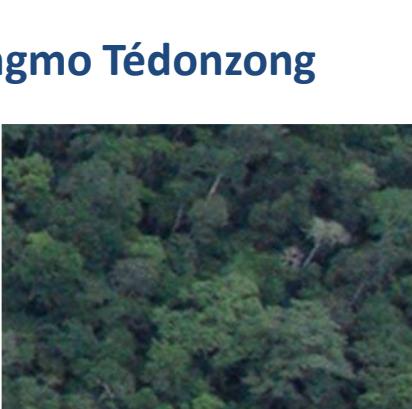
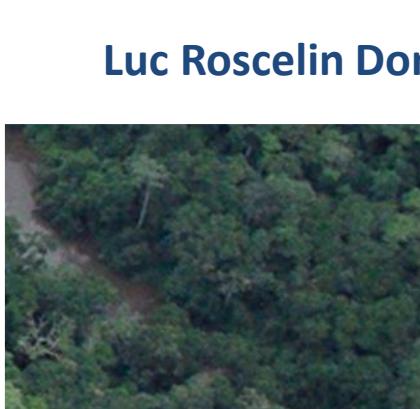
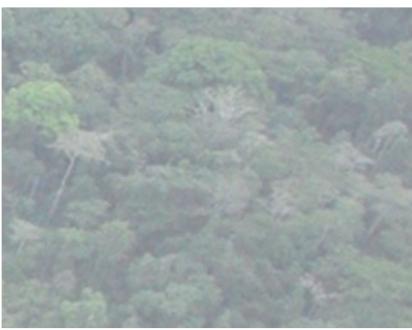
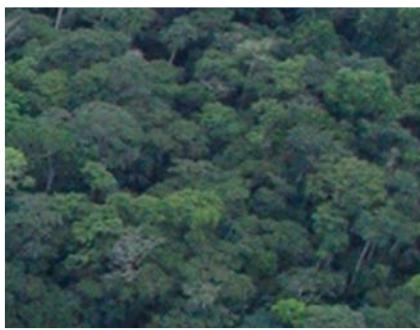
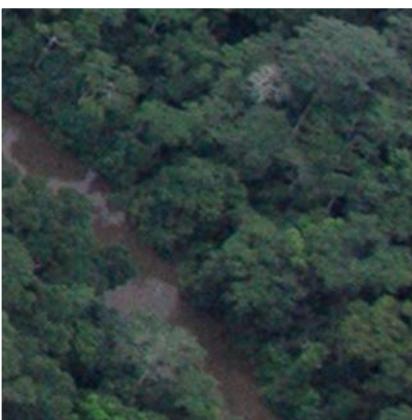
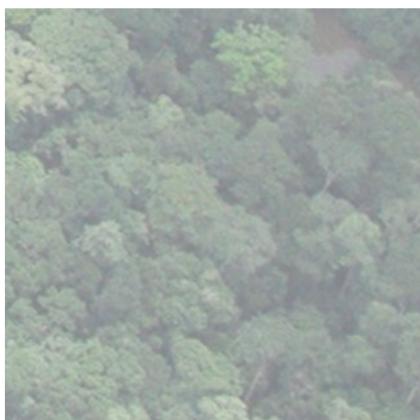




# **Ecological and anthropogenic drivers of the distribution and abundance of two Afrotropical rain forest mammals**



**Luc Roscelin Dongmo Tédonzong**





# ECOLOGICAL AND ANTHROPOGENIC DRIVERS OF THE DISTRIBUTION AND ABUNDANCE OF TWO AFROTROPICAL RAIN FOREST MAMMALS

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*Thesis submitted in fulfilment of the requirements for the degree of Doctor (PhD) in Sciences, Biology*

*Proefschrift voorgelegd tot het behalen van de graad van Doctor in de wetenschappen, biologie*

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**Cover photo:** Jean-Louis Doucet

**Layout:** Luc Tédonzong, inspired by Jasmijn Hillaert

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Printed by: University Press, Zelzate, Belgium

Date of public defence: 28<sup>th</sup> June 2019

The research presented in this thesis was funded by Centre for Research and Conservation of the Royal Zoological Society of Antwerp and Conservation Action Research Network.

For citation to the published work reprinted in this thesis, please refer to the original publications (as mentioned at the beginning of each chapter).

Please refer to this thesis as:

Tédonzong, L. R. D. (2019). Ecological and anthropogenic drivers of the distribution and abundance of two Afrotropical rain forest mammals. PhD thesis, Ghent University, 204 pp.

# DEDICATION

To

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# CHAPTER 1

## GENERAL INTRODUCTION

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LUC ROSCELIN DONGMO TÉDONZONG

Humans have long been interested in understanding the patterns of distribution and abundance of animals for many reasons, including curiosity about natural history and ecological relationships, ecotourism, and hunting for food and for sport (Morrison *et al.*, 2006; Mugume *et al.*, 2015). This knowledge has contributed to defining biogeographical regions of animal species across the globe and enabled the delineation of species' ranges (Soberon and Ceballos, 2011). More importantly, this information has helped to evaluate the status of wild animals (Kelt and Meserve, 2014; Jacobson *et al.*, 2016) and has contributed to the field of conservation biology (Orme *et al.*, 2006; Lascelles *et al.*, 2014). Over time, it was possible to evaluate the changes occurring in mammal populations. The information on the abundance and distribution of animals revealed that more than 20% of vertebrate species of almost all guilds are now threatened by extinction (Butchart *et al.*, 2010; Hoffmann *et al.*, 2010; Dirzo *et al.*, 2014). The threats faced by animal populations such as overexploitation, habitat degradation, habitat fragmentation are induced by humans (Bodmer *et al.*, 1997; Brooks *et al.*, 2002; Laurance *et al.*, 2012; Pekin and Pijanowski, 2012; Alroy, 2017; Estrada *et al.*, 2017). Climate change is also having profound impacts on biological diversity (Walther *et al.*, 2002; Thuiller *et al.*, 2006) and may exacerbate the negative impacts already being experienced by species from other threats, such as habitat destruction and fragmentation (Selwood *et al.*, 2015; Reed, 2017). The patterns of species' loss observed so far at the global scale is the result of how each threat operates at the local scale (Thompson *et al.*, 2001; Collen *et al.*, 2009). The process of species' extinction may occur naturally, but some authors assume that we are experiencing the sixth mass extinction, this time perpetuated by humans ((Baillie *et al.*, 2010; Corlett, 2016). This situation has led ecologists to shift from understanding the patterns of distribution and abundance of species to figuring out what factors actually cause the abundance and distribution of species to change in space and time (Wang *et al.*, 2018). Such knowledge is of paramount importance to helping avert the ongoing decline in wild animal populations (Di Fonzo *et al.*, 2016). Hence, an urgent need is to understand how the ranging behaviour of mammal species determines their response to anthropogenic change (Wong and Candolin, 2015). This relies on the ecological requirements of species (such as habitat quality and its use and diet) (Sepulveda *et al.*, 2007; Wilkin *et al.*, 2009) and their interactions with other species (such as predation and competition) (Bonnot *et al.*, 2015; du Preez *et al.*, 2015; Jutapruet *et al.*, 2015).

## 1.1. ECOLOGICAL DETERMINANTS OF MAMMALIAN POPULATION ABUNDANCE AND DISTRIBUTION

A population can be defined as a group of individuals of the same species living in a delimited area at a specific time period (Ives, 2009). This definition of a population has some implications, namely that there may be some level of interaction between all individuals of the population, and also that the boundaries of the area should be clearly defined (Berryman and Kindlmann, 2008; Ives, 2009). However, the area could be ecologically relevant (e.g. an island) or not (e.g. an administrative boundary), and the boundaries may constitute a barrier or be open so that the members of the population can migrate to and emigrate away from the population (Ives, 2009).

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### 1.1.1. ECOLOGICAL NICHE

The concept of the ecological niche has several meanings. First, it refers to the habitat requirements of a species, determined by abiotic (e.g. temperature, humidity) and biotic (e.g. food preference, competition, avoidance of predators) requirements necessary to its survival; it also refers to the ecological role of a species in the ecosystem and its dynamics; and finally ecological niche corresponds to the position of a species in the community (Polechová and Storch, 2008). To define the ecological niche of a species ( $S_1$ ), Hutchinson (1957) considered two independent environmental variables ( $E_1$  and  $E_2$ ) for which values could be distributed along ordinary rectangular coordinates. For each variable, the limiting value that can permit the survival and reproduction of species  $S_1$  was considered –  $E'_1$  and  $E''_1$  for the environmental variable  $E_1$ , and  $E'_2$  and  $E''_2$  for the environmental variable  $E_2$ ; this combination translated into an area for which the limits form an environmental condition that can allow the species to survive indefinitely (Hutchinson, 1957). Considering that species respond independently to the two environmental variables, the area formed is also a rectangle with the coordinates  $(x'_1, x''_1)$ ,  $(x''_1, x'_2)$ ,  $(x''_1, x''_2)$ ,  $(x''_1, x''_2)$ ; the existence of that area is then conditioned by the existence of independence in the response to the two environmental variables (Hutchinson, 1957). The process could further be extended to  $n$  environmental variables, which results in an  $n$ -dimensional hypervolume  $H$  inside which the species  $S_1$  could survive indefinitely, and this is called the “fundamental niche” (Hutchinson, 1957). Just like for species  $S_1$ , the same process could be used to define the fundamental niche for a second species ( $S_2$ ) with the same environmental variables. However, Hutchinson (1957) raised three concerns

about the theoretical definition of the “fundamental niche. The fundamental niche considers that the survival of the species at all points of the hypervolume is the same while normally, there may be a gradient in the optimality of conditions from the edge to the centre of the hypervolume. The assumption is such that the values of the environmental variables can be distributed in a linear manner, and only a single instant in time is considered; so, for example, species active in the day and those active at night do not show separated niches. Additionally, the model cannot consider many species at the same time (Hutchinson, 1957). All the points of the n-dimensional hypervolume H may correspond to a number of points in the physical space P.

When two species are present, their fundamental niches may overlap or not; in those cases, their fundamental niches are said to intersect or to separate, respectively (Hutchinson, 1957). Hutchinson (1957) then proposed a principle called the “Volterra-Gause principle” emphasizing that two species can coexist in the same environment if and only if they differ in some way in their fundamental niches; otherwise, they must compete, and one species (the inferior competitor) may be excluded by the other (the superior competitor). Consequently, for each species there are different parts of the overlapping area of the fundamental niches H' that allow their survival; those parts of the fundamental niche added to the non-overlapping parts were called “realized niches” (Hutchinson, 1957). In general, the realized niche is a product of not only the presence of competitors but also of the avoidance of predators (Polechová and Storch, 2008). This coexistence can only occur if individuals of the same species inhibit each other more than they inhibit individuals from the other species, meaning that the coexistence implies some interaction between species (Tilman, 2007). Competitive interactions may indirectly influence the abundance and distribution of species by changing their growth rate; a species with the highest density may increase its consumption of the limiting resource so that the remaining level of the resource may cause a change in the abundance of the other species (Pianka, 1981; Tilman, 2007). The differentiation of niches in coexisting species is predicted by the appearance of the different species; the most striking difference that allows the species to partition their feeding resources in spite of their similarity in ecological requirements concerns body size (e.g. the size of one species should be greater than the other; Chave, 2009).

In this case, when a new species enters the community, three outcomes are possible: (i) old species can be replaced by the new one, (ii) the new species can find a niche that is free of occupation, or (iii) the new species will proceed to

partition a niche that is occupied by a pre-existing species (Hutchinson, 1959). The exclusion of an existing species by the new one may not necessarily result in changing the stability of the ecosystem, but if the population of the new species is more stable, then the stability of the community could be changed (Hutchinson, 1959). As such, Hutchinson (1959) considers that the most important aspect of the animal system is food related and stresses that the great diversity of terrestrial fauna is the consequence of the high diversity of terrestrial plants.

---

### 1.1.2. HABITAT

Whittaker *et al.* (1973) found that the definition of “ecological niche” might lead to confusion between “niche” and “habitat”. However, the difference between “niche” and “habitat” resides in the fact that niche differentiation in a community is concerned with the evolution of the genetic characteristics of one species in relation to others in the community while habitat differentiation is concerned with the evolution of the response of species to the gradients of exogenous environmental variables, though the environmental factors can be influenced by the community itself (Whittaker *et al.*, 1973). Then the results of niche differentiation in the community occur within-habitat, measured by alpha diversity, while the result of habitat differentiation occurs between-habitat, measured by beta diversity (Whittaker *et al.*, 1973).

The habitat of a species comprises the range of environmental variables (elevation, slope, soil fertility, humidity, etc.) over which it occurs (Whittaker *et al.*, 1973). Hall *et al.* (1997) further defined a habitat as the resources and environmental conditions occurring in a place and that are necessary for a species to establish, reproduce, and survive in that area. They emphasized that defining a habitat must convey with some characteristics such as its specificity to a particular organism and that there must be a relation between an organism (species, population, individual) and biotic and abiotic characteristics of the area of concern. Habitat is then all resources that an organism needs in order to survive rather than simply vegetation or a vegetation structure (which should be termed as “vegetation association” or “habitat type” instead of “habitat”) (Hall *et al.*, 1997). The habitat quality is a measure of the impact of the capacity of the environment to provide conditions necessary to support the persistence of a population, while habitat availability is how animals have access to its physical and biological components (Hall *et al.*, 1997). Habitat quality is generally linked to another term “carrying capacity” which represents the maximum number of individuals of a population that the habitat can support (Morris and Mukherjee, 2007; Donovan *et al.*, 2012; Lyons *et al.*, 2018).

Estimating the carrying capacity often gives an indication of the quality of the habitat (Morris and Mukherjee, 2007).

Three parameters evaluate the interactions between animals and their habitat: habitat use, habitat selection, and habitat preference (Fretwell and Lucas, 1969). The first (habitat use) refers to the quantity that is used by an animal in a defined period of time or the time that an animal spends in a habitat; the second term (habitat selection) refers to the underlying behavioural processes that condition the choice of a particular habitat type by an animal; and the third expression represents the probability of choosing a particular habitat type if all habitats are given the same chance to be used by the animal (Johnson, 1980). When the proportion of use of a habitat type is greater than its availability, it is said to be “preferred”; but when that proportion is less than its availability, it is said to be “avoided” (Fretwell and Lucas, 1969; Johnson, 1980). Fretwell and Lucas (1969) defined the habitat distribution of a species as the proportion of the total number of individuals of the same population in each habitat type, considering that the habitat of a species could be divided into different sub-habitats. They then explained that if a species selects for the habitat that is best suited for its persistence and reproduction, its habitat selection behaviour conforms to the ideal free distribution (Fretwell and Lucas, 1969). If the distribution of a species conforms to the ideal free distribution hypothesis, that distribution can be compared to the carrying capacity of the habitat (Hobbs and Hanley, 1990).

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#### 1.1.3. ECOLOGICAL CONSTRAINTS ON HABITAT USE

Several ecological factors may constrain the use of habitats such as the risk of predation, competition, etc. (Grand and Dill, 1999; Johnson, 2007). Habitat use by individual organisms is context-dependent because it must be able to track the environment at scales that vary temporally and spatially (Tellería, 2016).

Predation risk may cause an animal to reduce the intensity of habitat use by avoiding the area where the risk of predation is present, and this may affect foraging activities (Moenting and Morris, 2006). Understanding animal behaviour is crucial to figuring out how they may adapt to habitat disturbance because if animals are coping with a disturbance, the dynamics of their population, community structure, and the patterns of distribution can be affected by adaptive behaviours (Moenting and Morris, 2006). The changes in the spatial distribution of animals due to the presence of a risk of predation may have implications on the patterns of habitat use and its interpretation, namely the increase in the availability of a preferred habitat type relatively to its use, or the decrease in the availability of

a non-preferred habitat type relatively to its use (Beyer *et al.*, 2010). Because of the conditionality of habitat preference on its availability, the fact that availability can vary spatially due to disturbance prevents the transferability of habitat suitability models from one area to another with different landscape configurations (Aarts *et al.*, 2008; Beyer *et al.*, 2010). The change in habitat use when its availability changes, generally indicated by an increasing deviation of habitat use from what could be expected by chance, is a consequence of the existence of functional response in habitat use (Johnson and Seip, 2008; Boyce *et al.*, 2016; Holbrook *et al.*, 2019). At the landscape level, when the spatial variation of resources is seasonal, a seasonal migration may cause a seasonal change in abundance (Boyce *et al.*, 2016). These source-sink dynamics resulting from inclusive habitat selection may facilitate the persistence of a population, its variability, and its spatial synchrony (Morris *et al.*, 2001). When a population presents an inclusive habitat selection pattern, its abundance will change both spatially and temporally, that is, the habitat exceeding its carrying capacity will show a declining density while the habitat below its carrying capacity will display an increasing density (Morris *et al.*, 2001).

The existence of competition between two species can be indicated by their adaptation in reducing the overlap between their niche axes by changing their diet or the pattern of habitat use (Wiens *et al.*, 2014). Competitive interactions affecting habitat use are characterized by the avoidance of habitats associated with the presence of competing species (Razgour *et al.*, 2011). For example, Razgour *et al.* (2011) found differential use of different pond sizes associated with different prey abundance by competing species. Competitive interactions influencing dietary niche axes are translated by differences in feeding resources consumed (different prey species or plant species) because of their limited supply (Kleynhans *et al.*, 2011). When the availability of resources varies seasonally, the overlap in feeding resources may also vary seasonally (Prins *et al.*, 2006; Owen-Smith *et al.*, 2015). For example, Kleynhans *et al.* (2011) found that the overlap of feeding resources was low when their availability was low, indicating that shortening feeding resources may increase competition between two ecologically similar species. Competition may also be indicated by the differential exploitation of several niche axes (Sexton *et al.*, 2017). However, in some cases, a random appointment of food items may be observed, and cannot translate to the existence of competition (Prins *et al.*, 2006). A competitive interaction at any time can only be inferred if it can be shown that resources at that time are in limited supply (Prins *et al.*, 2006). Amarasekare (2009) distinguished two types of competition: non-linear competition and the storage effect. The non-linear competition occurs when animals respond to a limiting

resource for which availability varies seasonally due to the influence of environmental or abiotic factors such as precipitations; while the storage effect is when the animals respond to an abiotic environmental factor which varies seasonally (Tilman, 2007; Amarasekare, 2009). Therefore, in the non-linear competition, competitors are affected directly by their differential responses to the limiting seasonal resource itself; while in the storage effect, competitors are affected indirectly by their differential responses to the abiotic environmental variable whose variation determines the timing of species engagement in the competition (Amarasekare, 2009).

Habitat segregation due to competition may result in differences in space use, which can occur vertically or horizontally (Booth and Murray, 2008). Vertical stratification was originally observed in Warbler by MacArthur (1958), searching for insects in spruce trees; from that observation, it resulted that different bird species fed at different heights of the tree. Vertical stratification was also observed in primates occupying different tree heights, due to the type and the size of trees the species fed on (Sushma and Singh, 2006). Niche differentiation can occur in the same habitat on diet resources, and then competition is materialized by morphological differences that induce behavioural modifications allowing species to exploit different diet resources in the same habitat (Kotler and Brown, 1988; Vleut *et al.*, 2015). When competition is translated by vertical stratification or behavioural differentiation, the different species may present a complete overlap in habitat use even when there are different habitat types (Vleut *et al.*, 2015). In such a case, a difference in horizontal patterns of abundance and distribution may not be due to the existence of competition between species. Horizontal stratification in space use due to competition between species can be facilitated by the spatial heterogeneity of habitat types (Amarasekare and Nisbet, 2001). Under these circumstances, species competing for the same dietary resources can select different habitat types (Ritchie, 2002). When habitat heterogeneity results in different patterns of habitat use, the abundance of species may increase in their preferred habitat type, and this may induce spatial dynamics in animal populations (Amarasekare, 2009). These dynamics can vary seasonally if the availability of feeding resources in different habitats also varies with seasons (Kotler and Brown, 1988; Head *et al.*, 2012).

Generally, predation risk may cause behavioural responses in animals, and this leads them to find safer places; consequently, there is a change in the spatial distribution of the “prey” in relation to the location of the risk (Oriol-Cotterill *et al.*, 2015). The sensitivity to predation risk may increase the endocrine stress to the

extent that reproduction is suppressed over the years through the maternal effects (Hik, 1995; Boonstra *et al.*, 1998). Sheriff *et al.* (2009) found that the increasing level of glucocorticoid concentration due to predation risk induced a decline in the number and the quality of snowshoe hare offspring. They then concluded that whatever the origin of stress, any factor causing glucocorticoid concentration to increase may result in decreasing fitness (Sheriff *et al.*, 2009). The direct consequences of stress induced by predation risk are increased level of cortisol, reduced testosterone, and reduced index of body condition (Boonstra *et al.*, 1998). Reducing the risk of predation can help to overcome the effects of predation risk on reproductive success and stress physiology (Boonstra *et al.*, 1998). The low survival rate of offspring resulting from induced stress of predation risk in mothers may cause poor breeding conditions in one reproductive season, and this may have negative consequences in the next generation (Hik, 1995). The intergenerational effects of stress induced by predation was reported by Sheriff *et al.* (2009); these effects are the result of a reduced ability to reproduce (Sheriff *et al.*, 2010). The sub-lethal effects of predation risk can influence the abundance and distribution of a population (Boonstra *et al.*, 1998). Even after a sudden decline in predation risk, a time of recovery may be necessary for a species to reproduce successfully; this corroborates the findings that predation risk may have intergenerational consequences (Boonstra *et al.*, 1998; Sheriff *et al.*, 2010).

Predation risk may induce behavioural modifications in animals with consequences for foraging activities (Cherry *et al.*, 2015). For some species, though, finding food may be more important than the risk of predation, as was the case for the zebra, the oribi, and the wildebeest (M'Soka *et al.*, 2017). Similarly, Dupke *et al.* (2017) observed a seasonal variation in habitat use by Roe dear that was primarily governed more by the variation in food resource availability than by the avoidance of predation risk. Species respond differently to the risk of predation, and the level of vigilance of a species to a risk of predation may vary according to how the species perceives the risk of predation (Brown, 1989). While the risk of predation negatively affects some species, others remain uninfluenced and others are even positively influenced (Koerner *et al.*, 2017; Dias *et al.*, 2019). At the community level, the differential responses of species to predation risk may result in a different spatial dynamics of populations and modify the community structure (Hernandez *et al.*, 2005). The different levels of vigilance can have an impact on the resources available to the animal; when the predation-induced risk is high for an animal, it may avoid a larger area than when the predation-induced risk is low (Brown, 1989). Hence, a low-risk perception by an animal is equivalent to a lower resource loss

than when the animal perceives the risk to be high (Brown, 1989). Whether the risk of predation induces a shift in space use followed by a shift in habitat selection or not, the risk of predation can reduce access to resources (which are particularly important in animal population abundance and distribution) and affect the long-term survival of the animal (Frid and Dill, 2002). In some cases, the negative effects of predation risk on foraging stems from the fact that it increases vigilance which reduces the time the animal spends feeding (Frid and Dill, 2002). For example, in Patas monkeys, although access to feeding resources determined habitat preference, the presence of predators altered their patterns of habitat use despite the potential feeding opportunities (Enstam, 2007). In the Plitvice Lakes National Park (Croatia), the risk of predation by wolves increased the giving up density (the quantity of food left behind because of species interactions) in foxes (Haswell *et al.*, 2018).

The outcome of competition may depend on the risk of predation if the two competing species respond to the same risk of predation (Chase *et al.*, 2002). The pattern of species responses to the risk of predation determines the output of the effects of predation risk on competitive interaction (Holt, 2009). If the two competing species respond negatively to the same risk of predation, finding refuge may lead to a new form of competition called “competition for enemy-free space”, resulting in a new axis of differentiation to allow coexistence which is not present without the risk of predation (Holt, 2009). If the two species respond differently to the risk of predation, the effects of predation risk may depend on the distribution of resources, that is, it may prevent a species to access a resource for which the two species compete for, allowing the other species to take advantage of that resource (Chase *et al.*, 2002; Holt, 2009). The abundance of species from competitive interactions therefore decreases due to the effects of predation risk (Chase *et al.*, 2002).

## 1.2. ANTHROPOGENIC DRIVERS OF VARIATION IN POPULATION ABUNDANCE AND DISTRIBUTION

The main threats to mammal populations described up until now influence animals in several ways: they may involve direct killing of animals through illegal and sport hunting (Muchaal and Ngandjui, 1999; Fa *et al.*, 2005; Velho *et al.*, 2012); they may also affect animals indirectly by modifying the physical habitat through forest fragmentation and degradation (Robertson and van Schaik, 2001). Habitat fragmentation and degradation affect mammal species depending on forests for shelter and for food resources (Meijaard and Sheil, 2008; Potts, 2011; Behie and

Pavelka, 2015). However, the effects of human disturbance resulting from the non-consumptive use of natural systems have received less attention.

Frid and Dill (2002) defined disturbance in animal behavioural ecology as any divergence from the patterns observed in nature in the absence of humans. Stimuli related to human disturbance include roads, damage to plants, human settlements, and noise (Frid and Dill, 2002). The study of human disturbance goes back to the late sixties when Walther (1969) used a vehicle to evaluate its effects on the flight initiation distance of Thomson's gazelle. Since then, research has shown that the non-lethal effects of human disturbance on animals can be compared to those of natural predators (Frid and Dill, 2002). Human features such as roads may constrain space use by animals; however, some species remain unaffected (Van Vliet and Nasi, 2008). This can cause changes in the spatial distribution of animals due to habitat disturbance (Beyer *et al.*, 2010). Courbin *et al.* (2014) found that wolves changed their movement patterns when encountering cues of human presence (human voices, roads, and cut plants) and increased their speed of movement. Pandas avoided areas near human features (roads, residence, hydropower stations, and tree-felling sites) and carried out activities at a certain distance from those human-affected environments (Zhao *et al.*, 2017). Avoiding areas of high predation risk has consequences for the abundance and distribution; for example, the abundance of the wildebeest, the oribi, and the zebra changed in response to the presence of humans and other carnivores (M'Soka *et al.*, 2017). In anthropogenic landscapes, predation cues related to human presence include villages, roads, farms, logging sites, mining sites, etc. (Theuerkauf and Rouys, 2008; Polfus *et al.*, 2011; Koerner *et al.*, 2017). Natural predators such as lions also perceive humans as predators, and they modify their ranging patterns by avoiding areas occupied by humans; the extent of avoidance increases with the intensity of human activities (Valeix *et al.*, 2012). It has been shown that human –induced stress is higher than stress caused by natural predators (Zhao *et al.*, 2017; Zbyryt *et al.*, 2018). Clinchy *et al.* (2016) found that human voices delayed feeding, increased vigilance, and decreased the feeding time and the number of feeding scats in wolves. In comparison to other natural predators, Clinchy *et al.* (2016) showed that wolves respond to humans more than they respond to their natural predators. The effects of human disturbance vary among species (Koerner *et al.*, 2017; Dias *et al.*, 2019). For example, while the abundance of certain animal guilds (birds and rodents) decreases with the distance from human settlements, the abundance of others increases with the distance from human features (monkeys, apes and ungulates) (Koerner *et al.*, 2017).

Overall, studies show that changes in the abundance and distribution of mammal populations due to ecological and human disturbance can vary from one species to another (Wijesinghe and Brooke, 2005), and a question arises as to why species respond differently (Vazquez and Simberloff, 2002). Another important question is how the ecological characteristics of species determine their responses to human disturbance (Vazquez and Simberloff, 2002). Authors suggested that the niche breadth of a species may govern how it responds to a disturbance (Vazquez and Simberloff, 2002). Under such conditions, the species with the narrowest niche breadth (the more specialized species) may be more negatively affected by disturbance than the species with the larger niche breadth (the more generalist species), which may even benefit from that disturbance; this was termed the “specialisation-disturbance hypothesis” (Vazquez and Simberloff, 2002). The more specialized species have a particular diet, or they use habitat types with particular physiognomy contrary to generalized species with broader diet and habitat requirements (Futuyma and Moreno, 1988). The evaluation of the level of specialization is likely to be correct if the range of preferred diet or habitat types of the specialist species is included in that of the generalist species (Futuyma and Moreno, 1988). Behavioural modifications such as polymorphism and individual flexibility are mechanisms through which species may cope with the inadequacy of food or unfavourable abiotic factors by exploring new opportunities (Futuyma and Moreno, 1988). Hence, a species tends to be more specialized when the cost of food search decreases, when the cost of morphological and physiological adaptation increases, and when the availability of its preferred habitat types increases (Futuyma and Moreno, 1988). Galan-Acedo *et al.* (2019) showed that the more generalist species on the basis of habitat types are more resilient to human disturbance than the specialist. The higher level of resilience of the generalist species compared to the specialist is related to their dispersal abilities (Kneitel, 2018). In fact, generalist species were found to disperse actively, while the specialist dispersed passively; under such circumstances, the accessibility to habitat types by the generalist may be greater than that of the specialist (Kneitel, 2018).

The differential response of animal species to a disturbance is likely a consequence of their behavioural differences (Cosset *et al.*, 2019). Understanding the effects of behavioural factors on the persistence of species through differential changes in their abundance and distribution will improve knowledge of the drivers of population abundance and distribution. Such knowledge is relevant to the conservation of different species. For example, understanding how behavioural modifications affect the change in species abundance and distribution will improve

methods for designing high conservation value forests necessary for their long-term survival in human-dominated landscapes.

### 1.3. TROPICAL RAIN FORESTS AND TARGET SPECIES

The tropical rain forest is a biome spanning four biogeographic realms, namely Afrotrropic, Neotropic, Indo-Malayan, and Australia (Figure 1.1). Tropical rain forests have several other denominations: tropical moist forests, tropical evergreen forests, humid tropical forests, tropical deciduous rain forests, and tropical broadleaf forests (Goldsmith, 1998; Olson *et al.*, 2001). The term tropical rain forest was first coined by Shimper (*Tropishe Regenwald*) to designate evergreen forests; in this original view, the tropical rain forest was regarded as evergreen (hygrophilous), with tree heights greater than 30 m, and with high abundance of lianas and woody and herbaceous epiphytes (Mabberley, 1992). However, tropical rain forests are divided into five major regions: America, Africa, South Asia, Madagascar, and New Guinea (Primack and Corlett, 2005). The Afrotropical rain forest is the second largest tropical rainforest after the Neotropic, and the Congo River Basin is its main geographic feature (Primack and Corlett, 2005). Although the diversity of terrestrial mammals and other species is high in tropical rain forests, the rate of species extinction is also high (Stenseth, 1984).

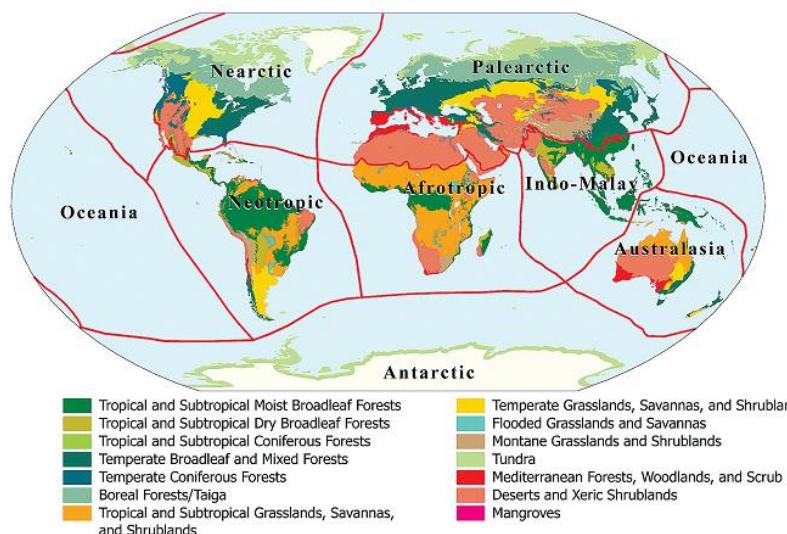


Figure 1.1: Biogeographic realms and biomes of the world (Olson *et al.*, 2001)

Primates are a particularly important mammal group because they characterize tropical rain forest regions better than any other animal group (Primack and Corlett, 2005). Given the multiple roles they play in tropical rain forest ecosystems (e.g. predators of invertebrates and vertebrates in some cases, leaf eaters, seed disperser agents), primates are considered to be a keystone group of mammals (Poulsen and Clark, 2001; Primack and Corlett, 2005; Deblauwe and Janssens, 2008; Deblauwe, 2009). Primates are the group of mammals that depend the most on plants for shelter, food, nesting, and locomotion (Fleagle, 1999). Most primate species are arboreal, that is they use trees and lianas as support for their movements (Fleagle, 1999). Plant families bearing fleshy fruits appeared long before frugivorous mammals, and fruit consumption has contributed to the evolutionary development of primates (Fleming and Kress, 2011). Based on all these characteristics, primates are suitable mammals for ecological studies aiming to understand the dynamics of tropical forest ecosystems.

Great apes are the largest primate species, and they perform almost all the functions (insectivorous, folivorous, frugivorous and predator) performed by the primate group (Kuroda *et al.*, 1996; Uehara, 1997; Mitani and Watts, 1999; Doran *et al.*, 2002; Deblauwe and Janssens, 2008; Head *et al.*, 2011). The ecology of great apes is relatively easy to study in natural habitats for a number of reasons: (i) great apes have visible footprints that allows scientists to track them without frightening them; (ii) they swallow the majority of seeds they consume (Wrangham *et al.*, 2009; Haurez *et al.*, 2013; Chancellor *et al.*, 2017); this facilitates studies of their diet through indirect methods (Tutin and Fernandez, 1993b; Phillips and McGrew, 2013). Great apes build night nests every day to sleep, and these nests are surveyed to determine their abundance (Kühl *et al.*, 2008). Western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) are sympatric across their range and, they are the only great apes in Africa whose ranges almost completely overlap (Figure 1.3). In addition, western lowland gorillas and central chimpanzees consume roughly the same fruits, and the availability of those fruits varies seasonally (Tutin and Fernandez, 1993a); hence, competition for food is therefore likely. As a result, it is possible to study the effects of competition and other ecological factors (e.g. habitat use, seasonal variation in fruit availability, level of specialization in fruit consumption, etc.) on the abundance and distribution of these two species. Great apes were found to respond differently to human features (Kalan *et al.*, 2019); as such they are suitable model species to study the influence of anthropogenic factors (such as forest trails, research camp, villages, village trails, etc.) on the abundance and distribution of mammal species in

tropical rain forests (Frishkoff *et al.*, 2019). Furthermore, the ranges of great apes cover almost all the tropical rain forests of Africa (Figure 1.1, Figure 1.3), and most mammal studies in the Paleotropics (tropical areas of Africa, Asia, and Oceania, excluding Australia and New Zealand) involve these species (Marshall *et al.*, 2016).

#### 1.4. OBJECTIVE

In this study, I aimed to evaluate how ecological and anthropogenic factors affect the abundance and distribution of mammal populations using sympatric great apes (gorillas and chimpanzees) as focal species. To achieve this aim, I addressed the following research questions: (i) How does the distribution of preferred and fallback foods determine the patterns of habitat use and the coexistence of sympatric mammals? (ii) How do human settlements modify the distribution of sympatric mammals? (iii) Does high nest abundance necessarily correspond to high habitat quality or high resource availability (fruits) when identifying high conservation value forests? (iv) Does the non-consumptive use of natural systems affect the persistence of mammal populations?

#### 1.5. OUTLINE OF THE THESIS

I wrote four data chapters (chapters 2-5) to provide answers to the questions raised above. Chapter 2 addresses niche partitioning in great apes by examining the seasonal patterns of fruit consumption and habitat selection and by evaluating woody fruiting plant abundance across habitat types and patterns of fruit availability; this knowledge contributes to the understanding of the mechanisms of coexistence in frugivorous mammals. In Chapter 3, I evaluated the influence of ecological and biophysical variables on the spatial distribution of great apes and assessed how human settlements modify the spatial distribution of these mammals. In Chapter 4, I determined the patterns of habitat selection by great apes and their important fruiting species and combined this information with the distribution of their nests to identify areas that are most suitable for their survival (high conservation value forests). In Chapter 5, I used a long-term dataset (2001-2016) on great ape population censuses to evaluate the influence of research presence on great ape population trends.

## 1.6. STUDY SPECIES: WESTERN LOWLAND GORILLAS AND CENTRAL CHIMPANZEES

### 1.6.1. CLASSIFICATION AND DISTRIBUTION

Gorillas, chimpanzees, bonobos, orang-utans, and humans are related (Figure 1.2) (Groves, 2018). Western lowland gorillas and central chimpanzees belong to the family Hominidae (order: Primates) (Butynski, 2001). Gorillas (genus *Gorilla*) represent the largest primates (Groves, 2003). This genus comprises two species: *Gorilla gorilla* and *Gorilla beringei*. Each of these species comprises two subspecies: *Gorilla gorilla gorilla* and *Gorilla gorilla diehli* (sub-species of *Gorilla gorilla*), and *Gorilla beringei beringei* and *Gorilla beringei graueri* (sub-species of *Gorilla beringei*) (Groves, 2003). Chimpanzees (*Pan troglodytes*) together with bonobos (*Pan paniscus*) constitute the two species of the genus *Pan*. *Pan troglodytes* is divided into four subspecies (central chimpanzee, *Pan troglodytes troglodytes*; eastern chimpanzee, *Pan troglodytes schweinfurthii*; Nigeria chimpanzee, *Pan troglodytes vellerosus*; western chimpanzee, *Pan troglodytes versus*) (Butynski, 2001).



Figure 1.2: Phylogenetic tree displaying the relatedness among great apes: orang-utan (genus *Pongo*), gorilla (genus *Gorilla*), chimpanzee and bonobo (genus *Pan*) and human (genus *Homo*) (Groves, 2018).

Both western lowland gorillas and central chimpanzees share approximately the same range that extends over seven countries namely Cameroon, Central African

Republic, Congo, Democratic Republic of Congo, Gabon, Equatorial Guinea, and Angola (enclave of Cabinda). The range of western lowland gorillas and central chimpanzees is estimated at 709 000 km<sup>2</sup> and 700 000 km<sup>2</sup>, respectively. (Butynski, 2001). Gorillas are larger than chimpanzees (an adult gorilla weights between 136-227 kg while an adult chimpanzee weights 68 kg on average) (Benson and Nagel, 2004). Figure 1.3 presents the distribution of great apes and their sub-species in Africa. *Gorilla gorilla gorilla* and *Pan troglodytes troglodytes* are the great apes whose geographical distributions overlap the most in Africa (Figure 1.3)

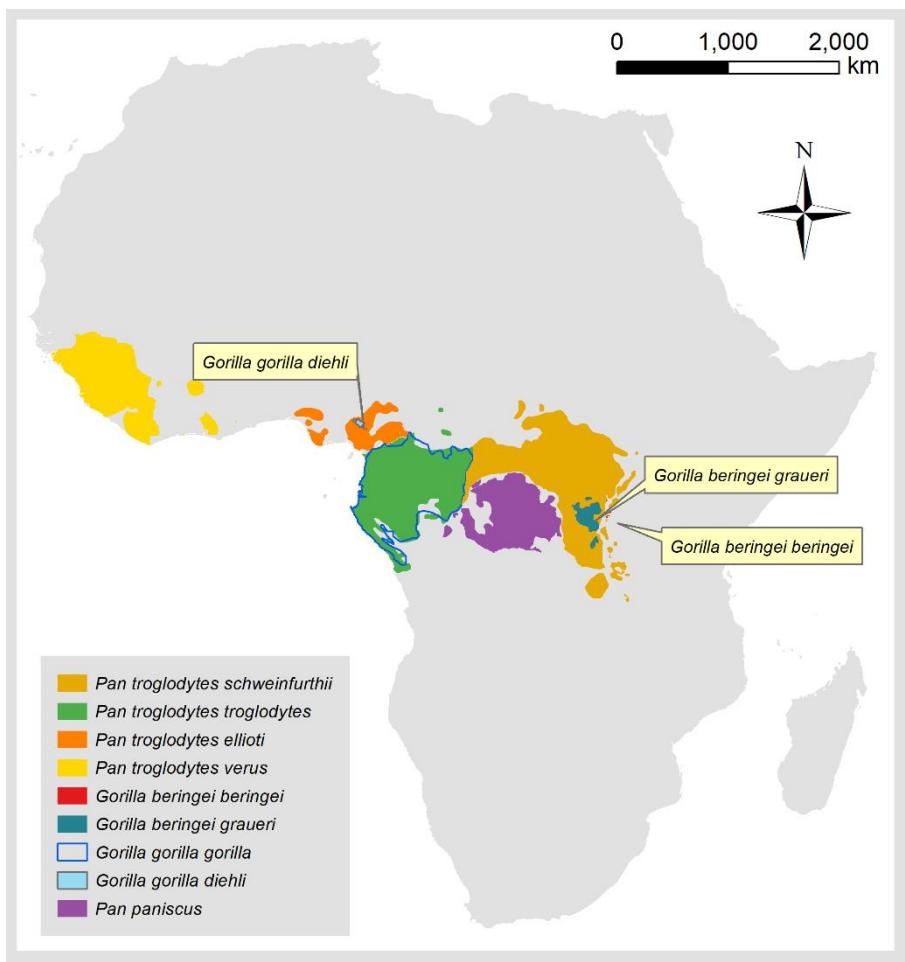


Figure 1.3: Geographical distribution of great ape species and sub-species in Africa (spatial data downloaded from <https://www.iucnredlist.org/resources/spatial-data-download>, on the 28 May 2019).

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### 1.6.2. HABITAT USE AND NESTING BEHAVIOUR

Gorillas and chimpanzees live in tropical rain forests. Highest densities of gorillas were found in swamps and secondary forests (Fay and Agnagna, 1992; Nishihara, 1995; Bermejo, 2004; Poulsen and Clark, 2004). A study of Willie *et al.* (2013) revealed a high preference of young secondary forests, swamps, and light gaps by western lowland gorillas. These habitats are favoured because they harbour a high abundance of herbaceous plants (mainly Marantaceae and Zingiberaceae) which are used to build nests and constitute important food sources when fruit availability is low (Rogers *et al.*, 1990; Williamson *et al.*, 1990; Remis, 1997; Willie *et al.*, 2014). However, Yamagiwa *et al.* (1995) emphasized that herbaceous plants may not be crucial for the long-term survival of western lowland gorillas although the density of these apes can be positively correlated with the density of herbaceous plants. Contrary to gorillas, chimpanzees prefer nesting in mature forests (Arnhem *et al.*, 2008). Chimpanzees tend to build nests in trees and gorillas usually build nests on the ground (Stanford, 2006). However, gorilla nests were also found in trees (Stanford and O'Malley, 2008), while chimpanzee nests were also found on the ground (Tagg *et al.*, 2013). Hence, the determination of the nest builder identity is not always straightforward when collecting data to estimate the abundance of these apes (Sanz *et al.*, 2007). For chimpanzees, patterns of habitat use based on nests and other signs (vocalization, direct observations, feeding remains, and dung) are consistent with patterns of habitat use based on nests only; however, this is not the case for gorillas (Morgan *et al.*, 2006). This indicates that chimpanzees range in their preferred nesting habitats, while gorillas also frequent habitats not preferred for nesting.

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### 1.6.3. FEEDING ECOLOGY

Western lowland gorillas are generalist herbivores, but fruits constitute the dominant part of their diet and herbs and foliage the second part (Doran *et al.*, 2002; Cipolletta, 2004; Rogers *et al.*, 2004; Head *et al.*, 2011). Western lowland gorillas consume fruits year-round but the consumption of fruits fluctuates with their availability (Cipolletta, 2004; Head *et al.*, 2011). The diet of chimpanzees is also dominated by fruits, as they spend much of their time consuming fruits (71% of the time), and 78% of the time spent consuming fruits is spent on the consumption of ripe fruits (Twehey *et al.*, 2004). When fruits are available, both chimpanzees and gorillas increase their fruit intake, but when fruits are scarce, while gorillas shift their diet to incorporate herbs and foliage, chimpanzees continue to maintain a fruit-dominated diet (Nishihara, 1995; Yamagiwa, 1999;

Doran *et al.*, 2002; Oelze *et al.*, 2014). In this case, the time spent travelling as well as the distance travelled by gorillas increased when fruit availability is high (Doran-Sheehy *et al.*, 2004; Masi *et al.*, 2009). Nutritional analyses show that fruits contain more energy and sugar than vegetative foods, while the quantity of fibres and proteins in fruits is lower than in herbs and foliage (Rogers *et al.*, 1990; Remis *et al.*, 2001). Among the fruits consumed, preferred fruits contain more sugar while fallback fruits are more fibrous and contain more tannin and lignin. When preferred fruits are available, gorillas increase their consumption of those fruits but shift to the consumption of fallback fruits when the availability of preferred fruits is low (Remis *et al.*, 2001). The majority of fruits consumed by great apes are from trees and lianas, and there is an overlap between the fruiting species consumed by gorillas and chimpanzees (Tutin and Fernandez, 1985, 1993a). Overall, chimpanzees consumed 57% of food items found in the gorilla diet while gorillas consumed 73% of foods consumed by chimpanzees; but when taking into account only fruit consumption, chimpanzees consumed 82% of gorilla fruits while gorillas consumed 79% of chimpanzee fruits (Tutin and Fernandez, 1985, 1993a). This indicates that the overall diet of gorillas is more diversified than that of chimpanzees and that chimpanzees consume more fruits than gorillas. The overlap between gorilla and chimpanzee diet varies seasonally due to the high flexibility of gorillas to shift their diet when fruits are scarce (Oelze *et al.*, 2014). The overlap between gorilla and chimpanzee diet varies from 0.3% and 69%, and the maximum value is observed in high fruit availability season (Head *et al.*, 2011; Oelze *et al.*, 2014). The different responses of gorillas and chimpanzees to fruit availability is linked to difficulties in processing vegetative food (Marshall and Wrangham, 2007). The dental morphology of gorillas may have adapted to allow them to easily consume herbaceous vegetation and foliage when preferred fruits are scarce; this feature gives gorillas an advantage over chimpanzees (Marshall and Wrangham, 2007). Additionally, the nutritional composition of vegetative foods and fallback fruits (high fibre, low energy, and high antifeedants) requires a digestive gut that is more specialised to process them (Marshall and Wrangham, 2007). This is an advantage that gorillas have over chimpanzees which do not have a long gut retention time that facilitates the consumption of low-quality foods when fruits are scarce (Tutin *et al.*, 1991; Remis, 2000; Remis *et al.*, 2001).

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#### 1.6.4. SOCIAL BEHAVIOUR AND GROUPING PATTERNS

Gorillas and chimpanzees all live in groups and the number of individuals per group may vary with the species. Gorilla males emigrate from their natal groups before

their complete maturation; then births, deaths, and emigration are the main factors determining group size in gorillas (Tutin, 1996; Parnell, 2002; Robbins *et al.*, 2004). In gorillas, the mean number of individuals per group varies from 6 to 11, and only one male dominates the group (Tutin, 1999; Yamagiwa *et al.*, 2003; Gatti *et al.*, 2004). Western lowland gorillas do not defend territories and their groups move in home ranges of about 5.6-15.4 km<sup>2</sup> (Bermejo, 2004; Doran-Sheehy *et al.*, 2004). However, intergroup interactions may arise, but the silverback generally respond with tolerance (about 64% of the time) (Bermejo, 2004). The intra-group competition in western lowland gorillas do not constraint the number of individuals per group (Bermejo, 1999). The home ranges of gorilla neighbouring groups overlap, and the groups generally use only a small part of their home range each month (20%) (Cipolletta, 2004). Unlike gorillas, fusion-fission social units, female transfer before their reproductive maturity, territoriality, and multiple males per groups are characteristics of chimpanzees (Pusey and Schroepfer-Walker, 2013). In chimpanzee, food availability and distribution can influence group size, and the time spent feeding is positively dependent on the party size (Lehmann and Boesch, 2004). The variation in group size results from the fission-fusion behaviour in chimpanzees that allows them to reduce intraspecific competition when fruit availability is low (Chapman *et al.*, 1995). Leopards are known to influence the grouping patterns of apes (Boesch, 1991), but their impact is not documented in La Belgique research site (Tagg *et al.*, 2013).

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#### 1.6.5. CONSERVATION STATUS

Both gorillas and chimpanzees are threatened species and are listed in the IUCN Red list of threatened species in different categories: Endangered (Chimpanzees, Humle *et al.*, 2016) and critically endangered (gorillas, Maisels *et al.*, 2018). Additionally, the two species are listed on appendix 1 of CITES and as Class A under the African Convention on the Conservation of Natural Resources. Major threats to their survival are hunting, habitat loss and fragmentation, and diseases (Plumptre *et al.*, 2003). At the national levels, gorillas have lost about 18.5 to 21.7% of their populations while no significant change was observed in chimpanzees (Strindberg *et al.*, 2018). However, the probability of occurrence of chimpanzee behaviours is reported to have decreased by 88% in communities where there was a high degree of the human footprint, in comparison to communities where there is a lower human footprint (Kühl *et al.*, 2019). Great ape densities were mainly influenced by natural variables (forest intactness and canopy height), and human-related variables (presence of guards, consumption of apes, and distance to roads) and

Ebola (Strindberg *et al.*, 2018). One of the major problems in great ape conservation is that a large part of their populations is present outside traditional protected areas (77.4% of gorillas and 80.7% of chimpanzees) (Plumptre *et al.*, 2003; Strindberg *et al.*, 2018). Efforts remain necessary to develop strategies in order to combat hunting pressure and habitat loss outside protected areas. Because they are wide-ranging and large-bodied species and have a longer generation time relatively to many other sympatric species, they represent important umbrella species in the study of the effects of anthropogenic variables on ecosystem integrity (Caro and O'Doherty, 1999).

## 1.7. STUDY AREA

Field work for this project was carried out in a tropical rain forest of Cameroon in the northern periphery of the Dja Faunal Reserve. According to Olson *et al.* (2001), the area falls within the northern Congolian lowland forest in the Afrotropic biome. The study area is about 200 km<sup>2</sup> and lies entirely within the Forest Management Unit 10 047a (which may be logged in the near future); vegetation types and great ape population abundance were found to be similar to patterns in the Dja Reserve (Tagg *et al.*, 2015). The geographic coordinates of the study site are longitude 3°01'00"E – 18°12'00"E and latitude 3°20'00"N – 3°30'00"N (Figure 1.4). Elevation is less variable across the site and ranges between 633 and 751 m (mean = 680.58; SD = 17.53 m) (Figure 4.1). The area is traversed by a hydrographic network comprising the Dja River and several tributaries. The mean annual precipitation is 1637.9 mm (SD = 105.1 mm). The average minimum daily temperature is 19.5°C (SD = 1.3°C) and the average maximum daily temperature is 26°C (SD = 2.4°C) (Willie *et al.*, 2014). In this area, there are four seasons (two rainy seasons and two dry seasons): the long dry season (November – February), the short dry season (July – August), the long rainy season (February – July) and the short rainy season (August – November) (Willie *et al.*, 2014). Local people live around the study area in the villages Doumo, Mimpala, Malen 5, and many others. The site was partially and selectively logged several decades ago, and the vegetation is composed of a mosaic of many habitat types (Figure 1.5a) (Willie *et al.*, 2013; Willie *et al.*, 2014). Near Primary Forests (NPF) are composed of large and tall tree species (Diameter at Breast Height (DBH) > 60 cm and height > 30 m); common species found in NPF are *Piptadeniastrum africanum* and *Distemonanthus benthamianus* of families Mimosaceae and Caesalpiniaceae, respectively. In Old Secondary Forests (OSF), large trees (DBH > 60 cm) relatively less tall than those of NPF (height 25-30 m) are found. Young Secondary Forests (YSF) comprise pioneer tree species with relatively

small diameters (DBH < 25 cm and height < 25 m) and a dense understory (with high abundance of *Tabernaemontana crassa*, Apocynaceae). Light Gaps (LG) are microhabitats created by tree or branch fall or by elephant activity resulting in an open canopy. NPF, OSF, YSF, and LG are *terra firma* forests. Swamps are characterized by hydromorphic soils and a high density of *Raphia* spp. as dominant species. Riparian Forests (RF) are periodically flooded areas located between swamps and *terra firma* forests; plant species from swamps and *terra firma* forests occur in RFs.

### 1.8. MAIN SAMPLING DESIGN

Several sampling designs were used for the collection of data pertaining to this thesis (Table 1.1). First, a sampling grid of 175-1x1 km grid cells was superimposed to the study area (Figure 1.4a,b); Within each grid cell, a transect of 1.2 km at 45° bearing was open; the transect extended diagonally 600 m either direction from the centre of the cell (Figure 1.4b). Along each transect, the habitat type was recorded at 50-m intervals. A number of transects were selected randomly each month from October 2015 to August 2016 (about 12-18 transects for 11 months, depending on the weather conditions and the effort that could be made by the team of field workers) and walked once to survey all great ape nests. Each 1x1 km grid cell was divided into four 500x500-km grid cells (Figure 1.4). At the centre of each 500x500-m grid cell, a botanical plot of 25x25 m was set; within each plot, all trees with DBH greater than 10 cm and all lianas with DBH greater than 5 cm were identified and measured. However, botanical inventories were performed in only 75% of the study area (133 grid cells, Figure 1.4b). In addition, another series of transects were used for great ape nest monitoring (Chapter 2 and Chapter 5) (Figure 1.4a). The first (20 transects) were walked each month for 13 months (from mid-April 2009 to mid-May 2010), and the second (10 transects) were walked four times (in 2001, 2008, 2014, and 2016).

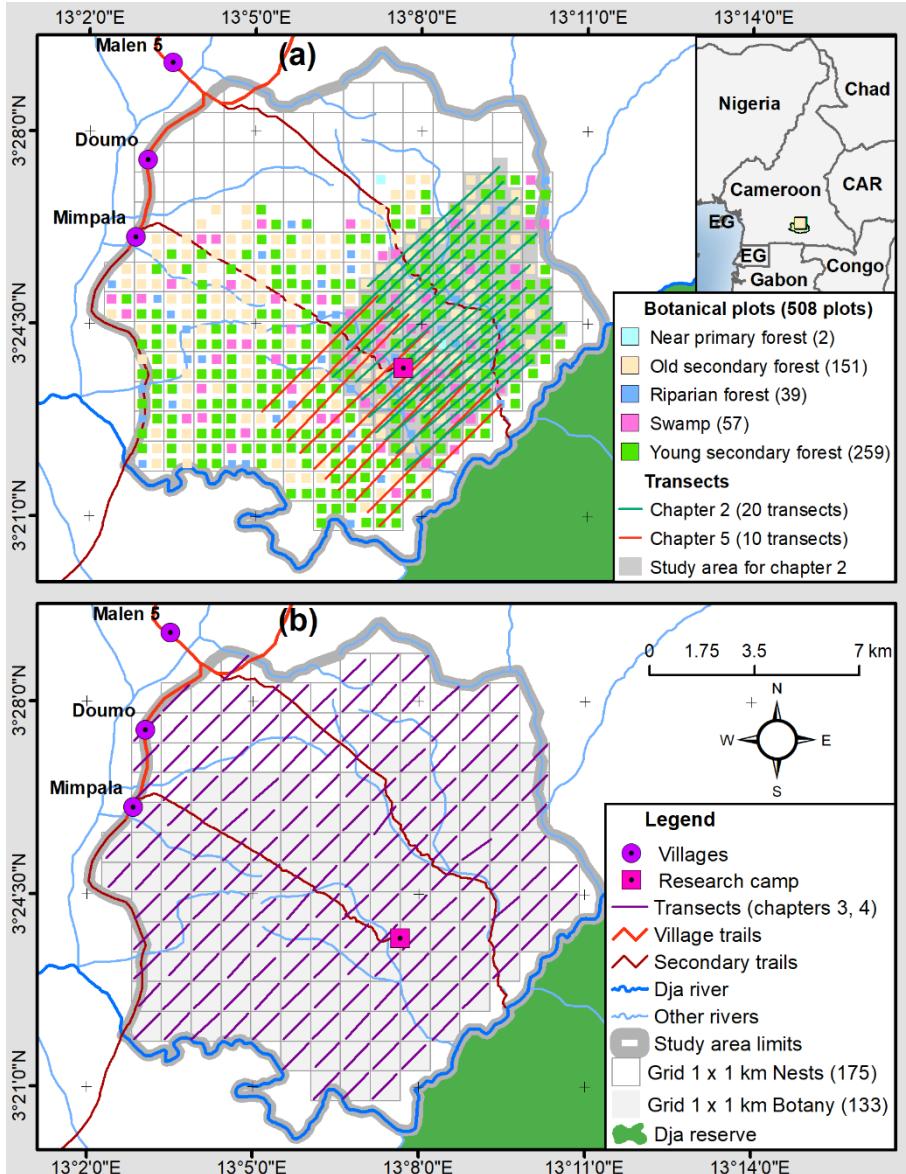
**Table 1.1: Overview of data collected and used in different chapters.**

Data collected	Chapter 2	Chapter 3	Chapter 4	Chapter 5
• Botanical inventories in 505 25x25-m plots	X		X	
• Monthly surveys of great ape nests 2009-2010 (along 20 6-km transects)	X			
• Great ape population monitoring along 10 6-km transects (in 2001, 2008, 2014, and 2016)			X	
• Great apes nest census within 1x1-km grid cells	X	X		
• Recording geographical references of human features in the study area		X		
• Recording of habitat points along 20 6-km transects	X			
• Mean fruit weight and mean number of seeds per fruit per species	X			
• Recording of habitat points in the 1x1 km sampling grid	X	X		
• Monitoring fruit phenology (2013-2016)	X		X	
• Fruiting plants consumed by great apes through faecal sample analyses (2013-2016)	X		X	

During great ape nest censuses, multiple nests of the same age category located within a radius of 20 m (gorillas) or 30 m (chimpanzees) were considered as belonging to the same nest group (Dupain *et al.*, 2004; Tagg and Willie, 2013). The distinction between gorilla and chimpanzee nests was made based on the presence of signs such as hairs, urine, feeding remains, dung, and prints (Morgan *et al.*, 2006). Old nests which often did not have those signs were regarded as built by gorillas if belonging to a group of nests built on the ground or in trees at less than 2

m height. For chimpanzees, at least one nest of a group must have been built in a tree at more than 2 m height (Tutin and Fernandez, 1984). In the study area, only 3.47% of chimpanzee nests were found on the ground, and only in few circumstances, all nests of the same group were built on the ground (Tagg et al., 2013).

Transects were open using a machete to cut understory vegetation at the minimum to allow the team to pass and make observations. Lianas were cut only if they were spiny or if they prevented passage. Distances were measured in the field with a decametre of 50 metres long. Transects starting points were identified on the map and uploaded in a GPS, along with the coordinates of the corners of all grid cells and those of the centre of each grid cell of 500x500 metre. Given that the topography of the site is relatively flat, the distance walked was not adjusted because this distance reflects the distance measured on the map.



**Figure 1.4: Study site and main sampling design: (a) 6-km transects and botanical plots with corresponding habitats; (b) locations of 1 x 1 km grid cells.**

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# CHAPTER 2

THE DISTRIBUTION OF PLANT  
CONSUMPTION TRAITS ACROSS  
HABITAT TYPES AND THE PATTERNS  
OF FRUIT AVAILABILITY SUGGEST A  
MECHANISM OF COEXISTENCE OF  
TWO SYMPATRIC FRUGIVOROUS  
MAMMALS

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## 2.1. ABSTRACT

Understanding the mechanisms governing the coexistence of organisms is an important question in ecology, and providing potential solutions contributes to conservation science. In this study, we evaluated the contribution of several mechanisms to the coexistence of two sympatric frugivores, using western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) in a tropical rainforest of south-east Cameroon as a model system. We collected great ape faecal samples to determine and classify fruit species consumed; we conducted great ape nest surveys to evaluate seasonal patterns of habitat use; and we collected botanical data to investigate the distribution of plant species across habitat types in relation to their ‘consumption traits’ (which indicate whether plants are preferred or fallback for either gorilla, chimpanzee or both). We found that patterns of habitat use varied seasonally for both gorillas and chimpanzees and that gorilla and chimpanzee preferred and fallback fruits differed. Also, the distribution of plant consumption traits was influenced by habitat type and matched accordingly with the patterns of habitat use by gorillas and chimpanzees. We show that neither habitat selection nor fruit preference alone can explain the coexistence of gorillas and chimpanzees, but that considering together the distribution of plant consumption traits of fruiting woody plants across habitats as well as the pattern of fruit availability may contribute to explaining coexistence. This supports the assumptions of niche theory with dominant and subordinate species in heterogeneous landscapes, whereby a species may prefer nesting in habitats where it is less subject to competitive exclusion and where food availability is higher. To our knowledge, our study is the first to investigate the contribution of plant consumption traits, seasonality, and habitat heterogeneity to enabling the coexistence of two sympatric frugivores.

**Keywords:** Fallback food; Habitat selection; Ecological niche; Fruit preference; Fruit phenology; Niche partitioning in primates

## 2.2. INTRODUCTION

A great challenge in ecology is, understanding the evolutionary and ecological implications of biotic interactions (Sutherland *et al.*, 2013), which has led researchers to question the mechanisms shaping the coexistence of closely related species (Hutchinson, 1961; Kotler and Brown, 2007; Benítez-López *et al.*, 2014). Many factors have been reported to control space use by animal species, including abiotic factors, such as climatic variables, and biotic factors, such as resource availability, resource overlap between two species and their relative positions in the food web (Kotler and Brown, 2007). The necessity to consider species interactions in species distribution models has advanced our understanding of how overlap in resource use and particular characteristics of those resources influences coexistence of two species (Benítez-López *et al.*, 2014; Leach *et al.*, 2016).

Resources within an animal's niche can be entirely available to them if no competitor or predator is present, and is thus referred to as a 'fundamental niche' (Hutchinson, 1957). However, the presence of competitors prevents the use of the entire fundamental niche, restricting the organism to its 'realized niche', which is a subset of its fundamental niche (Hutchinson, 1957). The niche overlap between two closely related species is a fundamental aspect of 'niche theory', which states that two closely related species occupying the same niche may undergo competition (Pianka, 1981). Competition may be direct (dealing with space), called 'interference competition', or indirect (dealing with resources), called 'exploitation competition' (Pianka, 1981). High levels of competition may lead to the competitive exclusion of one species by the most dominant competitor (Hutchinson, 1961) and are thus not consistent with species coexistence. Importantly, species may have become specialized through character displacement (e.g. morphological differentiation) by partitioning the shared resource (Walter, 1991). Such niche partitioning reduces exploitation competition (Rosenzweig, 1981), leading to a divergence of realized niches (Walter, 1991; Sinclair *et al.*, 2006) and facilitating coexistence. This implies that the sympatric species may have reached some equilibrium in the use of resources that allow them to coexist (Pianka, 1981). Spatial or temporal variations in resource availability can lead to changes in the pattern of habitat use by sympatric species (Rosenzweig, 1981; Grether *et al.*, 2009).

Studying a single species can help understand ranging patterns, but integrating the study of biotic interactions between two closely related species can inform on how their abundance and distribution may be influenced by their niche breadth or niche

position (Gaston *et al.*, 1997; Benítez-López *et al.*, 2014). Many aspects, such as reproductive success and resource use, are important to the niche theory, but of particular interest in understanding species interactions is the pattern of resource use (including food and space) (Pianka, 1981). Although shared resources are central to the concept of interspecific competition, the limited nature of resources is the ultimate cause of competition (Amarasekare, 2003). Resource supplies can be continuously reduced, but reduction can also occur on a temporal basis, leading to temporal niche differentiation between species (Hutchinson, 1961). In this case, understanding species interaction is only possible by analysing the various ways in which different resources are used by different species across time (Amarasekare, 2003).

Two hypotheses have been proposed to explain patterns of resource use by two coexisting species, namely the ‘optimal foraging theory’ and the ‘habitat selection theory’ (Rosenzweig, 1981). Both hypotheses have gained support from studies investigating the role of resource quality in niche partitioning (Kotler and Brown, 1988; Gregory and Gaston, 2000; Ritchie, 2002; Perrin and Kotler, 2005; de longh *et al.*, 2011; Kamilar and Ledogar, 2011; Martin and Garnett, 2013; Oelze *et al.*, 2014). Which hypothesis gains support depends upon how species alter their use of preferred resources in cases of high and low availability (Rosenzweig, 1981). Different feeding plant resources contain different nutritional compositions that make them either preferred or fallback for animal species (Remis *et al.*, 2001; Doran-Sheehy *et al.*, 2009), and their diversity and community structure are the resultant habitat heterogeneity (Myers and Harms, 2009). This implies that the availability of different food types may vary with habitat types, and seasons due to phenological patterns in plants (Poulsen and Clark, 2004; Yamagiwa *et al.*, 2008). However, the distribution of such resources, such as different food types (preferred and fallback) as an indication of food quality for the animal species, has rarely been considered when investigating mechanisms that may facilitate the coexistence of two closely related species in heterogeneous environments. Preferred foods are consumed whenever they are available, while fallback foods are consumed when preferred foods are scarce (Yamagiwa and Basabose, 2009). A few studies have considered the abundance of resources (Kotler and Brown, 1988; Brown, 1989; Steinmetz *et al.*, 2013) or their diversity (Kotler and Brown, 1988; Kleynhans *et al.*, 2011), but without taking into account the intrinsic value of each resource to the animal consumers, or considering food resource quality at the community level (Steinmetz *et al.*, 2013; Owen-Smith *et al.*, 2015). A study conducted by Vélez *et al.* (2017) investigated how the distribution of preferred fruits influenced habitat use

by lowland tapirs (*Tapirus terrestris*), but did not evaluate the implications for coexistence with closely related species.

We aimed to evaluate whether varying spatial and temporal availability of fruiting woody plant resources (comprising trees and lianas) can contribute to explaining the coexistence of two sympatric frugivores. Coexistence of two frugivorous species depends upon the outcome of species competition, which is in turn dependent upon the superiority and inferiority of the competitors (Perrin and Kotler, 2005). The superior competitors may be characterized as the species that rely the most on fruit (preferred fruits), while the inferior competitors tend to be more folivorous (Kinahan and Pillay, 2008), increasing their consumption of vegetation and lower quality fruits (fallback fruits) to reduce the interspecific competition when fruit availability is low (Kinahan and Pillay, 2008; Martin and Garnett, 2013).

We used sympatric great apes (western lowland gorillas *Gorilla gorilla gorilla* and central chimpanzees *Pan troglodytes troglodytes*) as target species, because they occur in the same habitats, share feeding habits to some extent (Tutin et al., 1991), and the availability of their preferred food (fruits) varies seasonally (Tweheyo and Lye, 2003; Yamagiwa et al., 2008). Fruit constitutes an important part of gorilla and chimpanzee diet with consequences in their ranging patterns (Doran-Sheehy et al., 2004), and the two species exhibit a high level of dietary overlap in terms of number of species (Tutin et al., 1991), and more than 93% of their fruits are obtained from woody plant species (Tutin and Fernandez, 1993). When fruit availability is high, both gorillas and chimpanzees increase their fruit consumption, but when fruit availability is low, chimpanzees maintain a diet dominated by fruit while gorillas incorporate large quantities of vegetative foods (herbs, leaves, flowers) (Basabose and Yamagiwa, 2002; Oelze et al., 2014). Fruits (preferred and fallback) are arguably the most influential aspects of great ape ecology (Poulsen and Clark, 2004; Lambert and Rothman, 2015), and represent the main cause of interspecific competitive interactions in primates (Yamagiwa et al., 1996). Additionally, studies have shown that chimpanzees prefer nesting in closed old growth forests, while gorillas prefer nesting in open young forests, as well as swamps and light gaps (Morgan et al., 2006; Willie et al., 2013). Therefore, we propose that chimpanzees may be more competitive and more specialized in fruit consumption than gorillas.

We tested two mechanisms that may promote the coexistence of gorillas and chimpanzees, described by the main niche axes (diet breadth and habitat

selection). As fruiting woody plant species are situated within habitat types, we tested a third mechanism described by a combination of the first two and defined by the spatial variation of the fruiting woody plants across the different habitat types based on whether they are preferred or fallback for either gorillas, chimpanzees or both, hereafter termed ‘plant consumption traits’. Consumption traits describe the quality of the fruiting species to the animal: high-quality fruits being ‘preferred’ and lower quality fruits, consumed when high-quality fruits are unavailable, being ‘fallback’. We asked whether differences in habitat selection and fruit preference and the distribution of fruiting woody plants could help explain the coexistence of gorillas and chimpanzees. We hypothesized that: (1) if habitat selection alone is the underlying mechanism of coexistence of gorillas and chimpanzees, the same pattern of habitat selection must be observed across all seasons; (2) if differential diet breadth alone is responsible for the coexistence of gorillas and chimpanzees, the pattern of habitat selection will not be different between the two species across all seasons; (3) the distribution of preferred and fallback woody fruiting plant species across habitat types may explain the coexistence of gorillas and chimpanzees; the seasonal availability of preferred and fallback fruits may vary between habitats, and the seasonal patterns of habitat use may vary between species. For this third hypothesis, considering chimpanzees as the superior competitor, we predicted that preferred species for both animals would be more associated with chimpanzee commonly preferred habitats (old secondary forests [Chapter 4]; Arnhem *et al.*, 2008); while fallback species would be more associated with gorilla commonly preferred habitats (young secondary forests, opened forests and swamps Willie *et al.*, 2013). In addition, gorillas may avoid nesting in habitats preferred by chimpanzees to escape competitive exclusion but may still forage in those chimpanzees-preferred nesting habitats when their preferred fruits are available there.

## 2.3. METHODOLOGY

### 2.3.1. DATA COLLECTION

#### 2.3.1.1 GREAT APE AND HABITAT SURVEYS

We conducted great ape nest surveys on 20 6-km transects from mid-April 2009 to mid-May 2010 using the marked nest count method (Kühl *et al.*, 2008). We set transects at a 45° bearing, to cross all major rivers (White and Edwards, 2000), and separated from each other by a distance of 300 m (Figure 2.1). We walked all the

20 transects every months for 13 months for nest censuses, during which recent night nests (less than one-month-old) were recorded and marked with red paint to avoid recounting in the next survey.

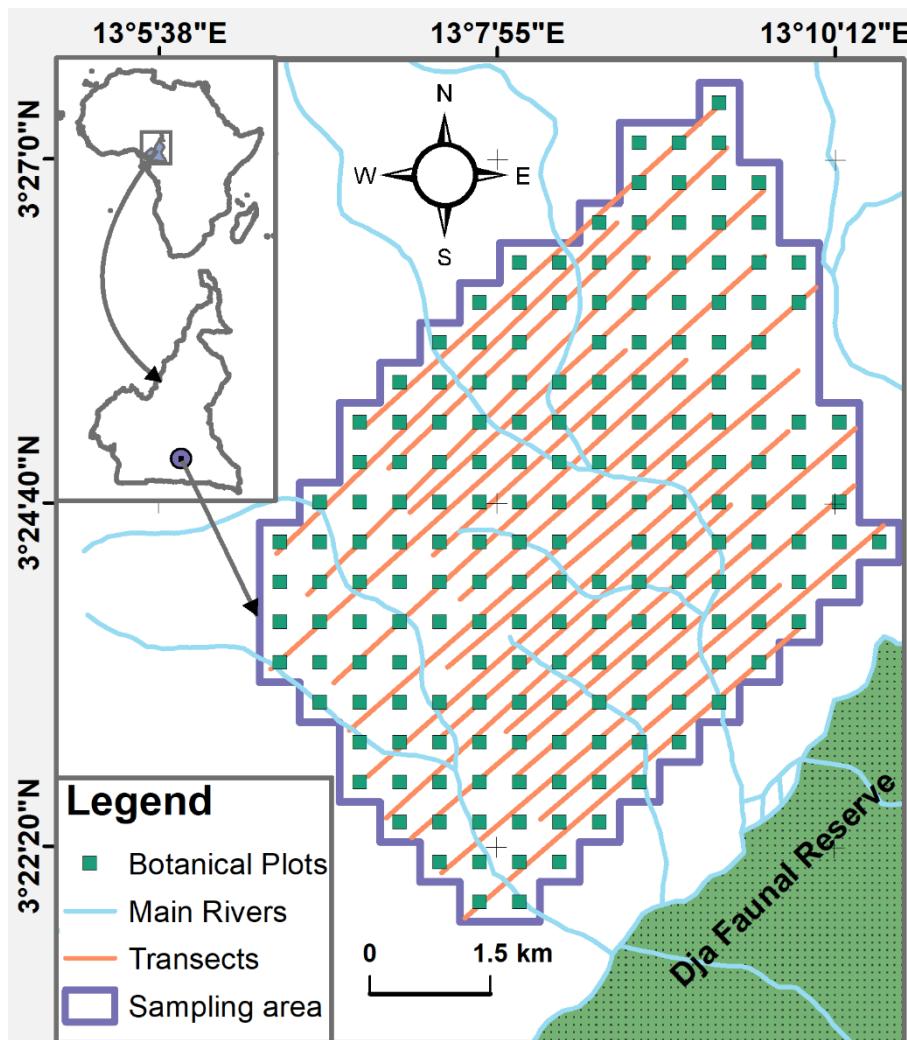
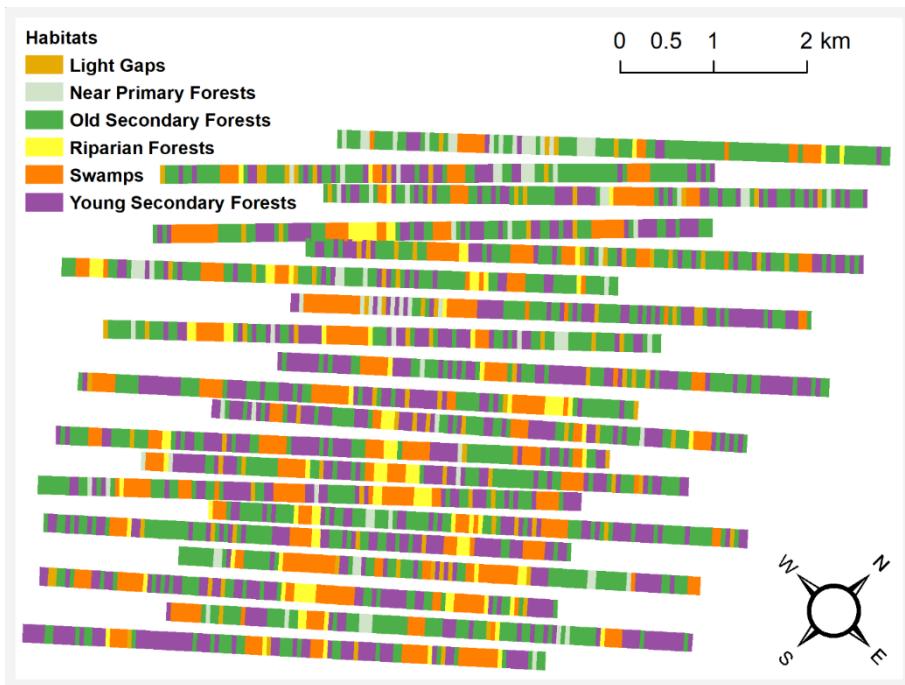


Figure 2.1: Study area and sampling design.

Additionally, along each transect, we noted the habitat type at every 50 m to evaluate habitat availability (Figure 2.2). We considered five habitat types in our study, based on the physical structure of the forest, the height of the dominant trees, and the hydromorphic status of the soil: Mature Forests (MF), Young

Secondary Forests (YSF), Light Gaps (LG), Swamps (SW) and Riparian Forests (RF), modified from Willie *et al.* (2013, 2014) (Figure 2.2). We decided to combine the categories Near Primary Forests (NPF) and Old Secondary Forests (OSF), as defined by Willie *et al.* (2013, 2014), into MF, as NPF are under-represented in our study site (less than 5%) and both NPF and OSF represent forests at advanced levels of stand development (Willie *et al.*, 2013).



**Figure 2.2: Distribution of the different habitat types along the transects.**

### 2.3.1.2 GREAT APE TRACKING, FAECAL SAMPLE COLLECTION, AND DIETARY ANALYSIS

From January to December 2014, we collected faecal samples of gorillas and chimpanzees, by tracking one-day-old great ape trails to locate fresh nests. We differentiated faeces and trails based on the presence of signs such as shape, size, associated odour, hairs (Head *et al.*, 2011), sightings and vocalizations. We washed faecal samples through a 1-mm sieve and identified extracted seeds to species level where possible, or to genus level (e.g. *Uapaca* spp., *Landolphia* spp. and *Trichoscypha* spp.), and counted them (Doran *et al.*, 2002).

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### 2.3.1.3 BOTANICAL INVENTORIES

We overlaid a grid of 184 500×500-m cells on the area covered by all transects, with one plot of 25×25 m at the centre of each cell, using ArcGIS 10.3.1 (Figure 2.1). In each plot, from May 2015 to September 2016, we counted all tree and liana species with DBH  $\geq 10$  and  $\geq 5$  cm, respectively, that were found in great ape faecal samples. We collected specimens for all plant species that could not be identified on site and sent them for identification at the National Herbarium of Cameroon. In 11 of the plots (6%, N=184), we found no fruiting tree or liana species known to be consumed by gorillas or chimpanzees. We did not collect botanical data from LG as it represents a microhabitat that can occur in any habitat type.

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### 2.3.1.4 FRUIT PHENOLOGY AND FRUIT CHARACTERISTICS

We selected approximately 10 individuals of each of the fruiting plant species consumed by gorillas and chimpanzees (Djoufack *et al.*, 2007) across 10 of the 6-km transects, ensuring separation from each other by a distance of at least 600 m, and then measured their DBH and height. We monitored these focal trees monthly (from January 2014 to December 2014) for fruit phenological data. Using a three-level score (0 = none, 1 = few and 2 = many) we characterized the quantity of fruits seen in the tree or on the ground. We noted information regarding the quantity of unripe fruits and ripe fruits on the tree, and the quantity of unripe and ripe intact fruits on the ground. Each month, we collected random samples of 10 ripe intact fruits from at least three different individuals of each species, to measure their weight and count their seeds, to calculate the mean weight and mean number of seeds of each fruiting species.

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## 2.3.2. STATISTICAL ANALYSIS

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### 2.3.2.1 HABITAT SELECTION

We compared patterns of habitat selection of gorillas and chimpanzees using the Manly Selectivity Index (Manly *et al.*, 2002). We used the design 1 sampling protocol, meaning that we considered all nest building observations to have been made at the population level and that we did not identify individuals building nests (Thomas and Taylor, 2006). We then assigned each nest to one habitat type. Equation 2.1 of the Manly Selectivity Index calculates a selectivity ratio  $W_i$  (Manly *et al.*, 2002),

$$W_i = \frac{r_i}{p_i} \left/ \sum_{i=1}^m \left( \frac{r_i}{p_i} \right) \right. \text{ (Equation 2.1)}$$

$$W'_i = m \times W_i \text{ (Equation 2.2)}$$

where  $r_i$  is the percentage of nests in habitat  $i$ ;  $p_i$  is the proportion of habitat  $i$ , and  $m$  is the total number of habitat types. The selectivity ratio,  $W_i$ , varies on a scale from 0 (avoidance) to 1 (preference). We used the selectivity ratio to calculate a second value,  $W'_i$ , (Equation 2.2) which is used to decide whether a habitat is preferred or used in a proportion less than expected by chance. Values of  $W' < 1$  indicate that the habitat is used in a proportion less than expected by chance, while values of  $W' > 1$  indicate a preferred habitat. We applied a Chi-squared goodness of fit test to quantify the significance of the preference or avoidance status of a habitat type (Neu *et al.*, 1974). We evaluated patterns of habitat selection using the package *adehabitatHS* (Calenge, 2006) in R version 3.4.2 (R Core Team, 2018).

### 2.3.2.2 PREFERRED AND FALBACK FRUITS

We used three parameters [Stem density (D), Fruit Availability Potential (FAP), Mean Consumption Score (MCS)] to calculate Global Importance Score (GIS), that in turn was used to classify fruiting plant species into their order of preference by gorillas and chimpanzees, adapting the formulae used in (Doran *et al.*, 2002). D for each species was calculated as follows (Equation 2.3),

$$D_i = \frac{\sum_{k=1}^K n_{ik}}{K \times S} \text{ (Equation 2.3)}$$

where  $n_{ik}$  is the number of individuals of species  $i$  in plot  $k$ ,  $K$  is the total number of plots counted and  $S$  is the area of each plot (in this case,  $S = 625 \text{ m}^2$ ). We used D to calculate FAP, using an adaptation of the formula of Tutin *et al.* (1997) and Basabose and Yamagiwa (2002) (Equation 2.4),

$$FAP_{ij} = \left\{ \sum_{n=1}^N (SS_{nij} \times B_{nij}) \right\} \left/ N_i \right. \times D_i \text{ (Equation 2.4)}$$

where  $SS_{nij}$  is the sum of fruit scores of the individual  $n$  of species  $i$  in month  $j$ ,  $B_{nij}$  is the basal area of the individual  $n$  of species  $i$  in month  $j$ ,  $N_i$  is the number of monitored individuals of species  $i$ . Before calculating MCS, we first determined the quantity of fruits (QF) for each species occurring in each faecal sample. For each

species, the number of fruits in the sample was 1 if the number of seeds of the species in the sample was less than the species-specific mean number of seeds per fruit; otherwise, the number of fruits corresponded to the number of seeds in the faecal sample divided by the species-specific mean number of seeds (for decimal numbers, the higher integer was chosen). For species with uncountable seeds such as *Ficus spp.*, we calibrated the number of seeds per fruit, and then estimated the number of fruits consumed from seeds found in faecal samples. QF was then the number of fruits multiplied by the species-specific mean weight. MCS was subsequently calculated using Equation 2.5,

$$MCS_{ij} = \left( \frac{QF_{ij}}{\sum_{i=1}^{N_j} QF_{ij}} \right) \times \left( \frac{Pf_{ij}}{NPf_j} \right) \quad (\text{Equation 2.5})$$

where  $QF_{ij}$  is the quantity of fruits of species  $i$  in month  $j$ ,  $N_j$  is the number of species found in faecal samples in month  $j$ ,  $Pf_{ij}$  is the number of faecal samples of month  $j$  where species  $i$  was present, and  $NPf_j$  is the number of faecal samples analysed in month  $j$ . We calculated the GIS, using the FAP and the MCS (Equation 2.6),

$$GIS_i = \left\{ \sum_{j=1}^J (MCS_{ij} / FAP_{ij}) \right\} / J \times Pe_i \quad (\text{Equation 2.6})$$

where  $J$  is the number of months of study, and  $Pe_i$  is the proportion of months during which species  $i$  was consumed, calculated relative to the number of months during which the species was bearing fruit. We classified species based their GIS value, with higher values corresponding to more preferred species and lower values corresponding to less preferred species.

Our calculation is an improvement of previous methods that were solely based on the percentage of faecal samples in which the fruits were found (Basabose and Yamagiwa, 2002; Etiendem and Tagg, 2013). A classification based on importance types (Doran *et al.*, 2002) was recommended by Rogers *et al.* (2004); however, our approach can inform on the relative preference of a plant species by two animal consumers, by comparing their GIS values for that plant species. Another advantage of our approach is that the equations consider seasonal variation in fruit availability, and the combination of FAP and MCS facilitates the identification of fallback species.

We used the MCS to calculate the seasonal dietary overlap and the GIS to calculate the yearly overlap between the pattern of fruit consumption by gorillas and chimpanzees using Schoener's index of overlap (Equation 2.7; Warren *et al.*, 2008),

$$D(P_C, P_G) = 1 - \frac{1}{2} \left( \sum_{i=1}^N |P_{C_i} - P_{G_i}| \right) \quad (\text{Equation 2.7})$$

where  $P_{C_i}$  and  $P_{G_i}$  represent the proportion of the MCS or the GIS for chimpanzees and gorillas respectively. N is the number of species. In this analysis, we did not consider species for which the GIS was not calculated for either chimpanzees or for gorillas. An overlap of 0.6 may be considered as a biologically significant level of overlap between animal species (Salinas-Ramos *et al.*, 2015).

We used Non-Metric Multidimensional Scaling (NMDS) ordination to visualize how the FAP of each plant species and the MCS of each fruiting plant species by each great ape species respond to seasonal variation, using the Bray-Curtis dissimilarity (Oksanen *et al.*, 2018). We used PERMANOVA to test the hypothesis that the four seasons have different centroids, for FAP and MCS (Anderson and Walsh, 2013). We also tested for homogeneity within seasons to confirm the results of the PERMANOVA (Oksanen *et al.*, 2018).

We determined fallback fruiting plant species for gorillas and chimpanzees by considering the trend of the FAP of each plant species between seasons, and the MCS of each species, for gorillas and chimpanzees (Yamagiwa and Basabose, 2009; Harrison and Marshall, 2011). We divided the seasons into two groups: two seasons of higher total FAP and two seasons of lower FAP. We considered a species fallback for either gorillas or chimpanzees if it fruited in at least three seasons, and if the trend of MCS was negative to that of the FAP. Then, we considered as fallback those fruiting species with high FAP in seasons of high fruit availability, but with high MCS in a season of lower fruit availability. We produced the respective lists of preferred and fallback species for both gorillas and chimpanzees as follows: for each great ape species, we divided the number of fruiting plant species by 3. We started selecting fallback species before selecting preferred ones (Harrison and Marshall, 2011); this means that a species that could be classified as both preferred and fallback was considered fallback. We ran NMDS, PERMANOVA and the homogeneity test using the package *vegan* (Oksanen *et al.*, 2018) in R version 3.4.2 (R Core Team, 2018). The role of ordination is to synthesize multivariate data into a fewer number of dimensions (axes) to facilitate the interpretation by displaying the results graphically and the first two axes are generally used (Syms, 2008).

### 2.3.2.3 DISTRIBUTION OF PLANT CONSUMPTION TRAITS

We defined the plant consumption traits as: preferred by either gorillas or chimpanzees ('Preferred chimpanzee' and 'Preferred gorilla'), preferred by both gorillas and chimpanzees ('Preferred apes'), fallback for either gorillas or chimpanzees ('Fallback chimpanzee' and 'Fallback gorilla'), or fallback for both gorillas and chimpanzees ('Fallback apes'). We used Correspondence Analysis (CA) to analyse the multivariate data (Hill, 1974) of species traits, as proposed by Pla *et al.* (2012). CA is an indirect gradient ordination based on weighted averaging, which uses the position of the sample to identify that of plant species consumption traits (in our case), and vice versa (Lepš and Šmilauer, 2003). In CA, we calculated deviations from expected frequencies so as to have a mean weight of zero, and scores are chosen in a way that minimizes the correlation between rows and columns (traits and habitats) (Hill, 1974). CA is more accurate when the number of species is small (Fayolle *et al.*, 2014), and is, therefore, suitable for the limited number of plant traits and species in our study. We used the first two axes to illustrate the divergence of plant traits and plant species abundance across the different habitat types. The CA results are based on the hypothesis of independence between habitat types and fruiting plant traits (Casanoves *et al.*, 2012); it then calculates a matrix of Chi-squared deviation that measures the combination of habitat types and plant traits that have more inertia, and that contribute to the rejection of the null hypothesis (Casanoves *et al.*, 2012). Finally, CA also provides a row-column sum to zero contingency table, which represents coefficients of the relationship between the two variables in consideration. In this case, this table shows for each plant consumption trait or species, the habitat in which it has its highest abundance; and for each habitat type, with which plant consumption traits or species it is more closely associated. We excluded the 11 plots where no great ape consumed fruiting plant species were found before running the analysis. We used the software package *Infostat 2016* to conduct the CA (Casanoves *et al.*, 2012).

## 2.4. RESULTS

Overall, we monitored 19 plant species for fruit phenology (Table A2.3). We recorded 780 nests on the 20-transects, with 124 gorilla nests and 780 chimpanzee nests (Table A2.4). We collected 1314 faecal samples, of which 905 for gorillas and 409 for chimpanzees (Table A2.5).

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### 2.4.1. SEASONAL HABITAT SELECTION BY GORILLAS AND CHIMPANZEES

The selection of habitats by both gorillas and chimpanzees in all seasons was significantly different to habitat availability (Table 2.1).

**Table 2.1: Chi-square of Manly Selectivity test for habitat use by gorillas and chimpanzees in the different seasons. This is the summary of the statistical test of the patterns of habitat use by gorillas and chimpanzees if different seasons.**

Season	Chimpanzee			Gorilla		
	Chi-square	DF	p-value	Chi-square	DF	p-value
General	512.67	4	< 0.001	167.49	4	< 0.001
Long Dry	148.167	4	< 0.001	43.554	4	< 0.001
Short Dry	116.874	4	< 0.001	16.441	4	0.002
Long Rainy	141.601	4	< 0.001	78.267	4	< 0.001
Short Rainy	160.201	4	< 0.001	49.441	4	< 0.001

Gorillas significantly preferred nesting in SW (Swamp) in all seasons and nested in MF (Mature forest) in proportion significantly less than would be expected by chance in all seasons (Figure 2.3a). For gorillas, the use of LG (Light-gap) was proportional to its availability in all seasons and the use of YSF (Young secondary forest) was proportional to its availability in the long dry, short dry and short rainy seasons, but in proportion significantly less than would be expected by chance in the long rainy season (Figure 2.3a). In addition, RF (Riparian forest) was used proportionally to its availability by gorillas in the short dry and short rainy seasons but was in proportion significantly less than would be expected by chance in the long dry and long rainy seasons (Figure 2.3a). Chimpanzees significantly preferred nesting in MF in all seasons, and significantly nested in LG and YSF less than would be expected by chance in all seasons (Figure 2.3a). Chimpanzees significantly nested in SW in proportion significantly less than would be expected by chance in the short dry and long rainy seasons, used it proportionally to its availability in the short rainy season, and significantly preferred it in the long dry season (Figure 2.3a).

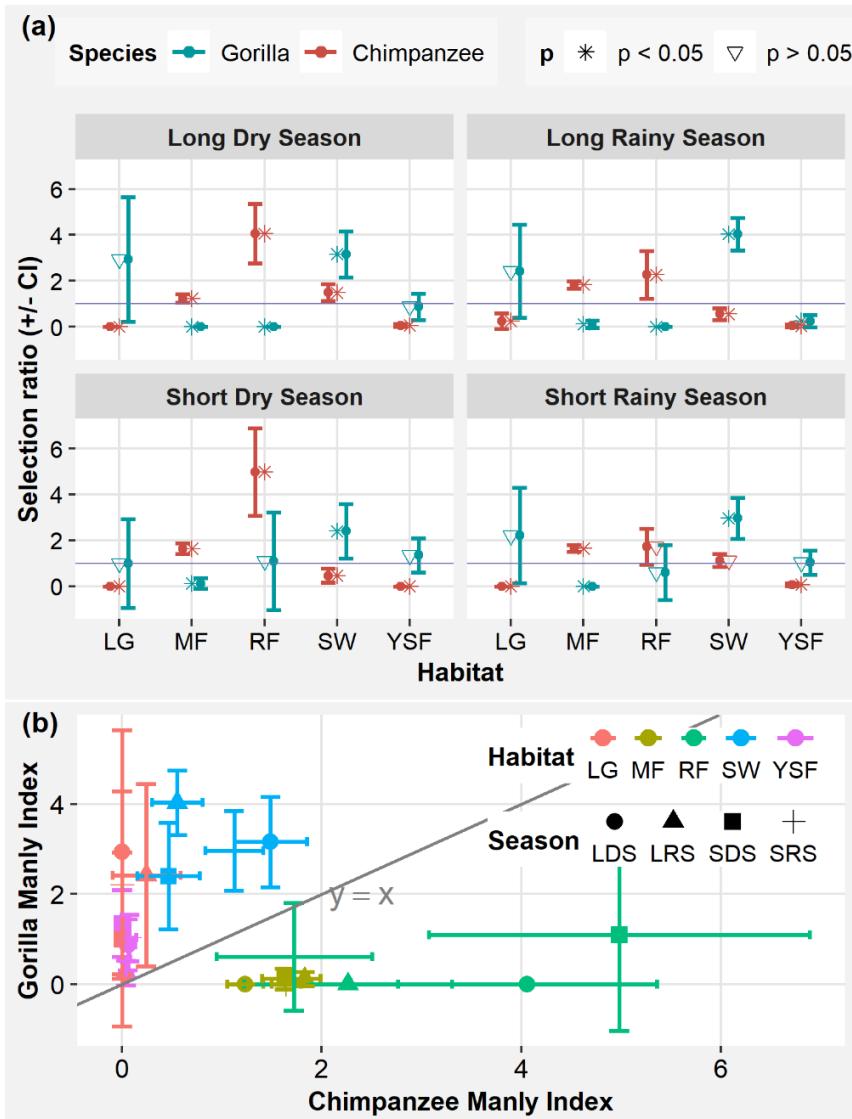
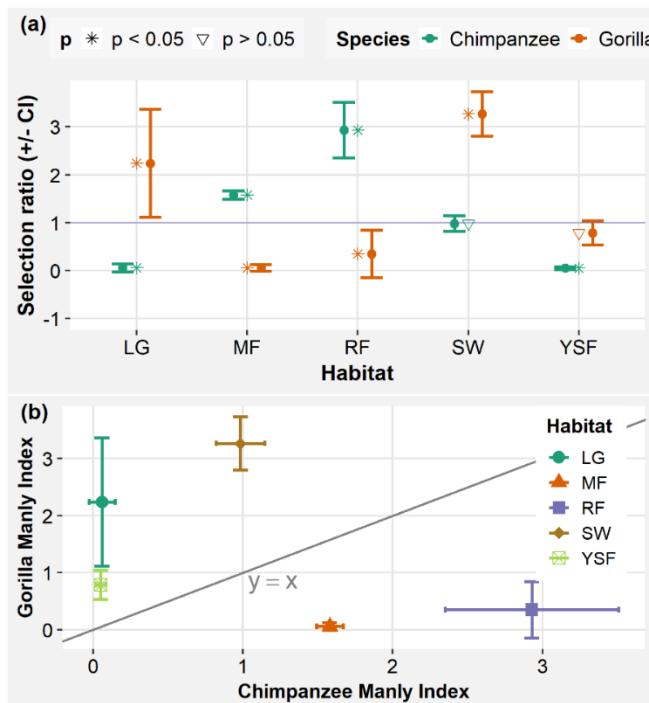


Figure 2.3: Seasonal patterns of habitat selection by gorillas and chimpanzees: (a) seasonal variation in habitat selection, habitats with selection ratio  $>1$  are significantly selected and those with selection ratio  $<1$  are significantly avoided; (b) relationship between gorilla and chimpanzee habitat selection indexes, habitat points above the oblique line represent the use by gorillas and those under the line represent the use by chimpanzees. LG = Light Gap; MF = mature forest; RF riparian forest; YSF = young secondary forest, SW = Swamp; LDS = Long dry season; LRS = Long rainy season; SDS = Short dry season; SRS = Short rainy season; the oblique line is the line of equality. Error bars represent confidence intervals.

Overall, chimpanzees and gorillas both preferentially used different sets of habitat types: gorillas commonly used LG, SW and YSF, while chimpanzees commonly used MF and RF (Figure 2.3b). Gorillas very rarely used MF, while chimpanzees very rarely used LG and YSF (Figure 2.3b). Gorillas seasonally increased their use of RF (in the short dry season), while chimpanzees seasonally increased their use of SW (in the long dry season) (Figure 2.3b), which are not their preferred habitats. In the analysis of all seasons pooled in the present study, we found light gaps to be significantly preferred by gorillas, and YSF to remain used proportionally to its availability (Figure 2.4a,b). However, the present study reveals a use of LG by gorillas across all seasons proportionally to its availability, but the mean selectivity indexes are greater than 1 in all seasons (Figure 2.3a). This non-significance may be due to the low number of data points of nests recorded in that habitat type, which would also explain the longer error bars in all seasons for light gaps (Figure 2.3a).



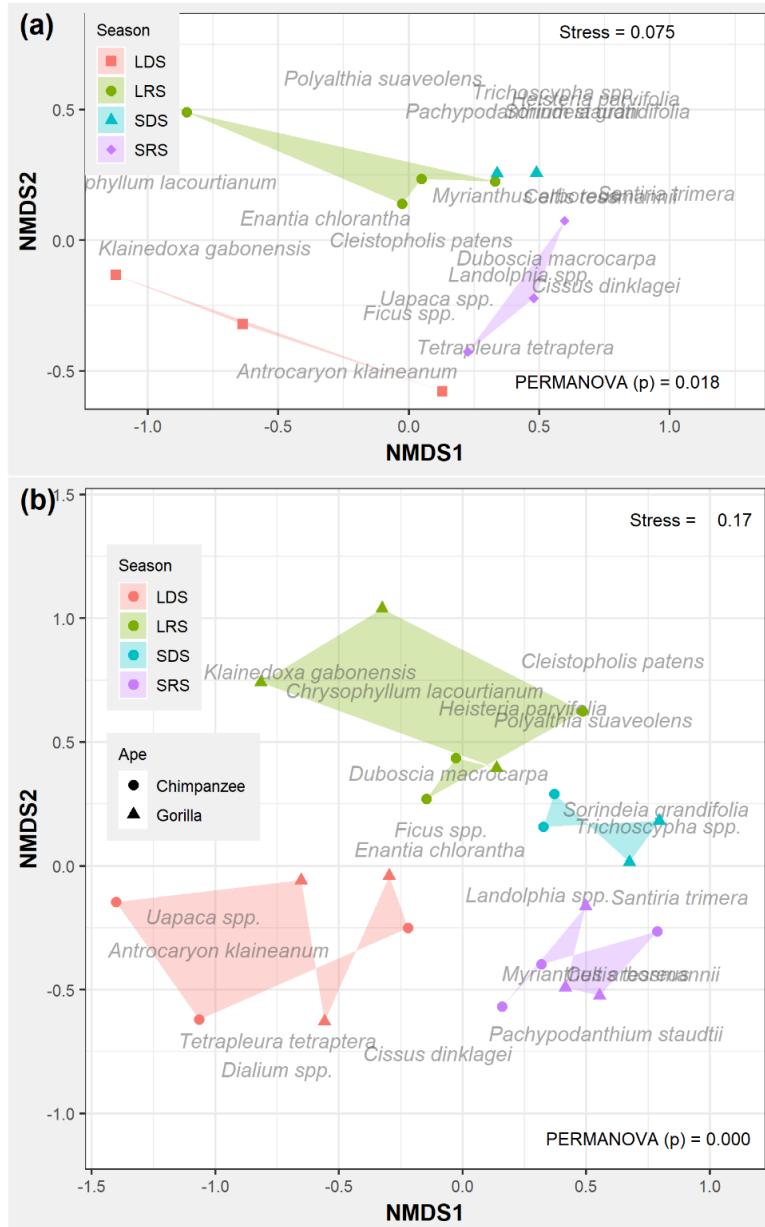
**Figure 2.4: General patterns of habitat selection by gorillas and chimpanzees:** (a) habitat selection, habitats with selection ratio  $>1$  are significantly selected and those with selection ratio  $<1$  are significantly avoided; (b) relationship between gorilla and chimpanzee habitat selection indexes, habitat points above the oblique line represent the use by gorillas and those under the line represent the use by chimpanzees. LG = Light Gap; MF = mature forest; RF = riparian forest; YSF = young secondary forest, SW = Swamp. Error bars represent confidence intervals.

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#### 2.4.2. PREFERRED AND FALBACK FRUITS FOR GORILLAS AND CHIMPANZEES

We used NMDS to evaluate whether FAP and MCS vary between seasons (Figure 2.5a,b). The stress values of the two plots are lower than 0.2, indicating that the two axes easily represent the configuration of theta (Quinn and Keough, 2002). Neither axis 1 nor 2 separates the diversity of FAP (Figure 2.5a) or MCS (Figure 2.5b) between seasons, but there seems to exist a separation between seasons.

The PERMANOVA results were significant for both MCS and FAP, confirming the observed differences (Figure 2.5a,b). Additionally, we obtained a non-significant within-season dispersion ( $p = 0.346$  for MCS, and  $p = 0.370$  for FAP), indicating a confidence in our PERMANOVA results. Meanwhile, it is notable that the seasonal variation in fruit consumption by gorillas and chimpanzees follows the same pattern, as approximately the same species were consumed by both gorillas and chimpanzees in all seasons (Figure 2.5b). Also, the ordination of MCS (Figure 2.5b) presents approximately the same configuration as that of FAP (Figure 2.5a), meaning that the MCS of many plant species for gorillas and chimpanzees vary according to their FAP. An exception is *Uapaca* spp., which produces fruits in almost all seasons, but was highly consumed by chimpanzees more than gorillas in the long dry season (Figure 2.5a,b). Similarly, *Klainedoxa gabonensis* produced more fruits in the long rainy season but was consumed more by gorillas in the long dry season (Figure 2.5b). Many species, such as *Trichoscypha* spp., *Sorindeia grandifolia* and *Santiria trimera* were more available in the short dry season and were highly consumed in that season, almost exclusively by chimpanzees (Figure 2.5a,b). Overall, gorillas and chimpanzees overlapped highly in fruit consumption (0.79) and there was a marked seasonal in that overlap in fruit consumption by gorillas and chimpanzees. The overlap was higher in the short rainy season (0.89), the short dry season (0.78) and the long rainy season (0.60) and lower in the long dry season (0.46).



**Figure 2.5: NMDS ordination results: (a) change in fruit availability potential (FAP) across seasons and (b) change in Mean consumption score (MCS) across seasons. LDS = long dry season, LRS = long rainy season, SDS = short rainy season, SRS = short rainy season. The closer the points (months), the more similar they are in terms of: the plant species bearing fruits as well as their corresponding FAP (a), the plant species consumed as well as their MCS (b).**

Table 2.2: Fruit preference orders for gorillas and chimpanzees.

Species name	Family	Chimpanzee		Gorilla	
		GIS	Rank	GIS	Rank
<i>Landolphia</i> spp. <sup>a</sup>	Apocynaceae	3285.33	1#	608.75	1#
<i>Chrysophyllum lacourtianum</i>	Sapotaceae	60.898	2#	17.899	4#
<i>Santiria trimera</i>	Burseraceae	22.911	3#	0.883	11#
<i>Uapaca</i> spp. <sup>b</sup>	Euphorbiaceae	16.803	4##	10.861	6##
<i>Enantia chlorantha</i>	Annonaceae	3.306	5#	0.053	14
<i>Celtis tessmannii</i>	Ulmaceae	3.276	6#	2.086	10#
<i>Antrocaryon klaineanum</i>	Anacardiaceae	1.581	7##	91.494	2##
<i>Heisteria parvifolia</i>	Olacaceae	1.554	8#	0.122	13
<i>Cleistostolis patens</i>	Annonaceae	1.350	9#	0	UC
<i>Ficus</i> spp. <sup>c</sup>	Moraceae	0.935	10	27.492	3##
<i>Duboscia macrocarpa</i>	Tiliaceae	0.835	11	0.461	12##
<i>Cissus dinklagei</i>	Vitaceae	0.517	12	0.011	15##
<i>Tetrapleura tetrapтера</i>	Mimosaceae	0.251	13##	9.947	7##
<i>Trichoscypha</i> spp. <sup>d</sup>	Anacardiaceae	0.178	14	8.014	8#
<i>Sorindeia grandifolia</i>	Anacardiaceae	0.175	15	13.175	5#
<i>Polyalthia suaveolens</i>	Annonaceae	0.050	16	*	UC
<i>Klainedoxa gabonensis</i>	Irvingiaceae	0.031	17	4.835	9#
<i>Myrianthus arboreus</i>	Urticaceae	**	UC##	0.004	16##
<i>Pachypodanthium staudtii</i>	Annonaceae	**	UC	**	UC
<i>Dialium</i> spp.	Ceasalpiniaceae	***	UC	***	UC

GIS Global Importance Score; UC= unclassified; 0= GIS <0.001; \* = not consumed; \*\* = consumed but not found during phenological surveys; \*\*\* = consumed but not found neither in phenological surveys nor in botanical inventories. <sup>a</sup>= Includes *L. glabra*, *L. jumellei*, *L. landolphioides*, *L. mannii*, *L. maxima*, *L. owariensis*, *L. violacea*, *L. jumellei* and two unidentified species; <sup>b</sup>= Includes *U. acuminata*, *U. guineensis*, *U. paludosa*, *U. vanhouttei*; <sup>c</sup>= Includes *Ficus mucoso*, and some stranglers; <sup>d</sup>= Includes *T. abut* and *T. acuminata*; # = Preferred species, ## = Fallback species

Gorillas and chimpanzees did not exhibit the same order of preference for fruits (Table 2.2). *Landolphia* spp. fruits are highly preferred by both great ape species, but many other species highly preferred by chimpanzees (namely *Santiria trimera*, *Enantia chlorantha* and *Celtis tessmannii*) are less preferred by gorillas. Similarly, *Ficus* spp., *Tetrapleura tetrapтера* and *Sorindeia grandifolia* are highly preferred by

gorillas and less preferred by chimpanzees (Table 2.2). Regarding fallback fruits, many species were consumed by both gorillas and chimpanzees in inverse proportion to the overall trend in fruit availability (Figure 2.6). Then, *Antrocaryon klaineanum*, *Myrianthus arboreus*, *Tetrapleura tetrapтера* and *Uapaca* spp., are fallback fruits for both gorillas and chimpanzees, while *Ficus* spp., *Cissus dinklagei* and *Duboscia macrocarpa* are fallback species for gorillas but not for chimpanzees (Figure 2.6). Because we first selected fallback species before selecting for preferred ones, a highly preferred species (e.g. *Uapaca* spp.), from our calculations, was classified as a fallback (Table 2.2, Figure 2.6). We attributed a species to either 'fallback' or 'preferred' using different criteria. Then it is likely that some species may appear in both categories. But in our case, we needed to assign a species to only one category before proceeding the analyses as recommended by Harrison and Marshall (2011). We found that four species (*Ficus* spp., *Uapaca* spp., *Tetrapleura tetrapтера*, *Antrocaryon klaineanum*) for gorillas and two species (*Uapaca* spp., *Antrocaryon klaineanum*) for chimpanzees were classified as both fallback and preferred and were then assigned to fallback.

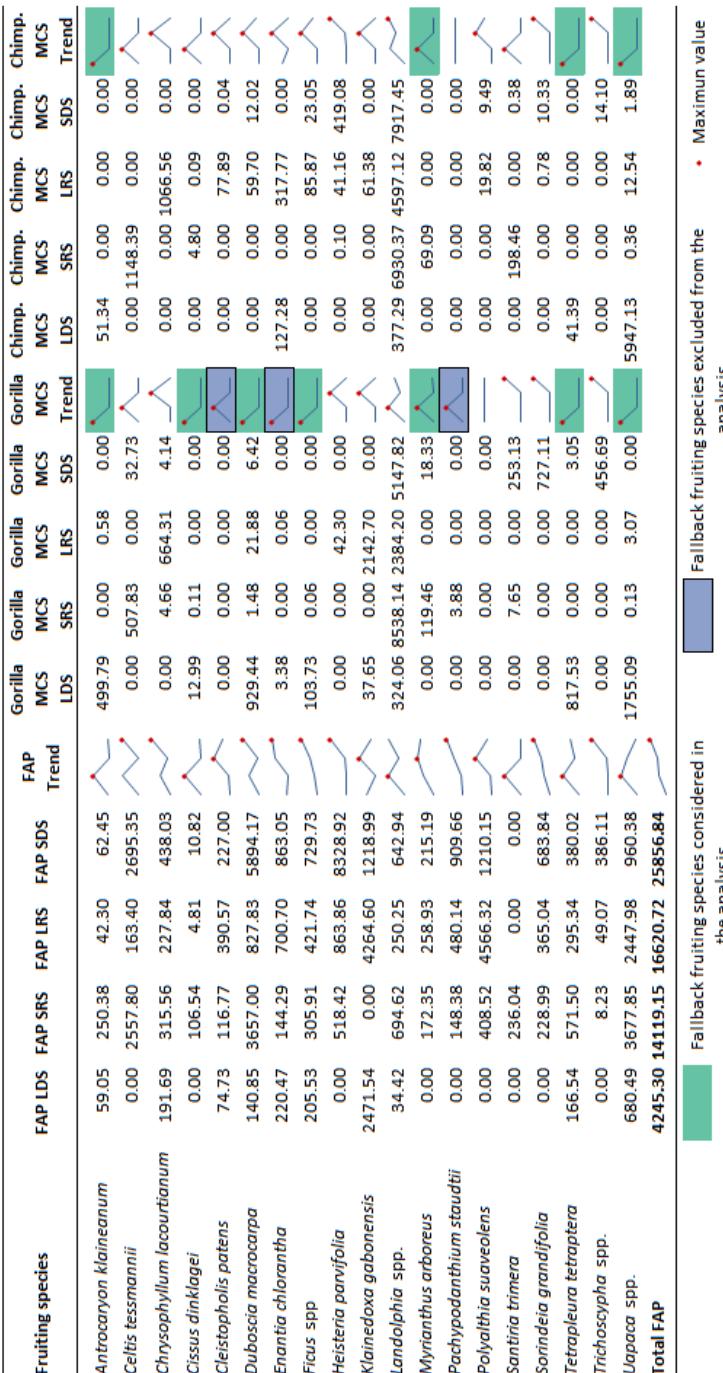
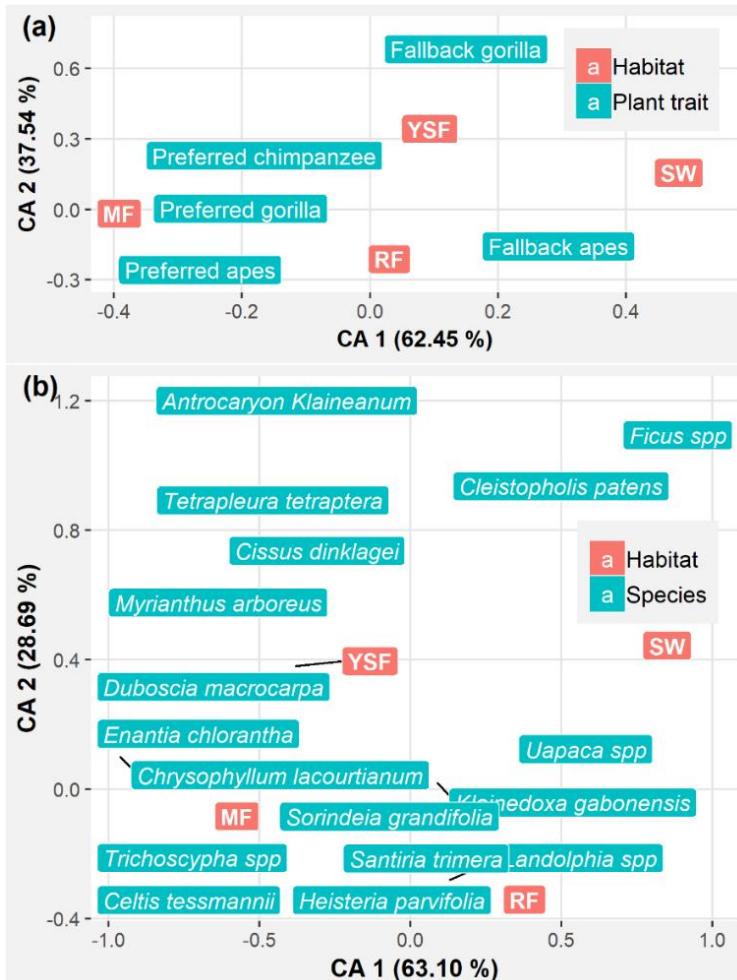


Figure 2.6: Determination of fallback fruit species. Lines present the trends of FAP and MCS; FAP = fruit availability potential, MCS = mean consumption score, LDS = long dry season, LRS = long rainy season, SDS = short rainy season, SRS = short rainy season, Chimpanzee = Excluded species have too low MCS values.

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#### 2.4.3. SPATIAL DISTRIBUTION OF FRUITING PLANTS IN RELATION TO THEIR CONSUMPTION TRAITS

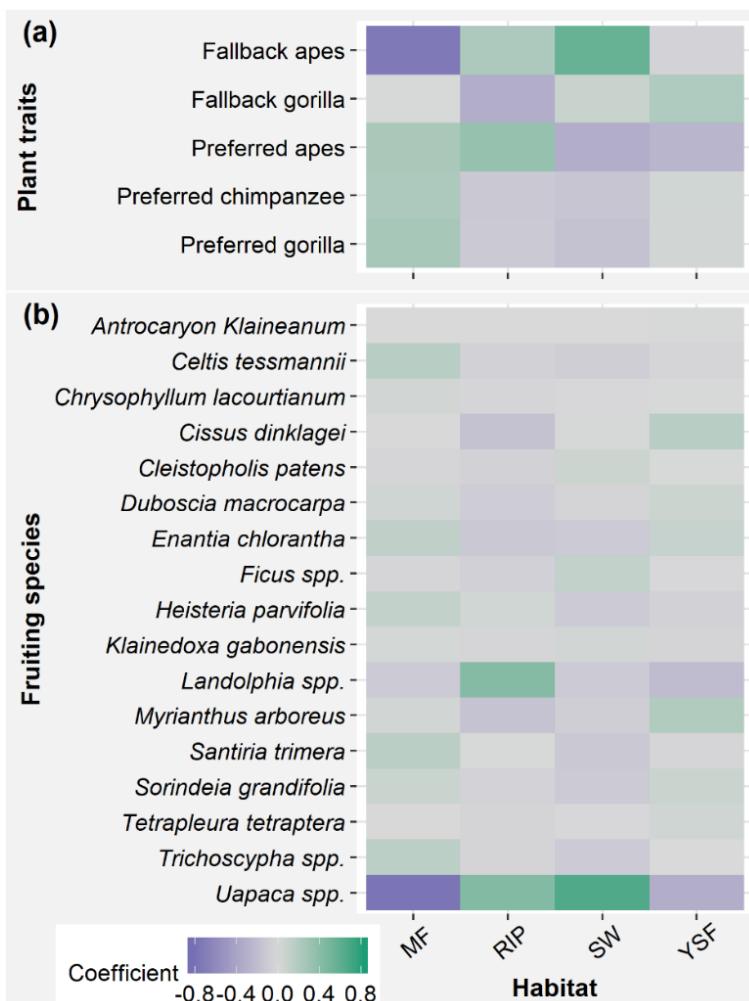
The results of CA indicate a high correlation between MF and SW and the first axis, while YSF and RF are weakly correlated with the first axis (Figure 2.7a). Additionally, YSF and RF have their highest correlation with the second axis, but YSF and SW have a similar correlation with the second axis (Figure 2.7a). MF and SW are farther from the centre and are located on both sides of the centre, meaning that these habitat types contribute the most to the differences in the distribution of plant consumption traits (Figure 2.7a) and species (Figure 2.7b) across all habitats. Their different correlation signs (the projection of each object to the axis) to the first axis mean that the abundances of plant consumption traits (Figure 2.7a) and species (Figure 2.7b) are different between those two habitats. The proximity of YSF and RF to the centre on the first axis indicates that they weakly contribute to the separation of the plant consumption traits. The ordination plot has separated two plant consumption traits categories: the group of preferred plant species negatively correlated with the first axis as MF, and fallback species positively correlated with the first axis as SW (Figure 2.7a).



**Figure 2.7: Results of the Correspondence Analysis showing the distribution of fruiting species and their consumption traits in different habitat types: (a) plant consumption traits; (b) individual species. MF = mature forest; RF = riparian forest; YSF = young secondary forest; SW = Swamp. The black lines indicate the exact location of the labels to which they are linked and are used to avoid overlap of several labels at the same location; the percentages represent the relative quantity of inertia ‘extracted’. Fallback gorilla and Fallback apes are fallback species for gorillas and apes respectively; Preferred Gorilla, Preferred Chimpanzee and Preferred Apes represent preferred plant species for gorillas, chimpanzees and apes respectively.**

The first two axes of the ordination plots (Figure 2.7a,b) explained the high percentages of total variability (99.99% for plant consumption traits [Figure 2.7a] and 91.79% for individual species [Figure 2.7b]). The same pattern of correlation between habitat types and ordination axis for plant consumption traits was

observed for individual species (Figure 2.7a,b). The highest abundances of most species are shifted towards MF, YSF and RF, while just a few sets of species are associated with SW, indicating that the abundance of fewer species may influence the association of plant traits to habitat types (Figure 2.7).



**Figure 2.8: Relationship between plant consumption traits and individual species and habitat types:** (a) plant consumption traits; (b) individual species. MF = mature forest; RF = riparian forest; YSF = young secondary forest; SW = Swamp. The data used in this graph are from the row-column sum to zero contingency tables of the Correspondence Analyses. The coefficients used here are the coordinates of each species or plant consumption traits in the Correspondence Analysis result (Figure 2.7).

Under the assumption of independence between variables, the relationship between plant traits and individual species reveals that fallback fruiting species of gorillas alone, and those of both gorillas and chimpanzees are the most indicating plant traits (Figure 2.8a), meaning that they are more associated with some habitat types than other plant traits. As indicated by the ordination plot (Figure 2.7a), the strongest discriminating nature of MF and SW is due to the distribution of fallback species common to both gorillas and chimpanzees, that are highly abundant in SW, but almost absent from MF (Figure 2.8a). The trait of fallback species for gorillas is more abundant in YSF; while that of preferred species of chimpanzees and of gorillas are positively associated with both RF and MF (Figure 2.8a). All strictly preferred plant traits are only positively associated with MF. The abundance of *Uapaca* spp. is the most influenced by habitat types, with the highest values in SW, and may be responsible for the high abundance of fallback fruits for both gorillas and chimpanzees in SW (Figure 2.8a,b). *Myrianthus arboreus*, *Landolphia* spp., *Celtis tessmannii* and *Santiria trimera* are also highly differentiated, with their highest abundance respectively in YSF and RF for the first two, and MF for the rest (Figure 2.8b). Many species, such as *Antrocaryon klaineanum*, *Chrysophyllum lacourtianum* and *Klainedoxa gabonensis*, do not relatively show any association pattern with habitat types (Figure 2.8b). They certainly influence less the abundances of plant consumption traits by habitat types (Figure 2.8a). It should be noted that *Uapaca* spp. is the only fruiting plant species accounting for the high abundance of fallback fruits to both gorillas and chimpanzees (fallback apes) in swamps (Figure 2.8a,b). Given that this species was mostly consumed in the long dry season by gorillas and chimpanzees, with chimpanzees consuming more than gorillas (Figure 2.5b), and that *Uapaca* spp. is the most abundant great ape fruiting plant species found in swamps (Figure 2.7b), this may explain why chimpanzees significantly selected swamps for nest building in the long dry season (Figure 2.3a). Furthermore, *Landolphia* spp. was found to be highly preferred by both gorillas and chimpanzees and is the principal determinant of the higher abundance of joint preferred fruiting species (preferred apes) in riparian forests (Figure 2.8). Its consumption by gorillas and chimpanzees was higher in the short dry and short rainy seasons (Figure 2.5b), possibly explaining the slight increase in gorilla nests found in riparian forests during the short dry and short rainy seasons (Figure 2.3b).

## 2.5. DISCUSSION

Resource competition (interference and exploitation) is an important factor structuring ecological communities (Pianka, 1981). In these cases, coexistence may

only be possible if species use different habitat types or resources, or if they partition shared resources, according to their temporal availability or spatial distribution (Amarasekare, 2003). The results of this study indicate that gorillas and chimpanzees preferred different sets of habitat types, but seasonal variation in the pattern of habitat use was observed, thus not supporting the hypothesis that the pattern of habitat use promotes coexistence of gorillas and chimpanzees. We also found that gorilla and chimpanzee preferred and fallback fruiting species were different, but due to the non-random pattern of habitat use, this does not support the hypothesis of dietary niche separation as a mechanism of coexistence of gorillas and chimpanzees. However, considering the differential distribution of fruiting woody plant consumption traits, we found that chimpanzees may prefer habitat types where their preferred fruiting plant species are more abundant, while gorillas may prefer habitat types where their fallback fruiting species are more abundant, thus supporting the hypothesis of interaction between two niche axes (dietary and habitat niche) in the promotion of coexistence of gorillas and chimpanzees.

The main limitation of our study is that we used data on great ape habitat use and fruit consumption collected in different years. Due to the inter-annual variability in fruit phenology, the results of fruit preference and plant consumption traits distribution may not reflect exactly the pattern of habitat use when nest surveys were conducted. However, we still consider our results to be reliable because similar patterns of fruiting periods and FAP, fruit preference and fallback were observed in other sites for several common plant species (Nishihara, 1995; Remis, 1997; Rogers *et al.*, 1998; Doran *et al.*, 2002; Doran-Sheehy *et al.*, 2009; Harrison and Marshall, 2011; Head *et al.*, 2011), and through previous research in our research site (Deblauwe, 2009; Petre, 2016). We consider our results of fruit availability and fruit consumption by sympatric gorillas and chimpanzees to reflect a general pattern that can be used to explain other aspects of their ecology in the same site. An additional limitation is that the patterns of habitat use in this study are based only on nesting data because we did not collect data from other signs, such as footprints, feeding remains and vocalizations, to evaluate the pattern of habitat use; although our mechanism of coexistence suggests a possible movement of ape species between habitat types. Our interpretations are based on the results of Furuichi *et al.* (2001) and Morgan *et al.* (2006) that great apes range in habitats that are not their preferred nesting habitats.

We calculated the FAP using fruiting scores rather than the true quantity of fruits in the trees; however, our results are still useful in that our FAP provides a relative

fruit quantity as the calculation integrates the DBH. Studies have considered the ‘fallen fruit phenology’ method to quantify fruit availability (Chapman *et al.*, 1994). But the ‘fallen fruit phenology’ method has a disadvantage that it misses all species whose fruits do not fall on the ground or species whose fruits are consumed by animals before they fall on the ground (Takenoshita *et al.*, 2008). We then considered the method based on fruit observation in trees to be more appropriate in order to provide an estimation for all species.

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#### 2.5.1. SEASONAL CHANGE IN PATTERNS OF HABITAT USE AND GREAT APE COEXISTENCE

We found seasonal variation in habitat use by both gorillas and chimpanzees. We noted that both species consistently preferred or avoided certain habitats but that there was also a seasonal increase in the selection index of other habitat types. Our results report a niche partitioning based on habitat use between gorillas (preferring swamps) and chimpanzees (preferring mature forests), except in the long dry season when both species significantly preferred the same habitat (swamps). Niche partitioning via differential habitat selection by gorillas and chimpanzees has been shown in previous studies (Morgan *et al.*, 2006; Arnhem *et al.*, 2008). Patterns of habitat use by gorillas and chimpanzees observed in other studies have shown chimpanzees to preferentially nest in mature forests and gorillas in swamps, open canopy forests and young secondary forests (Fay and Agnagna, 1992; Bermejo, 1999; Rainey *et al.*, 2010; Willie *et al.*, 2013; Ogawa *et al.*, 2014). However, our results are not consistent with these observations. Our seasonal analysis revealed a significant increase in swamp use by chimpanzees in the long dry season, as observed elsewhere (Poulsen and Clark, 2004; Morgan *et al.*, 2006), and in the same site in a previous study (Tagg *et al.*, 2013). We found gorillas to randomly use LG and YSF in all seasons, except in the long rainy season when they used YSF in proportion significantly less than would be expected by chance; however, a general analysis revealed that gorillas preferred LG, but again used YSF in proportion significantly less than would be expected by chance. A recent study in the same region but using a different data set also found a general use of YSF proportionally to its availability and a preference of LG by gorillas and subsequently considered young secondary forests to be an important habitat for gorilla survival because of the higher percentage of nests built (Chapter 4).

Due to the spatial heterogeneity, gorillas and chimpanzees may have reached a stable local coexistence across their range on the basis of general habitat partitioning (Ritchie, 2002; Amarasekare, 2009). However, our results showed a

significant increase in swamp use in the long dry and short rainy seasons relative to the short dry and long rainy seasons by chimpanzees, and an increase in the use of riparian forests from significantly avoided in the long dry and long rainy seasons to randomly used in the short dry and short rainy seasons by gorillas (Figure 2.3a). This suggests that the niches of the two great ape species may overlap in swamps in the dry season, and therefore does not support the suggestion that coexistence is enabled because of differential habitat use. An explanation that supports the increased use of swamps by chimpanzees in the long dry season is that chimpanzees do so to avoid hunters (Dupain *et al.*, 2004; Poulsen and Clark, 2004; Kalan *et al.*, 2010; Willie *et al.*, 2013), in contrast to the proposition that mature forests may constitute a refuge for chimpanzees (Ogawa *et al.*, 2014).

It is possible that chimpanzee nesting patterns may be influenced by the presence of gorillas (Head *et al.* (2012), and may be linked to the seasonal availability of fruits (Head *et al.*, 2012). Our results support this, as they reveal patterns of habitat segregation between chimpanzees and gorillas in different habitat types and seasons, therefore suggesting competitive avoidance between gorillas and chimpanzees. However, patterns of habitat separation may be biased if we focus our analysis only on nests. A combination of direct (sightings, vocalizations, etc.) and indirect (nest surveys, etc.) observations reveal different patterns of habitat use for both gorillas and chimpanzees being obtained depending on the method used (Furuichi *et al.*, 2001; Morgan *et al.*, 2006). Although the pattern of habitat selection by chimpanzees estimated via nest counts reflected that obtained in Kalinzu Forest (Uganda) through direct observations (Furuichi *et al.*, 2001), patterns of habitat preference by gorillas estimated via nest counts were not the same as that obtained through direct observation in the Goualougo Triangle (Republic of Congo ; Morgan *et al.*, 2006). This dichotomy in habitat use patterns based on methods of estimation coupled with seasonal variation in habitat selection indicate that other factors may be responsible for the coexistence of gorillas and chimpanzees. Foraging is a principal determinant of habitat use, and as frugivores, the seasonal nature of fruit availability may influence the seasonal patterns of habitat use by gorillas and chimpanzees (Poulsen and Clark, 2004; Basabose, 2005). Then examining the patterns of fruit seasonal partitioning between gorillas and chimpanzees may provide additional insights into their coexistence.

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### 2.5.2. FRUIT PREFERENCE, FALBACK FRUITS AND COEXISTENCE OF GORILLAS AND CHIMPANZEES

Coexistence between great apes may be possible due to differences in fruit consumption (Morgan and Sanz, 2006; Schreier *et al.*, 2009; Vleut *et al.*, 2015). Our results indicate that gorillas and chimpanzees consumed almost the same fruiting plant species, which is consistent with the high overlap in fruit consumption observed in other sites (Tutin *et al.*, 1991; Basabose and Yamagiwa, 2002; Oelze *et al.*, 2014). Although gorillas and chimpanzees consume a similar array of fruiting species, they may differ in their seasonal changes in the MCS of different species. Fruits from *Dialium* spp. were found in faecal samples but were not found in botanical inventories (Table 2.2), maybe because its density is very low in the site. A study conducted in an adjacent site in the Dja Reserve reported several species of *Dialium* spp. (Sonké and Couvreur, 2014); however, we cannot confirm the presence of *Dialium* spp. in the present study site. If the species is not present, great apes may be migrating beyond the study area to consume fruits from *Dialium* spp. However, the high consumption of *Dialium* spp. fruits in the dry season, when fruit availability is low, was also observed by Masi and Breuer (2018) in the Republic of Congo and in the Central African Republic.

Chimpanzees and gorillas also exhibited a differing order of preference for fruiting plants (Table 2.2). In addition, as well as there being fruiting species used by gorillas and chimpanzees as fallback fruits, many other fruits are fallback for gorillas alone (Figure 2.6). Dietary niche partitioning between gorillas and chimpanzees has long been viewed at the level of diet guilds, considering fruits as preferred and herbaceous and other vegetative foods as fallback (Williamson *et al.*, 1990; Rogers *et al.*, 2004; Doran-Sheehy *et al.*, 2008, 2009). Although fallback foods have been viewed as those of low nutritional value (Rogers *et al.*, 2004; Doran-Sheehy *et al.*, 2008), determination of fallback foods has rarely been carried out at the species level (Basabose and Yamagiwa, 2002). However, the protein content of fruits may be an important source of energy for great apes (Felton *et al.*, 2009), and the nutritional content of fruiting species may differ (Masi *et al.*, 2015). Our results support the classification by many other studies of *Ficus* spp. as a fallback fruit for chimpanzees (Harrison and Marshall, 2011) and a preferred food for gorillas (Chapman *et al.*, 2005; Yamagiwa and Basabose, 2009). Our results also show that both gorillas and chimpanzees considerably increased their consumption of *Uapaca* spp. fruits in low fruit availability seasons (Figure 2.6). *Landolphia* spp. fruits were mostly available in the short dry, short rainy and long rainy seasons, and in those seasons they were highly incorporated into the diet of both great ape species

(Figure 2.6). Head *et al.* (2011) classified *Uapaca* spp. as one of the top 10 most consumed species by gorillas but not for chimpanzees, based on the frequency of faecal samples containing their seeds. Because this classification was only based on the frequency of consumption but did not consider the quantity consumed and the availability, this may explain why in our study *Uapaca* spp. fruits were classified as fallback and preferred for both gorillas and chimpanzees. The quantity of fruit consumed may increase the MCS and then the final GIS, but do not change the fact that the species is highly consumed when other fruiting species are scarce. Likewise, as shown by Felton *et al.* (2009) and Masi *et al.* (2009), gorillas and chimpanzees may maintain their protein intake consistently, increasing total energy intake by incorporating different food types with different nutritional compositions. This may explain why both gorillas and chimpanzees, while being highly frugivorous, generally incorporate non-fruit foods (herbaceous plants, tree leaves, tree barks) into their diets (Remis, 1997; Doran and McNeilage, 1999; Doran *et al.*, 2002; Twehey and Lye, 2005). Previous studies have found that gorillas shift their diet in response to lower fruit availability to consume non-fruit foods (generally herbaceous plants) while chimpanzees maintain a fruit-dominated diet (Basabose and Yamagiwa, 2002; Head *et al.*, 2011), and this process may be viewed as a niche partitioning mechanism. Based on the MCS, we observed a low overlap in fruit consumption in the LDS (0.46), the season when fruit availability was the lowest in the study site. This may be due to the fact that during the season of fruit scarcity, chimpanzees continue to seek fruit while gorillas increase their consumption of herbs. The present patterns of dietary overlap are similar to what was reported previously in other sites (Tutin and Fernandez, 1985, 1993), although they were based on the number of species. High overlaps were also found in mormoopid bats on the Pacific coast of Mexico in Chamela (reaching a maximum of 0.79) and between dogs and foxes in the Greater Blue Mountains Area (Mitchell and Banks, 2005). In addition, the dietary overlap between mammals was also found to vary seasonally (Agostini *et al.*, 2010; Salinas-Ramos *et al.*, 2015). The high dietary overlap was considered by Mitchell and Banks (2005) as evidence of the existence of competition between wild dogs and foxes.

Among the few species found to be important in the chimpanzee diet during low fruit availability periods by Head *et al.* (2011), it appeared that gorillas never consumed lipid-rich fruiting species such as *Staudtia gabonensis* and *Pycnanthus angolensis*, in any season; however, we found none of those species to be consumed by great apes in our study. Gorillas have been observed to avoid some fruit types, thus increasing the relative fruit dietary breadth of chimpanzees in

terms of fruits (Head *et al.*, 2011). If chimpanzees consume more fatty-rich fruits than do gorillas, this may contribute to enabling coexistence between the species, as competitive exclusion can be avoided if there exists an exclusivity in the use of certain resources, in addition to other shared resources (Ritchie, 2002; Perrin and Kotler, 2005). However, this is not supported by observations from Lopé in Gabon where gorillas may consume more fruits than chimpanzees, and do not reduce their fruit consumption in low fruit availability seasons relative to chimpanzees (Tutin *et al.*, 1991). Indeed, the diversity of fruits consumed by gorillas and chimpanzees may result in sufficiently large fruit niche breadths so that competition is reduced, despite the high fruit dietary niche overlap (Sushma and Singh, 2006). The fission-fusion behaviour exhibited by chimpanzees may be influenced by seasonal variation in fruit availability, enabling large groups to divide into smaller subgroups when fruits are scarce (Chapman *et al.*, 1995). Large party size in chimpanzees affords them an increase in dominance over gorillas for access to fruit trees (Basabose and Yamagiwa, 2002; Lehmann and Boesch, 2004), thus suggesting that intraspecific competition among chimpanzees is higher than interspecific competition between gorillas and chimpanzees, enabling their coexistence (Lehmann and Boesch, 2004; Amarasekare, 2009). Meanwhile, chimpanzees may be globally more specialized in fruit consumption than gorillas, and the more dominant species (Tutin *et al.*, 1997; Morgan and Sanz, 2006; Lambert and Rothman, 2015).

A mechanism of coexistence of gorillas and chimpanzees based on fruit food partitioning is plausible. However, it does not help understand differences in habitat use between species and between seasons and thus do not fully explain the mechanism of coexistence of great apes. We, therefore, continue by exploring if the combination of mechanisms of fruit choice and habitat use may lead to additional explanations.

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#### 2.5.3. SPATIAL DISTRIBUTION OF PREFERRED AND FALBACK FRUITS AND COEXISTENCE OF GORILLAS AND CHIMPANZEES

We found that all preferred fruiting species for both gorillas and chimpanzees (preferred apes) were more abundant in mature forest and riparian forest than in other habitat types, while all fallback fruiting species for both great apes (fallback apes) were more abundant in SW and YSF (Figure 2.8a). As chimpanzees significantly preferred mature forest, this suggests they may prefer nesting in habitats which hold higher abundances of their preferred fruits. Our results, therefore, suggest that great ape patterns of habitat use may be influenced by the

difference in abundance of preferred and fallback woody fruiting plants, the phenology of these plant species and the season in which they are most commonly consumed. This suggests a nonlinear competition, where competitors are affected by temporal variation in food availability (Amarasekare *et al.*, 2004; Amarasekare, 2009). However, although all gorilla preferred fruiting plants were highly abundant in mature forest, gorilla nests were not found in that habitat in this study. This may be a consequence of the indirect data collection methodologies adopted for this study: studies using direct observational methods have found gorillas to frequently use mature forests and chimpanzees to use habitat types other than mature forest where they preferably build nests (Furuichi *et al.*, 2001; Morgan *et al.*, 2006), suggesting overlap in terms of ranging habitats (Morgan *et al.*, 2006). A potential mechanism of coexistence of gorillas and chimpanzees, therefore, may be driven by the seasonal variation in habitat selection, and the seasonal movements between the different habitats (Amarasekare, 2009). As the dominant species, chimpanzees may nest in habitats where preferred woody fruiting plant species are more abundant, while gorillas nest in habitats where preferred fruiting plants are less abundant, but forage in habitats where preferred fruits are more available, for example in mature forest, to reduce competitive exclusion. This mechanism may create a negative density-dependent effect in great ape habitat use (Amarasekare, 2003). Our results support the evidence that central chimpanzee densities are closely linked to a higher fruit availability as was found in other chimpanzee subspecies (Stanford and Nkurunungi, 2003; Potts *et al.*, 2011). The suggestion that chimpanzee densities are determined by the availability of fruits is supported by Basabose (2005), who observed chimpanzees visiting gorilla preferred nesting habitats to consume their preferred *Ficus* spp. fruits but remaining close to mature forest, their preferred nesting habitat. Furthermore, this dynamic might increase intraspecific competition in chimpanzees (Amarasekare, 2003), as party sizes increase to defend foraging territories (Lehmann and Dunbar, 2009).

This argument, however, does not explain why both gorillas and chimpanzees significantly preferred swamps in the long dry season where *Uapaca* spp., the species with the highest FAP of the season, is more abundant. Competitive exclusion may be avoided if fruit availability (*Uapaca* spp.) is high in that habitat during the long dry season (Prins *et al.*, 2006; Head *et al.*, 2012). This may explain the simultaneous selection of swamps by gorillas and chimpanzees in the long dry season. First, the long dry season is the season of lowest fruit availability, when great apes are expected to show the greatest niche divergence, but the contrary is observed. Second, the availability of *Uapaca* spp. fruits may be sufficiently high in

swamps in the long dry season to sustain both apes, as both are observed to increase *Uapaca* spp. consumption in the long dry season (Figure 2.6). Swamps are with YSF and TA the habitats with the highest densities in herbaceous plants, and those plants are available year-round (Rainey *et al.*, 2010; Willie *et al.*, 2013). The ranging patterns of western lowland gorillas in SW at Mondika were found to be correlated with the consumption of herbaceous vegetation, and this consumption occurred occasionally when fruit availability in *terra firma* forests was low (Doran and Greer, 2002). Thus, additionally to the high quantity of *Uapaca* spp. fruits in swamps in the long dry season, competition between gorillas and chimpanzees may be avoided in swamps by the increasing consumption of herbs by gorillas in the long dry season. Meanwhile, it has been found that herbaceous plants suitable for gorilla nest building are less abundant in mature forest than in old secondary forest in this region (Willie *et al.*, 2013), while chimpanzee nesting trees are less abundant in young secondary forest than in mature forest (Tagg *et al.*, 2013). Adding to the lower abundance of chimpanzee preferred fruiting plants in young secondary forest found in this study, this observation may explain the near absence of gorillas and chimpanzees in MF and in YSF, respectively, in all seasons. The year-round availability of herbaceous plants makes it non-responsible for the seasonal ranging patterns of great apes across habitats. Coexistence of gorillas and chimpanzees has been suggested to be favoured by a difference in nest height for both species, whereby gorillas may prefer nesting on the ground and chimpanzees in trees, to avoid competition (Stanford, 2006). Certainly, it is widely observed that gorillas commonly nest on the ground, using herbaceous vegetation (Willie *et al.*, 2013).

## 2.6. CONCLUSION

This paper addresses how the consumption traits of fruiting woody plant species consumed by sympatric great apes may contribute to shaping their local coexistence. We find that the spatial distribution of fruiting plants according to their extrinsic traits and the temporal availability of fruits for different fruiting woody plant species may account for the coexistence of gorillas and chimpanzees, via a mechanism of seasonal movement between habitats. As predicted, preferred fruiting plants for both gorillas and chimpanzees were most abundant in chimpanzee preferred nesting habitat types, while their fallback fruiting species were more abundant in gorilla preferred nesting habitat types. Tree species may differ in their abundance across habitat types, and the choice of a set of species to be logged will imply different levels of perturbation in different habitat types. This

study proposes using the spatial distribution of resources to understand mechanisms of coexistence of two competing species, by defining consumption traits for each fruiting plant consumed, based on its preference and fallback status. Our results conform to the assumption of niche theory. Gorillas and chimpanzees used similar habitat types and fruits, but to avoid competition, they partitioned those resources in space and time. The seasonal nature of fruit availability and the different abundances of the different fruiting plant species of different quality across habitats are two ecological factors that have facilitated niche partitioning between gorillas and chimpanzees. Also, the general tendency of preferred fruiting species for both gorillas and chimpanzees to be more abundant in chimpanzee preferred habitats confirm the competitive superiority of chimpanzees over gorillas. The results of this study can contribute to conservation in human-modified landscapes in two ways: the findings are helpful in predicting the outcome of environmental change on great ape community structure, and they can be employed in the restoration of degraded habitats.

## 2.7. APPENDIX

**Table A2.3: Number of individual plants monitored for each species for fruits phenology in 2014.**

Species name	January 2014	February 2014	March 2014	April 2014	May 2014	June 2014	July 2014	August 2014	September 2014	October 2014	November 2014	December 2014
<i>Antrocaryon</i>	4	4	2	4	4	4	4	4	4	4	4	4
<i>Klaineanum</i>	4	4	2	4	4	4	4	4	4	4	4	4
<i>Celtis tessmannii</i>	10	10	9	10	10	10	10	10	10	10	10	10
<i>Chrysophyllum lacourtianum</i>	8	8	8	8	8	8	8	8	8	8	8	8
<i>Cissus dinklagei</i>	9	9	8	9	9	9	8	8	8	9	9	9
<i>Cleistopholis patens</i>	9	9	9	9	8	9	8	8	8	9	9	9
<i>Duboscia macrocarpa</i>	19	19	17	19	19	19	19	19	19	19	19	19
<i>Enantia chlorantha</i>	11	11	10	11	11	11	11	11	11	11	11	11
<i>Ficus spp.</i>	14	14	13	14	14	14	14	14	14	14	14	14
<i>Heisteria parvifolia</i>	10	10	10	10	10	10	10	10	10	10	10	10
<i>Klainedoxa gabonensis</i>	10	10	9	10	10	10	10	10	10	10	10	10
<i>Landolphia spp.</i>	37	37	37	37	36	37	36	36	37	37	37	37
<i>Myrianthus arboreus</i>	10	10	9	10	10	10	10	10	10	10	10	10
<i>Pachypodanthium staudtii</i>	10	10	9	10	10	10	10	10	10	10	10	10
<i>Polyalthia suaveolens</i>	10	10	9	10	10	10	10	10	10	10	10	10
<i>Santiria trimera</i>	15	15	14	15	15	15	15	15	15	15	15	15
<i>Sorindeia grandifolia</i>	10	10	10	10	10	10	10	10	10	10	10	10
<i>Tetrapleura tetrapтера</i>	9	9	8	9	9	9	9	9	9	9	9	9
<i>Trichoscypha spp.</i>	19	19	17	19	19	19	19	19	19	19	19	19
<i>Uapaca spp.</i>	37	37	34	37	37	37	37	37	37	37	37	37
<b>Total</b>	<b>261</b>	<b>261</b>	<b>242</b>	<b>261</b>	<b>259</b>	<b>261</b>	<b>258</b>	<b>258</b>	<b>259</b>	<b>261</b>	<b>261</b>	<b>261</b>

**Table A2.4: Number of nests recorded for each species (gorilla and chimpanzee) per season per habitat type.**

Species (season)	Light gap	Riparian forest	Young secondary forest	Mature forest	Swamp	Total
<b>Chimpanzee</b>	<b>2</b>	<b>88</b>	<b>10</b>	<b>435</b>	<b>121</b>	<b>656</b>
Long Dry	0	32	3	89	48	172
Long Rainy	2	17	2	126	17	164
Short Dry	0	21	0	63	8	92
Short Rainy	0	18	5	157	48	228
<b>Gorilla</b>	<b>14</b>	<b>2</b>	<b>29</b>	<b>3</b>	<b>76</b>	<b>124</b>
Long Dry	4	0	7	0	16	27
Long Rainy	5	0	3	2	31	41
Short Dry	1	1	8	1	9	20
Short Rainy	4	1	11	0	20	36
<b>Total</b>	<b>16</b>	<b>90</b>	<b>39</b>	<b>438</b>	<b>197</b>	<b>780</b>

**Table A2.5: Number of faecal samples analysed for each animal species (gorilla and chimpanzee), per month, and per season in 2014. No faecal sample was collected in March 2014.**

Season	Month	Chimpanzee	Gorilla	Total
Long dry season	January 2014	53	44	97
	February 2014	4	66	70
	December 2014	19	105	124
	March 2014	0	0	0
Long rainy season	April 2014	9	8	17
	May 2014	7	25	32
	June 2014	98	58	156
	July 2014	105	97	202
Short dry season	August 2014	51	129	180
	September 2014	6	65	71
	October 2014	43	261	304
	November 2014	14	47	61
<b>Total</b>		<b>409</b>	<b>905</b>	<b>1314</b>

## 2.8. DATA ACCESSIBILITY

The botanical, phenological, dietary and nest survey data supporting our findings can be downloaded on [Dryad](#) (Tédonzong *et al.*, 2019).

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## CHAPTER 2

# CHAPTER 3

## MODELLING THE INFLUENCE OF RESEARCH PRESENCE AND HUMAN SETTLEMENTS ON THE DISTRIBUTION OF TWO SYMPATRIC FRUGIVOROUS MAMMALS

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### 3.1. ABSTRACT

Habitat loss and degradation are among the most important causes of recent decline in wildlife populations. Ecological factors such as predation can cause a shift in habitat utilization by inducing fear in their prey. Humans are also contributing to the problem; they are now considered to be super predators and are more and more present in most natural areas. Therefore, it is crucial to determine how human presence can cause the degradation of wildlife habitat at the community level. We applied this study to sympatric great apes (*Gorilla gorilla gorilla* and *Pan troglodytes troglodytes*). We collected data on great ape nest locations and habitat distribution, and we used other spatial features such as trails, villages, a research site, permanent rivers, and topographic data to determine how different types of variables (ecological and anthropogenic) affect wildlife species. Here, we show that human disturbance is an important predictor of the distribution of wild animals. In the resource model (including ecological requirements of the species), the distribution of gorilla nests was predicted by the availability of their preferred nesting habitats, while chimpanzee nests were predicted first by elevation followed by their preferred nesting habitats. When including human settlements in the models, the major predictors of gorilla nesting changed to human features, while the major predictors of chimpanzee nesting remained elevation and the availability of their preferred nesting habitats. Great apes avoided nesting near almost all human features. Our results demonstrate that the long history of human presence in natural systems has modified ecosystems, and they highlight the fact that although habitat may be available for a species, it may not be accessible to that animal. We anticipated our essay to be a starting point for defining conservation measures for animal communities in human-dominated landscapes even when their hunting is controlled. For example, evidence suggests that chimpanzees may survive in human-encroached areas whenever the availability of their nesting habitat and preferred fruits can support their population, while a certain level of human activities may threaten gorillas. This research extends our knowledge of predator-prey systems and emphasizes the need to consider the effects of humans on animal behaviour.

**Keywords:** Western lowland gorilla; Central chimpanzee; Predator-prey system; Ecological niche; Species distribution modelling; Anthropocene

### 3.2. INTRODUCTION

Habitat loss and degradation are the most important threats to wildlife (Johnson, 2007; Pereira *et al.*, 2012). Several trade-offs often influence the dynamics of wildlife populations which determine their survival in the natural system. Those trade-offs relate to food acquisition, nesting, territoriality, and mating and are conditioned by ecological factors such as competition, predation, and habitat quality (Chapter 2; Frid and Dill, 2002; Cresswell, 2008). Understanding the ecological impact of those factors on wildlife populations is inherent to their conservation in human-dominated landscapes.

Predation is an important ecological factor shaping wildlife species distribution. The effects of predation on wildlife species can be lethal (direct killing of animals) (Cherry *et al.*, 2015) or non-lethal (behavioural modification or induced physiological stress) (Lima, 1998; Messina *et al.*, 2018). The latter effect has received attention in scientific literature and has been characterized as being a consequence of a perceived predation risk (Frid and Dill, 2002; Cresswell, 2008; Chutipong *et al.*, 2015). Previous studies have reported that animal species may respond to predation risk in several ways: (i) species can alter their movements by changing direction or moving more slowly in the presence of the predation risk (Courbin *et al.*, 2014); (ii) animals may become more vigilant due to fear, and this can contribute to reducing the foraging effort as well as the time spent on feeding (Cherry *et al.*, 2015; Clinchy *et al.*, 2016; Haswell *et al.*, 2018); (iii) animals may also respond to predation risk by avoiding areas used by the predator (Wereszczuk and Zalewski, 2015; Dröge *et al.*, 2017; Plante *et al.*, 2018). Change in the spatial distribution of a species is a common response to predation risk, and this response can make some parts of the landscape unsuitable for the animal (Gill *et al.*, 2001; Oriol-Cotterill *et al.*, 2015). These various responses to predation risk have important physiological consequences on animals – results have shown an increase in the level of the stress hormone, cortisol (Bleicher, 2017; Messina *et al.*, 2018; Zbyryt *et al.*, 2018). The stress produced by the increasing level of cortisol negatively impacts the fitness of a species through indirect effect on survival and reproduction and then on population dynamics (Frid and Dill, 2002; Cresswell, 2008; Clinchy *et al.*, 2013; Benitez-Lopez, 2018). Hill and Weingrill (2007) have defined four determinants of predation risk: predator encounter, predator attack, prey capture, and individual capture probability. This means that the perceived risk of predation may vary according to the individual species considered in the predator-prey system (Linder and Oates, 2011). Each prey species in a predator-

prey system adopts a level of vigilance in response to its perception of the risk of predation in presence; the higher the level of apprehension of the predation risk, the higher the space which will be unsuitable for the animal species (Brown *et al.*, 1999; Frid and Dill, 2002). Hence, the perceived risk of predation can cause the reduction of suitable habitat patches if the areas avoided contain valuable feeding opportunities or are important nesting habitat types (Brown *et al.*, 1999; Norum *et al.*, 2015).

So, although in some systems, the risk of predation does not prevent the use of suitable habitat patches by select species (Enstam, 2007; Turkia *et al.*, 2018), in other systems, predation risk does prevent some species from accessing certain habitat patches to forage, or it may increase the quantity of food they left behind due to the presence of predation (Kuijper *et al.*, 2013; Courbin *et al.*, 2014; Hornseth and Rempl, 2016; Haswell *et al.*, 2018). The cost of increasing the GUD (Giving-Up Density, the density of food left behind in the presence of a competitor or a predator) may depend on whether the animal has other feeding opportunities or suitable habitats in the landscape (Frid and Dill, 2002). This is consistent with the “predation-sensitive food” hypothesis defined by Sinclair and Arcese (1995) stipulating that food and predation are limiting factors of animal population because animals may take higher risks against predation when food availability is low. Body size may influence the vulnerability to predation; in this case, larger body-sized animal species may withstand higher risk of predation than smaller ones (Davidson *et al.*, 2009; Preisser and Orrock, 2012; Benitez-Lopez, 2018; Navarro-Castilla *et al.*, 2018). Also, the perceived risk of predation may be relatively higher in terrestrial than arboreal species (Wereszczuk and Zalewski, 2015). Efforts invested into anti-predation behaviour have profound consequences on species’ population size by decreasing the net energy intake, body conditions, and reproduction success (Frid and Dill, 2002). Those “trait-mediated interactions” (the change in the prey phenotype or behaviour in response to predation risk) (Preisser *et al.*, 2005) may cause mortalities in the prey species as a result of non-consumptive effects due to the risk of predation (Gehr *et al.*, 2018).

Despite the negative effects of predation risk on wildlife population dynamics, studies have often been limited to carnivores even though the presence of humans may have the same effects on species as those resulting from the presence of natural predators. The avoidance of an area by an animal species due to the presence of another ecologically different species is evidence that the first species considers the second as a predator (M’Soka *et al.*, 2017). Because large carnivores respond negatively to human presence (Schuette *et al.*, 2013; Oriol-Cotterill *et al.*,

2015), humans can be seen as “super predators” (Clinchy *et al.*, 2016; Zbyryt *et al.*, 2018) and should be considered in studies of “predator-prey” systems (Frid and Dill, 2002; Alberti *et al.*, 2003). Humans are now either permanently present (Leblond *et al.*, 2011; Bortolamiol *et al.*, 2016; Scholte and Iyah, 2016) or temporarily present (Gehr *et al.*, 2017; Paton *et al.*, 2017) in almost all ecosystems, and human settlements are often found close to wildlife populations. Human activities such as hunting, gathering, and logging, as well as the proximity of human infrastructures such as villages and roads are perceived as threats by wildlife species (Frid and Dill, 2002; Koerner *et al.*, 2017; Lindshield *et al.*, 2017; Paton *et al.*, 2017; Tagg *et al.*, 2018).

Studies have shown that human settlements induce some gradients in the abundance of wildlife species with implications for their spatial distribution (Blom *et al.*, 2005; Vanthomme *et al.*, 2013; Koerner *et al.*, 2017; Schroeder *et al.*, 2018; Tucker *et al.*, 2018). Although, different types of human settlements may have different effects on animal species (Bowman *et al.*, 2010; Stokes *et al.*, 2010; Vanthomme *et al.*, 2013), proximity to villages, proximity to roads, and proximity to secondary roads represent the most influential variables to wildlife population abundance or presence (Blom *et al.*, 2005; Benitez-Lopez *et al.*, 2010; Koerner *et al.*, 2017). Understanding the patterns of niche dynamics is a requirement for spatial conservation planning of biodiversity, and niche shift or niche change can be used to measure niche dynamics (Pearman *et al.*, 2008; Guisan *et al.*, 2014).

Studies of the effects of human settlements on animal species were often done only considering anthropogenic variables (distance from roads, distance from villages, distance from logging activities, etc.) (Stokes *et al.*, 2010; Vanthomme *et al.*, 2013). However, when ecological variables are included, studies do not indicate how disturbance affects the basic requirements that are necessary to increase the fitness of the animal species (Blom *et al.*, 2005; Etiendem *et al.*, 2013; Bortolamiol *et al.*, 2016; Filla *et al.*, 2017; Koerner *et al.*, 2017; Schroeder *et al.*, 2018). As the domination of humans on the biosphere is becoming a rule (Hockings *et al.*, 2015), it is more and more crucial to evaluate the effects of anthropogenic factors on species’ distribution in order to figure out the structure of biological communities (Alberti *et al.*, 2003; Albuquerque *et al.*, 2018). At the community level, the use of ecological niche modelling to compare habitat quality involves running the model for each species under consideration and then comparing its predicted habitat suitability (geographical space comparison) or measuring the environmental niche similarities (environmental space comparison) (Hirzel and Le Lay, 2008). In this study, we focused on a community of great ape species (*Gorilla gorilla gorilla* and

*Pan troglodytes troglodytes*) in the northern periphery of the Dja Faunal Reserve. Western lowland gorillas and central chimpanzees are all threatened primate species – gorillas are considered to be “critically endangered” and chimpanzees “endangered”, according to the International Union for Conservation of Nature (Humle *et al.*, 2016; Maisels *et al.*, 2018). Field research is considered to be a form of human intrusion in the natural system (Salafsky *et al.*, 2008) because using a network of transects may indirectly contribute to the development of hunting activities in the research site (Gruen *et al.*, 2013). Questions regarding the effects of research presence on mammal populations have recently been raised (Laurance, 2013) making it imperative for researchers to evaluate the effects of their presence on mammal populations (Riley and Bezanson, 2018). If research presence is susceptible to favour hunting activities, it is likely that the distribution of mammal populations in the research site may be affected.

Using the current literature on great ape ecology, we aimed to determine the contribution of human activities in the research site and human settlements on their geographical niches and evaluate their implications for population dynamics. We hypothesized that (i) anthropogenic variables are more important than ecological variables in great ape distribution, and that (ii) the overlap between the distribution of gorillas and chimpanzees in the anthropogenic model is smaller than the overlap between their distributions in the resource model. We measured the shift in distribution as the change in distribution in the resource models due to the inclusion of anthropogenic variables (research presence and human settlements) used in the model as a proxy for predation risks (McLoughlin *et al.*, 2010).

### 3.3. METHODS

#### 3.3.1. STUDY AREA

Three villages are located at the proximity of the study area, which are linked by a main trail. A network of secondary trails is used by local people for hunting and collection of non-timber forest products and by researchers to enter the research site (Figure 3.1). Hunting activities are susceptible to occur on the transects and threaten mammals in the research site (Tagg and Willie, 2013).

We divided the study area into 175 grid cells of  $1 \times 1 \text{ km}^2$ . Inside of each grid cell, we established a 1.2 km transect, totalling 210 km of transect walked (Figure 3.1). We chose a  $45^\circ$  bearing so that all transects would traverse the drainage features.

Transects extended diagonally 600 m on both sides of the centre of the grid cell (Figure 3.1).

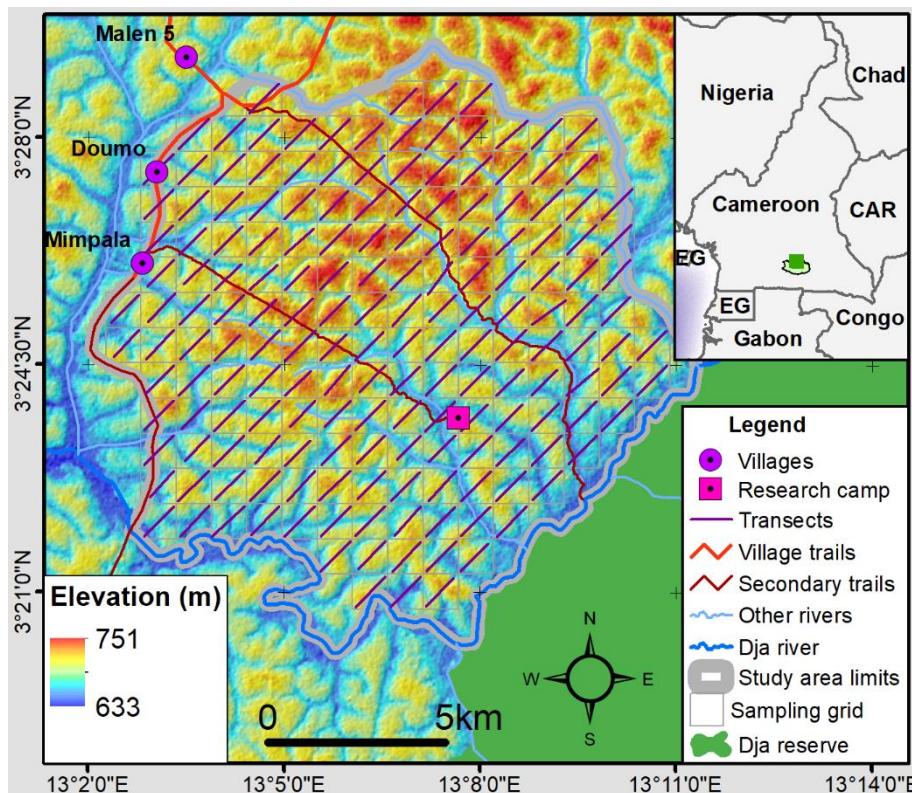


Figure 3.1: Study area and sampling design, with all human features (villages, trails, and research camp). The transects were drawn by joining the starting and the ending points.

### 3.3.2. DATA COLLECTION

#### 3.3.2.1 OCCURRENCE DATA

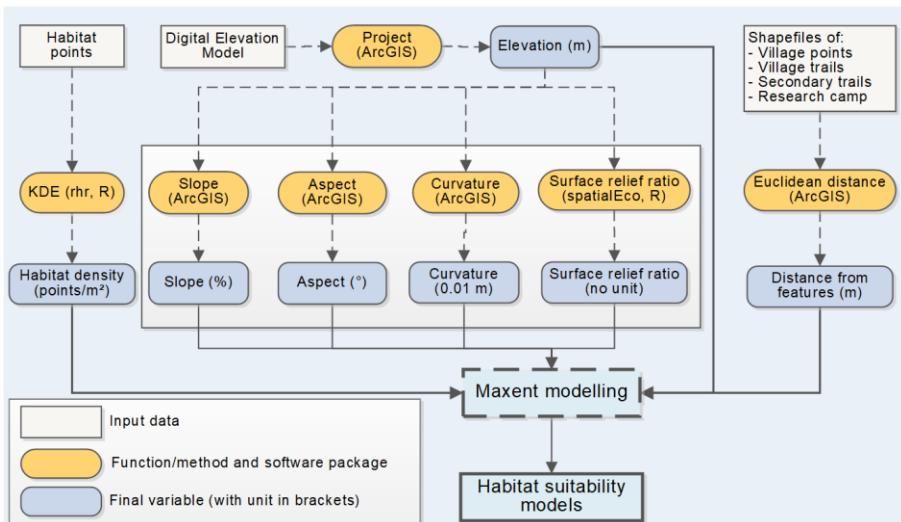
Each month, a team composed of a research assistant and local guides randomly selected a number of transects for data collection. Along each transect, the team searched for great ape nests and recorded the geographical locations of all nests encountered.

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### 3.3.2.2 ENVIRONMENTAL DATA

We used three categories in the modelling processes: ecological variables (habitat distribution), geophysical variables (elevation, slope, curvature, aspect, surface relief ratio, distance from permanent rivers and streams, and curvature), and anthropogenic variables (distance from villages, distance from village trails, distance from secondary trails, and distance from the research camp) (Figure 3.2). We considered the research camp as the barycentre of all research presence because it is located almost at the centre of the area covered by transects used for research purposes. Along each transect, we recorded the habitat type at each 50-m interval, resulting in 121 habitat points per transect. For habitat distribution, we distinguished two variables for gorillas and chimpanzees, based on their preferred nesting habitats as defined in Chapter 4. Then, we used young secondary forest, swamp, and light gap to derive the habitat variable for gorillas, and we used old secondary forest to generate the variable for chimpanzees (Figure 3.2). We used the Kernel Density Estimation (KDE) to generate the habitat variables. The KDE is a non-parametric method used for animal home range estimation (Worton, 1989); it can also be used to evaluate the distribution of habitat availability (Chapter 4; Seaman and Powell, 1996). The KDE uses location points as input data to generate a utilization distribution (Kie *et al.*, 2010). Instead of the utilization distribution which relates to home range studies, we used the availability distribution in this study for habitat variables. We created random points in each cell corresponding to their weight. We conducted the KDE in the package *rhr* version 1.2.909 using the least square cross validation bandwidth (Signer and Balkenhol, 2015) in the R software version 3.3.3 (R Core Team, 2018).

To create the distance-based variables, we created a shapefile for each feature type and then used the function “Euclidean distance” in ArcGIS 10.3.1 to create the raster files of the distances from the corresponding features. For the topographic variables (elevation, aspect, curvature, slope, and surface relief ratio), we used the Digital Elevation Model (DEM) from the NASA Shuttle Radar Topography Mission (SRTM) Version 3.0, at 30 m resolution (<https://earthexplorer.usgs.gov>) as the base file, and processed it in ArcGIS 10.3.1. We projected the DEM to obtain the elevation raster file using the function “project”. We then used the elevation raster file to create the curvature, slope, and aspect raster files in ArcGIS. We created the surface relief ratio using the package *spatialEco* in the R software. We resampled the resulting raster files of all environmental variables at a resolution of 50 m to correspond to the 50 m applied when collecting habitat points. We summarized the process of creation of all environmental variables in Figure 3.2.



**Figure 3.2: Method and process of creation of predictor variables, including the software used to derive the variable as well as the units of each variable. m = metre; KDE = kernel density estimation.**

### 3.3.3. MODELLING TECHNIQUE

We used the maximum entropy modelling (Maxent) approach to study the suitability of great ape habitat in relation to ecological, geophysical, and anthropogenic variables through the Maxent software version 3.4.1 (Phillips *et al.*, 2006). Maxent is the most promising tool and among the most commonly used software for modelling species distribution (Elith *et al.*, 2006). Its advantages reside in the fact that it is a machine-learning process, and it requires presence-only data to model species distribution (Merow *et al.*, 2013). It is also considered to be the most powerful modelling method when using a small number of observations to produce good results (Hernandez *et al.*, 2006). Regularization in Maxent contributes to preventing overfitting better than the lasso method does in regression-based methods (Phillips and Dudík, 2008).

When using presence-only data, Maxent creates false absence points (background data) and is then called presence background method (Lahoz-Monfort *et al.*, 2014). To do this, Maxent considers that species have the same likelihood of being found across the landscape (Merow *et al.*, 2013). To overcome these problems, we collected our occurrence data through a random sampling design, as proposed by Yackulic *et al.* (2013). We allowed the background data to be selected randomly

across the entire study area because no area was assumed inaccessible by any species due to the presence of any geographical barrier (Phillips and Dudík, 2008). We used the Jackknife test to select the variables with the highest important individual effect.

We used the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) most frequently used in Maxent to evaluate the performance of each model (Yackulic et al., 2013). The AUC is a threshold measure that represents the probability that a random occurrence point is ranked higher than a random background point (Merow et al., 2013). It was criticized for its incapacity to measure model accuracy in Maxent (Lobo et al., 2008). This is because the AUC is traditionally used for the distinction between presence and absence points, while in Maxent, background points are used instead of true absence points (Merow et al., 2013). Therefore, a high AUC value does not necessarily mean that the model is more accurate (Shabani et al., 2018). However, the AUC represents the best alternative for model evaluation in Maxent when background points are selected randomly and uniformly from the study area (Phillips and Dudík, 2008); hence, it can be used to compare models on the same species in the same study area (Lobo et al., 2008). The AUC values are constrained to vary between 0.5 (the discrimination is similar to a random set of prediction) and 1 (random discrimination) and can be classified as such: excellent (0.90- 1.00), very good (0.8-0.9), good (0.7-0.8), fair (0.6-0.7), and poor (0.5-0.6) (Duan et al., 2014). We ran it for gorillas and for chimpanzees. The first model used ecological and geophysical variables to characterize the distribution of the species according to their ecological requirements, while the second model used ecological, geophysical, and anthropogenic variables to characterize the distribution of the species when humans are present. We compared distribution in the resource and anthropogenic models based on the geographical space (predicted habitat suitability). To do this, we performed the overlap between the different Maxent outputs using the Schoener's index of overlap (Warren et al., 2008), based on Equation 3.1

$$D(P_A, P_B) = 1 - \frac{1}{2} \left( \sum_{i=1}^N |P_{A_i} - P_{B_i}| \right) \quad (\text{Equation 3.1})$$

where  $P_{Ai}$  and  $P_{Bi}$  represent the normalized suitability scores of the Maxent-generated ecological niche models  $A$  and  $B$  in grid cell  $i$ ; these parameters were calculated so that the sum of the suitability scores in the geographic space is 1.  $N$  is the number of grid cells.  $D$  considers that the suitability scores  $P_{Ai}$  or  $P_{Bi}$  provided in

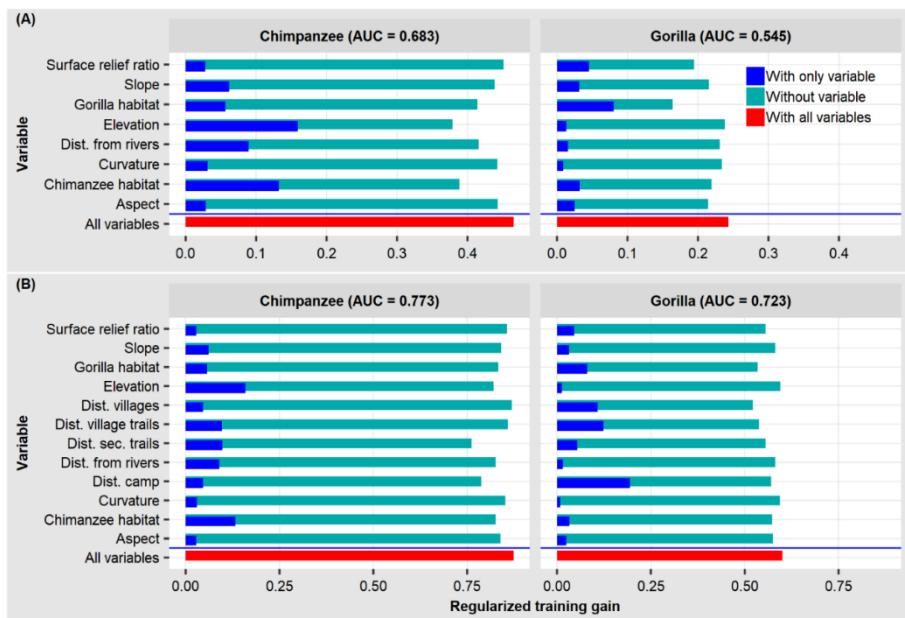
each Maxent output is a proportion of the species abundance.  $D$  was calculated in ENMTools 1.4.4 (Warren *et al.*, 2010).

### 3.4. RESULTS

Habitat quality was the most important determinant of gorilla distribution followed by surface relief ration in the absence of human disturbance. In contrast, elevation was the most important predictor of nesting site selection for chimpanzees, followed by abundance of their preferred nesting habitats, and then by distance from rivers and slope (Figure 3.3A). When we included research presence and human settlements in the models, elevation remained the most important predictor of chimpanzee nesting, followed by their preferred nesting habitats, then by distance from village trails, and finally, by distance from secondary trails. However, distance from the research camp became the most important predictor of gorilla nesting, followed by distance from village trails, then by distance from villages, and lastly by gorilla-preferred nesting habitats (Figure 3.3B). In the resource models, the two most important variables for gorillas (gorilla-preferred nesting habitats and surface relief ratio) and for chimpanzees (elevation and chimpanzee-preferred nesting habitats) decreased the gain the most when omitted and provided more information than was available in the rest of the variables (Figure 3.3A). While in the anthropogenic models the variables with the most information were not the most important for gorillas (gorilla-preferred nesting habitats and distance from villages) and for chimpanzees (distance from secondary trails and distance from villages) (Figure 3.3B).

The variable response curves (Figure 3.4) show that the probability to find chimpanzee nests was high at intermediate values of elevation; it increased with the density of their preferred nesting habitat types. The response of chimpanzee nesting to rivers simply shows that they avoided nesting near rivers. The probability to find chimpanzee nests increased with slope and became constant from intermediate values. The probability to find gorilla nests increased with the abundance of their preferred nesting habitats, while the latter was almost constant and intermediate with the abundance of chimpanzee-preferred nesting habitats. However, there was a lower probability of finding gorilla nests where gorilla- or chimpanzee-preferred nesting habitat abundance was very low (Figure 3.4). The probability of finding gorilla nests was also fairly constant with surface relief ratio but decreased above intermediate values of surface relief ratio. The probability of finding gorilla nests was almost constant and intermediate with a slope lower than 6 but increased at higher slope values (Figure 3.4). The responses to anthropogenic

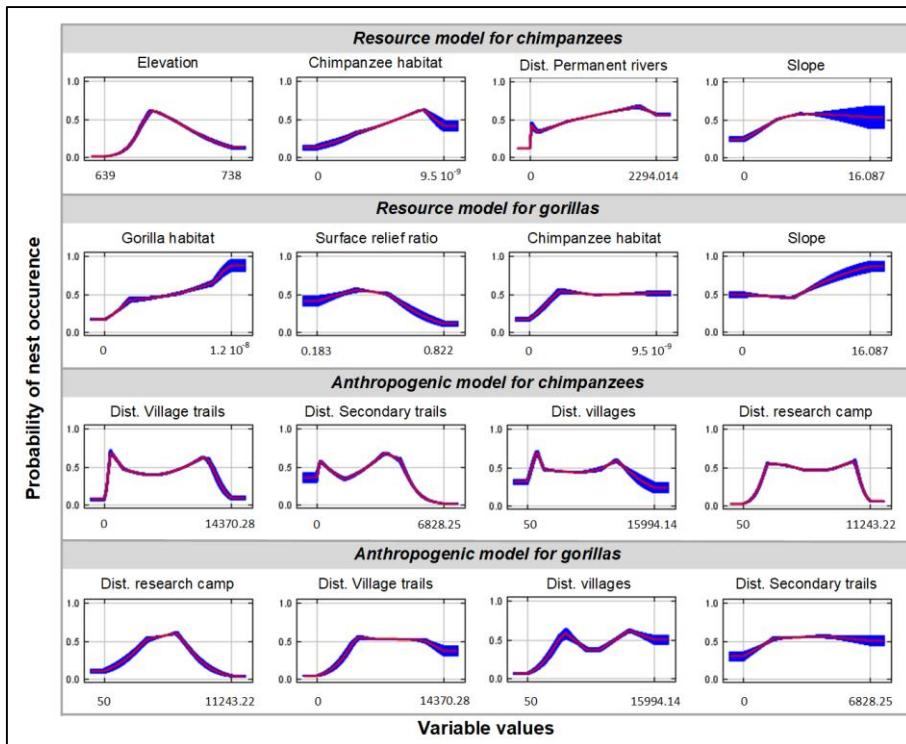
variables show that chimpanzees avoided nesting in areas located < 2 km from human features (village trails, research camp) but almost did not respond negatively to villages and secondary trails (Figure 3.4). Gorillas responded more to human features than chimpanzees; they tended to nest about 4–5 km away from human features (research camp, village trails, and villages); secondary trails had a lower impact on gorilla distribution compared to other human features (Figure 3.4).



**Figure 3.3: Results of the Jackknife test of variable importance for each Maxent model with their respective AUC values. A = Resource model, B = Anthropogenic model, Dist. = Distance; sec. = secondary; AUC = Area Under the Curve of the Receiver Operating Characteristic.**

It is worth noting that the inclusion of human-related variables in the models improved the predictions by increasing the values of AUC from poor to good (from 0.683 to 0.773 for chimpanzees and from 0.545 to 0.723 for gorillas; Figure 3.3). Habitat suitability maps show that without human presence, the study area was more suitable for gorillas than for chimpanzees and that shallows and rivers were not suitable for chimpanzee nesting (Figure 3.5). In the resource model, the distribution of high suitability scores, while being heterogeneous, covered almost the entire study area for both gorillas and chimpanzees. However, the habitat suitability maps in the anthropogenic model show that for both gorillas and chimpanzees, some areas that were suitable in the fundamental niche model were

no longer suitable in the anthropogenic model (Figure 3.5). For both gorillas and chimpanzees, the area around the research camp was not suitable when including anthropogenic variables in the models (Figure 3.5). Proximity to villages and village trails had more influence on gorillas than on chimpanzees, resulting in large areas unsuitable for gorilla nesting but not for chimpanzees nesting (Figure 3.5).



**Figure 3.4: Response of great ape nest occurrence to the four most important variables in the resource and anthropogenic models. For the anthropogenic models, the variables represent anthropogenic variables ordered by their order of importance in the model. For each model, we ordered the variables by their importance values from left to right. *Dist.* = Distance.**

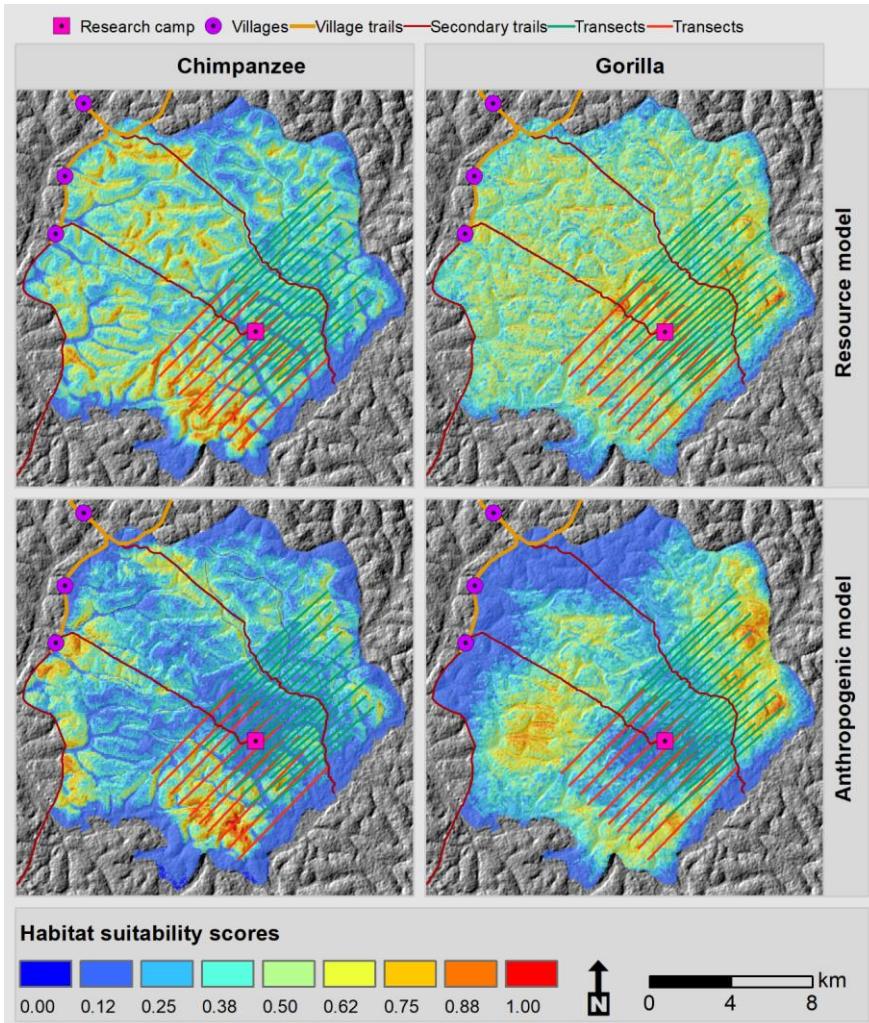


Figure 3.5: Great ape habitat suitability models displaying the spatial variation of suitability scores for gorillas and chimpanzees in two different models (resource and anthropogenic) throughout the landscape. The habitat suitability scores vary from 0 (low suitability) to 1 (high suitability). The background of each panel is a hillshade of the Digital Elevation Model of the area. Each map contains the location of each variable considered in the analyses (villages, research camp, and trails). We also added the transects used for research data collection in La Belgique.

The effects of anthropogenic variables on great ape distribution are highlighted in Figure 3.6. In the resource model, the distribution of chimpanzees included many pixels with suitability scores lower than 0.1, while the distribution of gorilla suitability scores followed a bell shape (Figure 3.6). The number of pixels where the

suitability score decreased because of the inclusion of anthropogenic variables in the models was greater for gorillas than for chimpanzees; this is indicated by a lower overlap between distributions of gorillas and chimpanzees in both the resource and anthropogenic models (Figure 3.6A). The mean suitability score was lower for chimpanzees than for gorillas in both the resource and the anthropogenic models, and the difference between the mean suitability scores of gorillas and chimpanzees was higher in the resource models than in the anthropogenic models (Figure 3.6B). The overlap between distributions in the resource models of both gorillas and chimpanzees was greater than that of their distributions in the anthropogenic models (Figure 3.6B).

### 3.5. DISCUSSION

Human presence and activities are changing the distribution of wildlife in landscapes, and this is becoming the rule in ecosystems. Hence, in order to inform conservation measures, human-related variables need be considered when predicting habitat suitability for wild animals. In this study, we evaluated the effects of field research presence and human settlements on great ape niches by comparing niches in a free system to niches in a system where there is a risk of predation represented by human presence, and we determined how two sympatric species respond to that predation risk. The results indicate that in the resource model, habitat variables were important predictors of great ape nesting, while in the anthropogenic model, anthropogenic variables were the most important predictors of gorilla nesting, although habitat variables and elevation continued to be the most important predictors of chimpanzee nesting in the anthropogenic model (Figure 3.3A, B). Human settlements and hunting activities occurring at the research site reduced the suitability scores for gorilla habitats more than they did for chimpanzee habitats.

The major limitation of this study is the assumption of no phenological variation in fruit availability occurring. Fruit phenology changes seasonally and annually (Yamagiwa et al., 2008), and this may cause seasonal change in the patterns of habitat selection and space use due to varying abundance of different fruiting species across habitats (Chapter 2). However, we did not collect data on a seasonal basis to evaluate the effects of seasons (Chapter 2). Instead, we used a random sampling design, and our data collection spanned different seasons.

The most important predictors of chimpanzee habitat suitability in the resource model were elevation, chimpanzee-preferred nesting habitat, distance to rivers,

and slope; for gorillas, on the other hand, the most important predictors were gorilla-preferred nesting habitat, surface relief ratio, chimpanzee-preferred nesting habitat, and slope (Figure 3.4). Elevation was the highest contributor to the chimpanzee resource model, but this factor was not important in the gorilla resource model (Figure 3.3). The shape of the relationship between the probability of occurrence of chimpanzee nests and altitude was comparable to the bell (Figure 3.4) indicating that an increase in altitude of up to 675 m corresponded to an increase in the probability of chimpanzee nest occurrence, after which it started to decline. Fitzgerald *et al.* (2018) have found a similar shape for chimpanzees in the Greater Nimba Landscape, where the probability of occurrence started to decline at 900 m. At Gombe, the suitability of chimpanzee habitat followed the same shape irrespective of land cover classes with optimum values of suitability being found between 850-1100 m of elevation (Foerster *et al.*, 2016). In the Tofala Hill Wildlife Sanctuary, chimpanzee nests were found at high elevations (800-1000m) (Njukang *et al.*, 2019). This indicates that elevation may be a good determinant for the choice of a nesting site by chimpanzees, where the areas with intermediate values of elevation are more suitable. Contrary to our results, Etiendem *et al.* (2013) found that elevation was an important predictor of the cross-river gorilla distribution at Mawambi Hills.

These contrasting patterns do not allow us to generalize the importance of elevation as predictor of nest building for either gorillas or chimpanzees, and they corroborate the finding of Hof *et al.* (2012) that elevation is a top predictor for many species but not all species. Nesting in high altitudes by chimpanzees in the Tofala Hill Wildlife Sanctuary (Cameroon) probably allowed them to minimize the encounter rates with logging and agricultural activities (Njukang *et al.*, 2019). Apart from elevation in the chimpanzee model, the distribution and density of preferred nesting habitats were the most important predictors in the resource models for both gorillas and chimpanzees (Figure 3.3). The fact that the most important habitat variable in a species' model was its preferred nesting habitat (Figure 3.3) corroborates the finding that the set of habitat types not preferred by one species is preferred by the other species (Chapter 2; Chapter 4).

Foerster *et al.* (2016) found that elevation and the Normalized Difference Vegetation Index (NDVI) were the top predictor variables of chimpanzee fruiting species. Also, the results of Pintea (2007) indicate that NDVI was positively correlated to the time chimpanzees spent feeding in Gombe (Tanzania). Similarly, macaques (in Japan) mostly consumed fruits when they lived in forest with higher NDVI (Tsuji *et al.*, 2015). We did not test for the contribution of fruiting trees in the

model, but in Chapter 2 we showed that chimpanzee-preferred fruiting species are more abundant in chimpanzee-preferred nesting habitats. This can explain why NDVI and elevation best predict chimpanzee nesting sites. The importance of elevation in chimpanzee ecology goes beyond the prediction of their local distribution to explain their abundance across their entire range (Strindberg *et al.*, 2018). NDVI is generally used as a surrogate of vegetation greenness or plant productivity (Evans *et al.*, 2006; McCormack *et al.*, 2010; Williams *et al.*, 2018) and is frequently used in animal ecology to study habitat suitability (Bellis *et al.*, 2008; Pettorelli *et al.*, 2011). The values of NDVI can vary through seasons and years due to leaf phenology (Pettorelli *et al.*, 2005), thus making different predictions difficult to compare among different studies. An approach for remediating issues related to the seasonal variation in NDVI is to calculate the mean value of the different seasons (Costa *et al.*, 2010). Our method based on the determination of the density of habitat points represents a good alternative to NDVI because it is not susceptible to seasonal variation. Analyses based on our method showed that areas with high densities of preferred nesting habitat points also correspond to areas with high densities of important fruiting plants for both gorillas and chimpanzees (Chapter 4). Additionally, the preferred plant species for both gorillas and chimpanzees are more abundant in chimpanzee-preferred nesting habitats (Chapter 2). This can explain why NDVI predicted chimpanzee nesting in previous studies and why their probability of occurrence increased with the density of their preferred nesting habitats in the present study.

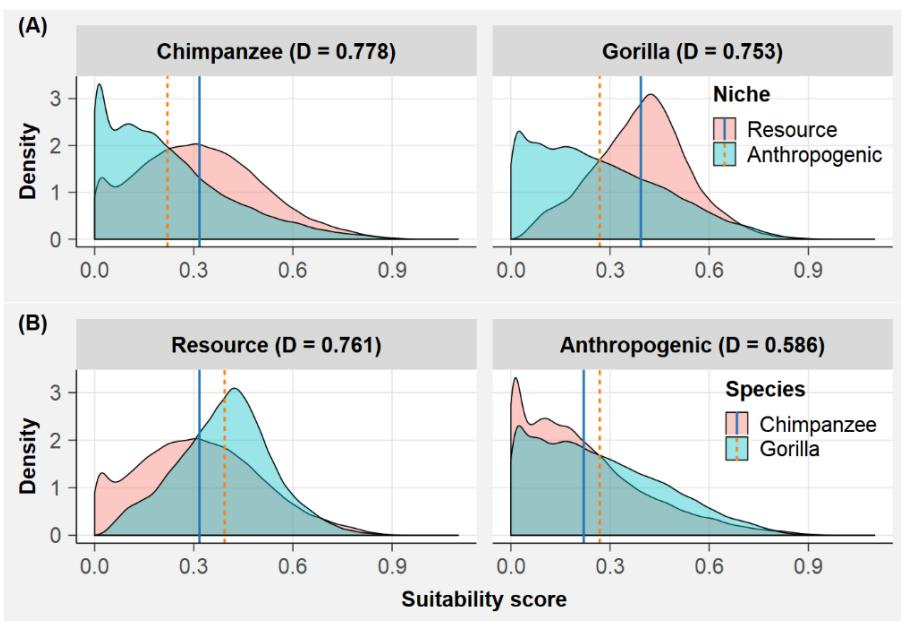
Instead of NDVI, Etiendem *et al.* (2013) and Bortolamiol *et al.* (2016) used land cover classes as the habitat variable in the predictive model, which necessitates a prior classification of Landsat satellite imagery to obtain forest classes. This method can be useful because it allows one to know the contribution of each individual habitat class to the model (Etiendem *et al.*, 2013). The use of habitat points to derive the habitat variables can be limited by the fact that the method cannot be used to make predictions beyond the area where data were collected; hence, Maxent is a more suitable approach (Fitzgerald *et al.*, 2018). However, with Maxent, the practice of using habitat points to predict the distribution beyond the study area was criticised due to the risk of decreasing the predictive power of the model in the regions where data were not collected (Warren and Seifert, 2011; Eger *et al.*, 2017). The response of gorilla nesting to chimpanzee-preferred habitat was almost constant and intermediate. This can be justified by the fact that due to the existence of competition between gorillas and chimpanzees and the competitive superiority of chimpanzees over gorillas, gorillas build nests in habitats

where their preferred fruiting species are not abundant, but they visit chimpanzee-preferred nesting habitats in search of fruits (Chapter 2). By searching for fruit in chimpanzee-preferred nesting habitats, gorillas may sometimes build their nests where the abundance of their preferred nesting habitats is low.

Our findings indicate that anthropogenic variables (research presence and human settlements) were more important than habitat variables for chimpanzees but not for gorillas (Figure 3.3). Anthropogenic variables also improved the predictive power of the models, as shown by higher values of AUC in the anthropogenic models than in the resource models (Figure 3.3). These variables contributed to the decrease of the suitability of great apes' habitats (Figure 3.5, Figure 3.6). The reduction of the habitat suitability scores due to research presence and human settlements indicates that great apes may avoid areas with signs of human presence up to a certain level. It is evident that great apes may face a risk of predation when moving to areas where humans are present. The increase in AUC values in the anthropogenic models is an indication that humans have modified the natural system and that the inclusion of human-related variables is crucial to the evaluation of species' responses to the environment (Lindshield *et al.*, 2017). This observation was made by several authors in previous studies (Frid and Dill, 2002; Alberti *et al.*, 2003), and Albuquerque *et al.* (2018) considered humans as niche constructors in animal ecology. The AUC values of our resource models were poor for both gorillas and chimpanzees (Figure 3.3), meaning that in a human-modified system, habitat and geophysical variables cannot adequately predict the distribution of great apes, particularly gorillas. Several authors highlighted the relevance of human-based variables in the prediction of wildlife habitats (Blom *et al.*, 2005; Bowman *et al.*, 2010; Schuette *et al.*, 2013; Koerner *et al.*, 2017). We can assimilate the effects of humans on wildlife distribution with those of natural predators. According to Salandre *et al.* (2017), species can use the presence or absence of predators' odours as the main cue of the risk of predation. Great apes may use such cues to assess threats from humans. In addition, noise made by humans can contribute to frightening animals (Clinchy *et al.*, 2016; Slabbekoorn *et al.*, 2018).

The variation of different cues for different human settlements makes the influence of anthropogenic variables on wildlife distribution very complex (Zhao *et al.*, 2017; Zbyryt *et al.*, 2018) and may cause species to respond differently to different variables. The most influential anthropogenic variables for gorillas were distance to the research camp, village trails, and villages, while distance to the village trails and secondary trails were the most influential anthropogenic variables

for chimpanzees (Figure 3.4). Regardless of the anthropogenic variable, all most important variables had a negative impact on great ape distribution, except for the distance from secondary trails. That is, the probability of nest occurrence was low near those human features and high away from them. Human presence may have caused a phenotypic and behavioural change in great apes (Preisser *et al.*, 2005). As predicted, human presence affected gorillas more than chimpanzees, as indicated by the response to individual variables and the reduction of habitat suitability scores (Figure 3.4, Figure 3.5). This means that research presence and human settlements contribute to reducing habitat suitability for gorillas more than they do for chimpanzees. The overlap between the distribution of gorillas and chimpanzees in the resource models was greater than the overlap between the distribution of gorillas and chimpanzees in the anthropogenic models (Figure 3.6B).



**Figure 3.6: Overlap between the distributions of great apes in the resource and anthropogenic models.  $D$ . Schoener's index of overlap.** (A) Overlap between the distributions from resource and anthropogenic models for chimpanzees and the overlap between the distributions from resource and anthropogenic models for gorillas. (B) Overlap between the distributions from the resource models of both gorillas and chimpanzees and overlap between distributions from the anthropogenic models of both gorillas and chimpanzees. The values obtained from the overlap analyses may be different from those observed in the graph because the index of overlap takes into account the spatial locations of suitability scores, while the graph only presents the density of those suitability scores. Each vertical line represents the average suitability score for the corresponding model.

The avoidance of human settlements was often attributed to hunting; under such circumstances, animal species may find refuge where hunting intensity is low (Blom *et al.*, 2005; Vanthomme *et al.*, 2013). Although, we did not consider hunting pressure in our analyses, Koerner *et al.* (2017) considered the distance from permanent human settlements as a surrogate to hunting pressure because they found that the increasing distance from a settlement corresponded to a decrease in hunting signs. This can indicate that the response of great apes to the research camp and human settlements may be due to a perceived hunting pressure. Authors have shown that along the transects, hunting signs not research activities determined space use by gorillas and chimpanzees for nesting (Tagg and Willie, 2013; Tagg *et al.*, 2018). Nevertheless, we found that gorillas negatively responded to the distance from research camp; the difference between gorillas and chimpanzees may be due to different behavioural adaptations. A study of Ávila *et al.* (2019) revealed that our focal species, gorillas and chimpanzees, were not the target of hunters in our study area; nevertheless, hunting activities occurring in the research site along the transects (Tagg and Willie, 2013) may be responsible for the change in the distribution of great apes. Additionally, Vanthomme *et al.* (2013) found that human activities such as logging concessions can constitute protection for some animals, specifically ungulates, but not for large mammals such as great apes. Because ungulates are more affected by hunting (Fa *et al.*, 2006), this activity was prohibited in logging concessions. If hunting pressure was the cause of niche contraction in great apes, these species may find refuge in logging concessions also. The same case applies to our results where gorillas were the most negatively affected by research presence. The fact that hunting of great apes is prohibited in the research site means that the presence of the research site or a logging concession may influence the distribution of great apes even when these species are not actually hunted. We speculate that hunting activities may have increased over time so that the intensity is now having an effect on the distribution of gorillas and chimpanzees.

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CHAPTER 3

# CHAPTER 4

## USING ABUNDANCE AND HABITAT VARIABLES TO IDENTIFY HIGH CONSERVATION VALUE FORESTS FOR THREATENED MAMMALS

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Adapted from: **Tédonzong, L. R. D., Willie, J., Keuko, A. M. P., Kuenbou, J. K., Njotah, G., Tchamba, M. N., Tagg, N. and Lens, L.** (2018). Using abundance and habitat variables to identify high conservation value areas for threatened mammals. *Biodiversity and Conservation* **27**, 1115-1137.  
<https://doi.org/10.1007/s10531-017-1483-9>

#### 4.1. ABSTRACT

The present study used abundance and habitat variables to design High Conservation Value Forests for wildlife protection. We considered great apes (*Gorilla gorilla gorilla* and *Pan troglodytes troglodytes*) as target species, and we used nest surveys, dietary analysis and botanical inventories to evaluate whether the traditional methods that use abundance data alone were consistent with the survival of the species. We assumed that setting a local priority area for animal conservation can be made possible if at least one variable (abundance or habitat variables) is spatially clustered, and that the final decision for a species may depend on the pattern of spatial association between abundance, nesting habitat and feeding habitat. We used Kernel Density Estimation to evaluate the spatial pattern of each biological variable. The results indicate that all three variables were spatially clustered for both gorillas and chimpanzees. The abundance variables of both animal species were spatially correlated to their preferred nesting habitat variables. But while the chimpanzee feeding habitat variable was spatially correlated to the abundance and nesting habitat variables, the same pattern was not observed for gorillas. We then proposed different methods to be considered to design local priority areas for the conservation of each great ape species. Alone, the abundance variable does not successfully represent the spatial distribution of major biological requirements for the survival of wildlife species; we therefore recommend the integration of the spatial distribution of their food resources to overcome the mismatch caused by the existence of biological interaction between congeneric species.

**Keywords:** Priority areas; High Conservation Value Forests; central chimpanzee; western lowland gorilla; Habitat variable; Kernel Density Estimation; Great apes; Spatial conservation planning

## 4.2. INTRODUCTION

One of the fundamental issues of wildlife conservation in production landscapes is the gazetting of high conservation value forests for endangered species (Camaclang et al., 2014). This process usually considers only abundance and distribution of the target species, ignoring the contribution of habitat quality (Berger-Tal et al., 2016). Two behavioural factors (animal dispersal and foraging) are closely linked to wildlife population decline due to habitat loss, and must ultimately be considered if conservation measures are to be successful (Berger-Tal et al., 2016). Animal dispersal is mainly controlled by species interactions and habitat quality and configuration (Bowler and Benton, 2005), and may consequently influence the abundance and spatial distribution of a species (Gaston et al., 2000). Food is the most obvious resource determinant of habitat quality (Sinclair et al., 2006). It is likely that relying only on abundance distribution to design high conservation values for an endangered species is insufficient and biased if the species ranging behaviour is influenced by the food they consume, and if their food does not predict their spatial distribution in their natural environment. In this sense, unoccupied habitat areas should be considered in high conservation value forests if they are to provide significant resources to a population for their long-term persistence and recovery after perturbations (Camphuysen et al., 2012; Camaclang et al., 2014).

As more than three quarters of the land surface is now dominated by human activities, a great challenge facing conservationists is to reconcile anthropogenic factors and the ecosystem (Ellis and Ramankutty, 2008). In order to mitigate the negative effects of human activities on habitat loss in non-protected areas, sustainable natural resource management via community-based management (Sinclair et al., 2006) features as a strategic goal of the Convention on Biological Diversity (Convention on Biological Diversity, 2010). This process is intended to extend the ecosystem integrity of small protected areas, and allow a proper conservation of wide-ranging and migratory species (Sinclair et al., 2006), and also to ensure the long-term persistence of wildlife in forests managed for timber production (Redford et al., 2015). That is the context in which forest certification schemes have grown and emerged as a conservation tool (Auld et al., 2008) and is viewed today as an important guide to foster sustainable forest management (Morgan et al., 2013). The major certification scheme for the management of tropical ecosystems, the Forest Stewardship Council (FSC) (Ramatsteiner and Simula, 2003; Auld et al., 2008) has outlined principles and criteria to improve the

sustainability of forest management (Cauley *et al.*, 2001) that are centred on forest management units (Rametsteiner and Simula, 2003). A very important concept in FSC principles and criteria is the concept of High Conservation Value Forests (hereafter referred as HCVF) which is treated in principle 9 (Jennings, 2004; Morgan *et al.*, 2013). It takes into account important values about biodiversity, ecosystem services, and, society and culture (Morgan *et al.*, 2013). A good consideration of HCVF in forest concessions is a guarantee of the persistence of biodiversity in general, and wildlife in particular (Jennings, 2004). The big challenge behind the concept of HCVF is how to identify and maintain high conservation values (Morgan *et al.*, 2013).

The concept of HCVF is synonymous with priority areas for conservation (Pinto *et al.*, 2007) or conservation areas (Denoël and Ficetola, 2015), and is widely used in conservation of endangered species (Ronconi *et al.*, 2012). It is also used to identify small habitat patches pertaining to the survival of threatened species before a perturbation (Jennings, 2004; Morgan *et al.*, 2013). Several techniques are often used to identify HCVF. The more commonly used is the abundance-based technique (Berger-Tal *et al.*, 2016), which considers the abundance and distribution of presence signs of a species (Vellend and Kharouba, 2013; Berger-Tal *et al.*, 2016). Other methods use ecological niche modelling (Araújo and Williams, 2000; Thorn *et al.*, 2009), where occurrence data are used to derive areas environmentally suitable for the persistence of a species (Hirzel *et al.*, 2002), where areas of high abundance of presence signs predict suitable environmental conditions (Hirzel and Arlettaz, 2003). High-quality absence data are often challenging to obtain (Hirzel *et al.*, 2002), but it is difficult to evaluate the predictive power of models based only on occurrence data (Hirzel and Arlettaz, 2003). In this case, ecological niche modelling (ENM) can be used for species for which distribution data are not easily obtainable (Araújo and Williams, 2000), and can also help identify corridors between protected areas (Thorn *et al.*, 2009). The combination of abundance information and habitat variables has rarely been used to design HCVF (Berger-Tal *et al.*, 2016).

Food and habitat are central to niche separation (Schreier *et al.*, 2009), which is the result of biotic interactions that may directly influence the abundance and distribution of two sympatric species on a local basis (Benítez-López *et al.*, 2014). However, food may not be a direct predictor of the abundance and distribution of some animal species (Van Horne, 1983; Arnhem *et al.*, 2008), while for others abundance is predicted by food availability (Balcomb *et al.*, 2000; Tweheyo *et al.*, 2004). This makes attempts to identify HCVFs based only on the abundance distribution of the species, or using ENM, biased (Vellend and Kharouba, 2013)

because it is susceptible to missing some specific requirements for the persistence of particular species living in the same site with their direct competitors (Benítez-López *et al.*, 2014). It is thus vital to delineate HCVF that include the distribution of all components necessary to the survival of individual species, rather than focusing only on where the species is present. In this context, considering habitat variables may improve the delineation of HCVFs if they are to favour the long-term persistence of species; however, empirical case studies using this approach are lacking.

The aim of this study was to evaluate whether using abundance variables alone to define priority areas is consistent with the long-term survival of sympatric species. Because niche partitioning may affect the distribution of sympatric animal species (Benítez-López *et al.*, 2014), we evaluated whether including habitat variables in the identification of priority areas for two sympatric species leads to different approaches for each species. To this end, we studied populations of sympatric great apes (*Gorilla gorilla gorilla* and *Pan troglodytes troglodytes*) in the northern periphery of the Dja Biosphere Reserve, as target species. Western lowland gorillas and central chimpanzees are highly frugivorous; fruit species represent 50 to 98% of their diet (Tutin and Fernandez, 1993; Cipolletta, 2004; Twehreyo *et al.*, 2004; Doran-Sheehy *et al.*, 2009), and more than 87% of those fruit species are trees and lianas (Tutin and Fernandez, 1993). Fruit consumption by great apes is generally significantly correlated with availability (Buij *et al.*, 2002; Doran-Sheehy *et al.*, 2009). Those fluctuations in fruit availability have important consequences on great ape ranging behaviour (Doran and Greer, 2002; Doran-Sheehy *et al.*, 2004; Wartmann *et al.*, 2010). When fruit is abundant, great apes increase the quantity and diversity in their diet, and gorillas increase their daily path lengths (DPL) (Doran and Greer, 2002; Cipolletta, 2004; Doran-Sheehy *et al.*, 2004; Doran-Sheehy *et al.*, 2009). Woody plant species are important to great apes as they provide fruits (Balcomb *et al.*, 2000) and nesting material (Stanford and O'Malley, 2008), but are more likely to be affected during logging operations, thus making it essential to establish sound approaches for identifying HCVF where conservation efforts will be more focused toward them. Great apes exhibit some preferences for nesting habitats (Morgan *et al.*, 2006; Willie *et al.*, 2013): gorillas prefer nesting in open canopy secondary forests and swamps (Morgan *et al.*, 2006; Willie *et al.*, 2013), while chimpanzees prefer nesting in closed canopy old secondary forests (Morgan *et al.*, 2006). It is evident that chimpanzees and gorillas may have become specialised in resource use due to their sympatry (Head *et al.*, 2011; Head *et al.*, 2012), and the distribution of their resources (nesting habitats and food) is likely to

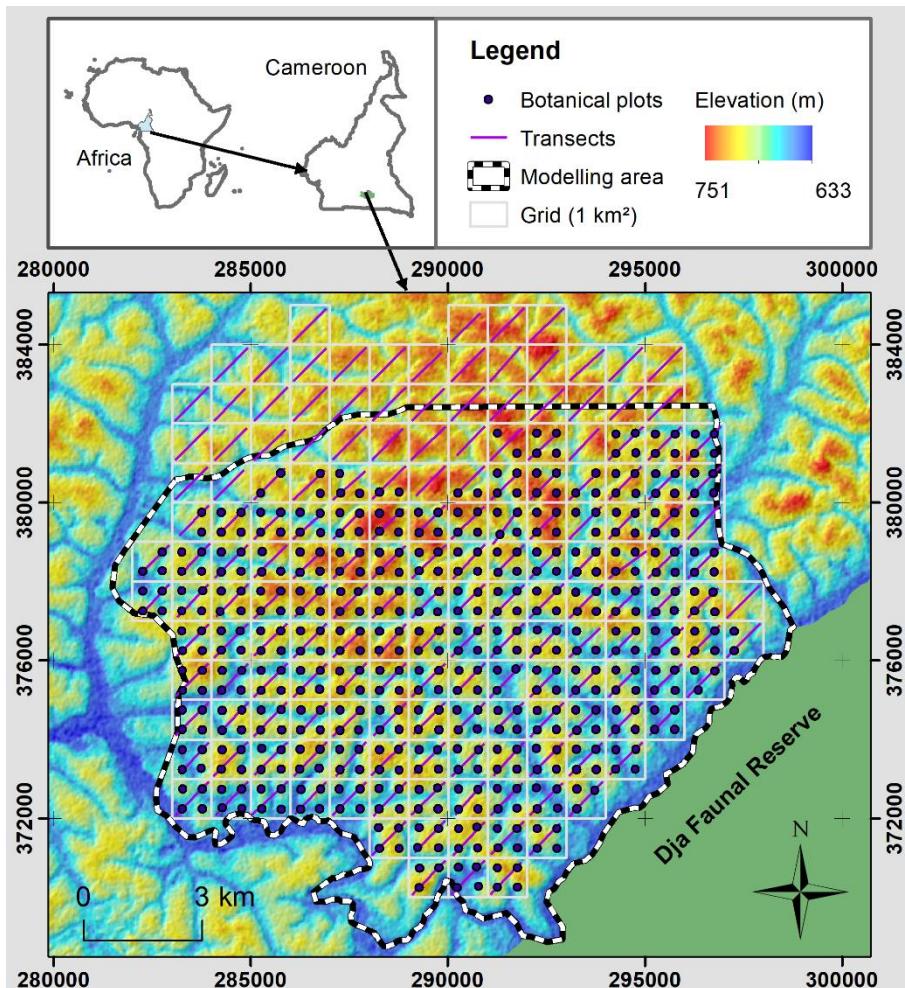
have affected their patterns of spatial distribution. Since all great ape species are threatened with extinction, and more than 50% of their populations lie in logging concessions (Morgan and Sanz, 2007), they are among the mammals most threatened due to habitat degradation (Schipper *et al.*, 2008). There is an urgent need to develop approaches to design HCVF for their preservation in managed forests (Morgan *et al.*, 2013), that consider both the spatial distribution of habitat variables and presence signs.

### 4.3. METHODS

#### 4.3.1. DATA COLLECTION

##### 4.3.1.1 TRANSECT SURVEYS

We set a sample grid with 1000×1000 m cell size. In each cell, we established a 1200 m transect at 45° bearing, extending diagonally 600 m both ways from the centre of the cell (Figure 4.1). A total of 175 cells was used, giving a total distance of 210 km of transect walked.



**Figure 4.1:** Study area drawn on the hill shade of the Digital Elevation Model obtained from the Shuttle Radar Topography Mission (SRTM) 1 Arc-Second global (<https://earthexplorer.usgs.gov/>). The modelling area is where all the data necessary to define the HCVF (botanical inventories, great ape nest surveys, habitat sampling points).

On each transect, we noted the habitat type as well as their geographical coordinates at each 50-m interval, with one point at the start and end of each transect, resulting in a total of 25 habitat points per transect. For each habitat type, availability was calculated as the number of points recorded for the selected habitat over the total number points recorded for all habitats. We also recorded the geographical location of all great ape nests of all ages and noted down the

habitat type. A random sample of grid cells was selected for survey each month for 11 months, from October 2015 to August 2016. Each cell was surveyed once.

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#### 4.3.1.2 GREAT APE TRACKING AND FAECAL ANALYSIS

Faecal analysis was employed to identify fruit remains consumed by great apes (Head *et al.*, 2011). Faecal samples were collected by two teams of local trackers from November 2013 to September 2016 (for chimpanzees) and January 2014 to September 2016 (for gorillas). Chimpanzee faeces were not found in March 2014, March–April 2015, January–February 2016 and June 2016; while gorilla faeces were not found in March 2014. Faecal samples were collected if the presence of signs such as the shape, size, associated odours, hairs or nests helped distinguish the primate species (Head *et al.*, 2011).

Faecal samples were washed through a 1-mm sieve, in order to identify the fruit species consumed by the great ape species via their seeds (Doran *et al.*, 2002), using a seed bank previously collected for our site. Many species were only identified to the genus level (e.g. *Uapaca* spp., *Landolphia* spp., *Nauclea* spp.) (Head *et al.*, 2011), genera for which seeds are similar.

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#### 4.3.1.3 BOTANICAL INVENTORIES

To carry out botanical inventories, we overlaid a second grid of 500×500 m cell size, in such a way that each of the original 1000×1000 m cells (big grid cell) comprised four 500×500 m cells (small grid cell). We regularly set a 25×25 m plot at the centre of each small grid cell (Figure 4.1). In each plot, we measured all trees with a DBH  $\geq$  10 cm, and all lianas with a DHB  $\geq$  5 cm. Plant specimens for species for which identification was not possible on site were collected for later identification at the National Herbarium of Cameroon. At least two botanical plots were set in each big grid cell to calculate the mean abundance of plant species in those cells; however, only 133 1000x1000 m cells were covered by botanical inventories and only that area was considered to define HCVFs.

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### 4.3.2. DATA ANALYSIS

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#### 4.3.2.1 NESTING HABITAT SELECTION

We evaluated habitat selection for nesting by gorillas and chimpanzees using the Cheason Index of selection, followed by a goodness of fit test (Manly *et al.*, 2002). The Cheason index allowed us to evaluate if a habitat was preferred, avoided or

randomly used by great apes as sleeping sites; and the goodness of fit test determined whether or not the avoidance or preference of a habitat was significant (Manly *et al.*, 2002). We calculated the Cheason index using the Equation 4.1:

$$\alpha_i = \frac{r_i}{\sum_{i=1}^m p_i} \quad (\text{Equation 4.1}) \quad \alpha'_i = m\alpha_i \quad (\text{Equation 4.2})$$

Where  $r_i$  is the proportion of nests in habitat  $i$  over all nests;  $p_i$  is the availability of habitat  $i$ ; and  $m$  is the total number of habitat types. The values of  $\alpha$  vary between 0 (complete avoidance) and 1 (complete preference). We calculated a second value  $\alpha'$  using equation 4.2. For  $\alpha'_i > 1$ , the habitat is considered preferred by the animal in function of its availability; for  $\alpha'_i < 1$ , the habitat is avoided in function of its availability; and for  $\alpha'_i = 1$ , the habitat is used randomly in function of its availability. All habitats preferred or avoided through the Cheason index, but not significant through the exact goodness of fit test, were considered randomly used for nesting.

We considered a habitat as a chimpanzee or gorilla nesting habitat if significantly preferred. We also considered habitats randomly used, but accounting for at least 20% of observed proportion of use for the great ape species (Gregory and Baillie, 1998). This is consistent with the assumption that a habitat may not be preferred by a species but, may nevertheless support a higher number of individuals of the population (Gregory and Baillie, 1998).

#### 4.3.2.2 IMPORTANT FRUIT SPECIES TO GREAT APES

We used the method described by Doran *et al.* (2002) to determine important fruit species consumed by gorillas and chimpanzees. Doran *et al.* (2002) defined four ‘importance types’, three of which we used: Importance type 1: present in more than 50% of faecal samples in at least one month and consumed for more than 50% of months; importance type 2: present in faecal samples for more than 50% of months; importance type 3: present in more than 50% of faecal samples in at least 1 month (Doran *et al.*, 2002). The fourth importance type deals with direct observations, but we conducted an indirect observation through faecal sample analysis. Before defining important plant species, we excluded from the plant list those for which remains were found in less than 1% of faecal samples (Doran *et al.*, 2002).

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#### 4.3.2.3 SPATIAL ANALYSES

We used three methods of spatial analyses: The Global Moran's I, the Kernel Density Estimation (KDE) and the spatial correlation. The Global Moran's I spatial autocorrelation statistic was used to measure the degree to which features were spatially associated (Scott and Janikas, 2010). A significant clustered pattern in each variable is an evidence of the existence of HCVFs (Lin *et al.*, 2017). KDE was used to describe the distribution of great ape nests as well as important fruit trees and suitable habitats.

**Table 4.1: Results of the Moran I test for spatial autocorrelation.**

Autocorrelation analysis	Moran's index (I)	Z-score	P-value
<b><i>Gorilla gorilla gorilla</i></b>			
Nesting site distribution	0.836	5.764	< 0.001
Nesting habitat distribution	0.967	118.771	< 0.001
Important fruit distribution	0.974	33.955	< 0.001
<b><i>Pan troglodytes troglodytes</i></b>			
Nesting site distribution	0.836	5.764	< 0.001
Nesting habitat distribution	0.857	67.925	< 0.001
Important fruit distribution	0.955	48.908	< 0.001

*Note.* Positive Mora's index (I) indicates that features are concentrated, while negative values indicate dispersion. The z-score is a summary value indicating the degree to which features of the measured variable are clustered or dispersed. Z-scores greater than 2.58 indicate that data points are clustered at more than 99% confidence level.

The KDE is a non parametric method that is generally used to estimate home range of individual animals (Worton, 1989), but it can also be used at population level to study their range, or applied on data other than animal locations, that are vital to a population such as habitat availability (Seaman and Powell, 1996). It uses location points recorded with GPS to derive a probability distribution that illustrates the likelihood that the study target is going to be present at any particular point (Kie *et al.*, 2010). The term utilization distribution is often used in home range studies to denote that probabilistic distribution, but in this work, we will use the terms abundance distribution and availability distribution for abundance and habitat variables respectively. An important aspect of KDE is that its output results vary according to several parameters such as the method (fixed or adaptive), the grid cell size, and the bandwidth (Worton, 1989; Powell, 2000). The fixed kernel method was used in KDE according to that all our variables presented a clumped

distribution (Table 4.1) (Lawson and Rodgers, 1997); and, it may produce less variable home rage sizes at different sampling sizes (Wartmann *et al.*, 2010). The value of the bandwidth, also called smoothing parameter, is evidently the most influential parameter in the KDE implementation (Hemson *et al.*, 2005). Several methods were developed to determine the bandwidth value for implementing KDE (Signer and Balkenhol, 2015). The best method for bandwidth selection is ideally the one that minimizes the mean integrated square error (MISE) (Worton, 1989; Seaman and Powell, 1996). In that sense, the Least Square Cross Validation (LSCV) was recommended for bandwidth selection in KDE (Seaman and Powell, 1996), and was widely used in home rage studies (Laver and Kelly, 2008). The KDE used with LSCV though producing accurate results (Seaman and Powell, 1996), was criticized because it yields smaller bandwidths and then produces utilization distributions (home ranges) that are more fragmented (Powell, 2000). A recent study show that the LSCV produces home ranges with negative bias for smaller samples and positive bias for larger samples (Kie, 2013). Using KDE with LSCV may be missing important corridor areas between important feeding sites and nesting sites (Kie *et al.*, 2010). An alternative to the LSCV is the reference bandwidth proposed by (Worton, 1989). This method yield large bandwidths that lead to oversmoothing of the sampling points, particularly when data points are clumped (Kie *et al.*, 2010). An ah-hoc method is proposed to overcome the probleme of undesmothing by the LSCV method and oversmoothing by the reference method, that consist of reducing the value of reduicing the value of the reference bandwidth until the extent of the home range satrts splitting into two parts (Kie, 2013). The ad-hoc method was used to determine the smothing parameter of all variables. We used 50% and 95% isopleths to represent the abundance and availability distribution from KDE (Hemson *et al.*, 2005). Following Laver and Kelly (2008), we also performed a distribution core analysis using an objective method based on the abundance and availability distribution of our data. It allows us to draw a third contour level of the abundance and availability distributions, which was further used to define HCVFs. The method produces different percentages at different probalities of abundance and availability (Powell, 2000).

We choose the smallest bandwidth obtained from abaundance variables to produce a unite shape of distribution cores. Certainly, our sampling interval made the data points spatially irregular (Katajisto and Moilanen, 2006). This is due to the fact that data were collected on predefined transects, that were established at a certain distance from each other, leading to missed observations and spatial aggregation of data points (Katajisto and Moilanen, 2006). To solve this probleme,

we weight each variable by grid cell and rounded all decimal values to one (Katajisto and Moilanen, 2006). We then generated random points in each grid cell corresponding to its weight for each variable. The weight for abundance variables was the number of nesting sites recorded in each grid cell. For suitable habitat, the weight was the total number of points of all suitable habitats in the grid cell. We calculated the weights ( $W_k$ ) for important plant species as follow (Equation 4.3):

$$W_k = \sum_{i=1}^X \sum_{j=1}^Y \frac{B_{ij}}{N} \quad (\text{Equation 4.3})$$

Where X is the number of important fruit species in the cell k; Y is the number of individuals of species i in the cell k; N is the number of plots counted in the cell; and  $B_{ij}$  is the basal area of the plant j.

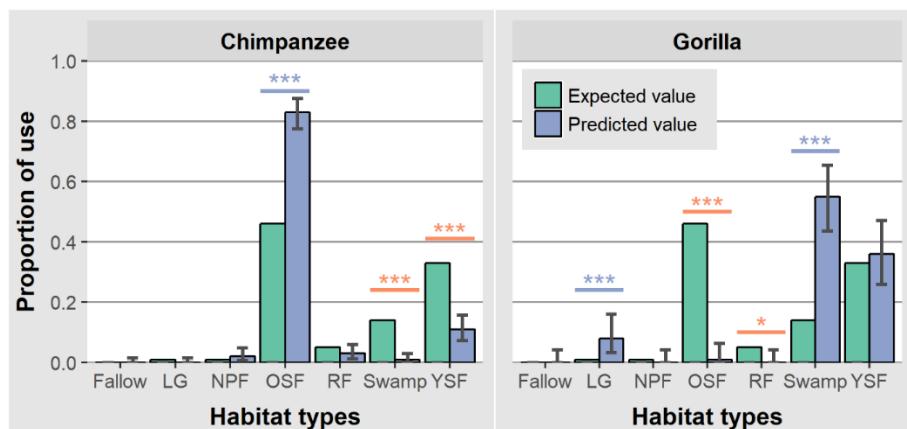
The spatial correlation was conducted to evaluate the local relationship between two abundance or availability distributions. We applied two techniques to delineate HCVF if the two species show different patterns of habitat use: (1) if a larger part of nesting site distribution was correlated to both the distribution of nesting habitats and important fruit species, the HCVF comprised a single area composed of the zone where high abundance of nesting sites, high densities of important fruit species and preponderance of preferred nesting habitats overlapped; (2) if the distribution of nesting sites was not simultaneously correlated to nesting habitats and important fruit species, the HCVF was composed of two areas, one where nesting sites are more abundant in high nesting habitat availability area and one where high densities of important fruits and high densities of nesting sites overlap.

The R software version 3.3.1 (R Core Team, 2018) was used to conduct exact goodness of fit test, KDE and core analysis distribution (package *rhr* version 1.2.909; Signer and Balkenhol, 2015), and spatial correlation (package *spatialEco* version 0.1-7). We used ArcGIS 10.3.1 to conduct the The Moran's I index of spatial autocorrelation and draw maps. HCVFs was defined using the *raster calculator* tool, an ArcGIS tool used to select in one or several raster files different cells that have a certain value. All variables were resampled at 50 m spatial resolution to correspond to the distance between two habitat points.

## 4.4. RESULTS

### 4.4.1. GREAT APE HABITAT USE

From the 175 1000×1000 m cells, we recorded 272 chimpanzee nests and 89 gorilla nests. Great ape nests were absent from 59 cells. Chimpanzee nests were found in 55 cells, while gorilla nests were found in 33 cells. Only 14 grid cells were recorded to contain both chimpanzee and gorilla nests. Mean nest encounter rate per kilometre was 4.97 ( $SD = 4.5$ ) for chimpanzees and 3.48 ( $SD = 4.7$ ) for gorillas. A total of 4375 habitat points was recorded and assigned to either Fallow (26), Old secondary forest (2069), Near primary forest (57), Young secondary forest (1396), Swamp (575), Riparian (191) and Light gap (61).



**Figure 4.2: Gorilla and chimpanzee habitat use.** Expected values are presented with confidence intervals as error bars. The observed values are significantly higher or lower than the predicted values if that value  $\pm$  the confidence value is always greater or lower than the expected value, otherwise, they are non-significant at a probability of 0.05. Significant values are marked with significance asterisks (\* = “ $p<0.05$ ”; \*\*\* = “ $p<0.001$ ”). Blue asterisks indicate habitats significantly preferred, and red asterisks indicate habitats significantly avoided. The expected value for an habitat is the number of points for that habitat divided by the total number of points recorded for all habitat types; the predicted value is the value calculated (using the Cheason Index of selection) based on the number of nests found for each species in that habitat. LG Light Gap; NPF Near Primary Forest; OSF Old Secondary Forest; RF Riparian Forest; YSF Young Secondary Forest.

**Table 4.2: Important fruit species to great apes.**

Scientific name	Family	Life form	Importance type
<b><i>Pan troglodytes troglodytes</i></b>			
<i>Chrysophyllum lacourtianum</i>	Sapotaceae	Tree	1
<i>Landolphia spp<sup>a</sup></i>	Apocynaceae	Liana	1
<i>Uapaca spp<sup>b</sup></i>	Euphorbiaceae	Tree	1
<i>Celtis tessmannii</i>	Ulmaceae	Tree	2
<i>Cissus dinklagei</i>	Vitaceae	Liana	2
<i>Dialium pachyphyllum</i>	Ceasalpiniaceae	Tree	2
<i>Enantia chlorantha</i>	Annonaceae	Tree	2
<i>Ficus spp<sup>c</sup></i>	Moraceae	Tree and stranglers	2
<i>Heisteria parvifolia</i>	Olaceaceae	Tree	2
<i>Milicia excelsa</i>	Moraceae	Tree	2
<i>Nauclea spp<sup>d</sup></i>	Rubiaceae	Tree	2
<i>Polyalthia suaveolens</i>	Annonaceae	Tree	2
<i>Santiria trimera</i>	Burseraceae	Tree	2
<i>Cleistostolis patens</i>	Annonaceae	Tree	2
<i>Duboscia macrocarpa</i>	Tiliaceae	Tree	3
<b><i>Gorilla gorilla gorilla</i></b>			
<i>Chrysophyllum lacourtianum</i>	Sapotaceae	Tree	1
<i>Duboscia macrocarpa</i>	Tiliaceae	Tree	1
<i>Landolphia spp<sup>a</sup></i>	Apocynaceae	Liana	1
<i>Uapaca spp<sup>b</sup></i>	Euphorbiaceae	Tree	1
<i>Antrocaryon Klaineanum</i>	Anacardiaceae	Tree	2
<i>Celtis tessmannii</i>	Ulmaceae	Tree	2
<i>Cissus dinklagei</i>	Vitaceae	Liana	2
<i>Dialium pachyphyllum</i>	Ceasalpiniaceae	Tree	2
<i>Ficus spp<sup>c</sup></i>	Moraceae	Tree and stranglers	2
<i>Heisteria parvifolia</i>	Olaceaceae	Tree	2
<i>Klainedoxa gabonensis</i>	Irvingiaceae	Tree	2
<i>Santiria trimera</i>	Burseraceae	Tree	2
<i>Sorindeia grandifolia</i>	Anacardiaceae	Tree	2
<i>Tetrapleura tetraptera</i>	Mimosaceae	Tree	2

<sup>a</sup> Includes *L. glabra*, *L. jumellei*, *L. landolphoides*, *L. mannii*, *L. maxima*, *L. owariensis*, *L. violacea*, *L. jumellei* and two unidentified species; <sup>b</sup> Includes *U. acuminata*, *U. guineensis*, *U. paludosa*, *U. vanhouttei*; <sup>c</sup> Includes *Ficus mucoso*, and some stranglers; <sup>d</sup> Includes *N. diderrichii*, *N. pobeguinii*

Note for Table 4.2: Importance type 1: present in more than 50% of faecal samples in at least one month and consumed for more than 50% of months; importance type 2: present in faecal samples for more than 50% of months; importance type 3: present in more than 50% of faecal samples in at least 1 month

The Cheason indexes indicate that chimpanzees and gorillas exhibit habitat preferences for nesting, as confirmed by the exact goodness of fit test ( $df = 6$ ;  $p = 0.000$ ). Chimpanzees significantly preferred nesting in old secondary forests ( $\alpha_i = 2.772$ ), while gorillas preferred nesting in swamps ( $\alpha_i = 2.389$ ) and light gaps ( $\alpha_i = 3.914$ ) (Figure 4.2). It is noteworthy that all habitats preferred by chimpanzees were not preferred by gorillas and vice versa. Riparian forests and young secondary forests were randomly used by either species, though this pattern was insignificant and varied: riparian forests constituted only 2.98% of use by chimpanzees, while young secondary forests constituted 36.05% of use by gorillas. We found no nest in fallows for neither chimpanzees nor gorillas.

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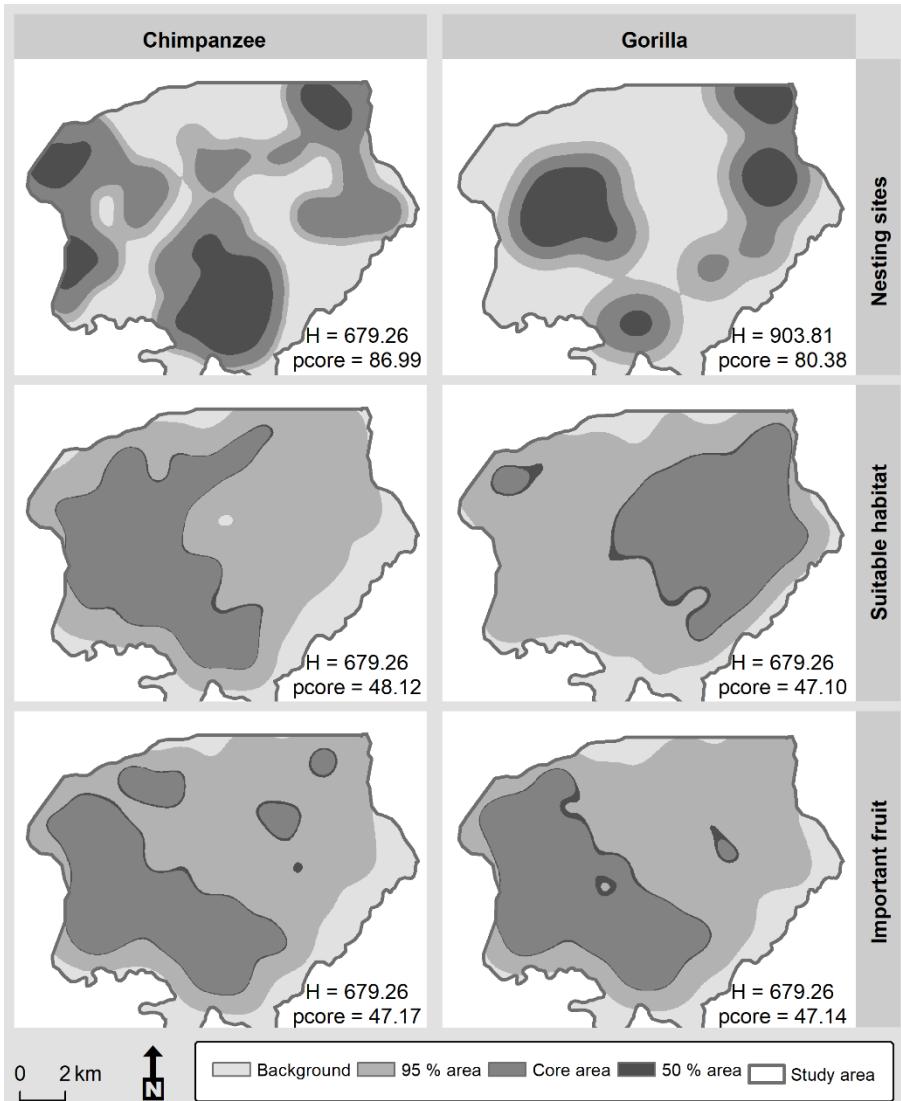
#### 4.4.2. IMPORTANT FRUIT SPECIES

We classified 15 and 14 fruit species as important for chimpanzees and gorillas, respectively, based on the analysis of faecal samples (Table 4.2). Three species were classified as type 1, 11 species as type 2 and one as type 3 for chimpanzees; while four species were classified as type 1 and 10 species as type 2 for gorillas. No species was classified as type 3 for gorillas. *Duboscia macrocarpa* classified as type 3 for chimpanzees appeared in type 1 for gorillas.

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#### 4.4.3. SPATIAL DISTRIBUTION OF GREAT APE NESTS, SUITABLE HABITATS, AND IMPORTANT FRUITS SPECIES

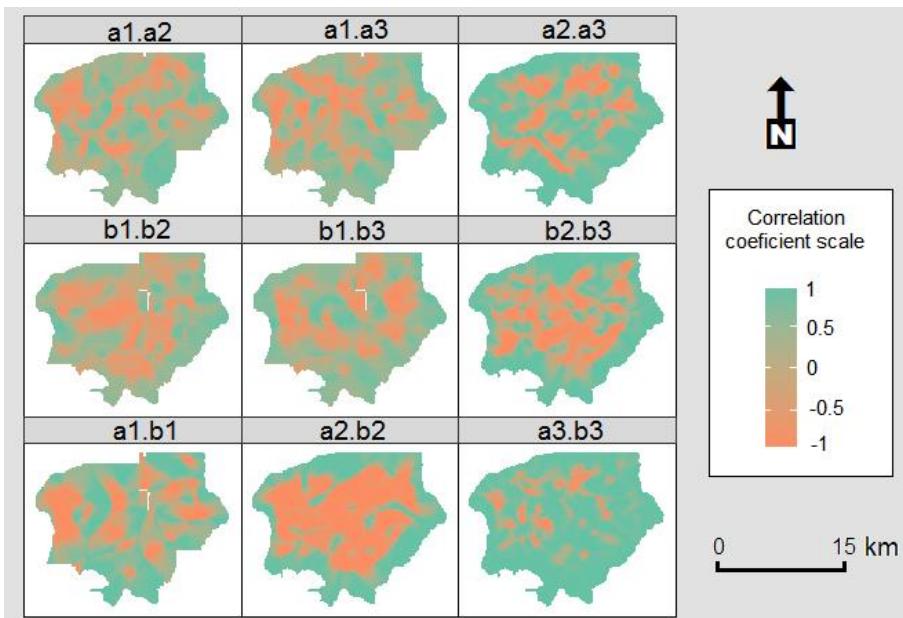
Features of all variables (nest abundance distribution, suitable nesting habitats, and important fruit species) were spatially clumped for both chimpanzees and gorillas (Table 4.1). This means that the distribution of great ape nesting sites, suitable nesting habitats, and important fruit species exhibit high values in some areas, that can be set as HCVF. Aggregation areas differ from one variable to another (Figure 4.3). Chimpanzee nesting sites are more abundant in the southern and south-western areas, with some small patches in the north-eastern area; while gorilla nesting sites are more abundant in the eastern, north-eastern and central areas (Figure 4.3a). Chimpanzee suitable nesting habitats are more present in the southern and north-western areas; while gorilla suitable nesting habitats are more present in the eastern areas (Figure 4.3b). The distributions of important fruit species for both chimpanzees and gorillas are all concentrated in the south and southeast of the site (Figure 4.3c).



**Figure 4.3: Spatial distribution of great apes' nests and resources; H = bandwidth, pcore = percentage of the core. The abundance is classified in three categories using 95% and 50% contours and the core area.**

The correlation maps indicate that the spatial correlation between nesting sites abundance and nesting habitat and important fruit distribution do not show a clear pattern for both animal species. But we can see that chimpanzees show more affinity to the distribution of their nesting habitat and important fruits than gorillas. Gorillas nesting sites distribution is locally correlated with nesting habitats (east)

and important fruit species distribution (centre and south) (Figure 4.4b1.b2 and Figure 4.4b1.b3). The correlation between chimpanzee nesting habitats and their important fruit distribution is high (Figure 4.4a2.a3), but relatively low for gorillas (Figure 4.4b2.b3). Also, the correlation between chimpanzee and gorilla nesting habitat is very low (Figure 4.4a2.b2), while it is very high between chimpanzee and gorilla important fruit species distribution (Figure 4.4a3.b3). This means that chimpanzees and gorilla habitats are available at different spatial locations, while gorilla important fruits species are more abundant at high chimpanzee habitat availability.

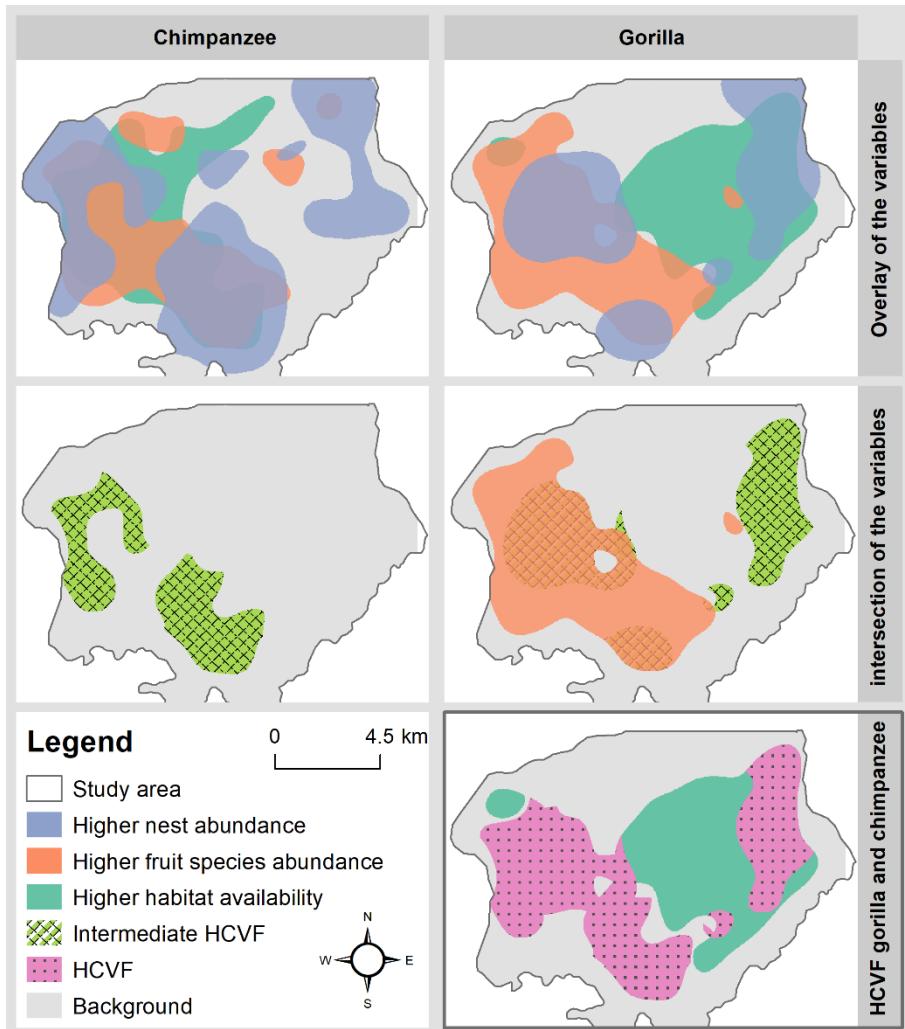


**Figure 4.4: Spatial correlation between the different variables for each species: a = Chimpanzee, b = Gorilla, 1 = nesting site distribution, 2 = nesting habitat distribution, 3 = important fruit species distribution.**

#### 4.4.4. HIGH CONSERVATION VALUE FORESTS FOR GREAT APE PROTECTION

The assessment of the spatial relationship between abundance and habitat variables led to the designation of one area HCVF for chimpanzees and two separate areas as HCVF for gorillas (Figure 4.5). The chimpanzee HCVF covers the south and western part of the study area (Figure 4.5b). For the two gorilla HCVF (Figure 4.5b and Figure 4.5c), one is in the centre area, where gorilla nesting sites

and their important fruits intersect, and the other area is in the north-eastern part of the study area where their nesting habitats are more available. Between the two areas, is a transitional zone composed of gorilla high quality nesting habitats (Figure 4.5c), and may be considered as corridor.



**Figure 4.5:** Delimitations of high conservation value forests for great apes' conservation considering: the overlay of high nesting site abundance distribution, high nesting habitat availability and high fruit plant density, the intersection of all spatially correlated variables, and then joining the final maps obtained after the intersections to draw the HCVF for both Gorillas and Chimpanzees with a corridor for Gorilla movements between the two HCVF.

#### 4.5. DISCUSSION

In contrast to techniques based solely on species abundance distribution, incorporating habitat variables such as nesting habitat and fruit tree distribution allowed us to objectively define HCVFs that do not only designate areas of high densities of great apes, but that also consider other factors that are indispensable to their long-term survival. Gorillas and chimpanzees significantly preferred different sets of different habitat types but a comparable set of fruit species are important for their survival. In addition, those habitat variables and nesting site locations present a clumped distribution. Spatial correlations between variables show different patterns for both animal species. Chimpanzees nesting sites present a high aggregation in areas of high fruit and high nesting habitat availability; while gorillas present two important clumps, one in areas of high-preferred nesting habitat availability and another in areas of important fruit availability. Areas of high nesting habitat availability do not overlap between gorilla and chimpanzee, while high important fruit availability areas greatly overlapped between the two species. The results show that animals may move seasonally according to the distribution of their resources. However, our data do not allow us to confirm the effect of seasons on the spatial distribution of nesting sites. Then using a method that integrates habitat variables with abundance distribution results in HCVFs that are consistent with ecological requirements of the animal species. Additionally, we showed that considering the distribution of fruit species would result in different approaches for defining HCVF when dealing with two competing species that coexist in the same environment. This method provides more valuable supplement to other techniques based only on the animal abundance distribution, especially when character displacement may have been at the centre of sympatry between the species and its competitor (Hickman Jr *et al.*, 2008). The patterns observed are due to the evidence of niche partitioning between gorillas and chimpanzees (Oelze *et al.*, 2014). Seasonal variation of fruit availability in great ape habitat results in a shift in fruit consumption by gorillas in terms of diversity, quantity and quality, in comparison to chimpanzees (Oelze *et al.*, 2014). Recent works underlined the importance of adding habitat features to design HCVF, as a mean to enhance the protection of important ecological processes that govern the maintenance of ecosystem integrity (Camphuysen *et al.*, 2012; Berger-Tal *et al.*, 2016). Camphuysen *et al.* (2012) found that birds are generally in transit to or from food sources. This imply that relying solely on inventory data without considering species behaviours may lead to setting priority areas that cannot protect key food sources necessary for the survival of those bird populations. Using camera traps, Matsuda *et al.*

(2015) show that orang-utans and other mammals require natural licks for their mineral contents, and then proposed the inclusion of natural licks in HCVFs. Buij *et al.* (2002) found that due to seasonal variation in fruit availability between different altitudes, orang-utans seasonally show high densities in habitats where fruit availability was the highest. They then concluded that HCVFs should include a range of different altitudes to allow the survival of orang-utans in the forest. Using ecological niche modelling, Brambilla and Saporetti (2014) found that habitat suitability with nesting habitats and feeding habitats resulted in different spatial distributions. Consequently, nesting habitats and feeding habitats were functionally different and should be considered separately when designing priority areas for conservation (Brambilla and Saporetti, 2014). This is congruent the case of gorillas in our study where their nesting and feeding habitats were not spatially correlated and have resulted in different functional responses (Figure 4.4).

We collected data over 11 months, but our analysis did not focus on seasonal spatial variations in the different variables. In addition, we did not consider the nest decay rate in our analyses. Evaluating patterns of habitat use by great apes often requires the use of signs other than nests (footprints, feeding remains, etc.) (Morgan *et al.*, 2006). Those additional signs are generally difficult to observe after several days or even when fresh in the dry season in *terra firma* habitats (Sanz *et al.*, 2007). As such, we used nest data as the only available ecologically sound and unbiased information on abundance distribution. Nest decay rate was shown to vary between gorilla and chimpanzee, and is also influenced by habitat types, nesting material and seasons (Morgan *et al.*, 2016). It is evident that such variable nest decay rate may have influenced our observed nesting site distribution. By using nesting sites instead of individual nests (Funwi-Gabga and Mateu, 2012), we reduced not only the effect of variability in the number of nests per site, but also minimized the influence of nest decay rate. Great apes are social primates, and many nests of the same site may have disappeared at time the nesting site is discovered. The distribution of different variables obtained from KDE is not a unique output, because it depends on several variable parameters. It is likely that a change of a parameter like the bandwidth may result in a different distribution. The different parameters and the model are chosen based on some properties and constraints defined in the literature. Now, no single method is consistent with all studies (Laver and Kelly, 2008), and the intended use of KDE outputs remain the important factor governing the choice of a parameter for KDE (Worton, 1989). The resultant HCVF do not consider factors that can affect the distribution of animals, such as roads and human settlements (Clark *et al.*, 2009). This is an important issue

that need to be considered, because some areas may be set as HCVFs that is not reachable or unsuitable for the animal. Our results showed that unoccupied areas should be included in HCVF to allow long-term survival of wildlife (Camaclang *et al.*, 2014). In this case, Ecological Niche Modelling appears to be a good complement to KDE to design HCVFs (Denoël and Ficetola, 2015), as it will help to focus conservation efforts only on areas that may support population persistence.

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#### 4.5.1. HABITAT REQUIREMENTS AND HCVFs

Using a combination of abundance and habitat variables, it was possible to set HCVF that differ from those set from abundance data alone. Our results are consistent with those of Balcomb *et al.* (2000) when considering chimpanzees alone. They found that the abundance of chimpanzees can be predicted by the distribution of large fruiting trees and high fruit species density may be a proxy of habitat chimpanzee quality. However, great apes are generally sympatric range wide, and sound conservation measures are those that consider the evolutionary factors that condition the coexistence of two sympatric species. Our study demonstrates that the prediction of the abundance of an animal species by habitat quality holds true under the assumption that it is a dominant species, but not necessarily when dealing with its direct competitor. In this viewpoint, considering the distribution of nesting habitats and fruit species made it possible to set less subjective HCVF that are more compatible with the persistence of the animals. HCVF are at the centre of biodiversity mainstreaming (Morgan *et al.*, 2013; Redford *et al.*, 2015), and considering both abundance distribution and habitat variables to delineate them provides a tool that should be incorporated in conservation decisions. A similar approach was used by Martins *et al.* (2013), considering animal abundance distribution and the intensity of anthropogenic activities. In addition, abundance alone was considered by Murai *et al.* (2013) to address hunting pressures in large mammals. It is then evident that the approach used to design HCVF may differ depending on the conservation objectives, but sound conservation measures that intend to favour the long term survival of animals are those that put forward the distribution of suitable habitat components such as food sources [see Balcomb *et al.* (2000)].

The importance of our study resides in the combination of the distribution of important components of the diet in defining HCVF. The study considers the distribution of plant species providing fruits to great apes. However, not all trees considered will bear fruits at the same time, and can then not reflect the actual distribution of fruits available to great apes. As the phenology of fruit species can

vary annually within the same species (Tweheyo and Lye, 2003; Chapman *et al.*, 2005; Yamagiwa *et al.*, 2008), it is possible that the distribution of fruits available to great apes may vary from year to year. A good way to solve this issue may be to consider foraging sites instead of fruit species bearing fruits consumed by the animal species (Camphuysen *et al.*, 2012; Brambilla and Saporetti, 2014; Soanes *et al.*, 2016). Recording foraging sites is somehow difficult for unhabituated great ape species, because dietary analysis based on trails is insufficient to describe great ape diet and is generally used in complement with faecal analysis, and is more useful for the identification of herbaceous plant species that are not identifiable in faecal samples (Doran *et al.*, 2002). Then relying on feeding sites to derive feeding habitat suitability (Brambilla and Saporetti, 2014) may lack the spatial pattern of the consumption of fruit species, the important resources for great ape survival. Our study is among the few that consider feeding habitat suitability by incorporating the spatial distribution of potential sources of important feeding resources (Buij *et al.*, 2002; Brambilla and Saporetti, 2014; Matsuda *et al.*, 2015). A similar approach was used by Martins *et al.* (2013) to consider important breeding areas in priority area setting.

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#### 4.5.2. MANAGEMENT OF HCVFs

Delineating HCVFs should involve several stakeholders (Lascelles *et al.*, 2012), which can have great implications on its area (Hanski, 2011). Thus our HCVF (Figure 4.5c) is the potential area suitable for animal species in consideration based on the criteria setup (Ronconi *et al.*, 2012). Our design can be applied in many ecosystems where HCVFs are useful for the protection of wildlife species. While we just focused on two wildlife species in our study, those species are all classified at least as endangered species. This is an important criterion for setting conservation areas (Galetti *et al.*, 2009). Additionally, our final HCVF encompasses many habitat types as it covers both chimpanzee and gorilla preferred nesting habitats, and is then suitable for the preservation of many other species for which the survival depends on habitats preferred by gorilla and chimpanzees. In addition, our design considers areas of high fruit species densities. This is important because many primate species other than great apes, many birds, and many other mammal species are frugivores (Fleming and Kress, 2011). This makes the choice of great apes as focal species to identify HCVF very useful if it is intended to the preservation of many species in the community. This could have some implications in the effort needed to identify HCVF. Considering many species at the same time may require additional efforts, expertise, finance and time, and focusing solely on great apes

can offer an objective alternative to define conservation areas for many species. This method can be assimilated to the umbrella species approach defined by Rainho and Palmeirim (2013) and was applied by Martins *et al.* (2013) to drive conservation decision for a coral reef ecosystem.

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#### 4.5.3. IMPORTANCE OF HABITAT BASED HCVFs FOR GREAT APES

The frugivorous character of great apes necessitates conservation practices that consider fruit species protection. In the context of human disturbance, this implicates the management of logging practices. Although selective logging seems not to affect plant species richness, diversity and evenness (Testolin *et al.*, 2016), it can significantly reduce species abundance (Meijaard and Sheil, 2008) and affect plant community and structure (Potts, 2011; Testolin *et al.*, 2016), resulting in a significant dissimilarity in species composition between logged and unlogged forests (Testolin *et al.*, 2016). These affected plant species may comprise those preferred by great apes: for example, in Kanyawara logging led to a change in the basal area of 18 fruit species consumed by chimpanzees, and many additional species of chimpanzee diet were directly extracted for commercial purposes (Potts, 2011). However, the seven most consumed fruit species were not extracted (Potts, 2011), therefore suggesting that logging may not detrimentally affect chimpanzee food supply (McLennan, 2013). Selective logging also appears not to negatively affect great ape abundance: gorillas appear temporally resilient to logging activities (Haurez *et al.*, 2016) and to exist at higher abundances in logged forests (Clark *et al.*, 2009); and chimpanzees exhibit no spatial changes in range use during logging activities (Arnhem *et al.*, 2008). Velázquez-Vázquez *et al.* (2015) found similar results in a study on the distribution of spider monkeys in logged and unlogged forests. Great apes exhibit a positive significant response to the distance from logged forest gradient (Clark *et al.*, 2009); however, the spatial or temporal patterns of great apes abundance may be due to a spatial relocation of great apes populations in relation to logging activities, but not a loss of individuals (Morgan *et al.*, 2015). Great apes are highly frugivorous, but exhibit some flexibility in their diet (Meijaard and Sheil, 2008), as they increase their consumption of non-fruit food when fruits are scarce (Yamagiwa and Basabose, 2009; Head *et al.*, 2011), thus enabling a degree of resilience to disturbance (Milton *et al.*, 2005). However, fruit does play a crucial role in great ape socio-ecology (Doran *et al.*, 2002), and it is important to differentiate between short term fluctuations in fruit availability to which great apes exhibit resilience (Milton *et al.*, 2005), and long term loss of fruits

in the forest because of habitat degradation, that could ultimately lead to great ape extinction (McLennan, 2013; Behie and Pavelka, 2015; Rosa *et al.*, 2016).

#### 4.6. CONCLUSION

HCVF appears to be an important management tool that favours sustainable natural resource management outside protected areas. The major challenge of HCVFs is to define areas that comprise important resources necessary for populations to survive (Morgan *et al.*, 2013). We demonstrated that setting priority areas for species conservation considering abundance alone is inappropriate for their survival, and then recommend considering the distribution of their resource in conservation decisions. HCVFs are just areas with high availability in animal's habitat variables, and highest abundance of presence signs. This means that extractive activities should always be controlled in those areas allocated to resource production, and avoiding habitat fragmentation that may lead to the isolation of the priority area (Fahrig, 1999). It is then required that restoration activities be planned just after resource extraction have taken place (Shi *et al.*, 2005). The designation of priority areas for conservation means setting an area for conservation and leaving the other areas where extractive activities can take place. It is worth noting that areas set as HCVFs are not the only areas where animal presence indices were observed. The HCVF set is composed of two separate zones due to the relationship between gorillas and their habitat requirements. Meanwhile, the distribution of gorilla suitable nesting habitats offers the possibility to consider corridor in the final HCVF map (Figure 4.5c), that will allow them to move to areas with high fruit availability when necessary. Our results clearly show that great apes nests are more abundant in area of high availability of suitable nesting habitats (Figure 4.3), but there are areas of high availability of suitable nesting habitats that do not actually support high nesting site abundance (mainly gorillas). This may be a consequence of the fact that additional factors such as human settlements may shape the distribution of great apes. A great contribution of research for the improvement of great ape conservation may be the evaluation of factors affecting their spatial distribution. As a home range estimation technique, using KDE allowed us to derive spatial distribution of density probabilities of our survey data. This particularity of KDE makes it more suitable than other methods like Minimum Convex Polygons (Laver and Kelly, 2008) to design HCVFs. However, combining KDE and ENM is certainly a good compromise between considering areas not actually occupied by the animal and removing unsafe areas or barrier (Denoël and Ficetola, 2015) from the HCVF.

#### 4.7. REFERENCES

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# CHAPTER 5

## LONG-TERM CHANGES IN MAMMALIAN POPULATION ABUNDANCE IN A RESEARCH SITE IN SOUTH-EASTERN CAMEROON

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### 5.1. ABSTRACT

Several types of human activities are known to impact mammal populations, but the fate of mammal populations has often been overlooked in research sites which can be subject to the intrusion of hunters. We evaluated mammal population trends in a permanent research site using sympatric great apes (*Gorilla gorilla gorilla* and *Pan troglodytes troglodytes*) as focal species. We conducted nest censuses in 2001, 2008, 2014, and 2016 and recorded signs of human activities in 2008 and 2016. Results show that abundance of gorillas and chimpanzees significantly decreased between 2001 and 2016. Great ape populations remained relatively stable between 2001 and 2008; however, after 2008, they started to decline. We found that the transect set developed for research purposes indirectly facilitated the intrusion of hunters and the development of hunting activities in the research site. In addition, the change of hunting methods, from traps to guns, may have increased disturbance in the research site. The recent decline in the abundance of hunted mammal species in adjacent forest patches is arguably the ultimate cause of the encroachment of the research site by hunters. Thus, we advocate that as long as wildlife populations continue to be threatened either by humans or by environmental factors such as climate change, the promotion of research on animal ecology and conservation biology is of foremost importance. In the light of our results, efforts should be put towards combating hunting in research sites. At the same time, researchers should re-evaluate their conservation efforts and develop new suitable strategies to ensure the sustainability of hunting in forest patches surrounding permanent research sites to avoid wildlife depletion.

**Keywords:** Central chimpanzee, Dja Biosphere Reserve, Ecological monitoring, Human settlement, Population trend, Western lowland gorilla, Research site, Sustainability

## 5.2. INTRODUCTION

Mammal species are experiencing an increasing risk of extinction (Hoffmann *et al.*, 2011), with the highest number of threatened species occurring in the tropical forests (Schipper *et al.*, 2008). Almost a quarter of terrestrial mammal species are threatened by extinction, and the abundance of their populations has dropped by 25% over the past two decades (Baillie *et al.*, 2010). The challenge of understanding what causes mammal populations to change over time remains. Such knowledge can contribute to the development of conservation measures to prevent the rapid decline in wild animal populations. To this end, ecological monitoring is an important tool that may help conservation to take effective actions to overcome the ongoing population decline (Yoccoz *et al.*, 2001; Sauer and Knutson, 2008; Lindenmayer and Hunter, 2010; Campbell *et al.*, 2011). Monitoring is indispensable to wildlife population conservation, and an important aspect of it is understanding the different threats associated with such decline (Devos *et al.*, 2008). Monitoring wildlife populations can also improve understanding of the effects of different environmental and socioeconomic contexts on their status (Nichols and Williams, 2006).

The main threats facing mammal populations are land-use change, fragmentation, climatic change, and hunting (Bennett *et al.*, 2002; Smith *et al.*, 2006; Brook *et al.*, 2008; Collen *et al.*, 2011; Ripple *et al.*, 2016; de Almeida-Rocha *et al.*, 2017; Estrada *et al.*, 2017). Land-use change and fragmentation generally result from logging and agricultural expansion (Hoffmann *et al.*, 2011; Gonzalez-Suarez and Revilla, 2014). The direct effects of hunting consist of killing the animals, generally for human consumption or trade for the purpose of supplementing household income (Rogan *et al.*, 2018; Tagg *et al.*, 2018). The effects of hunting on mammal populations have been assessed through the comparison of protected areas (where hunting is controlled) with unprotected areas (where hunting is not controlled) (Rovero *et al.*, 2012; Rovero *et al.*, 2015) or by the evaluation of temporal changes of hunted mammal populations in response to changes in the intensity of hunting activities (Muchaal and Ngandjui, 1999; Remis and Robinson, 2012; Nzooh Dongmo *et al.*, 2015; Cronin *et al.*, 2016; Nzooh Dongmo *et al.*, 2016). At a global scale, Benitez-Lopez *et al.* (2017) showed that the rate of decline in mammal populations is higher in hunted areas than in unhunted areas. On Bioko Island (Equatorial Guinea), primate populations declined with the increase in intensity of gun hunting (Cronin *et al.*, 2016). In the Udzungwa Mountains (Tanzania), primate (*Cercopithecus* and *Colobus*) populations were stable in the protected area but declined in the

unprotected area, likely due to hunting (Rovero *et al.*, 2015). In the Campo National Park (Cameroon), the abundance of elephants, great apes, and duikers did not vary between 2008 and 2014 due to reduction in hunting pressure (Nzooh Dongmo *et al.*, 2015); while in the National Parks of Boumba Beck and Nki (Cameroon), increasing hunting pressure led to a decline in large mammal populations (Gorillas, chimpanzees, and elephants; Nzooh Dongmo *et al.*, 2016). However, the abundance of some cercopithecines seemed not to be affected by hunting activities in Bioko (Equatorial Guinea; Cronin *et al.*, 2016) and in Udzungwa (Tanzania; Rovero *et al.*, 2012).

More importantly, in addition to disturbance caused by logging activities (increased intensity of human activities or change in resource or habitat availability; Arnhem *et al.*, 2008; Meijaard and Sheil, 2008; Remis and Kpanou, 2011; Haurez *et al.*, 2016; Morgan *et al.*, 2018), logging is also reported to exacerbate hunting pressure in remote forest areas (Bowen-Jones and Pendry, 1999; Morgan *et al.*, 2013). Increasing hunting pressure may also decrease mammalian population abundance (Matthews and Matthews, 2002; de Almeida-Rocha *et al.*, 2017). Although it was found that the effects of hunting on primate abundance were greater than the effect of logging (Remis and Robinson, 2012), the rate of decline increased by about 30% when hunting was combined with logging (de Almeida-Rocha *et al.*, 2017); nonetheless, the response of mammals to hunting or logging may vary between species (Rist *et al.*, 2009). In general, hunting pressure is higher in easily accessible areas than in remote areas (Espinosa *et al.*, 2018). For example, in the Yasuní Biosphere Reserve (Ecuador), Espinosa *et al.* (2018) found that the abundance of jaguars' prey (the species targeted by hunters) declined in areas where hunters had more access. However, in those areas, the abundance of jaguars declined disproportionately compared to that of their prey species, indicating that the abundance of jaguars was affected not only by a decrease in the abundance of their prey, but also by the hunting activity itself (Espinosa *et al.*, 2018). Currently, the effects of hunting pressure, apart from the direct killing of animals, are poorly understood. Studies on the impact of hunting pressure do not clearly differentiate between the effects due to the direct killing of the animals and those caused by the hunting activity itself (Rovero *et al.*, 2015; Cronin *et al.*, 2016; Nzooh Dongmo *et al.*, 2016). Long-term monitoring can help assess hunting impacts in a site where hunting does occur but where hunters do not target some species.

Field research is another form of human encroachment in natural systems, associated with non-consumptive use of organisms (Salafsky *et al.*, 2008).

Researchers generally use a network of transects that may facilitate the intrusion of hunters in the study site (Gruen *et al.*, 2013). Ethically, researchers must ensure the persistence of animal populations in their sites (Fedigan, 2010; Riley and Bezanson, 2018), but the effects of research presence on mammal populations have just started to be questioned (Laurance, 2013). Nowadays, it becomes imperative for researchers to evaluate the effects of their presence on mammal populations (Riley and Bezanson, 2018) and take corrective actions in order to participate in nationwide and global initiatives in biodiversity conservation (Nekaris and Nijman, 2013). Generally, studies have documented that researchers in a site may contribute to the protection of wildlife species (N'Goran *et al.*, 2012; Piel *et al.*, 2015; Tagg *et al.*, 2015). N'Goran *et al.* (2012) and Campbell *et al.* (2011) showed that the abundance of monkeys (Tai National Park, Ivory Coast) was higher near a research site than in an area subject to hunting. Tagg *et al.* (2015) compared the present research site (this study) with a protected area and a non-protected area and found that the abundance of great apes was more similar between the research site and the protected area than between the research site and the non-protected area; in addition, they also showed that great ape abundance was greater in the research site than in the non-protected area. They concluded that the mechanism of deterring poachers due to the presence of researchers in the forest or sensitisation in villages might contribute to the maintenance of animal populations; nevertheless, evidence suggests that hunting activities still occur in the research site (Tagg and Willie, 2013). Comparing animal abundance between different forest sites with varying levels of management is common in wildlife management (Roopsind *et al.*, 2017). The problem with using the spatial method for evaluating animal population status as a surrogate for animal persistence in the area by comparing sites with varying levels of influence (Morrison *et al.*, 2008) is that such approaches do not inform any baseline population sizes (Magurran *et al.*, 2010), therefore making it difficult to detect temporal environmental effects (Haurez *et al.*, 2016). Additionally, Campbell *et al.* (2011) reported that research sites are generally set in areas with high wildlife populations. An alternative approach to studying the status of animal populations is to monitor them in a site for a long period of time (Morrison *et al.*, 2008). This method can contribute to understanding the direct influence of a disturbance on wildlife populations (Morrison *et al.*, 2008). Hence, using a four-year change in animal populations to assess the effects of research, Piel *et al.* (2015) found that the abundance of primates slightly increased from 2009 to 2012, with the abundance of the common duiker increasing the most and being the highest. The increase in mammal populations can be explained by the fact that researchers' presence deters hunting

activities (Piel *et al.*, 2015), but the patterns in a research site where hunting activities occur are yet to be examined.

This study aims to evaluate whether the long-term use of a site for research purposes may indirectly affect animal population abundance using sympatric great apes (western lowland gorillas [*Gorilla gorilla gorilla*] and central chimpanzees [*Pan troglodytes troglodytes*]) as focal species. Here, great apes are chosen as target species because they are suitable indicators of the status of many other wildlife populations (White and Edwards, 2000; Morrison *et al.*, 2008). For example, the abundance of chimpanzees was shown to be positively correlated to the diversity of other mammals (Tweh *et al.*, 2015). Great apes are commonly found in mammal study sites; that is, most mammal research activities in the Afrotropics were implemented where at least one great ape species occurs (Marshall *et al.*, 2016), thus facilitating the comparison of results among several research sites. The present research site is part of an area where hunters do not primarily target gorillas and chimpanzees (Ávila *et al.*, 2019). However, given that the frequent use of transects by researchers may facilitate hunting activities, we hypothesize that great ape population abundance will change in the research site, and we predict that their populations will decline over time. This study will provide important insights into the potential indirect effects of permanent research presence on the persistence of wildlife populations.

### 5.3. METHODS

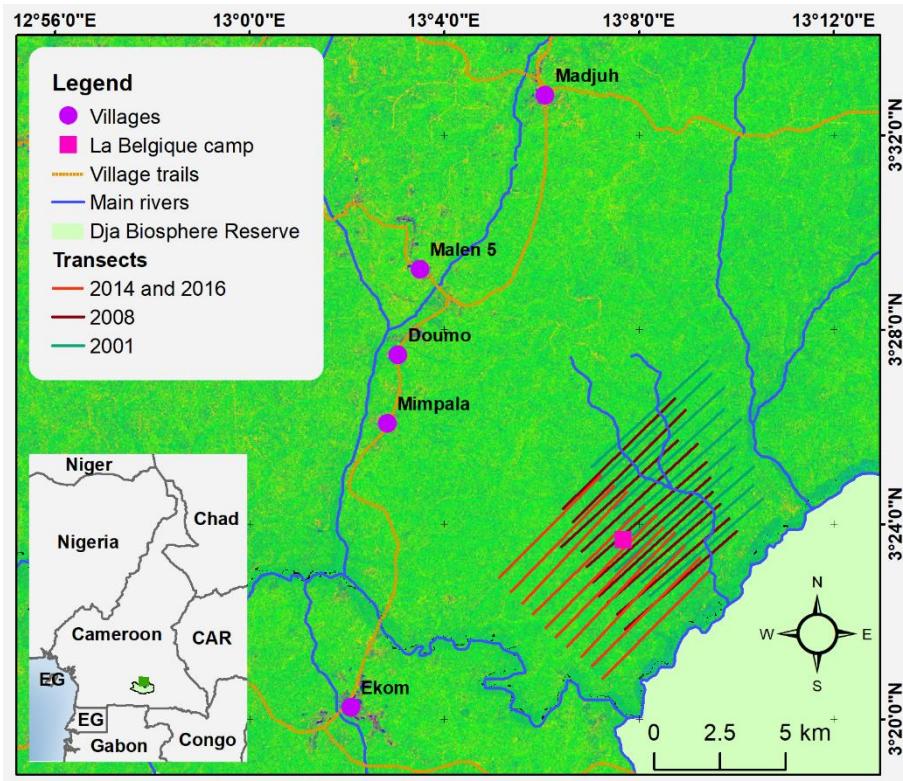
#### 5.3.1. STUDY AREA

The study was conducted in the research site La Belgique between 13°2'–13°11' East and 3°20'–3°27' North in the Forest Management Unit 10 047a; this site is adjacent to the Dja Reserve at the northern periphery (Figure 5.1). The research site La Belgique was established in 2001. In this site, research projects on wildlife surveys, great ape diet and nesting, fruit phenology, and botanical inventories were implemented intermittently until 2009, at which point data started to be collected on a regular basis.

### 5.3.2. DATA COLLECTION

#### 5.3.2.1 GREAT APE NEST SURVEYS

In the study site, great ape (gorilla and chimpanzee) nests were surveyed in 2001, 2008, 2014, and 2016 along ten 6-km transects, set 600 m apart. Along each transect, observations were made by a team composed of one researcher and two local guides.



**Figure 5.1:** Location of the research site as well as the transects used for ecological monitoring. The background represents the status of the forest in the research site, a fractional cover of a Landsat 8 image (WRS Path 184, WRS Row 058, and acquisition date 2015/12/23), downloaded from Earth Explorer (<https://earthexplorer.usgs.gov>), and processed in CLASlite 3.3 (Asner *et al.*, 2009). The blue and red colours around the villages represent non-forests, areas cleared for agriculture or habitations; the green colour represents intact forests.

### 5.3.2.2 HUMAN ACTIVITIES

Along the transects, all signs of human activities (e.g. hunting, gathering, etc.) were recorded in 2008 and 2016. We considered three levels of human activities: hunting signs only, hunting signs and camps, and all human signs. Hunting signs included gunshots, spent cartridges, traps, and all other evidence of hunting (Tagg and Willie, 2013). Other signs included honey extraction, bark stripping, extraction of larvae, collection of palm wine, fishing, human footprints other than those of researchers (who generally walk with rubber boots), and abandoned items such as clothes and cigarette butts (Tagg and Willie, 2013).

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### 5.3.3. DATA ANALYSIS

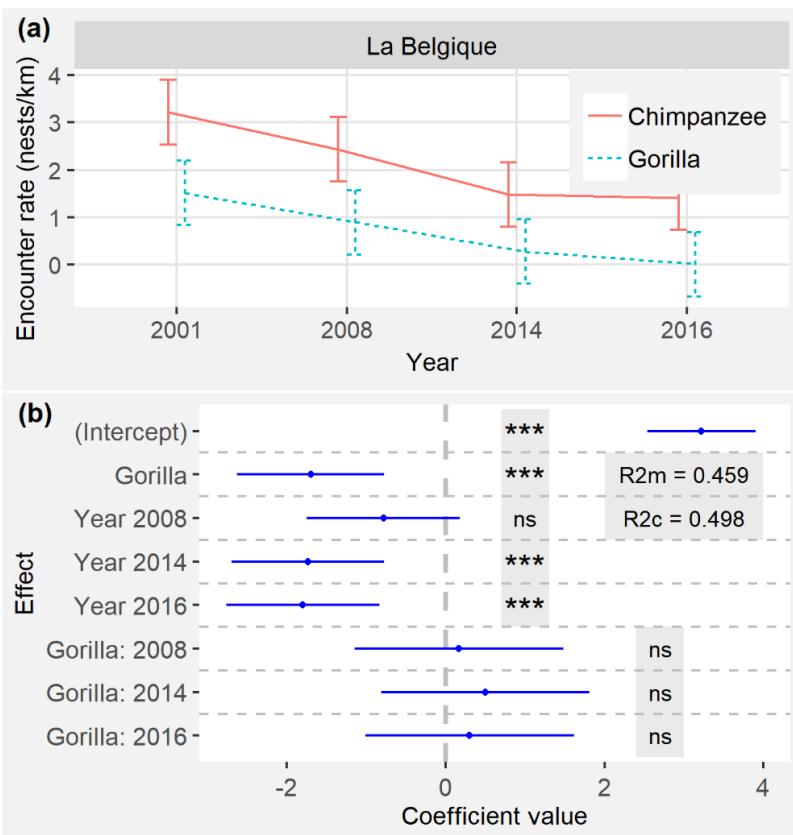
We used the *lme4* package (Bates *et al.*, 2015) in the R software version 3.5.1 (R Core Team, 2018) to run linear mixed effect models (LMMs). LMMs were used to investigate the variation of great ape abundance in different years (2001, 2008, 2014, and 2016). We included the number of nests per kilometre; Marsden *et al.*, 2016) for each species and for each transect as the dependent variable; year and species were independent variables included as fixed factors; the interaction between year and species was also used as a fixed factor, and transect was used as a random effect (Yoccoz *et al.*, 2001). The transect-to-transect variation (within-site variation) may represent micro-habitat effects or the influence of the very localised abundance of great apes (Schwarz, 2014).

We used the R square for mixed effect models to evaluate the fit of each model (Nakagawa and Schielzeth, 2013). Its advantage over the Akaike Information Criterion (AIC) is that it informs the absolute fit rather than the relative fit only; the amount of variance explained can be known, and it can help in the comparison of the fit of different models from different data sets (Nakagawa and Schielzeth, 2013). The LMMs were fitted using the Maximum Likelihood estimate (Nakagawa and Schielzeth, 2013). We calculated both the marginal and the conditional R square, which represent the variance explained by the fixed effects and the fixed and random effects, respectively (Nakagawa and Schielzeth, 2013). This means that a smaller difference between the conditional and the marginal R square indicates a smaller effect of random factors. To do that, two models were constructed, a null model with only random factors as the explanatory variable, and a full model with all fixed and random factors as explanatory variables. Then, the function *r.squaredGLMM* of the *MuMIn* package (Johnson, 2014; Bartoń, 2018) was used to determine the marginal and conditional R square from both models. Changes in the

abundance of human activities between 2008 and 2016 were tested using the Wilcoxon rank sum test. All data were analysed in the open software R (R Core Team, 2018).

#### 5.4. RESULTS

The change in great ape populations in La Belgique between 2001 and 2016 were analysed using Linear Mixed Effect Models. Table A5.1 presents the number of nests recorded per year for each species; in 2016, only one nest was recorded for gorillas.



**Figure 5.2: Results of the LMMs:** (a) mean encounter rate estimates from the model for each species and each year; (b) model estimated coefficients for each factor of the model. Chimpanzee was used as reference for “Species” and the year 2001 was used as the reference for “Year”. \* =  $p < 0.05$ ; \*\*\* =  $p < 0.001$ ; ns = non-significant; R2m = marginal R square; R2c = conditional R square; the interactions are represented by “:”. The error bars represent the standard errors.

In Figure 5.2a, there is clear evidence of decreasing populations of gorillas and chimpanzees in La Belgique and a consistent lower abundance of gorillas compared to that of chimpanzees. Figure 5.2b shows that the abundance of chimpanzees was significantly higher than that of gorillas. The mean encounter rate of chimpanzees was estimated at 3.21 nests per km ( $p < 0.001$ ) in La Belgique in 2001, while the abundance of gorillas was estimated at 1.70 nests per km (Figure 5.2b, Table A5.2). There was a significant decrease of 1.73 nests per km in great ape abundance between 2001 and 2014 and a decrease of 1.80 nests per km between 2001 and 2016 (Figure 5.2b, Table A5.2). The abundance of great apes was not significantly different between 2008, 2014, and 2016 (Figure 5.2b). However, the continuous decrease in abundance in 2008, 2014, and 2016 compared to 2001 indicates that there was a decline in great ape abundance over the years in the research site. There was not a significant interaction between species and year, meaning that the abundance of both gorillas and chimpanzees followed the same trend between 2001 and 2016.

When considering hunting signs only, hunting signs and camps, and all human activities together, the abundance of human activities was higher in 2016 than in 2008 (Figure 5.3).

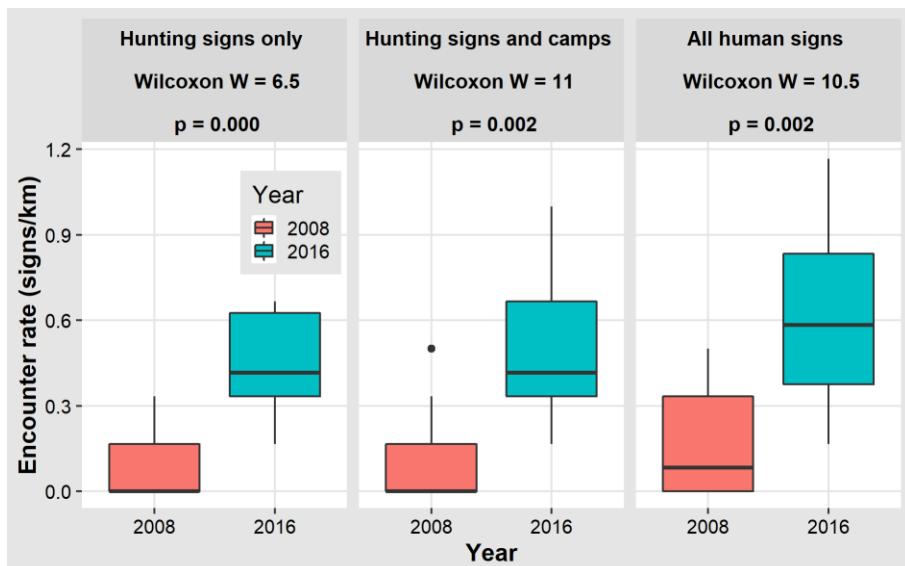


Figure 5.3: Variation of the abundance of human activities in La Belgique between 2008 and 2016.

## 5.5. DISCUSSION

Understanding the different mechanisms leading to mammal population change at the local level is an urgent need, and this knowledge can help conservationists take appropriate actions to invert the ongoing negative trend at the global scale (Estrada *et al.*, 2017). The presence of researchers in a site is reported to have a direct positive effect in biodiversity conservation (by deterring poachers; Piel *et al.*, 2015) or an indirect one (by providing alternatives to bushmeat, by employing former hunters, by increasing awareness of the need to protect biodiversity, and by promoting ecotourism; Laurance, 2013; Tagg *et al.*, 2015). We predicted that a decrease in great ape population size would be an indirect consequence of the extensive use of transects for research purposes. In this study, the abundance of gorillas and chimpanzees declined between 2001 and 2016. Although the abundance of gorillas was consistently lower than that of chimpanzees, population trends for both species followed the same pattern (Figure 5.2). We showed that the abundance of great apes remained relatively constant between 2001 and 2008 but declined afterwards (Figure 5.2). Evidence suggests that human activity, including hunting, increased significantly between 2008 and 2016 in the research site (Figure 5.3). Using long-term datasets on human activity and great ape census helped us to quantify the effects of human disturbance resulting from the use of transects for hunting activities by local people in the research site and to reconsider the implications of research presence for mammal persistence. Our findings both conform to and contrast with results and observations of previous studies conducted elsewhere (Campbell *et al.*, 2011; Laurance, 2013; Piel *et al.*, 2015) and in the present study site (Tagg *et al.*, 2011; Tagg *et al.*, 2015); these studies suggested that the presence of research sites may promote the persistence of mammal populations.

Several factors may explain the negative trend observed in our study: diseases, climatic variations (with emphasis on resource availability), deforestation, and fear (caused by intense hunting activities). The importance of climatic variation on mammal populations can be direct (Smith, 2013; Hall and Chalfoun, 2019) or indirect (by influencing resource availability; Dunham *et al.*, 2018). Great apes are mostly frugivorous mammals, and their pattern of habitat use may vary seasonally depending on fruit availability (Chapter 2). The variation in fruit availability is dependent on seasons that are generally defined by the variation in rainfall (Willie *et al.*, 2014). Also, fruit phenology was shown to vary with rainfall (Dunham *et al.*, 2018). Because we did not collect long-term data on fruit phenology, it is difficult to

derive strong conclusions about the effects of fruit availability on great ape populations. However, gorillas and chimpanzees were found to consume fruits from *Dialium* spp. and some other species whose trees were not found in the research site (Chapter 2) but occurred in the adjacent Dja Reserve (Sonké and Couvreur, 2014), meaning that great apes may move from the research site to find fruits in nearby areas. However, those fruits do not constitute the essential component of their diet (Chapter 2); hence, temporal changes in great ape abundance are less likely to be caused by emigration from the research site in response to fruit scarcity. Forest in the research site is not degraded (Figure 5.1), meaning that deforestation cannot be regarded as the cause of the decline in great ape populations, as previously documented by Yuh *et al.* (2019) in Lobeke National Park (Cameroon) and by Chapman and Lambert (2000) in Kibale National Park (Uganda). However, we are not able to confirm that the plant community structure remained the same over the years in our study site. In fact, in Kibale National Park, over a 20-year period, Chapman *et al.* (1997) noted a change in tree species abundance (27% of tree species increased in abundance, 33% decreased, and 40% remained stable).

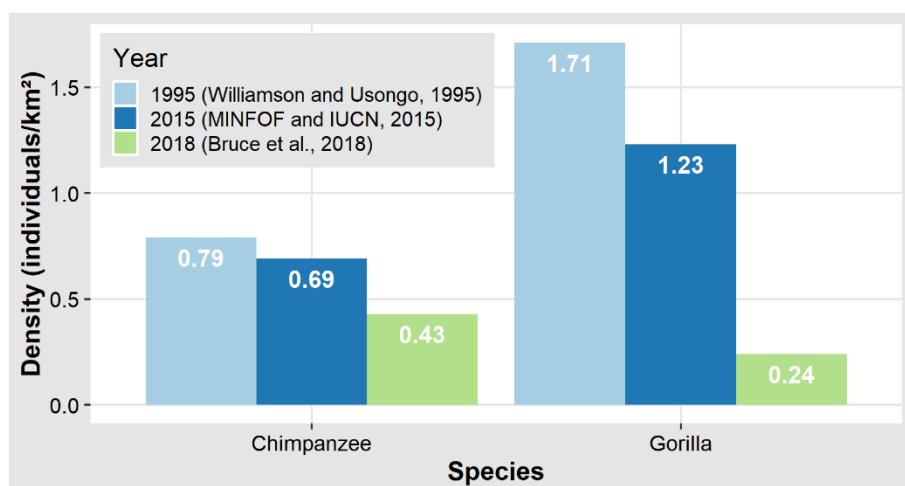
The causes of wildlife population decline in many studies, particularly for great apes, were linked to diseases such as Ebola (Huijbregts *et al.*, 2003; Caillaud *et al.*, 2006; Devos *et al.*, 2008). In addition to hunting and habitat loss, diseases are an important threat to wildlife populations; they are predicted to cause an extinction rate of more than 50% of species over the next several decades (Walsh *et al.*, 2003). While the presence of Ebola has not been noted in our study area, anthrax (*Bacillus anthracis*) was confirmed in La Belgique between December 2004 and January 2005, and it was the first time mortalities due to anthrax were reported in both gorillas and chimpanzees in the same site (Leendertz *et al.*, 2006). Great ape mortalities due to anthrax were also observed in other sites (Leendertz *et al.*, 2004). The epidemiology of anthrax is different from that of Ebola (Caillaud *et al.*, 2006); outbreaks do not occur because the pathogen is not transmitted between individual animals. Nevertheless, anthrax can contaminate the soil of an area and continue infecting animals for several decades (Leendertz *et al.*, 2006). Like Ebola, anthrax is predicted to cause the extinction of chimpanzees in the Tai National Parc (Ivory Coast) in the next 150 years; this adds anthrax to the list of infectious diseases threatening wildlife populations (Hoffmann *et al.*, 2017). However, after 2005, only one incident of death was recorded in La Belgique (Jacob Willie, personal observation); hence, anthrax is less likely to be the cause of great ape population decline in this research site.

A plausible explanation of great ape population decline in La Belgique may be associated with increasing hunting activities or even continuous hunting activities in the research site. It is likely that the regular use of transects for research purposes facilitated access to hunters. The most important determinant of the positive effects of research presence on mammal population abundance was the relatively low intensity of hunting activities in the research site compared to surrounding areas (Campbell *et al.*, 2011; Tagg *et al.*, 2015) and the regular undertaking of anti-poaching patrols (Tagg *et al.*, 2011; Piel *et al.*, 2015). The abundance of great apes was nearly constant in the research site between 2001 and 2008 (Tagg *et al.*, 2011). It is likely that during that time, the intensity of hunting activities was low in the research site, and the presence of humans was not perceived as a threat by great apes. For example, chimpanzees in the Goualougo triangle (Republic of Congo) were mostly curious (84% of time) about the arrival of researchers (Morgan and Sanz, 2003). In this context, great ape populations can be expected to be at least constant (Sugiyama, 1984) because they do not have natural predators. Although hunting pressure was lower in the research site than in other sites, hunting activities kept occurring (Tagg and Willie, 2013); these activities may have had an impact on mammal populations in the research site. The decline observed in the site after 2008 corresponds to the change in hunting technology from traps to firearms (Ávila *et al.*, 2019). In fact, the use of traps as a hunting method decreased from 2003 to 2016; while the use of guns increased from 2009 onwards (Ávila *et al.*, 2019). In addition, a long-term monitoring of mammal populations in forest patches located between the villages and the research site (Figure 5.1) in 2002, 2006, 2009, and 2016 showed that mammal abundance and species richness drastically decreased from 2009 to 2016 (Meigang, 2018). Our results show that hunting activities not only occurred in the research site but also increased between 2008 and 2016 (Figure 5.3). In addition to the conservation measures taken by “Projet Grand Singes” (PGS, a research and conservation project with an emphasis on great apes), a memorandum of understanding prohibiting the hunting of great apes was signed between PGS and local people. Although this strict regulation may have been adhered to (Ávila *et al.*, 2019), great apes have probably been affected in the long-term by hunting activities targeting other species. Local perception and law enforcement may improve the conservation status of large threatened mammals but not necessarily that of small mammals (Chen *et al.*, 2019). This may be associated with the economic benefit brought to local people by the large animals through ecotourism and conservation projects (Wade *et al.*, 2019). This may explain why in La Belgique great apes (charismatic species in the region) were not hunted (Ávila *et al.*, 2019) even though hunting

activities increased. The same pattern was observed in the Mone-Oku Forest Complex (Cameroon) where gorillas and chimpanzees were not hunted, but other mammals species were consistently hunted (Wade *et al.*, 2019).

Hunters frequently visited the research site possibly due to the depletion of hunted species in the forests located between the villages and the research site in the years 2008-2009. The changing behaviour of hunters due to the reduction of captures around the villages was also observed in the Dzanga-Sangha Dense Forest (Central African Republic) where an increase in primate hunting resulted from a decrease in ungulate abundance (Remis and Robinson, 2012). The combination of those two factors (decreasing game abundance around the villages and changing hunting technique from traps to guns) with easy access to the forest through transects may be the proximate cause that induced a high disturbance in the research site leading to a decline in great ape abundance starting from 2008. Similar conclusions were made in tropical forests of southeast Asia where improved access to forest and hunting technology were among the causes of overhunting (Harrison *et al.*, 2016). Tagg and Willie (2013) showed that in 2009, hunting activities were already influencing the abundance of gorilla and chimpanzee nesting, as their abundances were higher in newly opened transects than in transects used for research since 2001. With the increase in hunting activities over time and the increase in use of guns, the effects may have become more acute resulting in the patterns observed in this study. One of the measures recommended to combat hunting is to increase the revenue of households (Rogan *et al.*, 2018). PGS did indeed employ local people as field guides and involved them in the research programme. However, many guides are former hunters and many of them often use their PGS salary to buy cartridges (Luc Tédonzong, Personal observation). As they walk through the transects, they identify areas with high abundance of bushmeat species and then return there once the PGS research work is done. A strategy adopted by PGS was to sanction any guide who was involved in hunting activities by suspending him for a certain period of time. However, hunters are generally active at night or when researchers leave the site and return to the city in order to avoid meeting a research team on the transects. In some research sites in East and West Africa where hunters did not target chimpanzees, they were nevertheless accidentally injured by snares, despite the contribution of researchers to deter hunting activities (Quiatt *et al.*, 2002). In addition, hunting activities also occur in some protected areas where research is conducted such as the Salonga National Park (Democratic Republic of Congo), Bwindi Impenetrable Park (Uganda), Kibale National Park (Uganda), etc. (Nekaris and Nijman, 2013).

However, current patterns in great ape population abundance in the adjacent protected area may indicate that great apes are facing a general threat that is not related to research presence. In fact, successive population censuses conducted in the Dja Reserve indicated that great apes populations have declined between 1995 and 2018 (Williamson and Usongo, 1995; Latour, 2010; MINFOF and IUCN, 2015; Bruce *et al.*, 2018) as indicated in Figure 5.4. Around the reserve, great apes are targeted by some specialist hunters (Tagg *et al.*, 2018). It is possible that great apes may have been hunted by people who were not from the villages surrounding the research site. Great apes are integrally protected by the local faunal law (Cameroon); as a result, these species may be secretly hunted (Tagg *et al.*, 2018).



**Figure 5.4: Trends in great ape population size in the Dja Reserve between 1995 and 2018.**

Although the magnitude of hunting activities may be different from that of logging, the process occurring in our research site is comparable to that of some logging concessions where hunting is facilitated by logging roads (Robinson *et al.*, 1999). In addition, disturbance resulting from hunting activities in our site may be similar to disturbance caused by active logging in Gabon which led to an avoidance of active logging areas by gorillas (Haurez *et al.*, 2016). Similarly, the noise regularly made by guns in the research site may cause great apes to vacate the site and hide in areas where shooting disturbance is minimal (Chapter 3, Figure 3.5). However, the indirect effects of logging are different from those induced by research activities – logging implies opening large roads that can be used by wildlife hunters to enter deep into the forest, sometimes by car (Robinson *et al.*, 1999); while in the research site, only minimal openings specifically suitable for hikes are the norm.

In light of our results, it is likely that illegal hunting was indeed facilitated by transects used by researchers; this, in turn, altered the abundance of gorillas and chimpanzees, although great apes are not targeted by hunters in the area (Ávila *et al.*, 2019). As emphasized by Steklis and Steklis (2008), wildlife research remains an important aspect of the biological sciences and provides numerous benefits which can be scientific (recording rare events, collecting accurate life history data, and stimulating research), relevant to conservation (the application of research techniques and results to managing wildlife populations), or economic (international publicity and habituation of animals which are precursors of ecotourism and which will stimulate economic development). Hence, a question that may need to be answered is how to make research sustainable for wildlife persistence while research activities are going on. The most important mechanism that was put in place to ensure sustainability in logging concessions is forest certification, with the most common scheme being the Forest Stewardship Council (FSC; Auld *et al.*, 2008). Principle 6 of the FSC (Environmental values and impacts) in its criteria 6.6 requires logging organizations to prove that they have taken effective measures to manage and control hunting, trapping, and other forms resource collection (Forest Stewardship Council, 2015). Up until now, implementing conservation measures in research sites has been non-mandatory and generally prescribed by ethical guidelines (Gruen *et al.*, 2013). In addition, many ethical guidelines relate to animals captured for research purposes (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists, 2016). PGS contributed to the conservation of wildlife in the area through awareness-raising, environmental education, the provision of alternative sources of protein, and financial benefits to local people (Tagg *et al.*, 2011), all of which are generally recommended measures for research sites (Gruen *et al.*, 2013; Bowyer *et al.*, 2019). The high vulnerability of research sites lies in the fact that researchers use local people (often former hunters) as field guides, and as they work through transects, they identify areas where game species are abundant and later return to the forest to hunt them (Luc Tédonzong, personal observation). This means that research activities may not only provide hunters with access into the forest but may also facilitate their hunting efforts. At this point, although further investigations are required to understand the precise cause of great ape population decline in La Belgique research site, the precautionary principle (in environmental laws) requires us to take adequate actions to avoid further impacts. We then recommend that permanent protection (instead of temporal law enforcement) must be the rule in research sites. We propose, like in forest certification, that the presentation of a clear plan of how wildlife hunting will be managed should be a

requirement for the establishment and maintenance of a research site (Costello *et al.*, 2016). Ethical rules of wildlife field research often require that researchers comply with national and international laws in wildlife protection (Fedigan, 2010). Because researchers generally cannot arrest hunters, we recommend awareness-raising-campaigns among government officials regarding the potential influence of research presence on wildlife populations. Special efforts should be made to regulate research activities, and park rangers should be permanently assigned to protect biodiversity in research sites in collaboration with research organisations.

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### 5.5.1. APPENDIX

**Table A5.1:** Number of nests recorded per year per species in La Belgique.

Year	Species	Nest count
2008	chimpanzee	146
2008	gorilla	54
2016	chimpanzee	85
2016	gorilla	1
2001	chimpanzee	193
2001	gorilla	91
2014	chimpanzee	89
2014	gorilla	17

**Table A5.2:** Fitted values from the LMMs great apes population change in La Belgique. *CL* confidence limit.

Year	Species	Fitted value	Standard error	df	Lower CL	Upper CL
2001	chimpanzee	3.22	0.34	71.64	2.54	3.90
2001	gorilla	1.52	0.34	71.64	0.84	2.20
2008	chimpanzee	2.43	0.34	71.64	1.75	3.11
2008	gorilla	0.90	0.34	71.64	0.22	1.58
2014	chimpanzee	1.48	0.34	71.64	0.80	2.16
2014	gorilla	0.28	0.34	71.64	-0.40	0.96
2016	chimpanzee	1.42	0.34	71.64	0.74	2.10
2016	gorilla	0.02	0.34	71.64	-0.66	0.70

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CHAPTER 5

# CHAPTER 6

## GENERAL DISCUSSION

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While it is well recognized that predation can strongly affect the spatial distribution of mammal species and that the presence of humans and their activities may be associated with a risk of predation by animals, studies have rarely considered the distribution of feeding resources, their temporal availability, and competition in evaluating how mammals respond to humans. In addition, knowledge is lacking on the implications of non-consumptive use of natural systems such as research presence and its corollaries on the long-term persistence of mammal populations. In this chapter, I provide an overview of the main findings of studies reported in Chapters 2-5. I integrate these findings to discuss the ecological drivers of mammal population abundance and distribution. Additionally, I discuss how different behavioural adaptations of mammal species determine their response to anthropogenic threats and how human settlements affect the dynamics of mammal populations. Finally, I suggest implications for conservation and propose some prospects for future research.

## 6.1. OVERVIEW OF THE MAIN FINDINGS

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### 6.1.1. GREAT APE ABUNDANCE AND SPATIAL DISTRIBUTION OF THEIR PREFERRED NESTING HABITATS AND IMPORTANT FRUITS

In a general analysis of the patterns of habitat selection at a large spatial scale, both gorillas and chimpanzees exhibited different patterns of habitat preference by each selecting a different set of habitats (Chapter 4, Figure 4.2). Chimpanzees highly favoured nesting in old secondary forests, while gorillas preferred swamps and light gaps (Figure 4.2). I noted that the habitats preferred by gorillas were not preferred by chimpanzees and vice versa. Chimpanzees and gorillas randomly used riparian forests and young secondary forests respectively (Figure 4.2). However, only 2.98% of chimpanzee nests were found in riparian forests, while 36.05% of gorilla nests were found in young secondary forests. Habitat types in the study area were represented by small patches (Figure 2.2). However, after applying a kernel density estimation to a regular sampling point of preferred habitats, it appeared that the distribution of preferred habitat types was clustered for both gorillas and chimpanzees (Table 4.1). At the spatial scale, the preferred nesting habitats for chimpanzees were more available where gorilla-preferred nesting habitats were less present, and vice versa (Figure 4.3b). The abundance of chimpanzee-important fruits correlated to the abundance of their preferred nesting habitats, but this was not the case for gorillas. Gorilla-important fruits were mostly found where the

density of their preferred nesting habitats was low and where the density of chimpanzee-preferred nesting habitats was high.

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#### 6.1.2. CONTRIBUTION OF THE DISTRIBUTION OF PREFERRED AND FALBACK FRUIT SPECIES TO NICHE SEPARATION AND COEXISTENCE BETWEEN GREAT APES

Gorillas and chimpanzees consumed mostly the same fruit species; however, they exhibited different orders of fruit preference among fruit species (Table 2.2). Despite the fact that some fruit species were highly preferred by both apes (eg. *Landolphia* spp.), many other species were highly preferred by only chimpanzees (eg. *Santiria trimera*, *Enantia chlorantha*, *Celtis tessmannii*), and still others were highly preferred only by gorillas (eg. *Ficus* spp., *Tetrapleura tetrapтера*, *Sorindeia grandifolia*) (Table 2.2). Some species such as *Antrocaryon klaineanum*, *Myrianthus arboreus*, *Tetrapleura tetrapтера*, and *Uapaca* spp. were fallback for gorillas only. *Ficus* spp., *Cissus dinklagei*, and *Duboscia macrocarpa*, on the other hand, were fallback for both gorillas and chimpanzees (Figure 2.6, Table 2.2). The consumption of the different fruit species varied between seasons (Figure 2.5a,b). Similar patterns of fruit consumption were observed in gorillas and chimpanzees between seasons (Figure 2.5b), and the patterns of fruit consumption reflected the patterns of fruit availability (Figure 2.5a). However, certain species which produced fruit year-round (e.g. *Uapaca* spp.) were only consumed during the long dry season; similarly, *Klainedoxa gabonensis* produced fruit during the long rainy season but was consumed by gorillas in the long dry season (Figure 2.5). The overall overlap in fruit consumption between gorillas and chimpanzees was high but varied seasonally, with the lowest value occurring in the long dry season.

Across all seasons, gorillas and chimpanzees consistently preferred mature forests and swamps, respectively, for nest building (Figure 2.3a). While in the general analysis chimpanzees avoided swamps, they significantly preferred it in the long dry season and randomly used it in the short rainy season (Figure 2.3a). Out of the habitats avoided by gorillas in the general analysis, riparian forests were randomly used by them in the short dry and short rainy seasons (Figure 2.3a). Gorillas avoided mature forests in all seasons, and chimpanzees avoided young secondary forests in all seasons (Figure 2.3a). On a large spatial scale, riparian forests were only randomly used by chimpanzees, but on a smaller spatial scale, they preferred riparian forests in the general analysis (Figure 2.4a). However, chimpanzees only preferred riparian forests in the long dry season, the long rainy season, and the short rainy season (Figure 2.3a).

The fruiting species most preferred by both gorillas and chimpanzees were more abundant in mature forests (i.e. near primary forests and old secondary forests) and riparian forests (Figure 2.8a). All species most preferred by chimpanzees and those most preferred by gorillas were more abundant in mature forests (Figure 2.8a). The abundance of all fallback fruit species was lower in mature forests than in other habitats. Fruiting species that were fallback for both gorillas and chimpanzees were more abundant in riparian forests and swamps, while fruiting species that were fallback for gorillas only were more abundant in young secondary forests (Figure 2.8a). The differential abundance of preferred fruiting species among habitats resulted in a predictable spatial distribution of those species. The preferred fruiting species for both gorillas and chimpanzees were more abundant in areas where chimpanzee-preferred nesting habitats were more available, contrary to the spatial distribution of gorilla-preferred nesting habitats (Figure 4.3c).

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#### 6.1.3. INFLUENCE OF ECOLOGICAL AND ANTHROPOGENIC FEATURES ON GREAT APE SPATIAL DISTRIBUTION

In the resource model, habitat quality was the most important predictor of gorilla nesting patterns, while elevation and habitat quality were the most important predictors of chimpanzee nesting patterns (Figure 3.3A). However, after including anthropogenic features in the model, the results indicated that chimpanzee nesting patterns remained predicted mostly by elevation and distribution of their preferred nesting habitats; in contrast, distance from the research camp, distance from village trails, and distance from villages became the most important predictors of gorilla nesting patterns (Figure 3.3B). In response to anthropogenic variables, chimpanzees avoided building nests within a 2-km radius of human features (i.e. village trails, research camp), while gorillas avoided building nests within a radius of 4-5 km of human features (i.e. research camp, village trails, and villages) (Figure 3.4). As shown in Figure 3.6, anthropogenic variables increased the predictive power of the models for gorillas (AUC increased from 0.545 to 0.723 – a difference of 0.178) about two times more than for chimpanzees (AUC increased from 0.683 to 0.773 – a difference of 0.09).

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#### 6.1.4. CHANGE IN GREAT APE ABUNDANCE IN A HUMAN-DOMINATED LANDSCAPE

A 15-year trend in great ape populations in the research site showed that the abundance of gorillas and chimpanzees did not greatly change in the research site

from 2001 to 2008, then started to decline (Figure 5.2). Unlike great ape populations, the intensity of hunting activities in the research site increased significantly between 2008 and 2016 (Figure 5.3).

## 6.2. ECOLOGICAL DRIVERS OF MAMMAL POPULATION ABUNDANCE AND DISTRIBUTION

Temporal changes in the abundance of animal populations may be the result of several factors, namely, resource quality, seasonal availability of resources, and interaction with other species (i.e. competition and predation; Hastings, 2013). The quality of resources is a fundamental component that directly affects animal fitness and the abundance of their populations (Law and Dickman, 1998; Hastings, 2013). For many primate species, fruit quality and availability influences their ranging patterns and densities (Hanya *et al.*, 2006; Hanya *et al.*, 2011; Hanya and Chapman, 2013). I found that gorillas and chimpanzees consumed fruit species with different levels of preference (Table 2.2). This pattern of fruit consumption is predicted to maintain populations stable as long as there is a constant supply of those preferred fruit species (Hanya and Chapman, 2013). However, frugivorous primates can cope with seasonal variation in fruit availability (Chapter 2). This, coupled with the seasonal variation in the diversity of fruit-bearing species across habitats (Chapter 2), means that the quality of different habitats may change through time. Consequently, gorillas and chimpanzees exhibited seasonal changes in the patterns of habitat selection that were correlated to the consumption of preferred and fallback fruits (Chapter 2). The seasonal changes in habitat selection were then facilitated by the differential abundance of fruiting species across habitat types (Chapter 2).

At the landscape level, the maintenance of different populations is possible if the availability of fruits in each season is sufficient to support all the individuals in the community (Head *et al.*, 2012). However, the coexistence of both gorillas and chimpanzees at the same site indicates that despite the existence of a superior competitor in a competition system, a competitive exclusion does not exist between the two species. In such a case, the abundance and distribution of great ape populations may change on a seasonal basis. This is consistent with the findings of Haugaasen and Peres (2007) who showed that primate species' abundance increased with fruit availability and concluded that the dynamics of primate populations are a consequence of landscape heterogeneity constituted by a mosaic of several habitat types. In addition to landscape heterogeneity, I found that the preferred habitat types for gorillas and chimpanzees were clustered,

indicating that the seasonal changes in the patterns of habitat selection may result in a change in the spatial distribution of each animal species (Chapter 4). It therefore results that the local abundance of each species may vary depending on the season when the abundance is evaluated and the scale considered.

The change in abundance and distribution of animal populations not only varies seasonally but can also vary over the years. Fluctuation in population abundance is possible when fruit availability is variable across the year. Interannual phenological variation was reported in tropical forests (Yamagiwa *et al.*, 2008; Polansky and Robbins, 2013; Adamescu *et al.*, 2018), marked by fruiting peaks in some species. This may cause interannual population changes if the phenological changes concern preferred or fallback species. Evidence of annual changes in animal population abundance due to change in fruit availability was presented by Sakai (2001) and Nakagawa *et al.* (2007). Curran and Leighton (2000) found that the abundance of nomadic vertebrates increased during years of general fruiting; similarly, Granados *et al.* (2019) found that general fruiting increased immigration and reproduction in bearded pigs (*Sus barbatus*). Consequently, I suggest that the different populations of great apes may form a meta-community within which groups may migrate from areas where fruit availability is low to areas where fruits are available. For example, I found that both gorillas and chimpanzees intensely consumed fruits of *Dialium* spp. when fruit availability was low in the research site. However, during the study period, no individual tree of *Dialium* spp. was found in the study area. Meanwhile, according to Sonké and Couvreur (2014), fruits from *Dialium* spp. were found in adjacent sites. Hence, seasonal, annual, and spatial changes in fruit availability along with the patchiness of habitats may cause spatiotemporal changes in great ape abundance.

The distribution of intermediate suitability scores across the entire study area from the resource models for both gorillas and chimpanzees denotes the level of patchiness in the distribution of preferred nesting habitats in the site (Figure 3.5). When preferred fruits are available in an area, both gorillas and chimpanzees may consume them as long as the carrying capacity of the area exceeds the abundance of both species; otherwise, the less competitive species (gorillas) would concentrate on fallback fruits in other habitats (Chapter 2). After a migration due to fruit search, great apes may come back when the availability of preferred fruits has increased. In accordance with Chesson (2013), I conclude that the dynamics of great ape populations at the spatial scale may be associated with fruit availability.

The results show that in spite of the fact that a large proportion of gorilla nests were found in young secondary forests, they were not significantly preferred (Chapter 4). Additionally, chimpanzees significantly preferred riparian forests at a small spatial scale but not at a larger spatial scale (Chapter 2, Chapter 4). The change in the patterns of habitat selection at different spatial scales was reported in moose by Herfindal *et al.* (2009), where the local density did not modify the patterns of habitat selection, but the scale did. Chimpanzees and gorillas preferred habitats that provide high-quality forage but where risk of predation associated with human presence was reduced; then, at a larger spatial scale, the proportion of unsuitable habitat patches may be high as previously emphasized by Herfindal *et al.* (2009). This may reduce the observed proportion of use and consequently influence the selectivity of some habitats (Beyer *et al.*, 2010). Following the ideal distribution theory, the patterns of habitat selection may not be dependent on the scale (Fretwell and Lucas, 1969). Therefore, the reduction in the proportion of use at an increasing spatial scale is a consequence of functional response in habitat selection that may result from the presence of predators or humans (Herfindal *et al.*, 2009). Although leopards, which are the direct predators of sympatric great apes, occur in the present study site, they were not observed. Thus, the reduction in the proportion of use observed in this study suggests that human activities may induce functional responses in habitat selection in great apes (Tagg *et al.*, 2013).

### 6.3. INFLUENCE OF ANIMAL BEHAVIOURAL TRAITS ON THEIR RESPONSES TO HUMAN ACTIVITIES

Human settlements influenced chimpanzees relatively less than gorillas (Chapter 3, Figure 3.4, and Figure 3.6), indicating that chimpanzees may experience a trade-off between finding fruits and escaping predation. This trade-off was also documented in wildebeests (M'Soka *et al.*, 2017) and red squirrels (Turkia *et al.*, 2018). If a species experiences a trade-off between resource and predation risk, it may avoid predation or areas of high predation risk when it has an alternative area to find food (Frid and Dill, 2002). This can explain why chimpanzees did not systematically avoid areas with human settlements like gorillas did (Figure 3.5). Despite the fact that we collected data on a monthly basis, it is not possible to attest that the use of areas near village trails by chimpanzees was due to the absence of fruits in other areas. However, several studies have observed that chimpanzees move to villages to consume agricultural fruits when wild fruit availability is low in order to maintain a fruit-dominated diet (McLennan, 2013; Bryson-Morrison *et al.*, 2016). Those fruits were found to be relatively nutritious and procured energetic advantages to

chimpanzees (McLennan and Ganzhorn, 2017). This behavioural flexibility was also observed in many other primate species, such as *Colobus angolensis palliates* (Dunham, 2017) and *Cercopithecus albogularis labiatus* (Nowak *et al.*, 2017; Wimberger *et al.*, 2017). For these species, the risk of starvation and sensitivity to fruit availability may be more important than the risk of predation induced by human presence (McLennan, 2013; Nowak *et al.*, 2017; Weterings *et al.*, 2018). This may imply that the non-avoidance of human settlements by chimpanzees may be a consequence of their pursuit of agricultural foods. In the present study site, agricultural foods have not yet been identified in the great ape diet (Chapter 4; Petre, 2016). Consequently, the consumption of agricultural foods may not be the reason for the non-avoidance of human settlements by chimpanzees. There were villages and village trails located where the density of chimpanzee-preferred nesting habitats and important fruits was high (Figure 4.3). Hence, it can be concluded that in contrast to gorillas, chimpanzees are not highly influenced by human settlements because of the presence of their preferred nesting habitats and wild fruits near villages.

In accordance with the present results, Lindshield *et al.* (2017) found that anthropogenic landmarks at Fongoli in Senegal did not prevent chimpanzees from visit fruiting trees, which were highly abundant in close proximity to human features. Similarly, chimpanzees at Bili-Uele (in Northern Democratic Republic of the Congo) exhibited little fear in the presence of humans (Hicks *et al.*, 2012). At Bossou (Guinea), the high nutritional quality of agricultural fruits compensated for the stress induced by human presence in chimpanzees and reduced their concentration of glucocorticoid metabolite (McLennan *et al.*, 2019). The fact that the preferred nesting habitats and fruit species are more abundant near villages may reduce stress due to human presence in chimpanzees. However, the availability of forest fruits is subject to phenological changes. Hockings *et al.* (2012) found that because chimpanzees at Bossou (Guinea) consumed crop foods when fruit availability is low, they did not split into smaller groups as was observed in other sites (Itoh and Nishida, 2007). Thus far, fission-fusion behaviour has not been observed in gorillas (Parnell, 2002). Reducing party size may be a strategy for chimpanzees to cope with periods of low fruit availability not compensated by crop foods like at Bossou (Hockings *et al.*, 2012). This is because chimpanzees are highly territorial (Herbinger *et al.*, 2001), and intraspecific competition is also high among them (Mitani *et al.*, 2010). As a result, fatal attacks were observed between chimpanzees when population density was high (Mitani *et al.*, 2010; Wilson *et al.*, 2014).

Body size is also a key aspect in predator-prey interactions; large-sized animals may have a higher perception of the risk of predation than smaller-sized ones (Zuberbühler, 2007; McGraw and Zuberbuhler, 2008; Davidson *et al.*, 2009; Preisser and Orrock, 2012). The effects of body size on the response of different species to predation risk is related to the fact that different species present different flight initiation distances, and the flight initiation distance increases as body size increases (Gotanda *et al.*, 2009; Møller and Erritzøe, 2014). The lower sensitivity of chimpanzees to human settlements than that of gorillas may be due to their smaller size. While evaluating the effects of noise caused by oil prospection on mammals in the Loango National Park, Rabanal *et al.* (2010) found that mammals with large home ranges (e.g. elephants) were the most affected.

Chimpanzees are known to change their party size in response to fruit availability; they also increase in number to prevent gorillas from accessing fruiting trees (Basabose and Yamagiwa, 2002; Lehmann and Boesch, 2004). In the Ugalla area (western Tanzania), chimpanzees increased their party sizes in the evening to reduce the risk of predation by large nocturnal carnivores such as lions and leopards (Ogawa *et al.*, 2007). The fission-fusion behaviour in chimpanzees may be an advantage that allows them to cope with the presence of humans. Accordingly, Osmond and de Mazancourt (2013) have shown that evolutionary adaptions to competitive interactions may help species adapt to environmental change.

Furthermore, chimpanzees are more arboreal than gorillas because they tend to build nests in trees while gorillas tend to build nests on the ground (Tagg *et al.*, 2013); chimpanzees' building of night nests at higher heights may represent an antipredator strategy (Stewart and Pruetz, 2013). For instance, in two adjacent sites with varying levels of predation risk, Pruetz *et al.* (2008) found that the height of chimpanzee nests was lower in the site with a lower level of predation risk than in the site with a higher level of predation risk. Additionally, Last and Muh (2013) observed that chimpanzees in the Lebialem-Mone Forest Landscape (Southwest Region, Cameroon) tended to build nests in trees in sites with high human population density and to build terrestrial nests in sites with low human population density. Building arboreal nests in proximity to humans may constitute an advantage for chimpanzees in the form of reduced risk of predation. In Bili-Uele (northern Democratic Republic of the Congo), chimpanzees in trees withstood the presence of humans for a longer period of time than when they were terrestrial (Hicks *et al.*, 2012). This is consistent with the findings of Wereszczuk and Zalewski (2015) who suggested that the risk of predation may be higher for less arboreal than for more arboreal species. The differential responses to human settlements

and research presence in gorillas and chimpanzees imply that the abundance of their populations may vary differently across space and time.

#### 6.4. EFFECTS OF HUMAN SETTLEMENTS ON MAMMAL POPULATION DYNAMICS

Although the effects of predator densities have been associated with a decreasing survival of the prey species, support is lacking for the effects of non-consumptive use of natural systems on animal populations (Gibson *et al.*, 2018) despite the fact that the presence of human activities is more and more widespread in natural systems. Previous studies on great apes were conducted in logging concessions where the animals and their resources would most likely be affected by disturbance due to logging activities (Arnhem *et al.*, 2008; Haurez *et al.*, 2016; Morgan *et al.*, 2018); but there is limited knowledge on systems where animal resources are not affected.

Gorillas and chimpanzees select different habitat types; this selection varies seasonally in relation to the distribution of fruiting plants across habitats as well as their phenology (Chapter 2, Chapter 4). Great apes avoided areas around human settlements (Chapter 3), and a decline in population size for both species was observed in 15 years (Chapter 5). It is well acknowledged today that human presence has a negative influence on the distribution of animal species (Blom *et al.*, 2005; Young *et al.*, 2008; Gray *et al.*, 2010; Stokes *et al.*, 2010; M'Soka *et al.*, 2017). Great apes may escape areas where human activities are more intense and relocate to safer areas. The decline in great ape populations may be the result of the fact that their monitoring was only conducted around the barycentre of the research site (i.e. the research camp). The relocation of great apes may have occurred at the landscape level; as one can see in (Figure 3.5), there are areas of high suitability for both gorillas and chimpanzees around the research camp and the transects.

The research site might have served as a refuge for gorilla populations between 2001 and 2008, but after that period, the intensification of hunting activities and the increasing use of guns on research transects forced them to move away. The pattern of habitat availability was evaluated at multiple scales in the research site, and it appeared that the availability of all habitat types was the same at different spatial scales (Chapter 2; Chapter 4; Willie *et al.*, 2013). This means that by moving away from the research site, gorillas did not have to change their habitat selection pattern. It is worth noting that human settlements and research activities have

made a large area where the habitat suitability scores were greater than the mean suitability scores to become unsuitable (Figure 3.6). Tolerance is the common response of encounters between gorilla groups; peaceful intergroup encounters are common when accessing food and this seems not to affect their ranging patterns (Bermejo, 2004; Doran-Sheehy *et al.*, 2004). Tolerance may allow gorillas to disperse from disturbed areas to an undisturbed area without creating intergroup competition for food. This implies that the dispersal of gorillas from areas encroached by humans to safer areas can contribute to the maintenance of their population if the abundance in those areas is below the carrying capacity (Williamson *et al.*, 2014). However, measuring the carrying capacity is beyond the scope of this study.

Although I found that human presence affected the distribution of chimpanzees less than the distribution of gorillas (Chapter 3), their abundance also declined in the research site as hunting activities increased (Figure 5.3). The distance at which chimpanzees were affected by human presence was about half (around 2 km) the distance at which gorillas were affected by human activities (4 to 5 km) (Figure 3.4). However, no difference was found between the trends of gorilla and chimpanzee populations in La Belgique. This indicates that chimpanzee populations were more affected by research activities than gorillas contrary to what may be predicted from the response curves of human impacts on the nesting distribution (Figure 3.4). Figure 3.4 shows that chimpanzees responded negatively to research activities more than they did to all other human features. Transects used to monitor great ape populations were located in an area where the chimpanzee resource model indicated high habitat suitability (Figure 3.5). This means that even the slightest response of chimpanzees to human activities in the research site may have caused a higher decline in their abundance than was expected.

Gorilla-suitable habitats degraded faster than chimpanzee-suitable habitats (Figure 3.5). In addition, the abundance of preferred fruiting woody species was the main predictor of chimpanzee persistence, while gorillas preferred nesting in areas away from human presence. In the present research site, surveys of nests of great ape species in two sets of transects (the first set opened in 2001 and the second set in 2008) indicated that the density of chimpanzees was significantly higher in the newly established transects than the oldest, while not significantly different for gorillas (Tagg and Willie, 2013). This indicates that hunting activities in the research site were already influencing great ape populations before 2008, as illustrated by a monotonous negative trend in their abundance between 2001 and 2016 (Figure 5.2). The non-significant difference in gorilla densities between the new and old

transects may corroborate my results that gorillas prefer nesting a longer distance away from human features than chimpanzees. In that case, it is possible that chimpanzees may avoid transects (Tagg and Willie, 2013), but they may remain in an area covered by transects, while gorillas may have started to leave the transect area. This observation is consistent with the findings of Morgan *et al.* (2018) who showed that chimpanzees respond to human activities at the local level (within their home range), while gorillas can avoid the entire logging area by shifting their ranging patterns. In this vein, Arnhem *et al.* (2008) considered chimpanzees to be more spatially resilient to logging activities than gorillas; this is certainly because in their study area, logging did not affect fruit availability (Arnhem *et al.*, 2008). However, studies have reported that gorilla abundance decreased immediately during active logging operations and increased months later (Haurez *et al.*, 2016; Morgan *et al.*, 2018). This pattern corroborates my interpretation that gorillas as generalist species are able to move to adjacent areas where the intensity of human activities is low and come back when logging activities have stopped.

## 6.5. CONCLUSION AND RECOMMENDATIONS FOR FUTURE RESEARCH

Using sympatric great apes as model species, this study has investigated the ecological and anthropogenic drivers of mammal population abundance and distribution. Insights on great apes from the present study suggest that (1) When two closely related species coexist, they may exhibit some dietary and habitat preferences that may vary seasonally, and the distribution of their feeding resources across habitat types determines their seasonal movements and seasonal patterns of habitat use. (2) Several mammal traits (body size, intergroup interaction, competition, territoriality, degree of specialization/generalization, terrestrial/arboreal) may influence their response to anthropogenic disturbances. (2a) Large-sized mammal species may be more frightened by human presence. (2b) A species with a high tolerance of intergroup encounters may find refuge in areas not disturbed by human presence without increasing intraspecific competition; the more generalist species may be more flexible if dispersed in areas where food availability is low. (2c) The more specialized species may continue to use their preferred habitats despite the presence of human activities. (2d) Dominant species exhibit a grouping pattern characterized by an increase in the number of individuals to defend food resources against the other competitors; this strategy is an adaptive behaviour that may help them respond to human presence. (2e) Arboreality may be an advantage over territoriality to cope with human presence for space use. (3) The influence of human activities exacerbated by hunting

activities can be associated with the decline in mammal populations; despite the different mechanisms adopted by mammals to cope with the influence of human activities, the long-term presence of anthropogenic factors in a site may cause their populations to decline.

Dispersal from areas affected by human presence to areas where the intensity of human activities is low may partly explain fluctuations in great ape abundance and distribution in human-dominated landscapes. Human activities can induce spatial dispersal in great apes in different ways. Gorillas may respond to human disturbance by moving from the disturbed area to areas away from human presence, while the response of chimpanzees to human presence may be characterized by subtle changes in space use without shifting their range. Species differ in their response to anthropogenic disturbance based on how they interact with other sympatric mammals, their level of dietary specialisation, and the interaction they have with their physical environment. Understanding the physiological response of great apes to human disturbance may guide conservation efforts because stress may have negative influences on animal fitness and demographic rates (Gaynor *et al.*, 2019). As the non-consumptive use of natural systems by humans can affect species and their habitats, evaluating thresholds beyond which these effects are detrimental is of paramount importance to guiding conservation efforts. Further analyses may also be conducted to gain a deeper understanding of the contribution of forest structure to great ape spatial distribution. For this purpose, using laser scanner images provided by NASA at fine spatial resolution represents a good opportunity for advancing research in great ape distribution.

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GENERAL DISCUSSION

# SUMMARY

The ongoing global decline in mammal populations has led researchers and conservationists to question which factors drive their abundance and distribution. Specifically, there is an urgent need to understand how the ranging behaviour of mammals determines their response to human-induced environmental changes. Threats such as hunting and habitat fragmentation and degradation through agricultural expansion and logging have received considerable attention. However, a potential threat resulting from the non-consumptive use of natural systems by humans has often been overlooked. The ecological and anthropogenic factors influencing the abundance and distribution of mammal populations in tropical forests were evaluated using great apes (*Gorilla gorilla gorilla* and *Pan troglodytes troglodytes*) as focal species in order to improve understanding of the drivers of local extinction of species. To achieve this goal, data on diet, fruit phenology, botany, and nest abundance and distribution were collected in a design involving a sampling grid and line transects. Data were analysed using modelling techniques in R and ArcGIS. The preferred fruiting plants for both gorillas and chimpanzees were more abundant in chimpanzee-preferred nesting habitats, while their fallback fruits were more abundant in gorilla-preferred nesting habitats. The patterns of habitat use by both gorillas and chimpanzees varied seasonally. In the absence of human disturbance, the distribution of gorilla nests was predicted by the availability of their preferred nesting habitats, while the distribution of chimpanzee nests was predicted by elevation and their preferred nesting habitats. However, when considering the research camp and human settlements, the distribution of gorilla nests was predicted first by the distribution of human settlements and then by their preferred nesting habitats, while chimpanzee nests remained predicted by elevation and their preferred nesting habitats. The long-term monitoring of great ape nests in the research site revealed a decline in both gorilla and chimpanzee populations resulting from an increase in hunting activities in the site. Results suggest that in the absence of human disturbance, ecological factors (habitat preference, seasonal patterns of fruit availability, fruit preference, and spatial distribution of habitat types) may be responsible for seasonal changes in mammal population abundance and distribution. Animal species traits (body size, terrestrial/arboreal, level of specialization/generalization, and competitive inferiority/superiority) have a profound influence on the response of mammals to

human activities. Due to their spatial flexibility and their reliance on more available fallback food sources when preferred fruits are scarce, gorillas may vacate areas disturbed by hunting and non-hunting human activities and related noise. Chimpanzees, on the other hand, persist in their preferred nesting habitats despite human disturbance due to their high level of specialisation in fruit consumption. Additionally, the competitive dominance of chimpanzees over gorillas facilitated by their grouping patterns may allow them to cope with human disturbance better than gorillas. Human impacts other than direct killing of animals may influence the abundance and distribution of great ape populations and may account for the long-term decrease in population size. As habitat and resource heterogeneity facilitate the local coexistence of gorillas and chimpanzees, preserving both preferred and fallback fruiting plant species is crucial. Patterns observed in great apes may be an indication that human disturbance is also negatively influencing other mammals. However, species may respond differently to human disturbance, depending on their interaction with other sympatric mammals, their level of dietary specialisation, and their interaction with their physical environment. Further research is required to assess how these biological traits affect mammal response to anthropogenic disturbance. Furthermore, future studies should investigate the threshold beyond which the non-consumptive use of natural systems by humans becomes detrimental to species and their habitats.

# SAMENVATTING

De voortschrijdende, wereldwijde achteruitgang van zoogdieren noopt onderzoekers en natuurbeschermers tot een beter begrip van factoren die hun abundantie en verspreiding beïnvloeden. Er is in het bijzonder nood aan een beter begrip hoe ruimtelijk gedrag van zoogdieren de impact van door de mens veroorzaakte milieuveranderingen beïnvloedt. Daar waar effecten van jacht, verlies en versnippering van natuurlijk leefgebied (door intensificering van landbouw) en houtkap recent veel aandacht kregen, worden potentiële bedreigingen als gevolg van niet-consumptief gebruik van natuurlijke systemen door mensen vaak over het hoofd gezien.

In deze studie worden ecologische en antropogene effecten op de abundantie en verspreiding van zoogdierpopulaties in tropische bossen bestudeerd aan de hand van twee mensap soorten, *Gorilla gorilla gorilla* en *Pan troglodytes troglodytes*, dit met het oog op een beter begrip van processen die extinctie van zoogdierpopulaties kunnen bespoedigen. Om deze doelstelling te bereiken, werden gegevens over voeding, vruchtfenologie, vegetaties en het voorkomen van nesten verzameld langsheen lijntransecten, en werden deze data vervolgens geanalyseerd met behulp van state-of-the-art modelleertechnieken in R en ArcGIS. Vruchtdragende planten die geprefereerd werden door gorilla's en chimpansees bereikten een hogere abundantie in gebieden die door chimpansees werden geprefereerd voor het bouwen van nesten, terwijl 'fallback' vruchten overvloediger aanwezig waren in gebieden die door gorilla's voor nestbouw werden geprefereerd. Patronen van habitatgebruik door gorilla's en chimpansees varieerden per seizoen. In afwezigheid van menselijke verstoring werd de ruimtelijke distributie van nesten van gorilla's het best voorspeld aan de hand van de beschikbaarheid van geprefereerd voortplantingshabitat, terwijl de distributie van nesten van chimpansees bijkomend werd voorspeld door de hoogteligging. Echter, wanneer ook de locaties van het onderzoekkamp en van menselijke nederzettingen in rekening werden gebracht, werd de verdeling van nesten van gorilla's best voorspeld door de verspreiding van menselijke nederzettingen, en pas daarna door de beschikbaarheid van geprefereerd voortplantingshabitat. Bij

chimpansees leidde het betrekken van menselijke nederzettingen evenwel niet tot een wijziging in voorspellingen. Lange-termijn monitoring van nesten in het studiegebied toonde een afname voor beide soorten, dit als gevolg van een toename in jachtdruk.

Resultaten van deze studie suggereren dat bij afwezigheid van verstoring door de mens, ecologische factoren (habitat voorkeur, seizoenale variatie in beschikbaarheid aan vruchten, preferentie van vruchten en ruimtelijke verspreiding van habitat types) kunnen leiden tot seizoenale veranderingen in abundantie en distributie van zoogdieren. Soortspecifieke kenmerken zoals lichaamslengte, terrestrische versus boombewonende levenswijze, mate van specialisatie, competitief vermogen, ... beïnvloeden de impact van menselijke activiteiten op de response van zoogdieren. Ruimtelijke flexibiliteit van gorilla's en gebruik van beschikbare 'fallback' voedselbronnen wanneer hun geprefereerde vruchten schaars zijn, stelt deze soort in staat om gebieden die sterk beïnvloed worden door jacht of andere vormen van menselijke verstoring te verlaten. Chimpansees daarentegen tonen een hogere plaats trouw aan geprefereerd broedhabitat bij menselijke verstoring, wellicht als gevolg van hun meer uitgesproken specialisatie in fruitconsumptie. Bovendien stelt de competitieve dominantie van chimpansees over gorilla's - gefaciliteerd door hun groeps gedrag - hen in staat om beter om te gaan met menselijke verstoring. Naast gerichte jacht kunnen ook andere menselijke effecten de abundantie en verspreiding van populaties mensapen beïnvloeden, en tevens leiden tot een langdurige afname in populatiegrootte. Omdat heterogeniteit van leefgebieden en hulpbronnen het lokaal samenleven van gorilla's en chimpansees vergemakkelijkt, is het van cruciaal belang om zowel geprefereerde als 'fallback' vruchtdragende plantensoorten te vrijwaren. Waar patronen van menselijke verstoring bij mensapen een aanwijzing kunnen vormen voor soortgelijke effecten bij andere zoogdieren, kunnen soorten sterk variëren in hun response op menselijke verstoring - afhankelijk van hun interacties met sympatrische soorten en de abiotische omgeving en hun niveau van voedingsspecialisatie. Verder onderzoek naar effecten van biologische eigenschappen van soorten op hun gevoeligheid aan antropogene verstoring blijft daarom noodzakelijk. Daarnaast is een betere kennis gewenst van drempelwaarden waarboven niet-consumptief gebruik van natuurlijke hulpbronnen door mensen het voortbestaan van soorten en hun leefgebieden in het gedrang brengt.

# ACKNOWLEDGEMENTS

The present work was carried out from November 2013 to June 2019, with data contributions from previous studies. I am grateful to the Centre for Research and Conservation (CRC) of the Royal Zoological Society of Antwerp (Belgium) for supporting me as a PhD student by providing funds for research. The CRC provided sufficient funds to cover all research-related expenses, including costs for logistics and salaries of research assistants and field guides. In addition, I received financial support from the CRC to cover my travel and living costs in Belgium where I finalized and defended my PhD thesis. The extra financial and logistic support offered by the Terrestrial Ecology Unit of Ghent University was very helpful. The research grant offered to me by the Conservation Action Research Network through the Congo Basin Grant Program contributed significantly to advance the data collection process. The Cameroon Ministry of Scientific Research and Innovation issued research permits, thus making it possible to carry out research activities.

Throughout the implementation of my research project, I was a staff member of “Projet Grands Singes” (PGS) in Cameroon, under the coordination of Dr Nikki Tagg, where I benefited from a friendly work environment, without which this work could not have been completed successfully. Additionally, I am grateful to Dr Nikki Tagg as she actively reviewed and commented on all manuscripts, even when the time was very limited. As a PGS employee, I had the opportunity to use all the equipment and logistics at the PGS office and research facilities at La Belgique research station to implement my research project in the field. I sincerely thank Dr Jacob Willie because he has believed in me and put in much effort to help me succeed in this great project. Specifically, he designed this PhD research project and facilitated my registration at Ghent University as a PhD student, contributed to finding research grants to supplement the funding offered by PGS, and oversaw the entire research process starting from data collection planning to thorough comments on manuscripts. I really thank Prof Zjef Pereboom for endorsing me as a CRC PhD student and facilitating the provision of financial support. I sincerely thank Olga for carefully proofreading the final version of this thesis and sacrificing her

## Acknowledgements

sleep. Thank to Mathieu for letting me live with him during the finalization phase of this thesis. Charles-Albert has encouraged me to pursue a PhD. During my tenure in PGS, fellow researchers, including Charles, Veerle, John-Carlos, André, and Marcel, provided helpful advice for the organization and management of my field operations. Outstanding contributions of Sandra, Myriane, Jacques, Arnaud, Giscard, Michel, Patrick, and Maxwell during data collection and processing greatly helped obtain data used in this thesis. I also thank Donald, Bernadette, God Love, George, and Honorine for their administrative and logistic support. I cannot thank enough the many local field guides who substantially contributed to data collection, including Anicet, Jean-Baptiste, Casimir, Martial, Serge, Luc, Pascal, Jean, Pierre, Rodrigues, etc.

I enjoyed the environment at TEREC, under the direction of Prof Luc Lens. He offered me the unique opportunity to pursue a PhD study in his lab and defend my PhD thesis at Ghent University. I am also very grateful to Prof Luc Lens for adequate guidance and insightful comments on this PhD thesis. I also thank Angelica for administrative support. My thanks also go to all the reading committee members for taking time to review and comment on the early drafts of this thesis.

Finally, I thank my parents, my parents-in-law, my siblings Alain, Berenice, Aurelie, Roseline, Roderic, Erika and Dorienne, my uncle's family Demanou, and my sister-in-law Christelle and her husband, for assistance during the busiest phase of my PhD.

# CURRICULUM VITAE

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## PROFILE

I am a driven scientist, with a master of engineering in Forestry and Wildlife from the University of Dschang in Cameroon. After my master studies, I soon engaged in a PhD in Biology (Major – Wildlife Ecology and Conservation) at Ghent University. Since then, I have been working as an assistant researcher with the “Great Apes Project” in Cameroon, an in-situ project of the Royal Zoological Society of Antwerp (Belgium). I developed strong abilities and skills such as research design, professional writing, statistical analyses, teamwork, problem solving based on self-study and the sense of responsibility. Because those qualifications are not perfect, I am looking for new challenges and opportunities where I will grow my talents and knowledge.

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## COMPETENCIES

Languages      French – Mother's tongue

                    English – Academic, excellent knowledge

Informatics      Microsoft Office, R, ArcGIS, Python (Python for ArcGIS – Arcpy)

Coaching        Master theses (University of Dschang)

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## PREVIOUS WORK EXPERIENCE

2013 – 2019      Assistant researcher (Great Apes Project, Cameroon/ Centre for Research and Conservation, Royal Zoological Society of Antwerp, Belgium)

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## EDUCATIVE BACKGROUND

- 2013 – 2019      PhD student, Ghent University, Belgium  
Thesis title: Ecological and anthropogenic drivers of the distribution and abundance of two Afrotropical rain forest mammals  
Promotors: Prof. Dr. Luc Lens; Dr. Jacob Willie
- 2010 – 2013      Master of Engineering in Forestry and Wildlife, University of Dschang, Cameroon
- 2007 – 2010      Bachelor in Forestry and Wildlife, University of Dschang, Cameroon

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## RESEARCH GRANT

- 2015                Congo Basin Grant Program (Conservation Action Research Network)

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## DATA ARCHIVING

**Tédonzong, L.R.D.**, Willie, J., Tagg, N., Tchamba, M.N., Angwafo, T.E., Keuko, A.M.P., Kuenbou, J.K., Petre, C.-A., Lens, L., 2019. Data from: The distribution of plant consumption traits across habitat types and the patterns of fruit availability suggest a mechanism of coexistence of two sympatric frugivorous mammals. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.ms65f29>

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## SCIENTIFIC PUBLICATIONS

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#### INTERNATIONAL CONFERENCE TALKS

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Tagg, N., Mbohli, D., Willie, J., **Tédonzong, L.**, Kuenbou, J., Lens, L., 2018. Research as a critical conservation tool in non-protected forests of Cameroon, *XXVII Congress of the International Primatological Society, from 20-Aug-2018 to 25-Aug-2018*. International Primatological Society, United Nations Offices, Nairobi, Kenya. (*Presentation*)

Willie J., **Tédonzong, L. R. D.**, Tagg, N. (2017). Monitoring great ape abundance and distribution to assess conservation effectiveness and guide future efforts - 15 years of great ape monitoring in southeast Cameroon. *European Conference of Tropical Ecology*, 6-10 February 2017 in Brussels. (*Poster*)

Willie J., **Tédonzong, L. R. D.** (2016). Monitoring great ape abundance and habitat availability to determine high conservation value forests and assess conservation effectiveness. *Annual CRC Zoo Research Symposium*, December 15, 2016 in Antwerp, Belgium. (*Presentation*)

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#### ONLINE TRAINING COURSES

- 2018: **Editing in ArcGIS Desktop** (ESRI - Environmental Systems Research Institute)
- 2016: **Using ArcMap in ArcGIS Desktop 10** (ESRI - Environmental Systems Research Institute)
- 2016: **GIS for Humanitarian Mine Action: Data Types and Data Exploration** (ESRI - Environmental Systems Research Institute)

- 2016: **Basics of Geographic Coordinate Systems** (ESRI - Environmental Systems Research Institute)
- 2016: **Getting Started with GIS** (ESRI - Environmental Systems Research Institute)
- 2016: **Introducing conservation** (United for Wildlife)
- 2016: **Statistical Learning “using R”** (Stanford University Online)  
[https://verify.lagunita.stanford.edu/SOA/ced62a3ab11f4209a5e004a35d42bc  
52](https://verify.lagunita.stanford.edu/SOA/ced62a3ab11f4209a5e004a35d42bc52)
- 2016: **Forest Monitoring with CLASlite** (Carnegie Institution for Science)
- 2016: **Biological Diversity - Theories, Measures and Data sampling techniques** (Biological Institute National Research, Tomsk State University)  
<https://www.coursera.org/account/accomplishments/verify/VYC3PFYNM3KK>
- 2015: **Research Writing and Proposal Writing** (AuthorAID and INASP - International Network for the Availability of Scientific Publication)



