


Herbaceous plant community structure in south-east Cameroon: ecological drivers and use by western lowland gorillas



Jacob Willie

Front cover photographs:

A group of western lowland gorillas (*Gorilla gorilla gorilla*) in a forest clearing. ©Thomas Breuer, MPI-EVA / WCS

Herbaceous plants of the families Marantaceae and Zingiberaceae. © Jacob Willie, PGS

ISBN: 978-9-4619708-3-1

Ghent University Press, Zelzate

Herbaceous plant community structure in south-east Cameroon: ecological drivers and use by western lowland gorillas

Jacob Willie
Ghent University
Faculty of Sciences

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

Promotor: Prof. Dr. Luc Lens (Ghent University, Belgium)
Co-promotor: Dr. Nikki Tagg (PGS, Cameroon)

Reading committee:
Prof. Dr. Jean-Louis Doucet (University of Liège, Belgium)
Prof. Dr. Maurice Hoffmann (Ghent University, Belgium)
Dr. Nikki Tagg (PGS, Cameroon)
Prof. Dr. Zjef Pereboom (CRC-KMDA & University of Antwerp, Belgium)

Examination committee:
Prof. Dr. Dominique Adriaens (Ghent University, Belgium), Chairman
Prof. Dr. Dries Bonte (Ghent University, Belgium)
Prof. Dr. Jean-Louis Doucet (University of Liège, Belgium)
Prof. Dr. Luc Lens (Ghent University, Belgium)
Prof. Dr. Maurice Hoffmann (Ghent University, Belgium)
Dr. Nikki Tagg (PGS, Cameroon)
Prof. Dr. Zjef Pereboom (CRC-KMDA & University of Antwerp, Belgium)

Please refer to this work as:
Willie, J. (2012). Herbaceous plant community structure in south-east Cameroon: ecological drivers and use by western lowland gorillas. PhD thesis, Ghent University.

Contents

Acknowledgements

The present work was carried out from November 2007 through November 2012 and was made possible thanks to many contributors. I owe a great debt of gratitude to the Centre for Research and Conservation (CRC) of Antwerp Zoo for funding much of the research that led to this PhD. This substantial support from the CRC made it possible to access the necessary logistics for office and field work, research permits, salaries of research assistants and other technical staff and funded much of my stay in Belgium as a PhD student. Additional financial and logistic support was provided by the Flemish Interuniversity Council (VLIR) and the Terrestrial Ecology Lab (TEREC) of Ghent University. I am thankful to the Ministry of Forestry and Wildlife and to the Ministry of Scientific Research and Innovation, Cameroon, for kindly issuing the research permits.

The work environment within Projet Grands Singes (PGS), Cameroon has been conducive to successful implementation of my research ideas. The smooth running of PGS by Nikki greatly contributed to my success. She trusted me and permitted the use all available means to implement the activities pertaining to my PhD. She has always found time to read my manuscripts, and her constructive comments have significantly enhanced their content. I acknowledge Zjef for his contribution, with much gratitude. He has played a major role in the creation of my thesis by promoting PGS, endorsing my candidature as a PhD student in Belgium and ensuring that I always had access to the necessary resources. He trusted that I could make an efficient use of these means and finalize my work responsibly. Charles-Albert has been a great support and one of my best friends within PGS. He provided valuable assistance during data collection and processing. His scientific contribution as a co-author in some chapters of this thesis was remarkable. Without the assistance of Germain, Fabrice, Charles Yem,

John Carlos, Marcel, André, Luc Roscelin and the field guides of Malen V, Doumo Pierre and Mimpala, it would not have been possible to collect and process the data used for this thesis. Also, I thank Donald, Bernadette, Olivia, Victoria, Inge, Mélodie, Thomas and Honorine, who were also supportive.

The work environment at TEREC was empowering. I am deeply appreciative of Luc for his support. He believed that it was possible for me to successfully complete my PhD at TEREC, and offered me the opportunity to do so. Despite his busy schedule, he has always found time to work with me and has meticulously supervised my PhD work. Angelica was always available to help, assisting me in all administrative matters. I am also grateful to Hans, Greet, Lander, Eduardo and Jeroen as well as other members of TEREC for their technical assistance and help in data analysis. I thank the all members of the reading committee for their constructive comments on an earlier draft of the thesis.

Thanks are extended to my mom and my brothers Patrick and Arnaud for their help with shopping prior to field trips. I always had so much to arrange, and their assistance was a great relief. I am also grateful to Denis, Kris, Duane, Geoffrey, Leo, René, Penny, Janneke, Jasmijn, Eyram, Pieterjan, Kseniya, Jamie, Amie, Kate, Pieter, Mariale, Faysal, Kaitlin, Aimi and Wuga for their assistance and moral support during my PhD studies in Belgium.

Faith indeed tells what the senses do not tell, but not the contrary of what they see. It is above them and not contrary to them.

Blaise Pascal

A plant community dominated by raphia and herb species in a swamp clearing of “La Belgique” research site. © Jacob Willie, PGS

General introduction

A plant community can be defined as a set of individuals of different species that grow together within a specific site and show definite interactions with each other (Kent & Coker, 1992; Van Andel, 2005). As illustrated by Crawley (1997a), the physical structure of a plant community is determined by three features, namely the community physiognomy (types of life-forms present; e.g. trees, shrubs, lianas, herbs), the vertical structure (height of life-forms) and the horizontal structure (spatial variations in species composition and frequency). The factors that structure plant communities can be grouped into a number of major categories, namely progagule and site availability, light and other abiotic resources, environmental conditions and human impacts and interspecific interactions (Tilman, 1983; Wright, 1992; Malenky et al., 1993; Crawley, 1997a; Van Andel, 2005; Bonnefille, 2010; Matías et al., 2012). At sites where propagules are available, ecological and human factors affect plants in various ways, and the resulting effects on plant community structure vary spatially and temporally (Van Andel, 2005).

ABIOTIC RESOURCE AVAILABILITY AND PLANT PRODUCTIVITY

- **Light**

The amount of light energy available to plants influences photochemical reactions, thus determining the rate of incorporation of atmospheric CO_2 into organic compounds (Mooney & Ehleringer, 1997). Some plants grow faster in open canopy habitats where light is more readily available (Ticktin & Nantel, 2004). In circumstances of decreased photosynthetically-active radiation, plant photosynthetic rate is low (Mooney & Ehleringer, 1997) and this may reduce plant biomass and negatively affect other plant traits. For example, some understory plants produce small-sized leaves and slender stems due to shaded conditions (Meers et al., 2010; Van Breugel et al., 2012). Most tropical herbaceous species grow better in light gaps compared to the forest understory where shade conditions predominate (Wright, 1992). Nevertheless, other species, including ferns, lichens and mosses, can grow in permanently shaded conditions due to coping mechanisms that enable them to thrive despite the limited amount of light (Crawley, 1997b). Light is regarded as the major limiting factor to plant growth in tropical forests (White & Edwards, 2000). However, high light levels may also be detrimental to plants. For certain species, excessive light can inhibit photosynthesis (Costa & Magnusson, 2002).

- **Water**

Plants lose water via stomatal pores while incorporating CO_2 into organic compounds, and this loss is regulated using available water in the air and in the soil (Mooney & Ehleringer, 1997). Hence a drastic reduction in air humidity and soil moisture content can cause stress and severely affect plant growth. The structure of plant communities strongly depends on soil water availability (Crawley, 1997b). It has been observed that shallow-rooted species such as tropical herbaceous plants are very sensitive to drastic reductions in available moisture (Wright, 1992; Furuichi et al., 1997).

- **Nutrients**

About 15 chemical elements are essential to plants; but nitrogen, phosphorus, carbon, oxygen and hydrogen are crucial for function (Fitter, 1997; Tilman, 1997; Leuschner, 2005). However, in most cases, phosphorus and nitrogen alone largely determine photosynthetic performance (Fitter, 1997; Mooney & Ehleringer, 1997). For example, the enzyme responsible for CO_2 fixation contains a large proportion of the nitrogen found in a leaf, and when light is available, net photosynthesis is positively correlated with leaf nitrogen content (Mooney & Ehleringer, 1997). Nitrogen is the most limiting nutrient resource in grassland habitats (Tilman, 1997). In tropical forests, the density of shrubs and herbs is generally correlated with soil fertility, but patterns are variable for trees (Wright, 1992).

EFFECTS OF ENVIRONMENTAL CONDITIONS AND HUMAN IMPACTS ON PLANTS

Environmental conditions influence plant physiological processes and resource quality and availability. Plant photosynthetic rate is correlated with temperature, but decreases in extreme conditions (Mooney & Ehleringer, 1997). Soil quality, nutrient availability and nutrient uptake by plants are influenced by soil pH; which is the concentration of hydrogen ions in the soil solution (Crawley, 1997b). For instance, a low pH is an indication of soil toxicity, and a high pH may decrease the availability of phosphorus, potassium and iron, though this may also favor nitrogen fixation by symbiotic bacteria (see Crawley [1997b] and references therein). Plant species display varying levels of soil pH tolerance (Crawley, 1997b). Rainfall is a key determinant of plant distribution and density (Wright, 1992; Crawley, 1997b; Bonnefille, 2010). Drought partly accounts for mortality and low diversity of tropical herbaceous plants, epiphytes and shrubs (Wright, 1992). For annual species, germination is possible only after rainfall, and a high amount of water is needed for better growth (Crawley, 1997b). The amount of water in plant tissues is reduced, and the amino acid content in the phloem and leaves is increased due to water shortages; as a result, plants are more vulnerable to pathogens and pests (see Crawley [1997b] and references therein). Plants are also influenced by other environmental conditions such as soil erosion, wind, trampling and soil compaction, fire, landslides and other physical disturbances (Malenky et al., 1993; Wrangham et al., 1993; Crawley, 1997b; Mooney & Ehleringer, 1997; Givnish, 1999; Matías et al., 2012).

Humans can have direct and indirect influences on plant communities. Logging damage can severely affect populations of both exploited and untargeted tree species, thus leading to an overall reduction in tree density (Johns, 1985). Canopy modification and soil compaction during logging activities modify habitat conditions and affect plants. Although the amount of light available to plants increases as a result of logging, this may not automatically increase the density of herbaceous plants. Malenky et al. (1993) found higher herb density in lightly-logged compared to heavy-logged forest. Soil fertility gradients may also be caused by shifting agriculture and nomadic settlements. Muchiru et al. (2009) found high amounts of soil nutrients in previously settled savanna areas, and suggested that disturbance due to nomadic settlements affected nutrient distribution and resulted in “plant diversity hotspots”. Industrial pollutants influence plants in various ways. For example, an atmospheric pollutant such as SO_2 reduces leaf conductance, therefore decreasing the rate of photosynthesis (Mooney & Ehleringer, 1997). In general, plant physiology and productivity are negatively affected at low concentrations of pollutants—though there may be some exceptions when environmental conditions are suitable—and plants may be destroyed at high concentrations (Ashmore, 1997). Industrial pollution can also affect plants by modifying soil pH (Crawley, 1997b).

INTERSPECIFIC INTERACTIONS AND PLANT COMMUNITY STRUCTURE

The relationship that exists between individuals of two species is termed interspecific interaction, and the resulting effect on these species, whether positive, negative or neutral, can be assessed by changes in fitness (Van Andel, 2005). A mutualistic relationship between vascular plants and fungi is known as a mycorrhiza. Benefits to vascular plants include increased nutrient uptake and enhanced protection against root pathogens and soil toxicity; while fungi are supplied with carbon (Kuyper & De Goede, 2005; Van Andel, 2005). Nitrogen uptake by vascular plants is significantly increased via mutualistic associations with nitrogen-fixing bacteria, and this has been observed to increase the productivity of young forest stands (Kuyper & De Goede, 2005).

The attractiveness of plants to animals results in mutualistic relationships between plants and animals. In some cases, a plant species providing fruit as food for a single animal species will depend exclusively on that animal for seed dispersal, seed germination and seedling survival (e.g. Tutin et al., 1991a). Sometimes, secondary dispersers also play a crucial role for seed germination and the success of seed dispersal by primary dispersers (Andresen & Levey, 2004). Herbivore foraging activity can improve habitat quality and plant productivity, and such mutualistic interactions may largely explain feeding adaptations of herbivores across their range (Tilman, 1983; Watts, 1987). However, interactions between plants and animals may also be antagonistic, and most often plants are negatively affected (Smallwood, 2001). Herbivory may limit the expansion of some species despite the increased availability of nutrient resources (Tilman, 1983). In some cases, availability of nutrients to plants may be reduced as a result of folivory, and this may negatively affect flower traits, thus making them less attractive to pollinators (Poveda et al., 2005). However, despite the damage caused by animals, plants may develop coping mechanisms, resulting in improved primary productivity (Watts, 1987). Plant-animal relationships are therefore pivotal for the maintenance of ecosystems, and it can reasonably be concluded that habitats and animals positively shape each other, as noted by Nakaoka (2005). Similarly, Marshall & Wrangham (2007) reason that primate socioecology and life history traits are influenced by the availability of fallback food resources, referring to highly abundant food items of relatively lower quality consumed when preferred foods are scarce (e.g. Tutin et al., 1991b; Remis, 1997; Doran et al., 2002).

UTILIZATION OF HERBACEOUS PLANTS BY GORILLAS AND OTHER MAMMALS

Western lowland gorillas (*Gorilla gorilla gorilla*) have been observed in several sites to feed constantly on *Aframomum* spp., which are herbs of the family Zingiberaceae (Sabater Pi, 1977; Calvert, 1985; Rogers et al., 1990), showing that

Aframomum is an important genus in their diet, and reinforcing the conclusion of Kingdon (1997) that *Aframomum* constitutes a high proportion of the diet of western lowland gorillas. Herb species of the family Marantaceae are also known to be eaten by this great ape and *Haumania* spp. are widely consumed across Central Africa (Calvert, 1985; Nishihara, 1995; Remis, 1997; Tutin, 1998; Doran et al., 2002; Rogers et al., 2004; Doran-Sheehy et al., 2009). Although fruits from trees are the preferred foods of western gorillas, pith, fruits, shoots and young leaves of herbs—primarily Marantaceae and Zingiberaceae species—are consumed year-round, and proportions increase when fruits are scarce (Sabater Pi, 1977; Calvert, 1985; Tutin & Fernandez, 1985; Rogers et al., 1988; Williamson et al., 1990; Tutin et al., 1991b; Remis, 1997; Groves & Meder, 2001; Doran et al., 2002; Rogers et al., 2004; Head et al., 2011). Western gorillas also incorporate termites and other insects in their diet (Tutin & Fernandez, 1992; Remis, 1997; Deblauwe et al., 2003). Mountain gorillas feed more on herbaceous vegetation than do western and eastern lowland gorillas as a result of reduced fruit supply in their habitats (Ganas et al., 2004; Harrison & Marshall, 2011). Given this importance, Harrison & Marshall (2011) objectively concluded that herbaceous plants provide staple fallback food for gorillas. A review of chimpanzee dietary studies highlights marked differences among subspecies and roughly indicates that these apes primarily feed on fruits, but use figs, barks, leaves and pith from herbaceous plants as fallback foods (Harrison & Marshall, 2011). Chimpanzee populations have also been observed to consume honey, termites and other insects, and meat (Tutin & Fernandez, 1992; Tutin et al., 1995a; Deblauwe, 2006; Deblauwe et al., 2006; Fowler & Sommer, 2007; Sanz & Morgan, 2007; Head et al., 2011; Pruetz & Lindshield, 2012). Harrison & Marshall (2011) summarize the diet of the bonobo as fruit-dominated and point out that this species also relies on large amounts of pith from high-quality herbaceous plants, figs, roots, barks, flowers, leaves and occasionally meat. Termites and honey are also included in the list of bonobo food items (Badrian et al., 1981; McGrew et al., 2007). Both chimpanzees and bonobos use tools to feed on insects and honey (Badrian et al., 1981; Tutin & Fernandez, 1992; Tutin et al., 1995a; Deblauwe, 2006; Deblauwe et al., 2006; Fowler & Sommer, 2007; McGrew et al., 2007; Sanz & Morgan, 2007); and plant materials, including herbaceous species, are frequently incorporated into tool use, for example, as fishing probes to extract termites from termite nests (Deblauwe et al., 2006; McGrew et al., 2007; Sanz & Morgan, 2007). Aside from great apes, elephants and other mammals such as mandrills, buffalos, bongos, duikers and sometimes arboreal monkeys also consume herbaceous plants (Rogers & Williamson, 1987; Tutin et al., 1997). Gorilla and chimpanzee ground nests are commonly built using herbaceous plants (Groves & Sabater Pi, 1985; Tutin et al., 1995b; Rothman et al., 2006; Koops et al., 2007). Detailed studies on plant preference for nest building by western gorillas are rare. Gorillas rely more heavily on herbaceous plants than do sympatric mammals (e.g. chimpanzees; Tutin et al., 1991b; Head et al., 2011).

RELEVANCE TO GORILLA ECOLOGY AND CONSERVATION OF STUDIES OF HERBACEOUS PLANTS

Studies of herbaceous plants can help to assess the ecological interactions between these plants and the animals that depend on them, therefore establishing a link between resource availability and use (Fay, 1997). For example, information on the distribution of the resources used by gorillas may help to identify their most suitable habitats (Rogers et al., 2004), thus furthering knowledge required for conservation planning. Furthermore, thorough investigations of herbaceous plants will provide more evidence to help verify whether fluctuations in herb availability can explain documented changes in the consumption of herbs and the use of habitats by gorillas (Rogers et al., 1988; Williamson et al., 1990; Tutin et al., 1991b; White et al., 1995; Doran-Sheehy et al., 2004). In addition, understanding the effects of environmental factors on herb plants used by gorillas is particularly important because climate change can negatively affect food sources, thus threatening the existence of these critically endangered apes (Walsh et al., 2008; Musana & Mutuyeyezu, 2011). Such investigations can help to assess possible influences of meteorological conditions on resource availability to gorillas and highlight the abiotic factors that also influence gorilla ecology, thus contributing to the global picture of how climate change may affect the biotope and the resulting consequences on the faunal community.

HERBACEOUS PLANTS AS INDICATORS OF HABITAT QUALITY

The use of indicator species has been proposed as an efficient method for assessing forest quality (e.g. Moffatt & McLachlan, 2004) as their presence reveals the predominance of specific environmental conditions and disturbance regimes (White & Edwards, 2000; Webb et al., 2006). For example, detailed studies on herbs have been suggested in order to highlight their importance as indicator species to help define the successional status of secondary forests (Djoufack, 2003). Studying the composition and diversity of herbaceous plants, therefore, may contribute to the definition of ecological indicators of forest development for different successional stages (Moffatt & McLachlan, 2004), and enhance knowledge of forest ecology. In addition, ecological studies on understory herbs can provide some baseline data needed to monitor change in forest biodiversity (FAO, 2005). Collecting quantitative data on plots or transects to monitor forests is challenging due to constraints such as limited availability of funding, logistics and time (Nagendra & Ostrom, 2011). Indicator species can therefore have a practical importance: knowledge on these species may help to avoid full forest inventories and provide conservationists with readily available and effective management tools for the monitoring and mitigation of human-induced disturbances in natural habitats (Moffatt & McLachlan, 2004), which are serious threats to survival of the critically endangered western lowland gorilla (Walsh et al., 2008). Furthermore, the study of the composition of herbs in different forest types may help to verify if the occurrence of forest understory herb species in various habitat types can be validated as distinct community types (McCune & Grace, 2002). This knowledge and additional information on diversity and abundance of herbaceous plants may help to assess whether these plants can serve as effective criteria for arbitrary classification of forest types in categories.

ECOLOGICAL STUDIES OF HERBACEOUS PLANTS IN CENTRAL AFRICA

Ecological studies on forest understory herbs have been carried out in some sites in Central Africa. Rogers & Williamson (1987) measured stem density and available food biomass from pith and shoots of Marantaceae and Zingiberaceae (collectively termed terrestrial herbaceous vegetation, THV, in the study) in a restricted portion of the Lopé Reserve (Gabon). Although THV fruits are also eaten by gorillas (Sabater Pi, 1977; Calvert, 1985; Kingdon, 1997), their biomass could not be included since the THV stems did not have fruit in the dry season when the survey was conducted; nor could they estimate food biomass from new leaves of THV. Rogers et al. (1988) monitored the production of young leaves of a few THV species, but THV density was not measured. To fill these gaps, White et al. (1995) re-measured THV densities in more representative samples and seasonally monitored the production phenology of THV plant organs, including fruits and leaves. This resulted in a more accurate estimation of THV food availability for gorillas in this site. Fay (1997) later argued that the THV definition adopted by both studies (Rogers & Williamson, 1987; White et al., 1995) was too restrictive, especially as species from other monocotyledon families also provide food to many forest herbivores, and they constitute important elements of the herbaceous layer. Therefore in Ndakan (Central African Republic), Fay (1997) described the patterns of abundance, distribution and food availability of THV, including all other terrestrial species of monocotyledons, to have a more complete picture of their occurrence. However, the production phenology of herbs was not monitored. In other sites, herb availability was assessed as part of a global study, and these investigations were limited to stem density estimation (e.g. Malenky et al., 1993; Furuichi et al., 1997; Brugiere & Sakom, 2001; Doran et al., 2002; Head et al., 2011). Although many attempts have been made to study THV, less effort has been made to describe other ecological patterns (e.g. diversity, community composition and population dynamics) or the effects of abiotic factors such as meteorological conditions and soil fertility. Food biomass has been estimated using stem-density data measured during a given period of the year (e.g. Rogers & Williamson, 1987; Fay, 1997). Although this approach can provide an accurate estimation of biomass at the time of the survey, it does not assess temporal variations of food availability; especially if THV stem density, fruit or shoot availability vary throughout the year. In most cases, the estimation did not account for changes in population size because the abundance of THV stems was not monitored throughout the year. Monitoring is therefore needed to provide seasonal THV stem-density data. These data could be applied to potential food-biomass figures for each species to have a more precise assessment of THV food availability at any given moment of the year.

OBJECTIVES OF THE THESIS

The aim of this thesis is to describe ecological patterns of terrestrial herbaceous plants in order to understand their association with various successional stages of forest development and the resulting influences on the ecology of gorillas that depend upon them. A special emphasis is laid on the effects of abiotic factors on herbs that are used by gorillas in an attempt to establish a link between environmental variables and gorilla distribution. To achieve this goal, the specific objectives are as follows: (i) assessing the diversity, composition and abundance of forest understory herbs in different habitat types; (ii) evaluating the effects of abiotic factors on the spatial and temporal availability of herbaceous plants; (iii) determining the species of forest herbaceous plants that are important to gorillas; (iv) describing the influence of herb availability on gorilla distribution.

HYPOTHESES AND PREDICTIONS

Physiological responses of plants to environmental influences lead to changes in plant community structure (Tilman, 1983; Wilson & Tilman, 1991). I therefore hypothesize that there will be variations in herbaceous plant community structure across different habitats with contrasting ecological features. Given that photosynthesis is more likely to be water- than light-limited (Mooney & Ehleringer, 1997), and that tropical understory herbs are vulnerable to stresses caused by reduced moisture and soil fertility (Wright, 1992), I predict that: i) herb biomass, density and diversity will be high in flooded habitats with hydromorphic soils as compared to *terra firma* habitats; and that ii) the overall herb density will be correlated with precipitation. Moreover, I hypothesize that due to edaphic and floristic differences between habitat types, there will be spatial variation in soil fertility, and spatial patterns of herbaceous plant abundance will reflect this variation. As a result of variations in herbaceous plant biomass, abundance and diversity, I propose that habitat and herbaceous plant use by gorillas will show nonrandom spatial and temporal patterns.

OUTLINE OF THE THESIS

Chapter 1 addresses herb diversity questions by monitoring herb sampling processes across habitat types and by determining species richness and patchiness, thus contributing to the evaluation of herb resource availability. The monitoring is done using a set of species richness estimator curves, and diversity indices are calculated. In Chapter 2, the composition of herbaceous plants in different habitat types is assessed to study their association with forest stages. Because the availability of plants depends on the environment, Chapter 3 investigates possible environmental gradients in understory herbs. In this respect, soil fertility parameters and other abiotic variables are recorded in a set of plots, and herbaceous plants are monitored in these plots. In Chapter 4, plants used by gorillas for nest building are identified in order to classify them in terms of preference. This is achieved by describing the plant species composition of nests built by gorillas during an extended period. Chapter 5 provides a description of the relationship between herb availability and gorilla distribution. For this purpose, herb stems and gorilla nest sites are inventoried in different habitat types. Chapters 1, 2, 3 and 5 describe the ecological patterns of herbaceous plants and assess the influence of abiotic factors on their availability. Chapters 4 and 5 highlight the importance of herbaceous plants for gorillas and relate these plants to gorilla distribution. The data collected to answer the various questions raised in these five chapters are summarized in Table 1.

STUDY SPECIES

- **Terrestrial herbaceous plants**

The study subjects are all herb species of the ground layer (see Fig. 1 for some illustrations). The species inventoried belonged to 15 families, namely Araceae, Aspleniaceae, Balanophoraceae, Commelinaceae, Costaceae, Cyperaceae, Marantaceae, Melastomataceae, Poaceae, Pteridaceae, Rubiaceae, Selaginellaceae, Thelypteridaceae, Urticaceae and Zingiberaceae. Marantaceae and Zingiberaceae occur at high density in the study site (see Fig. 1 for some illustrations). These species are perennial plants, some having climbing stems (Koechlin, 1965). They are found in *terra firma* forests and swamps; and individuals can form clumps of more than two meters in height (Koechlin, 1965). They are used by humans for food-wrapping, medicinal purposes and handicraft, and some are traded (Betti, 2004; Brink, 2010).

Table 1 Summary of the data collected.

Data collected	**Chapter 1**	**Chapter 2**	**Chapter 3**	**Chapter 4**	**Chapter 5**
Herb stems identified and counted in > 8500 1-m^2 contiguous plots distributed in six habitat types	x				x
Canopy openness above the 1-m^2 plots					x
12-month monitoring of herbs in 250 4-m^2 plots placed along ten 6-km transects		x	x		
Soil fertility parameters and other environmental variables assessed in 50 monitored 4-m^2 herb plots			x		
Monthly temperature, rainfall and humidity			x	x	
32 months of monitoring of nest building by gorillas				x	x
Botanical inventories in 130 plots of 25 x 40 m				x	
Habitat type and visibility determined in 1200 systematically-chosen positions along ten 6-km transects					x

Fig. 1 Pictures of four plant species of the herbaceous layer in the study site. (A) *Halopegia azurea*; (B) *Hypselodelphys scandens*; (C) *Haumania danckelmaniana*; (D) *Aframomum polyanthum.* © Jacob Willie, PGS

- **Western lowland gorillas**

The subspecies of gorilla that occurs in the study site is the western lowland gorilla (*Gorilla gorilla gorilla* [Savage and Wyman, 1847]; Fig. 2). This gorilla subspecies is distributed in lowland rainforests and swampy areas, and it occurs in Cameroon (South of the Sanaga River), Central African Republic, Congo, Equatorial Guinea and Gabon (Groves & Meder, 2001; Walsh et al., 2008). This range might be modified because in Cabinda (Angola) and Ebo/Ndokbou, North of the Sanaga River (Cameroon), some gorilla populations with undefined taxonomic status have been found (Walsh et al., 2008). On average, western lowland gorilla groups are composed of about 10 individuals, but other individuals are solitary (Parnell, 2002; Walsh et al., 2008). There are considerable overlaps in group home ranges, and a single range can encompass 20 km^2 (Walsh et al., 2008). Gorillas can sleep in trees (Tutin et al., 1995b), but owing to their large bodies, they usually sleep in ground nests constructed using plant materials (Groves & Sabater Pi, 1985; Fay & Agnagna, 1992; Tutin et al., 1995b; Iwata & Ando, 2007). Seasonal fruits are the preferred food items of these apes, and fallback foods include pith, young leaves and shoots of herbs—mostly Marantaceae and Zingiberaceae species—as well as bark (Sabater Pi, 1977; Calvert, 1985; Kingdon, 1997; Rogers et al., 2004; Doran-Sheehy et al., 2009; Harrison & Marshall, 2011).

Fig. 2 Western lowland gorilla (male). © A.P.E.S 2012

Commercial hunting associated with logging, and epidemics of infectious disease, such as anthrax and Ebola, are the major documented threats to western lowland gorillas; in the near future, habitat loss and disturbance and climate change are likely to become more of a threat (Fay & Agnagna, 1992; Huijbregts et al., 2003; Tutin et al., 2005; Bermejo et al., 2006; Caillaud et al., 2006; Leendertz et al., 2006; Walsh et al., 2008). In some areas, populations have perished by 50%, and numbers are globally decreasing across their range (Walsh et al., 2003; Walsh et al., 2008). Western lowland gorilla populations cannot easily recover from such losses, and these primates are consequently classified as a critically endangered species (Walsh et al., 2008).

STUDY AREA

Field work was carried out in the northern buffer zone of the Dja Biosphere Reserve (DBR, 5260 km^2; 12°25'–13°35'E, 2°49'–3°23'N) in south-east Cameroon (Fig. 3). The DBR belongs to the Cameroon-Congo forest block and is located in the transition zone between the semi-deciduous forests of Equatorial Guinea and the evergreen forests of the Congo Basin (Letouzey, 1985). The canopy is predominantly formed by legumes of 30–40 meters (McGinley, 2008). In the 1940s, some village sites were abandoned, and this has resulted in the formation of secondary forests (McGinley, 2008). Lianas occur at high densities, and *Mapania* spp. and species of Marantaceae predominate in the herbaceous layer (McGinley, 2008). The climate is equatorial and humid with rainfall peaks in May and September and a mean annual rainfall of approximately 1600 millimeters (McGinley, 2008). Temperatures are fairly constant throughout the year, with average monthly minimum and maximum temperatures of 18 and 27°C in the coldest month and 19 and 30°C in the warmest month, and an annual mean of 23.3°C (McGinley, 2008). The Dja forest is situated on the Precambrian plateau, and the major part of the reserve is encircled by the Dja River; the altitude varies from 400 to 800 m and the relief is fairly flat in most areas, with shallow valleys and round-topped hills (Fomete & Tchanou, 1998; McGinley, 2008). The soil is ferralitic, porous and red, with an underlying substratum which mostly constitutes schist, gneiss and quartzite (McGinley, 2008). The DBR is one of the largest protected areas in Africa and the largest protected area in Cameroon. In 1950, it was classified as a Faunal Reserve, initially called 'Réserve de Faune et de Chasse', and later modified as 'Réserve de Faune' in 1973 (McGinley, 2008).

UNESCO recognized this protected area as a Biosphere Reserve in 1981 (McGinley, 2008), and it was inscribed in the list of World Heritage Sites in 1987 (Betti, 2004). The protected area is surrounded by logging concessions. The reserve and its buffer zone are biodiversity-rich, with high densities of apes and other species (Dupain et al., 2004; McGinley, 2008). The reserve and adjacent forest blocks have been referred to as the Dja Conservation Complex and considered an 'exceptional priority area' for great ape conservation (Tutin et al., 2005).

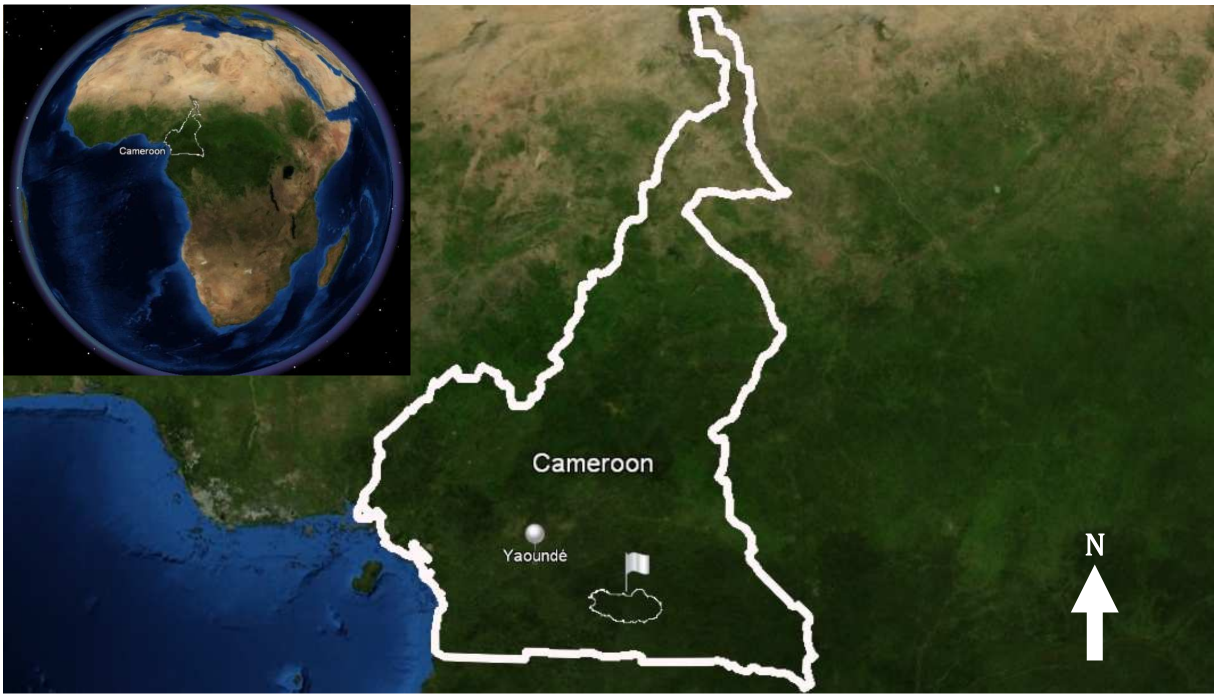
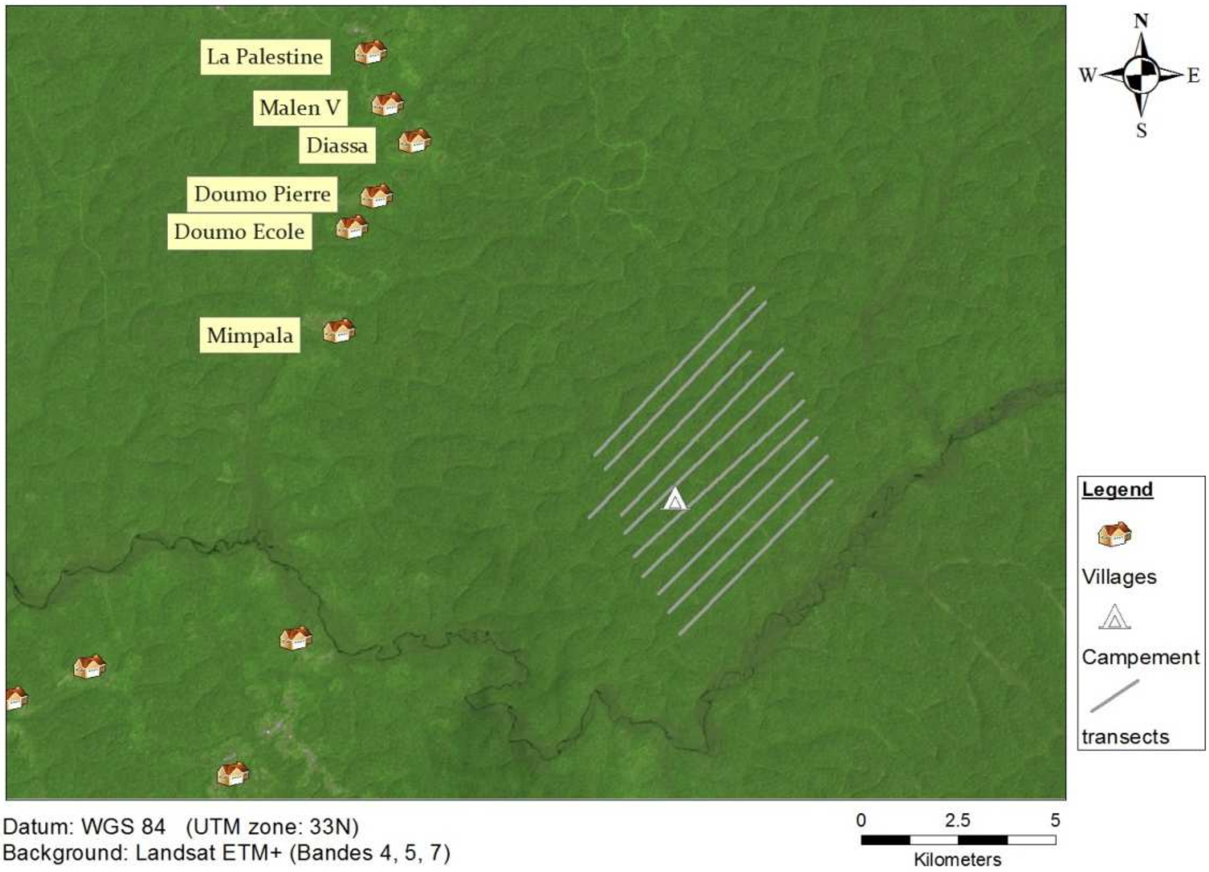


Fig. 3 Northern buffer zone of the Dja Reserve in Cameroon.

Specifically, data were collected in the research site called 'la Belgique' (40 km^2) of *Projet Grands Singes* (PGS), of the Centre for Research and Conservation, Royal Zoological Society of Antwerp (Fig. 4). Geographic coordinates range between 013°07'–013°11'E and 03°23'–03°27'N. The research site is officially unprotected and situated within the forest management unit 10 047; it comprises many seasonal swamps and watercourses, all tributaries of the Dja River. The research site was partially and selectively logged in the past.



Datum: WGS 84 (UTM zone: 33N)
Background: Landsat ETM+ (Bandes 4, 5, 7)

Fig. 4 Study site.

According to previous vegetation studies in the research site (Nguenang & Dupain, 2002; Djoufack, 2003), many vegetation types occur. They differ in terms of structure and floristic composition and they can be divided into sub-categories, resulting in a forest mosaic. Five vegetation types can be distinguished as follows:

- Young secondary forest. Canopy height of < 25 m, dominated by early successional species, including *Tabernaemontana crassa* and *Myrianthus arboreus*. The understory is dense, and shrubs such as *Alchornea floribunda* and A. *laxiflora* are abundant. This habitat type is also characterized by dense thickets of herbs from Marantaceae and Zingiberaceae families;

- Old secondary forest. Dominant canopy height is usually between 25—30 m, and dominant tree species include *Terminalia superba*, *Nauclea diderrichii*, *Polyalthia suaveolens*, *Uapaca* spp. and *Alstonia boonei.* The shrub layer (height < 20 m) is composed of young secondary forest species such as *Myrianthus arboreus*, *Desplatsia dewevrei* and *Tabernaemontana crassa*. Herb patches do occur, but the forest understory is more open than that of young secondary forest;

- Near primary or mature forest. Large and tall trees of height > 30 m dominate the canopy, such as *Omphalocarpum procerum*, *Uapaca* spp., *Polyalthia suaveolens*. Large individuals of *Piptadeniastrum africanum*, with a diameter > 90 cm and height > 35 m sometimes occur in this forest type. In addition, the canopy layer is more continuous and the understory is more open than in old secondary forest. The shrub layer is < 15 m, and species such as *Drypetes* spp. and *Rinorea* spp. are abundant. It is noteworthy that unlike inside the Dja Reserve, *Gilbertiondendon* spp. do not occur in the study site;

- Riparian forest. It is located in the transition zone between *terra firma* forest types (young secondary, old secondary and near primary forest) and swamps (see below). This forest is periodically flooded, and dominant canopy height is between 15–20 m. The floristic composition of this habitat type includes species of both *terra firma* forests and swamps;

- Swamps. This habitat type occurs on hydromorphic soils. Dominant species are *Raphia* spp., and trees such as *Uapaca* spp. are frequent. Raphia-free open areas (clearings) are sometimes found. Dense patches of herbaceous plants are common in this habitat.

In addition to these habitat categories, frequent tree and branch falls in the study site result in the formation of light gaps. The herbaceous vegetation is more developed in this microhabitat, and seedlings are abundant.

The research site is surrounded by villages and is situated about 8 km straight line from the nearest human settlement. Local people rely heavily on natural resources for subsistence and income, and exploitation activities include hunting, fishing and gathering of non-timber forest products (Nyaga, 2004; McGinley, 2008). Animal rearing is poorly developed, and the traditional agricultural system consists of slash-and-burn shifting cultivation; both food and cash crops are cultivated (Willie, 2006). Although human population density was low two decades ago, current density is likely to be higher (UICN, 2010). Pressure on natural resources is high (Muchaal & Ngandjui, 1999; Willie, 2006), and overexploitation and deforestation are real problems (McGinley, 2008; UICN, 2010).

MAIN SAMPLING DESIGN

Ten 6-km transects were opened at a bearing of 45°. Transects were 600 m apart (Fig. 4). At 50-m points along each transect, habitat type and horizontal visibility were determined. Along each transect, trees were inventoried in 13 25 x 40 m plots set 500 m apart (Fig. 5). Along each transect, all herbaceous plants were sampled and monitored in 25 2 x 2-m plots, set 250 m apart; Fig. 5). Other data were randomly collected in various habitat patches along and between transects. Plots of 1 x 1 m were used to sample herbs of two families, and larger plots (2 x 2 m) were used to sample all herb species. Both plot sizes are commonly used to sample herbs in African forests (White & Edwards, 2000).

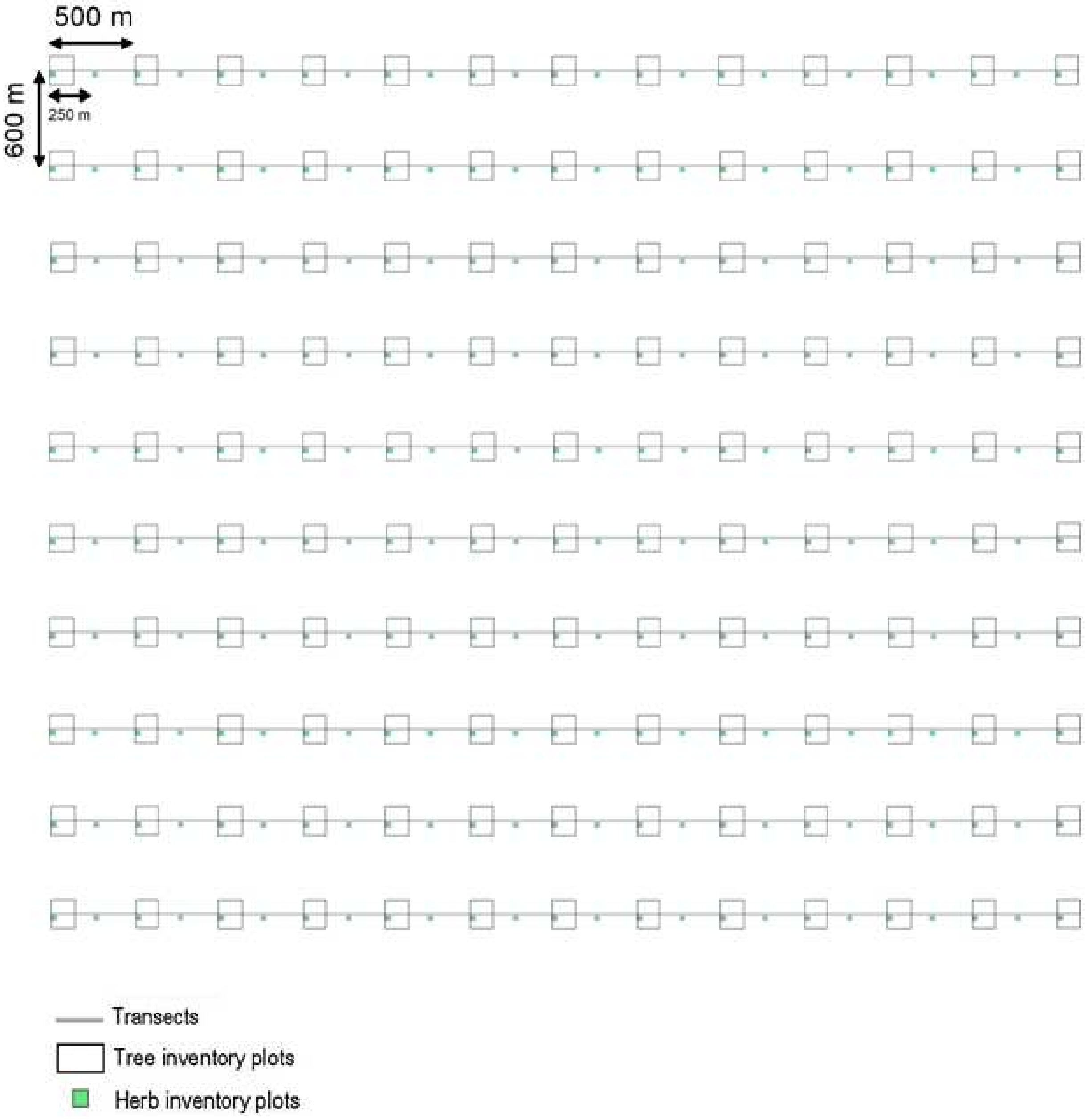


Fig. 5 Main sampling design.

REFERENCES

Andresen, E. & Levey, D.J. (2004). Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia* 139: 45–54.

Ashmore, M. (1997). Plants and pollution. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Badrian, N., Badrian, A. & Susman, R. L. (1981). Preliminary observations on the feeding behaviour of *Pan paniscus* in the Lomako forest of central Zaire. *Primates* 22: 173–181.

Bermejo, M., Rodriguez-Teijeiro, J.D., Illera, G., Barroso A., Vila C. & Walsh P.D. (2006). Ebola outbreak killed 5000 gorillas. *Science* 314: 1564.

Betti, L. (2004). An ethnobotanical study of medicinal plants among the Baka Pygmies in the Dja Biosphere Reserve, Cameroon. *African Study Monographs* 25(1): 1–27.

Bonnefille, R. (2010). Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change* 72: 390–411.

Brink, M. (2010). *Ataenidia conferta (Benth.) Milne-Redh*. [Internet] Record from Protabase. Brink, M. & Achigan-Dako, E.G. (Editors). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, Netherlands. <http://database.prota.org/search.htm>. Accessed 4 August 2012.

Brugiere, D. & Sakom, D. (2001). Population density and nesting behaviour of lowland gorillas (Gorilla gorilla gorilla) in the Ngotto forest, Central African Republic. *Zoologial Journal London* 255: 251–259.

Caillaud, D., Levrero, F., Cristescu, R., Gatti, S., Dewas, M., Douadi, M., Gautier-Hion, A., Raymond, M. & Menard, N. (2006). Gorilla susceptibility to Ebola virus: The cost of sociality. *Current Biology* 16 (13): 489–491.

Calvert, J.J. (1985). Food selection by western gorillas (G. g. gorilla) in relation to food chemistry. *Oecologia* 65:236–246.

Costa, F. & Magnusson, W. (2002). Selective logging effects on abundance, diversity, and composition of tropical understorey herbs. *Ecological Applications* 12: 807–819.

Crawley, M.J. (1997a). The structure of plant communities. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Crawley, M.J. (1997b). Life history and environment. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Deblauwe, I. (2006). New evidence of honey-stick use by chimpanzees in Southeast Cameroon. *Pan Africa News* 13(1): 2–4.

Deblauwe, I., Dupain, J., Nguenang, G. M., Werdenich, D. & Van Elsacker, L. (2003). Insectivory by Gorilla gorilla gorilla in Southeast Cameroon. *International Journal of Primatology* 24(3): 493–502.

Deblauwe, I., Guislain, P., Dupain, J. & Van Elsacker, L. (2006). Use of a tool-set by Pan troglodytes troglodytes to obtain termites (Macrotermes) in the Periphery of the Dja Biosphere Reserve, Southeast Cameroon. *American Journal of Primatology* 68: 1191–1196.

Djoufack, S.D. (2003). *Végétation et distribution des nids de gorilles (Gorilla gorilla gorilla) dans la périphérie Nord de la Réserve de Biosphère du Dja*. Mémoire de DEA, Université de Yaoundé I, Yaoundé.

Doran, D.M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. & Shah, N. (2002). Western lowland gorilla diet and resource availability: New evidence, cross-Site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology* 58: 91–116.

Doran-Sheehy, D., Mongo, P., Lodwick, J. & Conklin-Brittain, N.L. (2009). Male and female western gorilla diet: preferred foods, use of fallback resources and implications for ape versus old world foraging strategies. *American Journal of Physical Anthropology* 140: 727–738.

Dupain, J., Guislain, P., Nguenang, G.M., De Vleeschouwer, K. & Van Elsacker, L. (2004). High chimpanzee and gorilla densities in a non-protected area of the northern periphery of the Dja Faunal Reserve, Cameroon. *Oryx* 38: 1–8.

FAO (2005). *Global forest resources assessment*. FAO, Rome.

Fay, J.M. (1997). *The ecology, social organization, populations, habitat and history of the western lowland gorilla (Gorilla gorilla gorilla Savage and Wyman 1847).* Ph. D. thesis. Washington University, St. Louis.

Fay, J.M. & Agnagna, M. (1992). Census of gorillas in northern Republic of Congo. *American Journal of Primatology* 27: 275–284.

Fitter, A. (1997). Nutrient acquisition. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Fomete, N. T. & Tchanou, Z. (1998). *La gestion des écosystèmes forestiers du Cameroun à l'aube de l'an 2000*. UICN, Gland et Cambridge.

Fowler, A. & Sommer, V. (2007). Subsistence technology of Nigerian chimpanzees. *International Journal of Primatology* 28: 997–1023.

Furuichi, T., Inagaki, H. & Angoue-Ovono, S. (1997). Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: employing a new method to distinguish between nests of the two species. *International Journal of Primatology* 18(6): 1029–1046.

Ganas, J., Robbins, M.M., Nkurunungi, J.B., Kaplin, B.A. & McNeilage, A. (2004). Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology* 25(5): 1043–1072.

Givnish, T. J. (1999). On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87: 193–210.

Groves, C.P. & Sabater Pi, J. (1985). From ape's nest to human fix-point. *Man* 20: 22–47.

Groves, C. & Meder, A. (2001). A model of gorilla life history. *Australian Primatology* 15: 2–15.

Harrison, M.E. & Marshall, A.J. (2011). Strategies for the use of fallback foods in apes. *International Journal of Primatology* 32: 531–565.

Head, J.S., Boesch, C., Makaga, L. & Robbins, M.M. (2011). Sympatric chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: dietary composition, seasonality, and intersite comparisons. *International Journal of Primatology* 32: 755–775.

Huijbregts, B., De Wachter P., Ndong Obiang L.S. & Akou, A.E. (2003). Ebola and the decline of gorilla (*Gorilla gorilla*) and chimpanzee (*Pan troglodytes*) populations in Minkebe forest, north-eastern Gabon. *Oryx* 37: 437–443.

Iwata, Y. & Ando, C. (2007). Bed and bed-site reuse by western lowland gorillas (*Gorilla g. gorilla*) in Moukalaba-Doudou National Park, Gabon. *Primates* 48: 77–80.

Johns, A.D. (1985). Selective logging and wildlife conservation in tropical rain-forest: problems and recommendations. *Biological Conservation* 31: 355–375.

Kent, M. & Coker, P. (1992). *Vegetation description and analysis. A practical approach*. Belhaven Press, London.

Kingdon, J. (1997). *The Kingdon field guide to African mammals*. Academic Press, London.

Koechlin, J. (1965). *Flore du Cameroun* (Vol.4). Muséum National d'Histoire Naturelle, Paris.

Koops, K., Humle, T., Sterck, E.H.M. & Matsuzawa, T. (2007). Ground-nesting by the chimpanzees of the Nimba Mountains, Guinea: environmentally or socially determined? *American Journal of Primatology* 69: 407–419.

Kuyper, T.W. & De Goede, R.G.M. (2005). Interaction between higher plants and soil-dwelling organisms. In: *Vegetation Ecology* (Ed. E. van der Maarel). Blackwell Publishing, Oxford.

Leendertz, F.H., Lankester, F., Guislain, P., Néel, C., Drori, O., Dupain, J., Speede, S., Reed, P., Wolfe, N., Loul, S., Mpoudi-Ngole, E., Peeters, M., Boesch, C., Pauli, G., Ellerbrok, H. & Leroy, E.M. (2006). Anthrax in western and Central African great apes. *American Journal of Primatology* 68: 928–933.

Letouzey, R. (1985). *Notice de la carte phytogéographique du Cameroun au 1 / 500 000. Domaine de forêt dense humide toujours verte*. Institut de la Carte Internationale de la Végétation, Toulouse.

Leuschner, C. (2005). Vegetation and ecosystems. In: *Vegetation Ecology* (Ed. E. van der Maarel). Blackwell Publishing, Oxford.

Malenky, R., Wrangham R., Chapman, C. & Vineberg, E. (1993). Measuring chimpanzee food abundance. *Tropics* 2: 231–244.

Marshall, A.J. & Wrangham, R.W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology* 28:1219–1235.

Matías, L. Quero, J.L., Zamora, R. & Castro, J. (2012). Evidence for plant traits driving specific drought resistance. A community field experiment*. Environmental and Experimental Botany* 81: 55–61.

McCune, B. & Grace, J.B. (2002). *Analysis of ecological communities*. MjM software design, Oregon.

McGinley, M. (2008). Dja Faunal Reserve. In: *Encyclopedia of Earth*. (Ed. C.J. Cleveland). United Nations Environment Programme–World Conservation Monitoring Centre. http://www/eoearth.org/article/Dja_Faunal_Reserve,_Cameroon.

McGrew, W. C., Marchant, L.F., Beuerlein, M.M., Vrancken, D., Fruth, B. & Hohmann, G. (2007). Prospects for bonobo insectivory: Lui Kotal, Democratic Republic of Congo. *International Journal of Primatology* 28:1237–1252.

Meers, T.L. Kasel, S., Bell, T.L. & Enright, N.J. (2010). Conversion of native forest to exotic Pinus radiata plantation: Response of understorey plant composition using a plant functional trait approach. *Forest Ecology and Management* 259: 399–409.

Moffatt, S.F. & McLachlan, S.M. (2004). Understorey indicators of disturbance for riparian forests along an urban–rural gradient in Manitoba. *Ecological Indicators* 4: 1–16.

Mooney, H.A. & Ehleringer, J.R. (1997). Photosynthesis. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Muchaal, P. & Ngandjui, G. (1999). Impact of village hunting on wildlife populations in the Western Dja Reserve, Cameroon. *Conservation Biology* 13(2): 385–396.

Muchiru, A.N., Western, D. & Reid, R.S. (2009). The impact of abandoned pastoral settlements on plant and nutrient succession in an African savanna ecosystem. *Journal of Arid Environments* 73: 322–331.

Musana, A. & Mutuyeyezu, A. (2011)*. Impact of climate change and climate variability on altitudinal ranging movements of mountain gorillas in Volcanoes National Park, Rwanda. Externship Report*. The International START Secretariat, Washington DC.

Nagendra, H. & Ostrom, E. (2011). The challenge of forest diagnostics. *Ecology and Society* 16(2): 20.

Nakaoka, M. (2005). Plant–animal interactions in seagrass beds: ongoing and future challenges for understanding population and community dynamics*. Population Ecology* 47: 167–177.

Nguenang, G. M. & Dupain, J. (2002). *Typologie et description morpho-structurale de la mosaïque forestière du Dja : Cas du site d'étude sur la socio-écologie des grands singes dans les villages Malen V, Doumo-pierre et Mimpala (Est-Cameroun).* Rapport interne. SRZA.

Nishihara, T. (1995). Feeding Ecology of Western Lowland Gorillas in the Nouabalé-Ndoki National Park, Congo. *Primates* 36(2): 151–168.

Nyaga, Y.A. (2004). *Analyse des facteurs socio-économiques et culturels qui conditionnent la gestion communautaire de la chasse villageoise: Cas des villages Malen V, Doumo-Pierre et Mimpala à la périphérie Nord de la Réserve de Biosphère du Dja.* Mémoire présenté en vue de l'obtention du diplôme d'Ingénieur des Eaux, Forêts et Chasse. Université de Dschang, Dschang.

Parnell, R.J. (2002). Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *American Journal of Primatology* 56: 193–206.

Poveda, K., Steffan-Dewentera, I., Scheub, S. & Tscharntke, T. (2005). Floral trait expression and plant fitness in response to below- and aboveground plant–animal interactions. *Perspectives in Plant Ecology, Evolution and Systematics* 7: 77–83.

Pruetz, J.D. & Lindshield, S. (2012). Plant-food and tool transfer among savanna chimpanzees at Fongoli, Senegal. *Primates* 53(2): 133–145.

Remis, M.J. (1997). Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *American Journal of Primatology* 43: 87–109.

Rogers, M.E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., McFarland, K., Nishihara, T., Remis, M. & Tutin, C.E.G. (2004). Western gorilla diet: A synthesis from six sites. *American Journal of Primatology* 64: 173–192.

Rogers, M.E., Maisels, F., Williamson, E.A., Fernandez, M. & Tutin, C.E.G. (1990). Gorilla diet in the Lopé Reserve, Gabon: a nutritional analysis. *Oecologia* 84: 326–339.

Rogers, M.E. & Williamson, E.A. (1987). Density of herbaceous plants eaten by gorillas in Gabon: Some preliminary data. *Biotropica* 19: 278–281.

Rogers, M.E., Williamson, E.A., Tutin, C.E.G. & Fernandez, M. (1988). Effects of the dry season on gorilla diet in Gabon. *Primates* 22: 25–33.

Rothman, J.M., Pell A.N., Dierenfeld, E.S. & McCann, C.M. (2006). Plant choice in the construction of night nests by gorillas in the Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology* 68: 361–368.

Sabater Pi, J. (1977). Contribution to the study of alimentation of lowland gorillas in the natural state, in Rio Muni, Republic of Equatorial Guinea (West Africa). *Primates* 18: 183–204.

Sanz, C.M . & Morgan D.B. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution* 52: 420–433.

Smallwood, P.D. (2001). An integrative approach to the study of plant-animal interactions. *American Zoologist* 41: 807–809.

Ticktin, T. & Nantel, P. (2004). Dynamics of harvested populations of the tropical understory herb *Aechmea magdalenae* in old-growth versus secondary forests. *Biological Conservation* 120: 461–470.

Tilman, D. (1983). Plant succession and gopher disturbance along an experimental gradient. *Oecologia* 60: 285 –292.

Tilman, D. (1997). Mechanisms of plant competition. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Tutin, C., Stokes, E., Boesch, C. Morgan, D., Sanz, C., Reed, T., Blom, A., Walsh, P., Blake, S. & Kormos, R. (2005). *Regional action plan for the conservation of chimpanzees and gorillas in Western Equatorial Africa*. Conservation International, Washington DC.

Tutin, C.E.G. (1998). Gorillas and their food plants in the Lopé Reserve, Gabon. In: *Chorology, Taxonomy and Ecology of the floras of Africa and Madagascar* (Eds. C.R. Huxley, J.M. Lock & D.F. Cutler). Royal Botanic Gardens, Kew.

Tutin, C.E.G. & Fernandez, M. (1985). Foods consumed by sympatric populations of *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon: some preliminary data. *International Journal of Primatolology* 6: 27–43.

Tutin, C.E.G. & Fernandez, M. (1992). Insect-eating by sympatric lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *American Journal of Primatology* 28: 29–40.

Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E.A. & McGrew, W.C. (1991b). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philosophical Transactions of the Royal Society of London, Series B* 334: 179–186.

Tutin, C.E.G., Ham, R. & Wrogemann, D. (1995a). Tool-use by chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *Primates* 36: 181–192.

Tutin, C.E.G., Parnell, R.J., White, L,J,T. & Fernandez, M. (1995b). Nest building by lowland gorillas in the Lopé Reserve, Gabon: environmental influences and implications for censusing. *International Journal of Primatology* 16(1): 53–76.

Tutin, C.E.G., White, L.J.T. & Mackanga-Missandzou, A. (1997). The use by rain forest mammals of natural forest fragments in an equatorial African savanna. *Conservation Biology* 11(5): 1190–1203.

Tutin, C.E.G., Williamson, E.A., Rogers, M.E. & Fernandez, M. (1991a). A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 7(2): 181–199.

UICN (2010). *Rapport préliminaire sur l'état de l'environnement en Afrique centrale*. UICN, Yaoundé.

Van Andel, J. (2005). Species interactions structuring plant communities. In: *Vegetation Ecology* (Ed. E. van der Maarel). Blackwell Publishing, Oxford.

Van Breugel, M., Van Breugel, P., Jansen, P.A., Martinez-Ramos, M. & Bongers, F. (2012). The relative importance of above- versus belowground competition for tree growth during early succession of a tropical moist forest. *Plant Ecology* 213:25–34.

Walsh, P.D., Abernethy, K.A. Bermejo, M., Beyers, R., Wachter, P.D., Akou, M.E., Huijbregts, B., Mambounga, D.I., Toham, A.K., Kilbourn, A.M., Lahm, S.A., Latour, S., Maisels, F., Mbina, C., Mihindou, Y., Obiang, S.N., Effa, E.N., Starkey, M.P., Telfer, P., Thibault, M., Tutin, C.E.G., White, L.J.T. & Wilkie, D.S. (2003). *Nature* 422: 611–614.

Walsh, P.D., Tutin, C.E.G., Baillie, J.E.M., Maisels, F., Stokes, E.J. & Gatti, S. (2008). Gorilla gorilla ssp. gorilla. In: *IUCN 2012. IUCN Red List of Threatened Species*. Version 2012.1. <www.iucnredlist.org>. Downloaded on 05 August 2012.

Watts, D. P. (1987). Effects of mountain gorilla foraging activities on the productivity of their food plant species. *African Journal of Ecology* 25: 155–163.

Webb, E.L., Van de Bult, M., Chutipong, W. & Kabir, Md.E. (2006). Composition and Structure of Lowland Rain-Forest Tree Communities on Ta'u, American Samoa. *Pacific Science* 60 (3): 333–354.

White, L.J.T. & Edwards, A. (2000). Vegetation inventory and description. In: *Conservation research in the African rain forests: a technical handbook* (Eds. L.J.T. White & A. Edwards). Wildlife Conservation Society, New York.

White, L.J.T., Rogers, M.E., Tutin, C.E.G., Williamson, E. & Fernandez, M. (1995). Herbaceous vegetation in different forest types in the Lopé Forest Reserve, Gabon: implications for keystone food availability. *African Journal of Ecology* 33: 124–141.

Williamson, E.A., Tutin, C.E.G., Rogers, M.E. & Fernandez, M. (1990). Composition of the diet of lowland gorillas at Lopé in Gabon. *American Journal of Primatology* 21: 265–277.

Willie, J. (2006). *Contribution à l'évaluation de l'incidence de la chasse sur les populations de céphalophes de la périphérie Nord de la Réserve du Dja (Est-Cameroun).* Mémoire présenté en vue de l'obtention du diplôme d'Ingénieur des Eaux, Forêts et Chasse. Université de Dschang, Dschang.

Wilson, S.D. & Tilman, D. (1991). Components of plant competition along an experimental gradient of nitrogen availability. *Oecologia* 88: 61–71.

Wrangham, R.W., Rogers, M.E. & Basuta, G.I. (1993). Ape food density in the ground layer in Kibale forest, Uganda. *African Journal of Ecology* 31: 49–57.

Wright, S.J. (1992). Seasonal drought, soil fertility and the species density of tropical forest plant communities. *Trends in Ecology and Evolution* 6: 159–152.

Botanical inventory in young secondary forest. © Fabrice Ottou, PGS

During field work, J. Willie was assisted by Master's students, PGS researchers and Badjué guides of Malen V, Doumo Pierre and Mimpala.

Chapter 1

Evaluation of species richness estimators based on quantitative performance measures and sensitivity to patchiness and sample grain size

Jacob Willie, Charles-Albert Petre, Nikki Tagg and Luc Lens

Modified from Willie et al. (2012). *Acta Oecologica* 45: 31–41

ABSTRACT

Data from forest herbaceous plants in a site of known species richness in Cameroon were used to test the performance of rarefaction and eight species richness estimators (ACE, ICE, Chao1, Chao2, Jack1, Jack2, Bootstrap and MM). Bias, accuracy, precision and sensitivity to patchiness and sample grain size were the evaluation criteria. An evaluation of the effects of sampling effort and patchiness on diversity estimation is also provided. Stems were identified and counted in linear series of 1-m^2 contiguous square plots distributed in six habitat types. Initially, 500 plots were sampled in each habitat type. The sampling process was monitored using rarefaction and a set of richness estimator curves. Curves from the first dataset suggested adequate sampling in riparian forest only. Additional plots ranging from 523 to 2143 were subsequently added in the undersampled habitats until most of the curves stabilized. Jack1 and ICE, the non-parametric richness estimators, performed better, being more accurate and less sensitive to patchiness and sample grain size, and significantly reducing biases that could not be detected by rarefaction and other estimators. This study confirms the usefulness of non-parametric incidence-based estimators, and recommends Jack1 or ICE alongside rarefaction while describing taxon richness and comparing results across areas sampled using similar or different grain sizes. As patchiness varied across habitat types, accurate estimations of diversity did not require the same number of plots. We suggest that communities should first be sampled thoroughly using appropriate taxon sampling curves before explaining differences in diversity.

INTRODUCTION

Tropical biodiversity is being depleted at an alarming rate resulting in a crisis that highly preoccupies conservation biologists (Laurance & Wright, 2009). Lack of knowledge and detailed information on which to base management decisions regarding the flora of a particular site have been described, among other factors, as important threats to species survival (Broughton & McAdam, 2002). Survey work which is commonly carried out to define population status enables species to be determined as endangered or not, thus providing detailed biological data on which to base land-management decisions (Broughton & McAdam, 2002). Such decisions tend to be made using biodiversity richness for areas such as landscapes, reserves or parks (Colwell & Coddington, 1994). The critical and timely task of assessing global biodiversity therefore requires us to maximize the usefulness of our knowledge of small areas using estimation and extrapolation from censuses (Colwell & Coddington, 1994).

However, biodiversity data are often uneven and biased due to sampling artifacts (Rosenzweig, 2003; Hortal et al., 2007; 2008; Borges et al., 2009), and sampling protocols vary widely between studies. Common protocols include uniform sampling (balanced, equal or constant sampling effort), or proportional sampling, a method in which sampling effort is proportional to the area being sampled (Borges et al., 2009; Nufio et al., 2009). Nufio et al. (2009) made a critical assessment of these methods and found that both have similar inherent shortcomings including failure to determine inventory completeness and true species richness. Consequently, the observed picture of richness patterns emerging from studies has most often been different from the real one, resulting in incomplete descriptions of species niches, conservation theories severely underestimating the proportion of diversity that is at threat and many recommendations being biologically incorrect (Rosenzweig, 2003; Hortal et al., 2008; Borges et al., 2009). This emphasizes the need to accurately describe diversity and estimate the status of species by avoiding such constraints as sample-size bias. In this respect, Nufio et al. (2009) suggested the use of readily-available rarefaction and estimation tools which have been developed to assess census completeness and provide more accurate estimations of diversity (Colwell & Coddington, 1994; Chazdon et al., 1998; Colwell et al., 2004; Chao et al., 2005; Mao et al., 2005). They are generally referred to as species richness estimators.

Studies on species richness have been performed, but species richness estimations are lacking (Chiarucci et al., 2001). Although these novel approaches have been ignored in many studies, some pilot studies have emphasized the importance of carefully using species richness estimators to quantify biodiversity (Chazdon et al., 1998; Gotelli & Colwell, 2001), and some researchers have begun to apply them over the last two decades (e.g. Butler & Chazdon, 1998; Hofer & Bersier, 2001; Williams et al., 2007; Loya & Jules, 2008; Zhao et al., 2010). However, errors have been repeatedly made in choosing the appropriate tools, applying them and interpreting the results, and this has led to some misleading conclusions, as noted by Gotelli & Colwell (2001).

Chiarucci et al. (2001) tested the use of species richness estimators on floristic datasets. Although non-parametric estimators seemed to be more accurate, the power of different estimation methods was not definitively determined due to the small datasets used. According to Chazdon et al. (1998), useful evaluation of species richness estimators is possible in cases where thorough surveys of delimited areas have been done. Brose (2002) provided an evaluation of species richness estimators based on a pitfall trapping program of carabid beetles in a small habitat. He also found that non-parametric estimators, relative to other estimators, performed much better and significantly reduced the bias, but he suggested further investigations be carried out in order to determine if this conclusion could also be true for other taxonomic groups sampled using different methods and for larger habitats. Williams et al. (2007) used ethnobotanical data and showed that an asymptotic estimator was the best estimator because the curve approached a horizontal asymptote. However it did not perform well relative to a non-parametric estimator for one of the datasets when two of its subsamples were individually tested.

Walther & Moore (2005) highlighted common mistakes and limitations of many previous studies evaluating the performance of richness estimators. These included the lack of details on data simulation models and resampling schemes, the small number of estimators being compared and the lack of information on performance measures and their mathematical expressions. Moreover, the results were not scaled or were mostly presented in figures instead of numerical tables. This has led to confusing and incomparable results. Therefore, although their use for various datasets has been supported, it is apparent that the overall usefulness of species richness estimators requires further investigation using quantifiable performance measures. Studies using different datasets collected in various habitat types are still required in order to confirm the validity and generalization of previous conclusions.

The objective of this study is to test the performance of rarefaction and eight richness estimators (ACE, ICE, Chao1, Chao2, Jack1, Jack2, Bootstrap and MM) using a large understory herbaceous vegetation dataset obtained from a small area (about 40 km^2) of tropical forest habitat. Data from previous intensive floristic investigations (Djoufack, 2003; Ottou, 2009) and empirical observations reveal the existence of 22 *Marantaceae* and *Zingiberaceae* species in this site. As the actual *Marantaceae* and *Zingiberaceae* species richness of the study site is known with some certainty, testing the performance of the species richness estimators using inventory data of herbs from these two families is straightforward (Walther & Moore, 2005): an unbiased and accurate prediction of species richness (even for relatively lower levels of sampling effort) will suggest a good richness estimator. Given that previous evaluations of species richness estimators presented in the literature lacked information on performance measures or formulae and tested only a few estimators, this study offers a unique and thorough description of the differing properties of many richness estimators based on quantitative and qualitative performance measures and contributes to the determination of the appropriateness of these analytical tools for addressing biodiversity questions. Because patchiness and sampling effort affect the performance of richness estimators (Chazdon et al., 1998), we also provide an explicit evaluation of their effects on diversity estimation. This helps to assess the degree to which observed richness differences between habitat types can be attributed to differences in overall density or to differences in patchiness. Lastly, this study assesses the effect of variation in sample grain size on species richness estimators and provides helpful information for assessing survey exhaustiveness and determining adequate sampling efforts for valid comparisons among community types.

MATERIAL AND METHODS

Study area and species

Research was carried out in the northern periphery of the Dja Biosphere Reserve (DBR, 5260 km^2), Cameroon, specifically in the *Projet Grands Singes* (PGS) 'La Belgique' research site (about 40 km^2) located between 013°07'–013°11' E and 03°23'–03°27' N. This zone is located in the transition zone between the semi-deciduous forests of Equatorial Guinea and the evergreen forests of the Congo basin (Letouzey, 1985). The climate is equatorial and humid. Climatic data collected in the site from April 2009 to March 2010 show that rainfall is 1563 mm, with average temperatures ranging between 19.8 °C and 27.0 °C. The Dja forest is situated on the Precambrian plateau; its altitude varies from 600 m to 700 m and relief is characterized by shallow valleys (Fomete & Tchanou, 1998).

For the purpose of this study we targeted all species of *Marantaceae* and *Zingiberaceae* families and recorded a total of 22 species (14 *Marantaceae*; 8 *Zingiberaceae*). These species are perennial herbs and vines found in the rainforest understory and in flooded habitats; they can occur as clumps with individuals of > 2 m in height (see Koechlin [1965] for details). Some species of *Marantaceae* have many ramets. Ramets for each genetic individual always have a common base, which helps to differentiate between individuals during herb surveys.

Habitat types

Following previous vegetation classifications in the area (Nguenang & Dupain, 2002; Djoufack, 2003; Dupain et al., 2004), we distinguished six habitat types: 1) Near primary forest (NPF), where large tree species of height > 30 m predominate (e.g. *Polyalthia suaveolens*, *Omphalocarpum procerum*, *Uapaca* spp. and *Piptadeniastrum africanum*), and there is little undergrowth and a closed canopy; 2) Old secondary forest (OSF), with dominant canopy trees of height 25−30 m (e.g. *Terminalia superba*), a more dense understory than NPF, and a discontinuous canopy layer; 3) Young secondary forest (YSF), characterized by a canopy height of < 25 m dominated by early successional trees (e.g. *Myrianthus arboreus*, *Tabernaemontana crassa*), and a relatively dense undergrowth; 4) Light gaps (LG), with completely open canopies resulting from elephant activity or tree and branch fall; 5) Swamps (SW), with high densities of *Raphia* spp., rare (< 5%) raphia-free open areas (clearings), and a hydromorphic soil; and 6) Riparian forest (RF), growing in the transition zone between SW and other habitat types, with a highly heterogeneous floristic composition comprising species from all habitat types. NPF, OSF, YSF and LG are referred to collectively as *terra firma* habitats. SW and RF are (periodically) flooded habitats.

Sampling protocol

Species of Marantaceae and Zingiberaceae were sampled using a stratified sampling design. In November 2007, we identified and counted herb stems in a number of patches of each habitat type using a linear series of 1-m^2 contiguous square plots. In each case, plot direction avoided trails. We sampled each habitat type sporadically across the study area rather than sampling densely within a restricted portion of the site. Initially, 500 plots were sampled in each habitat type. For the undersampled habitat types, additional plots ranging from 523 to 2143 were subsequently surveyed in new patches until sampling was considered adequate (see below). All species were identified on the ground by the same trained local guides using consistent local names, and scientific names were later confirmed and assigned at the National Herbarium of Yaoundé, Cameroon.

Rarefaction and species richness estimators

We attempted to estimate species richness from our herb data in order to test the estimators and study diversity across habitat types. Michaelis–Menten asymptote (MM) and non-parametric methods were used as estimators of richness. Observed species richness was assessed using rarefaction (individual-based). Aside from rarefaction, all richness estimators were computed in EstimateS 8.2 (Colwell, 2009).

Rarefaction (individual-based) estimates the number of species observed for any smaller number of individuals, assuming that they are randomly mixed (see Colwell et al. [2004] and references therein). To obtain individual-based rarefaction estimates, the pool of n individuals is repeatedly re-sampled at random, and the average number of species represented by 1, 2,…, n individuals is calculated (Gotelli & Colwell, 2001). Rarefaction estimates were computed in EcoSim 7.72 (Gotelli & Entsminger, 2011) using the independent sampling algorithm. This software produces a computer-sampling algorithm of rarefaction, with a specified number of individuals randomly drawn from a community sample. This process is repeated several times to derive means and variances of species diversity indices. In each abundance level, simulations consisted of 1000 iterations.

Michaelis–Menten asymptote (MM) is the estimated true species richness (Colwell & Coddington, 1994); this asymptotic estimator was computed for each level of sample pooling using an asymptotic function (the Michaelis-Menten equation). Therefore, asymptotic estimates of total richness were generated for each pooling level and the average values among randomizations were used as final estimates.

Non-parametric richness estimators included the incidence-based estimators: first-order Jacknife (hereafter Jack1), second-order Jacknife (Jack2), Chao2, Bootstrap and Incidence-based coverage estimator, (ICE); and the abundance-based estimators: abundance-based coverage estimator (ACE) and Chao1 (see Colwell & Coddington, 1994 and Chazdon et al., 1998). Incidence-based estimators only require presence/absence data, whereas abundance-based estimators require relative abundance data. Estimating species richness using non-parametric methods requires the determination of the number of unseen species that are likely to be present in a larger sample of the community, but that are not found in the actual sample data (Chazdon et al., 1998; Chao et al., 2005). Non-parametric richness estimations are influenced by the proportion of discovered rare species (Chazdon et al., 1998).

The occurrence of rare species such as Uniques (species found in one plot) and Duplicates (species found in two plots) during the sampling process was also monitored. All estimators were computed in EstimateS 8.2 (Colwell, 2009). To generate independent richness estimates for performance measure calculation, sampling was done with replacement (Walther & Moore, 2005), and simulations consisted of 1000 runs.

Performance measures

We used bias, accuracy and precision as quantitative performance measures (see Walther & Moore, 2005 for more details). In addition, sensitivity to patchiness was used as a qualitative performance measure. As emphasized by these authors, the performance of estimators should be tested when estimates are still increasing, thereby providing informative performances. To exclude levels of sampling effort near the asymptote, sampling effort levels were truncated and only the first 50% of sampling effort levels were used to test the estimators. In order to compare between habitat types, with varying levels of species richness, performance measures of each estimator were calculated at each level of sampling effort and scaled. Each performance measure was then averaged over all levels of sampling effort. For each estimator, bias was defined as the mean error (ME), which is the mean of all differences between the estimated species richness values and the true value. Scaled bias was then calculated as

$$\mathrm{SME} = \frac{1}{\mathrm{An}}\sum_{j=1}^{n}\left(\mathrm{E_j} - \mathrm{A}\right)$$

where $\mathrm{E_j}$ is the mean estimated species richness for the $\mathrm{j^{th}}$ sample (computed from 1000 estimates derived from 1000 runs of randomized sampling order), A is the true species richness and n is the number of samples. Precision was used to provide statistical variances of species richness estimates. The coefficient of variation (CV) was used as a measure of scaled precision using the formula $\mathrm{CV} = 100SD/\mathrm{E}$, where E and SD are the mean and standard deviation of the estimates, respectively. The smaller the CV of an estimator, the higher its precision. The mean square error (MSE) was used as a measure of accuracy to assess how close species richness estimates are to the true value.

Scaled accuracy was then measured as

$$\mathrm{SMSE} = \frac{1}{\mathrm{A}^2\mathrm{n}}\sum_{j=1}^{n}\left(\mathrm{E_j} - \mathrm{A}\right)^2.$$

Performance measures were calculated for each habitat type separately and averages computed for all habitat types to give the overall estimator performance. We considered an estimator as a good one if it was unbiased or less biased (lower positive or higher negative value of SME) and accurate (lower value of SMSE), even for relatively low levels of sampling effort. Precision and sensitivity to patchiness and sample grain size (see below) were secondary criteria used to classify estimators.

Species richness estimations at different sample grain sizes

We defined seven grain sizes (i.e. sampling effort units; see Hortal et al. [2006] and references therein) to assess the effect of variation in sample grain size on species richness estimators. For each habitat type, the final dataset (1 m^2 plots) was the first grain size; these plots were subsequently grouped in grains of 4, 8, 16, 32, 64 and 128 m^2 by computing the sum of stems for each species at each level of grouping. For each grain, species richness estimates were computed in EstimateS; sampling was done with replacement and simulations consisted of 1000 runs. For each species richness estimator, richness estimates from all grain sizes were pooled together and the standard deviation (*SD*) was computed. Best estimators are those with smaller *SDs* (higher precision), indicating little variability in the estimates (Hortal et al., 2006).

Sampling adequacy

The level of completeness of censuses (sampling adequacy) was assessed for each forest type by studying the behavior of rarefaction and species richness estimator curves. So in addition to rarefaction, three non-parametric richness estimators

(ICE, Jack1 and Jack 2) and the asymptotic (MM) curves were fitted. Only incidence-based non-parametric estimators were chosen for this purpose because they are less sensitive to patchiness (Chazdon et al., 1998). However all sampling curves were computed in EstimateS using the default setting of sampling without replacement (e.g. Gotelli & Colwell, 2001; Loya & Jules, 2008). Although sample-based abundance data were used, EstimateS 8.2 computed the number of individuals for each level of sample pooling, allowing re-scaling of the x-axis and presentation of sampling effort in terms of number of individuals in order to represent species richness (Gotelli & Colwell, 2001).

By assessing the changes to these curves throughout the sampling process, their performance and usefulness for sampling purposes were also described. Sampling was considered adequate in a given habitat when the curves approached a horizontal asymptote (Gotelli & Colwell, 2001) because at that level it is less likely that the next individual sampled represents a new species (Colwell & Coddington, 1994; Williams et al., 2007). Thus, still-rising curves indicated inadequate sampling. However when the curves failed to stabilize completely, the close convergence of observed and estimated richness was still an indication of a relatively adequate sampling (Longino et al., 2002). Number of rare species in the dataset normally rises quickly with increasing sampling effort, then stabilizes and decreases as true richness is approached (Colwell & Coddington, 1994; Walther & Moore, 2005; Loya & Jules, 2008).

Average species richness and patchiness

Average species richness values for each habitat type were calculated in EcoSim 7.72 (Gotelli & Entsminger, 2011) once all species richness estimator curves indicated adequate sampling. Because the number of individuals collected affects most species diversity indices, resulting in erroneous comparisons of diversity indices in datasets of different samples size (Rosenzweig, 2003; Gotelli & Entsminger, 2011), we used the same number of individuals in all habitats to calculate diversity indices. For each habitat type, the simulation consisted of 1000 iterations of a single abundance level.

In order to derive patchiness values, we first calculated species evenness in each habitat type. The Probability of Interspecific Encounters (PIE) of Hurlbert (1971) was used as an index of evenness and was computed in EcoSim 7.72. This index is the probability that two randomly sampled individuals from a given habitat type represent two different species. The more random the species' distributions, the higher the resulting PIE value. Based on this assumption, we derived a coefficient of non-randomness as $(1 - \text{PIE}) \times 100$. This coefficient represents patchiness score and measures the degree of non-randomness of species distributions in each habitat type.

Spatial autocorrelation

For each habitat, we calculated a Moran's I score of spatial autocorrelation (Z_I) to assess patterns of similarity in number of species per plot. In each habitat type, the lag distance was constant (5 m; the last plot in each series of 5 consecutively surveyed 1-m^2 plots). Values of Z_I were calculated based on the number of species per plot, and tested for significance in SAS 9.2 using the variogram procedure. Negative values of Z_I (negative autocorrelation) highlight patterns of dissimilarity and positive values (positive autocorrelation) indicate that neighboring plots are more alike.

RESULTS

Rarefaction and MM curves were still rising in swamps (Fig. 1.1f), after the initial census of 500 plots, but approached an asymptote in many other habitat types, suggesting nearly all species had been discovered and that sampling was adequate in these habitats. However ICE, Jack1 and Jack2 curves did not stabilize, except in riparian forest (Fig.1.1e). Taken together, all the curves suggested that only riparian forest was thoroughly sampled after the initial census of 500 plots. Additional plots were therefore surveyed in the undersampled habitats, with a final sampling effort ranging from 1023 plots in light gaps to 2643 plots in near primary forest (Table 1.1). This resulted in the curves for observed richness (rarefaction) and estimated richness (MM, ICE and Jack 1) nearly stabilizing or converging in all habitat types (Fig. 1.2), suggesting a relatively adequate sampling of herbaceous vegetation. Nevertheless Jack 2 did not stabilize in most cases.

As indicated by rarefaction curves, the number of observed species increased in near primary forest, young secondary forest and swamps (Fig. 1.1 & 1.2; numerical results presented in Appendix I), but subsequent censuses in old secondary forest and light gaps did not result in the discovery of new species. Number of rare species remained constant in light gaps and slightly decreased in other habitat types despite increasing levels of sampling effort (Table 1.1).

The highest species richness was observed in riparian forest with an average number of 18 species and a corresponding patchiness score of 12, the lowest among all habitat types (Table 1.1). This habitat also exhibited the lowest sampling effort, in terms of both the number of plots and the number of individuals. Near primary forest showed an opposite trend, with the lowest richness of 13.41 species and the highest patchiness value of 22. The remaining habitats, old secondary forest, young secondary forest, light gaps and swamps, presented intermediate patterns of patchiness and sampling effort. Moran's I scores of spatial autocorrelation were high in near primary and riparian forest, and low in other habitat types (Table 1.1).

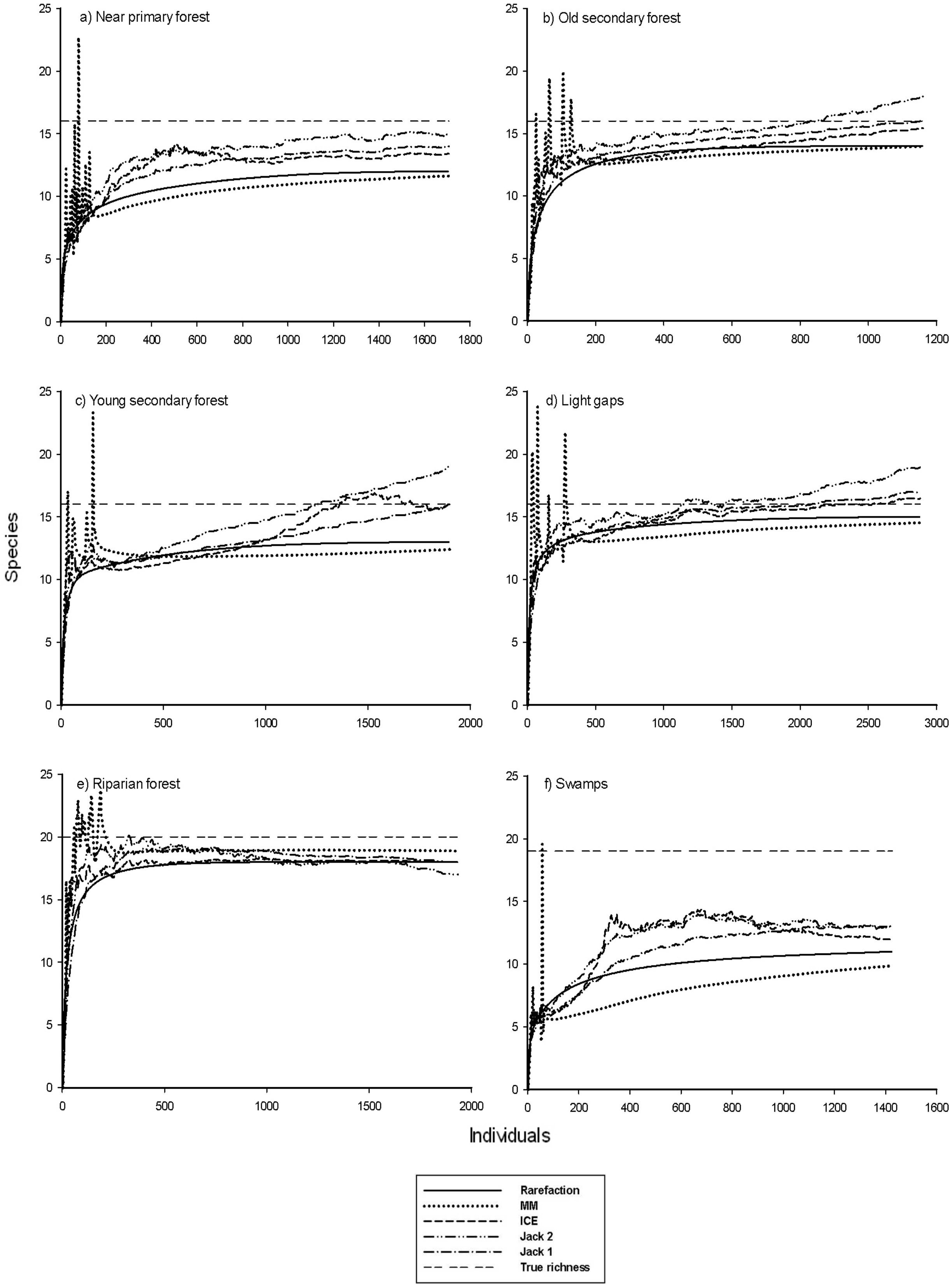


Fig.1.1 Rarefaction and species richness estimator curves for each habitat type based on data from the first set of plots.

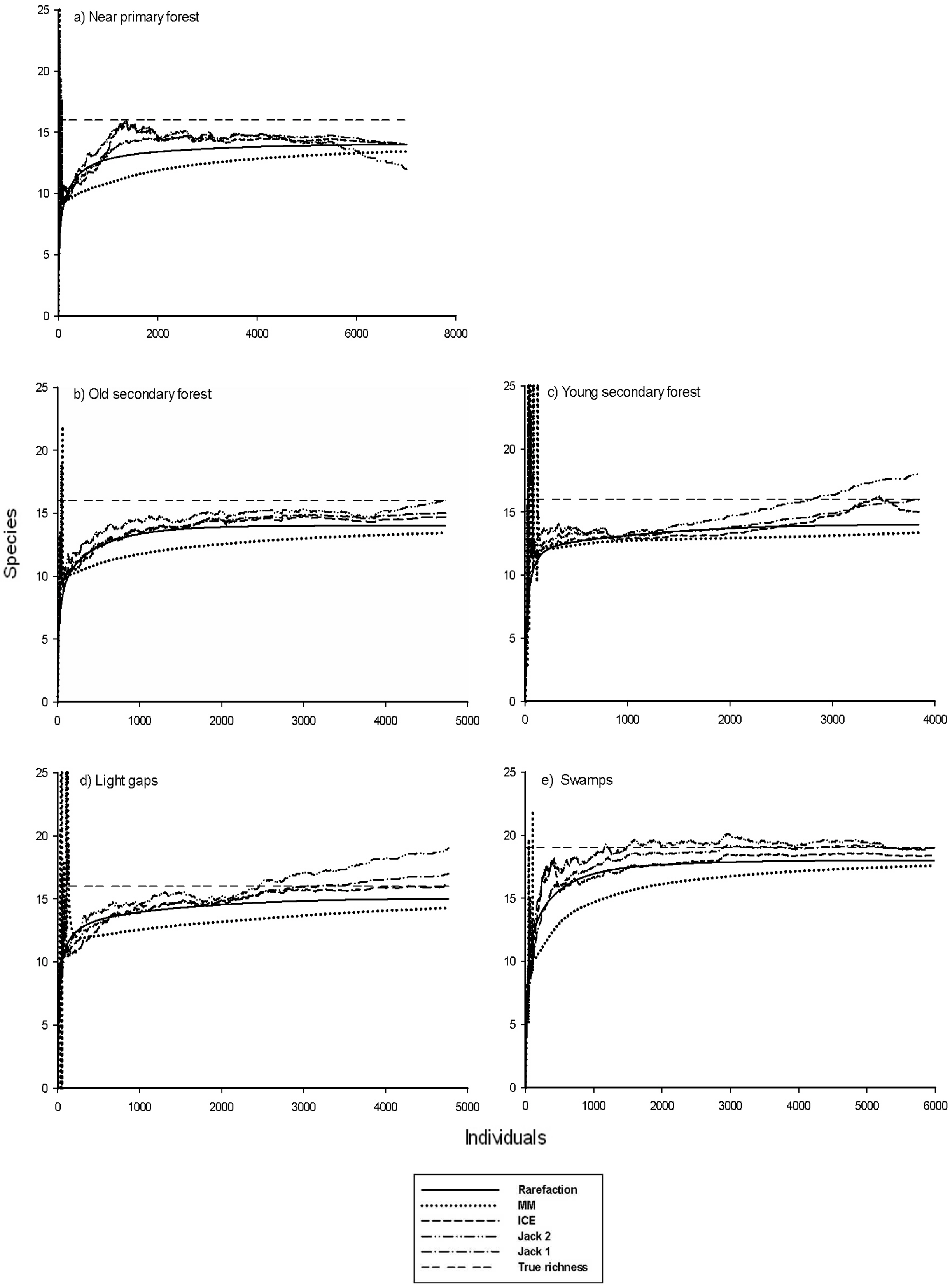


Fig.1.2 Rarefaction and species richness estimator curves for each habitat type at final sampling effort.

Table 1.1 Final sampling effort and diversity patterns across habitat types. 500 plots were initially sampled in each habitat type. Additional plots were added in all habitat types, except in riparian forest. Rare species are those found in only one or two plots. Species richness is the total number of species found in a habitat type. Patchiness scores can vary from 0 (perfectly random species distribution) to 100 (highest degree of non-randomness). Average species richness values and patchiness scores were estimated at final sampling effort, based on 1935 individuals, the smallest number of individuals among all habitat types. Positive values of Z_I suggest that plots are similar in terms of species density. Significance levels are indicated by *P*-values.

Parameter	**Near primary forest**	**Old secondary forest**	**Young secondary forest**	**Light gaps**	**Riparian forest**	**Swamps**
Total number of plots	2643	1582	1170	1023	500	1754
Total number of individuals	7005	4731	3844	4769	1935	5985
Number of rare species at initial sampling effort	3	2	3	2	1	4
Number of rare species at final sampling effort	2	1	2	2	–	2
Average species richness	13.41	13.89	13.68	14.52	18.00	17.68
Patchiness score	22	20	17	16	12	18
Moran's I score (Z_I)	4.68	1.57	1.26	1.94	3.04	1.74
P-value	<0.0001	0.115	0.207	0.052	0.002	0.083

Table 1.2 Overall performance measures of rarefaction and richness estimators. For each estimator, scaled performance measures were calculated in six habitat types and the average was saved as the overall performance measure. Detailed results for each habitat type are presented in Appendix II. Precision was not computed for MM because EstimateS did not yield a standard deviation for this estimator. Rarefaction results are shown to allow for comparisons. Higher negative values indicate lower levels of bias, while lower values of accuracy and precision indices indicate higher levels of accuracy and precision, respectively.

Estimator	**Bias**	**Accuracy**	**Precision**
Rarefaction	–0.19	0.06	5.42
ACE	–0.26	0.08	10.68
ICE	–0.18	0.04	18.41
Chao1	–0.27	0.09	1.87
Chao2	–0.21	0.06	13.06
Jack1	–0.17	0.04	8.44
Jack2	–0.13	0.03	21.88
Bootstrap	–0.22	0.06	10.80
MM	–0.19	0.14	–

Although species overlap was very high among habitat types, some exceptions did occur. Survey data and empirical observations in the field showed that *Ataenidia conferta, Marantochloa congensis, Aframomum* sp., *A. polyanthum, Halopegia azurea* and *Trachyphrynium braunianum* were indicative of and restricted to flooded habitats, a trend confirming the results of Djoufack (2003) and Ottou (2009) in the study site. These six species did not occur in *terra firma* habitats where 'true species richness' was limited to 16 species in each habitat. Similarly *Marantochloa filipes* and *Afrocalathea rhizantha* were restricted to *terra firma* habitats, and *Aframomum* sp. was restricted to riparian forest. As a result, 'true species richness values' in swamps and riparian forest were respectively 19 and 20.

Performance measures for each richness estimator were calculated in each habitat type based on true species richness values; in most cases, detailed results did not show important variations and the results were therefore summarized (Table 1.2; see Appendix II for detailed results). Although Jack2 was less biased and more accurate among the richness estimators, it exhibited the lowest degree of precision (Table 1.2); Jack2 was followed by Jack1 and ICE. On the contrary, Chao1 yielded the highest bias and the lowest accuracy, but was superior in precision compared to all other estimators. Rarefaction had better or equal performance in terms of bias, precision and accuracy compared to ACE, Chao2, Bootstrap and MM. MM was the most inaccurate estimator. Values of *SD* for all estimators tended to vary across habitat types, with consistently higher values in riparian forest (Table 1.3). Overall, ICE had the lowest *SD*, followed by Chao2, Jack2 and Jack1. MM exhibited the highest *SD*.

DISCUSSION

Performance of species richness estimators

Chao1, ACE, Bootstrap, Chao2 and MM performed very badly in terms of bias and accuracy (Table 1.2); among the non-parametric richness estimators, the abundance-based (ACE, Chao1) were highly biased and less accurate (although more precise) compared to the incidence-based estimators. The ranking of rarefaction and richness estimators in decreasing order of performance based on bias and accuracy is thus: Jack2, Jack1, ICE, rarefaction, Chao2, Bootstrap, MM, ACE and Chao1. Jack2 did not stabilize at final sampling effort, except in swamps where the number of rare species decreased slightly more, because it was more sensitive to patchiness. Although Jack2 best predicted species richness (lowest bias and highest accuracy), it was the most imprecise estimator and was very sensitive to patchiness (Table 1.2, Fig. 1.1 & 1.2). Assessing sampling thoroughness using Jack2 curves in habitats with highly patchy species distribution can therefore be misleading. However, the next two 'high scorers' for bias and accuracy, Jack 1 and ICE, presented curves which were moderately insensitive to patchiness and nearly stabilized in most cases, despite the persistence of rare species in the final dataset (Fig. 1.2). They had similar levels of bias and accuracy, and Jack1 was more precise. On the other hand, ICE richness estimates were highly independent of sample grain size (Table 1.3). The ranking of species richness estimators in decreasing degrees of independence from grain size is ICE, Chao2, Jack2, Jack1, Bootstrap, ACE, Chao1 and MM. This ranking suggests that non-parametric estimators were less sensitive to sample grain size compared to the asymptotic MM, and that among non-parametric estimators, incidence-based (ICE, Chao2, Jack2, Jack1 and Bootstrap) performed better than abundance-based (ACE and Chao1). Therefore, based on quantitative performance measures (bias, accuracy, precision) and the degree of sensitivity to patchiness and sample grain size, our results show that Jack1 and ICE are the ideal richness estimators. These findings reinforce the important points made by Chazdon et al. (1998), Walther & Martin (2001), Brose (2002), Walther & Moore (2005) and Williams et al. (2007) who suggested that non-parametric estimators have better performance than observed and asymptotic estimators, as they are less biased and more accurate, and they best approximate true richness. Interestingly, the small variability in the richness estimates given by these estimators supports the results of Hortal et al. (2006) who showed that these estimators, among others, are insensitive to sample unit size, yielding precise richness scores despite differences in sampling protocols. These findings emphasize the necessity of using species richness estimators in macro-ecological comparisons of diversity as sample grain size varies between studies. We therefore confirm and recommend Jack1 and ICE as the best estimators for diversity studies. They should however be used along with the rarefaction curve.

Table 1.3*SD* of species richness estimates obtained with the seven grains in each habitat type. For each habitat type, species richness estimates were computed seven times using data aggregated in 1, 4, 8, 16, 32, 64 and 128 m^2 plots. Results yielded by EstimateS for each estimator in each habitat type were pooled together to derive a standard deviation (*SD*). Low values of *SD* indicate small variability in the estimates.

Habitat	**ACE**	**ICE**	**Chao1**	**Chao2**	**Jack1**	**Jack2**	**Bootstrap**	**MM**
Near primary forest	1.55	1.21	1.56	1.35	1.32	1.21	1.47	3.89
Old secondary forest	1.42	1.25	1.50	1.33	1.25	1.25	1.40	1.25
Young secondary forest	1.32	1.23	1.36	1.21	1.10	1.25	1.24	1.53
Light gaps	1.63	1.68	1.68	1.74	1.46	1.54	1.59	3.38
Riparian forest	2.93	2.30	2.94	2.01	2.45	2.46	2.76	10.50
Swamps	2.49	1.64	2.53	1.91	2.09	1.88	2.36	1.95
Average value	1.89	1.55	1.93	1.59	1.61	1.60	1.80	3.75

Taxon sampling curves, sampling effort and survey exhaustiveness

Rarefaction and MM curves displayed similar patterns of species richness in all but one habitat type, swamps, based on the initial sampling effort of 500 plots (Fig. 1.1). Rarefaction curves stabilized in all habitat types. These curves were already suggesting that almost all habitat types were adequately sampled. Yet additional sampling revealed more species in near primary forest, young secondary forest and swamps. Moreover, in all habitat types, rarefaction and MM curves did not reach true species richness, even at final sampling effort. Rarefaction and MM curves tended to stabilize relatively earlier before true richness was reached. Therefore these curves alone cannot be used to ascertain sampling thoroughness. As discussed by Chazdon et al. (1998) and Loya and Jules (2008), comparisons of community types based strictly on observed richness can result to misleading conclusions.

Because there were still considerable numbers of rare species at initial sampling effort for most habitat types, it is likely that other species were present that were not captured by the earlier surveys (Gotelli & Colwell, 2001). A similar conclusion could be drawn in considering Jack1, Jack2 and ICE curves. At final sampling effort in some habitat types, species richness patterns changed; for example there was a drastic increase in swamps. Rarefaction, MM, Jack1 and ICE nearly converged in some cases (Fig. 1.2a, b, e), indicating the same pattern of species richness. Longino et al. (2002) also observed a similar convergence at large sample size. Jack1, Jack2 and ICE estimator curves helped to detect sampling biases that could not be detected by rarefaction and MM curves. In addition, they approached true richness sooner. These non-parametric richness estimator curves are therefore informative and appropriate tools for assessing survey exhaustiveness. These curves should stabilize to indicate adequate sampling.

At final sampling effort, the total number of plots differed between habitat types (Table 1.1). In habitats with patchy species distributions, accurate estimations of species richness require a large number of samples because species accumulation curves will rise slowly (Chazdon et al., 1998). For example, small-scale patches of individual species in near primary forest resulted in a higher number of samples (Table 1.1). The more we surveyed near primary forest, sampling all over the area, the more species were identified and the greater the observed species richness became. Before the richness estimator curves stabilized, they suggested that some species occurring in a given habitat could also occur in others. This assumption was subsequently confirmed after 'adequately' sampling all habitats. These results show that the number of samples needed to fully describe diversity varies between community types. This is likely to be due to idiosyncratic differences (Loya & Jules, 2008). The number of samples needed to fully capture diversity per habitat type should not necessarily be the same, and can only be known when taxon sampling curves have indicated adequate sampling. Balanced sampling designs may result in rich habitats being undersampled (Turner & Tjørve, 2005), and sampling protocols should not be guided by balanced designs in order to avoid biases resulting from sampling artifacts. As advocated by previous researchers (Colwell & Coddington, 1994; Walther & Martin, 2001), our results show that samples of insufficient size can consistently underestimate richness. Our sampling protocol indicates that many small samples distributed over a large area provide greater accuracy and precision in species richness estimations, confirming the trend already observed by Butler and Chazdon (1998) while studying species richness of the soil seed bank in Costa Rica.

Effect of sampling effort and patchiness on richness estimators and diversity estimation

Attention should be drawn to the fact that the number of rare species remained constant or slightly decreased in many cases at the highest level of sampling effort (Table 1.1), which may be interpreted as inadequate sampling. However, this is not necessarily the case. For instance, in old secondary forest and light gaps, additional sampling effort did not result in the discovery of new species. At final sampling effort, the number of rare species slightly decreased in near primary forest (Table 1.1). This may be a result of a high degree of patchiness; a less random (patchier) species distribution leads to a lower probability of multi-sampling that species. It is also likely that numbers of rare species did not drastically change in young secondary forest, light gaps and swamps as a result of patchiness. Still-rising Jack1, Jack2 and ICE curves (Fig. 1.2) under such circumstances therefore did not indicate undersampling. They occurred simply as a result of the presence of truly rare species, as these estimators are strongly influenced by the proportion of rare species. In fact, communities in general have few widespread species and many rare species due to the law of infrequency (Palmer, 1995). This lack of stabilization of estimator curves due to patchiness can be regarded as a limitation of richness estimators (Chazdon et al., 1998). Caution should therefore be taken in applying and interpreting any species richness estimator, especially in habitats with highly patchy species distributions (Chazdon et al., 1998). Nevertheless, still-rising curves can be considered as lower-bound estimates of richness, which can be of some use, or can be re-scaled to allow comparisons (Gotelli & Colwell, 2001; Longino et al., 2002); datasets can also be restricted to samples that are ecologically more homogeneous to have asymptotic curves (Gotelli & Colwell, 2001).

Average species richness in young secondary forest was slightly lower than old secondary forest (Table 1.1). But the possibility that old secondary forest is not actually richer than young secondary forest can be examined by looking at sampling effort and patchiness. Although richness was higher in old secondary forest, patchiness was also higher (Table 1.1). As such, for an equal number of individuals sampled in both forest types, one would expect more species to be recorded in young secondary forest where distributions are more random. Many more individuals were surveyed in old secondary forest than in young secondary forest (Table 1.1), which resulted in better sampling efficiency given the shapes of the curves (Fig. 1.2b, c). An extra effort in young secondary forest may have resulted in an accordingly higher richness. Differences in observed species richness between these two forest types were therefore due to differences in abundance of sampled individuals, a conclusion which reinforce the findings of Gimaret-Carpentier et al. (1998) and Walther & Martin (2001) who showed that sample size affects species richness estimation. One would not envisage a similar conclusion between light gaps or young secondary forest and swamps, simply because species composition significantly differs in those habitat types, with many species indicative of and exclusive to swamps (Djoufack, 2003; Ottou, 2009).

Data from the first set of plots showed important differences in observed richness between riparian forest and all other habitat types (Fig. 1.1). At that stage the differences could have been due to differences in overall plant density, as in the previous comparison between young secondary and old secondary forests, or it could have been due to the degree of non-randomness (patchiness) of species across plots (Chazdon et al., 1998). Rather than attempting to use a uniform sampling design based on the number of individuals sampled, we instead sampled all other habitats to the extent that most of the curves stabilized and became independent of sampling effort (Fig. 1.2), thus standardizing the sampling protocol. Such a use of species richness estimators avoids the effect of sampling unevenness and provides more unbiased richness values (e.g. Hortal et al., 2004). At maximum sampling effort, once both species sampling curves have stabilized and become independent of sampling effort, we could believe that differences in observed species richness between two habitats were due to differences in patchiness. These differences were therefore representing biological differences between communities. A similar effect is seen through the comparison of old secondary forest and light gaps.

Our analyses have confirmed that non-parametric richness estimators offer the better performance as they are less biased and more accurate, thus best approximating true richness. Our investigations have also shown that richness estimators are useful for defining informative levels of sampling effort for assessing species richness and comparing it among community types. While describing taxon richness, the rarefaction curve may always be used with a non-parametric incidence-based estimator, namely Jack1 or ICE which appeared to be the better-performing non-parametric estimators in this study. All these curves should at least stabilize and at best converge asymptotically in order to indicate thorough sampling. The curves should nevertheless be used with caution, and with careful consideration of both mathematical and ecological interpretations. This is particularly important because of the effects of sampling effort and patchiness. Richness increases with the number of individuals. Because this number varies across community types, equal-sized samples are highly likely to lead to misleading comparisons of richness across habitats. Instead, representative sampling designs with a large number of samples seem to be more suitable as they provide accurate and precise estimations of richness. Differences in observed richness between communities can be due to differences in the level of sampling completeness or to variations in patchiness which reflect biologically meaningful patterns. Researchers should first ensure thorough sampling with the help of suitable taxon sampling curves, carefully considering the effects of sampling effort and patchiness on these curves, before any explanation can be given in an attempt to justify differences in richness. The quality of the present evaluation is not affected by the relatively small number of species used because all estimators were tested using the same values of true species richness to assess their relative performance and rank them primarily using quantitative performance measures. However, other biological datasets with more abundant taxa are required for further analyses that can potentially help to assess the extent to which our conclusions may be generalized.

ACKNOWLEDGMENTS

Financial and logistical support was provided by the Centre for Research and Conservation of the Royal Zoological Society of Antwerp (Belgium), core-funded by the Flemish Government. Permission was given to conduct this research from the Ministry of Forestry and Wildlife and the Ministry of Scientific Research and Innovation, Cameroon. We thank Guilaume Djang Djang, Jean Tongo, Laurent Tiné, Jean Assimentsel, John Carlos Nguinlong and Geoffrey Decan who provided invaluable help during field work and data processing, and Fulbert Tadjouteu of the National Herbarium of Yaoundé for plant specimen identification. We are also grateful to Dr. Greet De Coster for help in SAS analyses. Constructive comments on the manuscript were received from Kasso Daïnou and a number of reviewers.

REFERENCES

Borges, P.A.V., Hortal, J., Gabriel, R. & Homem, N. (2009). Would species richness estimators change the observed species area relationship? *Acta Oecologica* 35: 149–156.

Brose, U. (2002). Estimating species richness of pitfall catches by non-parametric estimators. *Pedobiologia* 46: 101–107.

Broughton, D.A. & McAdam, J.H. (2002). A red data list for the Falkland Islands vascular flora. *Oryx* 36(3): 279–287.

Butler, B.J. & Chazdon, R.L. (1998). Species richness, spatial variation, and abundance of the soil seed bank of a secondary tropical rain forest. *Biotropica* 30 (2): 214–222.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* 8: 148–159.

Chazdon, R.L., Colwell, R.K., Denslow, J.S. & Guariguata, M.R. (1998). Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of Northeastern Costa Rica. In: *Forest biodiversity research, monitoring and modeling: Conceptual background and old world case studies* (Eds.

F. Dallmeier & J.A. Comiskey). UNESCO Paris and The Parthenon Publishing Group, Paris.

Chiarucci, A., Maccherini, S. & De Dominicis, V. (2001). Evaluation and monitoring of the flora in a nature reserve by estimation methods. *Biological Conservation* 101: 305–314.

Colwell, R.K. (2009). *EstimateS: Statistical estimation of species richness and shared species from samples*. Version 8.2. User's Guide and application published at: http://purl.oclc.org/estimates.

Colwell, R.K. & Coddington, J.A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London, Series B* 345: 101–118.

Colwell, R.K., Mao, C.X. & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85(10): 2717–2727.

Djoufack, S.D. (2003). *Végétation et distribution des nids de gorilles (Gorilla gorilla gorilla) dans la périphérie Nord de la Réserve de Biosphère du Dja.* Mémoire de DEA, Université de Yaoundé I, Yaoundé.

Dupain, J., Guislain, P., Nguenang, G.M., De Vleeschouwer, K. & Van Elsacker, L. (2004). High chimpanzee and gorilla densities in a non-protected area of the northern periphery of the Dja Faunal Reserve, Cameroon. *Oryx* 38: 1–8.

Fomete, N.T. & Tchanou, Z. (1998). *La gestion des écosystèmes forestiers du Cameroun à l'aube de l'an 2000*. UICN, Gland and Cambridge.

Gimaret-Carpentier, C., Pélissier, R., Pascal, J.P. & Houllier, F. (1998). Sampling strategies for the assessment of tree species diversity. *Journal of Vegetation Science* 9: 161–172.

Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379–391.

Gotelli, N.J. & Entsminger, G.L. (2011). *EcoSim: Null models software for ecology*. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim.htm.

Hofer, U. & Bersier, L.F. (2001). Herpetofaunal diversity and abundance in tropical upland forests of Cameroon and Panama. *Biotropica* 33(1): 142–152.

Hortal, J., Garcia-Pereira, P. & Garcia-Barros, E. (2004). Butterfly species richness in mainland Portugal: predictive models of geographic distribution patterns. *Ecography* 27: 68–82.

Hortal, J., Borges, P.A.V. & Gaspar, C. (2006). Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology* 75: 274–287.

Hortal, J., Lobo, J.M. & Jiménez-Valverde, A. (2007). Limitations of biodiversity databases: Case study on seed-plant diversity in Tenerife, Canary Islands. *Conservation Biology* 21 (3): 853–863.

Hortal, J., Jiménez-Valverde, A., Gómez, J.F., Lobo, J.M. & Baselga, A. (2008). Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos* 117: 847–858.

Hurlbert, S.H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577–585.

Koechlin, J. (1965). *Flore du Cameroun* (Vol.4). Muséum National d'Histoire Naturelle, Paris.

Laurance, W.F. & Wright, S.J. (2009). New insights into the tropical biodiversity crisis. *Conservation Biology* 23(6): 1382–1385.

Letouzey, R. (1985). *Notice de la carte phytogéographique du Cameroun au 1 / 500 000. Domaine de forêt dense humide toujours verte*. Institut de la Carte Internationale de la Végétation, Toulouse.

Longino, J.T., Coddington, J. & Colwell, R.K. (2002). The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology* 83(3): 689–702.

Loya, D.T. & Jules, E.S. (2008). Use of species richness estimators improves evaluation of understory plant response to logging: a study of redwood forests. *Plant Ecology* 194: 179–194.

Mao, C.X., Colwell, R.K. & Chang, J. (2005). Estimating the species accumulation curve using mixtures. *Biometrics* 61: 433–441.

Nguenang, G. M. & Dupain, J. (2002). *Typologie et description morpho-structurale de la mosaïque forestière du Dja : Cas du site d'étude sur la socio-écologie des grands singes dans les villages Malen V, Doumo-pierre et Mimpala (Est-Cameroun).* Rapport interne. SRZA.

Nufio, C.R., McClenahan, J.L. & Thurston, E.G. (2009). Determining the effects of habitat fragment area on grasshopper species density and richness: a comparison of proportional and uniform sampling methods. *Insect Conservation and Diversity* 2: 295–304.

Ottou, M. F. G. (2009). *Utilisation saisonnière des habitats par les gorilles (Gorilla gorilla gorilla) et les chimpanzés (Pan troglodytes troglodytes) dans la périphérie Nord de la Réserve de Biosphère du Dja (Est-Cameroun).* Mémoire présenté en vue de l'obtention du diplôme d'Ingénieur des Eaux, Forêts et Chasse. Université de Dschang, Dschang.

Palmer, M.W. (1995). How should one count species? *Natural Areas Journal* 15: 124–135.

Rosenzweig, M.L. (2003). Reconciliation ecology and the future of species diversity. *Oryx* 37(2): 194–205.

Turner, W.R. & Tjørve, E. (2005). Scale-dependence in species-area relationship. *Ecography* 28: 721–730.

Walther, B.A. & Martin, J.L. (2001). Species richness estimation of bird communities: how to control for sampling effort? *Ibis* 143: 413–419.

Walther, B.A. & Moore, J.L. (2005). The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* 28: 815–829.

Williams, V. L., Witkowski, E. T. F. & Balkwill, K. (2007). The use of incidence-based species richness estimators, species accumulation curves and similarity measures to appraise ethnobotanical inventories from South Africa. *Biodiversity and Conservation* 16: 2495–2513.

Zhao, J., Ouyang, Z., Xu, W., Zheng, H. & Meng, X. (2010). Sampling adequacy estimation for plant species composition by accumulation curves – a case study of urban vegetation in Beijing, China. *Landscape and Urban Planning* 95: 113–121.

APPENDICES

Appendix I Summary of numerical results of rarefaction and richness estimators presented in Figures 1.1 and 1.2.

Plots	Individuals	Rarefaction	MM	ICE	Jack1	Jack2
Near primary forest						
1	3	2.40	0.00	0.81	0.66	0.00
100	265	10.75	9.94	10.55	10.68	11.43
200	530	11.98	10.29	11.53	11.80	12.69
300	795	12.56	10.68	12.32	12.45	13.30
400	1060	12.85	11.00	13.14	12.98	13.78
500	1325	13.12	11.25	13.67	13.29	13.99
600	1590	13.27	11.47	13.94	13.62	14.30
700	1856	13.32	11.66	13.84	13.69	14.14
800	2121	13.45	11.81	13.85	13.81	14.19
900	2386	13.52	11.95	13.84	13.89	14.22
1000	2651	13.58	12.07	13.87	14.01	14.34
1100	2916	13.64	12.18	13.88	14.06	14.35
1200	3181	13.70	12.28	13.94	14.14	14.42
1300	3446	13.72	12.37	13.98	14.20	14.43
1400	3711	13.77	12.45	14.04	14.24	14.43
1500	3976	13.80	12.53	14.03	14.26	14.44
1600	4241	13.84	12.60	14.06	14.28	14.44
1700	4506	13.89	12.66	14.06	14.31	14.42
1800	4771	13.91	12.72	14.11	14.34	14.48
1900	5036	13.92	12.78	14.13	14.35	14.45
2000	5302	13.93	12.83	14.12	14.35	14.40
2100	5567	13.97	12.88	14.13	14.34	14.34
2200	5832	13.98	12.92	14.11	14.33	14.31
2300	6097	13.99	12.97	14.10	14.34	14.30
2400	6362	13.99	13.01	14.12	14.34	14.30
2500	6627	14.00	13.04	14.12	14.35	14.30
2600	6892	14.00	13.08	14.14	14.36	14.30
2643	7005	14.00	13.09	14.13	14.35	14.28

Appendix I (Continued)

Old secondary forest

Plots	Individuals	Rarefaction	MM	ICE	Jack1	Jack2
1	3	2.45	0.00	0.85	0.70	0.00
100	299	11.41	10.78	11.22	11.60	12.28
200	599	12.63	11.32	12.33	12.66	13.32
300	898	13.21	11.72	13.03	13.24	13.85
400	1197	13.54	12.00	13.33	13.48	13.95
500	1496	13.73	12.21	13.56	13.70	14.17
600	1796	13.86	12.37	13.65	13.82	14.20
700	2095	13.92	12.51	13.72	13.92	14.25
800	2394	13.97	12.62	13.81	14.00	14.28
900	2694	13.98	12.72	13.82	14.02	14.23
1000	2993	13.99	12.80	13.88	14.07	14.23
1100	3292	14.00	12.88	13.92	14.10	14.20
1200	3592	14.00	12.94	13.92	14.10	14.17
1300	3891	14.00	13.00	13.94	14.10	14.12
1400	4190	14.00	13.06	13.98	14.11	14.11
1500	4489	14.00	13.10	14.00	14.13	14.14
1582	4731	14.00	13.14	14.03	14.14	14.12

Young secondary forest

Plots	Individuals	Rarefaction	MM	ICE	Jack1	Jack2
1	3	2.54	0.00	1.02	0.81	0.00
100	329	12.38	12.26	12.16	12.65	13.02
200	659	12.85	12.50	12.52	12.96	13.06
300	988	13.14	12.65	12.79	13.09	13.21
400	1317	13.35	12.75	12.90	13.14	13.30
500	1646	13.58	12.81	12.98	13.21	13.47
600	1975	13.70	12.86	13.13	13.40	13.79
700	2305	13.82	12.91	13.30	13.56	13.98
800	2634	13.87	12.95	13.48	13.70	14.16
900	2963	13.96	13.00	13.66	13.82	14.28
1000	3292	13.98	13.04	13.77	13.90	14.33
1100	3622	14.00	13.08	13.86	13.97	14.36
1170	3844	14.00	13.10	13.88	14.00	14.34

Appendix I (Continued)

Light gaps						
Plots	Individuals	Rarefaction	MM	ICE	Jack1	Jack2
1	5	3.69	0.00	1.21	0.91	0.00
100	466	13.29	11.84	12.25	12.74	13.71
200	932	13.94	12.30	14.18	13.85	14.64
300	1398	14.26	12.66	14.43	14.35	15.00
400	1864	14.51	12.93	14.66	14.61	15.09
500	2330	14.65	13.14	14.69	14.74	15.07
600	2796	14.79	13.31	14.78	14.85	15.10
700	3262	14.90	13.46	14.79	14.94	15.16
800	3728	14.95	13.58	14.79	15.01	15.21
900	4194	14.98	13.68	14.77	15.07	15.28
1000	4660	15.00	13.77	14.79	15.10	15.30
1023	4769	15.00	13.79	14.80	15.11	15.32
Riparian forest						
Plots	Individuals	Rarefaction	MM	ICE	Jack1	Jack2
1	4	3.38	0.00	0.90	0.74	0.00
100	387	17.59	18.37	17.24	18.22	18.90
200	774	17.98	18.51	17.95	18.77	18.78
300	1162	18.00	18.62	18.05	18.62	18.40
400	1549	18.00	18.65	18.01	18.41	18.17
500	1935	18.00	18.64	18.00	18.25	18.03
Swamps						
Plots	Individuals	Rarefaction	MM	ICE	Jack1	Jack2
1	3	2.50	0.00	0.82	0.70	0.00
100	342	14.82	11.75	17.30	14.52	16.21
200	684	16.31	13.45	15.80	16.29	17.18
300	1026	16.99	14.37	16.25	17.03	17.75
400	1368	17.32	14.95	16.58	17.40	17.97
500	1710	17.58	15.36	16.79	17.64	18.17
600	2052	17.69	15.66	17.06	17.88	18.42
700	2394	17.77	15.90	17.28	18.00	18.48
800	2736	17.85	16.10	17.40	18.04	18.40
900	3078	17.88	16.26	17.57	18.11	18.38
1000	3420	17.92	16.40	17.74	18.21	18.46
1100	3762	17.95	16.52	17.87	18.27	18.49
1200	4104	17.98	16.62	17.85	18.26	18.39
1300	4446	17.99	16.71	17.87	18.26	18.34
1400	4788	17.99	16.79	17.86	18.25	18.27
1500	5130	18.00	16.86	17.91	18.27	18.29
1600	5472	18.00	16.93	17.96	18.31	18.33
1700	5813	18.00	16.99	17.97	18.31	18.30
1754	5985	18.00	17.02	17.96	18.28	18.25

Appendix II Performance measures of rarefaction and richness estimators in each habitat type.

Habitat	Bias								
	Rarefaction	**ACE**	**ICE**	**Chao 1**	**Chao 2**	**Jack 1**	**Jack 2**	**Bootstrap**	**MM**
Near primary forest	−0.22	−0.26	−0.18	−0.28	−0.24	−0.19	−0.15	−0.24	−0.28
Old secondary forest	−0.21	−0.27	−0.20	−0.28	−0.24	−0.19	−0.16	−0.24	−0.25
Young secondary forest	−0.22	−0.27	−0.22	−0.27	−0.22	−0.20	−0.19	−0.24	−0.20
Light gaps	−0.16	−0.25	−0.15	−0.26	−0.20	−0.15	−0.11	−0.21	−0.19
Riparian forest	−0.18	−0.27	−0.16	−0.28	−0.20	−0.15	−0.11	−0.22	0.01
Swamps	−0.14	−0.23	−0.14	−0.24	−0.18	−0.13	−0.09	−0.19	−0.23
Average measure	**−0.19**	**−0.26**	**−0.18**	**−0.27**	**−0.21**	**−0.17**	**−0.13**	**−0.22**	**−0.19**
	Accuracy								
	Rarefaction	**ACE**	**ICE**	**Chao 1**	**Chao 2**	**Jack 1**	**Jack 2**	**Bootstrap**	**MM**
Near primary forest	0.07	0.08	0.04	0.09	0.06	0.04	0.03	0.07	0.12
Old secondary forest	0.06	0.08	0.05	0.09	0.07	0.05	0.03	0.07	0.07
Young secondary forest	0.07	0.08	0.05	0.08	0.05	0.05	0.04	0.06	0.06
Light gaps	0.04	0.08	0.03	0.08	0.05	0.03	0.02	0.06	0.07
Riparian forest	0.06	0.10	0.04	0.11	0.06	0.05	0.03	0.07	0.44
Swamps	0.05	0.07	0.03	0.08	0.04	0.03	0.02	0.05	0.06
Average measure	**0.06**	**0.08**	**0.04**	**0.09**	**0.06**	**0.04**	**0.03**	**0.06**	**0.14**
	Precision								
	Rarefaction	**ACE**	**ICE**	**Chao 1**	**Chao 2**	**Jack 1**	**Jack 2**	**Bootstrap**	**MM**
Near primary forest	5.96	11.75	20.14	2.37	11.58	8.69	22.78	11.10	–
Old secondary forest	5.58	10.12	17.84	1.33	11.02	8.37	22.20	10.72	–
Young secondary forest	5.85	8.25	13.49	1.39	12.40	6.48	19.28	9.22	–
Light gaps	5.59	9.76	20.75	0.53	12.59	8.71	22.45	11.20	–
Riparian forest	4.66	13.06	20.63	3.11	16.72	9.57	23.07	12.04	–
Swamps	4.91	11.16	17.59	2.48	14.03	8.82	21.48	10.50	–
Average measure	**5.42**	**10.68**	**18.41**	**1.87**	**13.06**	**8.44**	**21.88**	**10.80**	–

Herbaceous plant community dominated by species of Marantaceae in a swamp.

© Jacob Willie, PGS

Chapter 2

Diversity and community composition of herbaceous plants in different habitat types in south-east Cameroon

Jacob Willie, Nikki Tagg and Luc Lens

ABSTRACT

Diversity patterns and community composition of plants vary across habitats and must be fully assessed in order to adequately describe forest types and to estimate forest age. Diversity and composition of herbaceous plants were evaluated with the aim of characterizing forests at various ages of stand development. Herb stems were sampled in 250 4-m^2 square plots distributed within 6 habitat types. A multinomial model was used to estimate asymptotic herb species richness. A total of 36 herb species belonging to 15 families was recorded. Observed species richness did not significantly differ between habitat types. Likewise, extrapolations to larger sample size using the multinomial model did not reveal significant differences between habitat types, and observed and predicted values of species richness for each habitat type were similar. Most herb species occurred in all habitat types, and were therefore generalists. However, a few indicator herb species were detected, and the results roughly suggested that herb species of the families Poaceae and Araceae were indicative of late successional forests; Zingiberaceae were indicative of early successional forests; and Commelinaceae, Costaceae, Cyperaceae and Marantacaeae were indicators of flooded habitats. These variations resulted in changes in the vertical structure of herbaceous plant communities. Contrary to our predictions, abundance and diversity of herbaceous plants did not change with forest succession as a decrease in abundance and frequency of occurrence of pioneer species in late successional forests was counterbalanced by the presence of generalist and late successional species. This study contributes to the definition of ecological indicators of forest stages at different levels of succession.

INTRODUCTION

African landscapes display considerable variability from deserts to rainforests (White, 1986). White (1986) grouped rainforests into two main types: semi-evergreen and evergreen forests; these broad categories represent forests that grow under different ecological conditions and display contrasting features (see also Dupuy [1998] and references therein). As reviewed by Dupuy (1998), basal area and stem density of trees > 10 cm DBH considerably vary in African forests, and can reach up to 40 m^2/ha and 680 stems/ha, respectively. Dominant canopy height is usually > 30 m, and dominant trees belong to many families, including, but not limited to, Leguminosae, Meliaceae, Sapotaceae, Irvingiaceae and Ulmaceae (White, 1986; Dupuy, 1998). The physiognomy and phytomass of rainforests are determined to a large extent by trees, and woody species are by far higher in number compared to herbaceous species (White, 1986).

It has been suggested that habitats or vegetation formations can be identified based on physiognomy (Kollmann, 2000). However, vegetation classification based solely on structural features (e.g. Tutin & Fernandez, 1984) helps to define the structure of a plant community without necessarily having precise knowledge of the species composition. This approach can be misleading as it does not accurately assess the stand age and the vegetation stage. For example, as various tree species differ in height when they attain maturity, forest classification based on tree heights or other structural features may be misleading, causing unnecessary differentiation of truly similar eco-units, and pooling together vegetation units that are largely different (White, 1986). Moreover, information obtained only from trees can inaccurately describe trends in forest biodiversity (Tchouto et al., 2006). Additional investigations on plant community composition and indicator species can therefore complement the classification based on structural features, and provide qualitative information for more accurate descriptions of vegetation stages (Moffatt & McLachlan, 2004; Loya & Jules, 2008). It has been shown that forest structure and tree species composition are modified as forest succession progresses from early to late successional stages (Martinez-Ramos et al., 1989; White & Edwards, 2000). However, further investigation is required in order to determine if herb community composition follows the same trend.

The objective of this study is to assess understory herb species composition and identify possible herb indicators of forest development for different successional stages. Herbs can be classified as generalists which occur in all habitat types, early successional species which occur in light gaps and young secondary forest, and late successional species which occur in old secondary and near primary forest. In addition, indicator herb species of flooded habitats will also be determined. This study will contribute to the classification of herbs into groups, and will help to verify whether herbs in various habitat types form distinct communities (McCune & Grace, 2002). Given that tropical herb species grow better with adequate light (Wright, 1992), we hypothesize that there will be variation in herb stem density and species diversity across habitat types which contrast in terms of light availability. We predict that stem density and diversity will be high in light gaps, and that herb community composition will vary across habitat types.

MATERIAL AND METHODS

Study area and species

Research was carried out in the northern periphery of the Dja Biosphere Reserve (DBR, 5260 km^2), specifically in 'La Belgique' research site (40 km^2) located between 013°07'–013°11' E and 03°23'–03°27' N. This area is located in the transition zone between the semi-deciduous forests of Equatorial Guinea and the evergreen forests of the Congo basin (Letouzey, 1985). The climate is equatorial and humid. Average rainfall during a two-year period (April 2009–March 2011) was 1637.9 ± SD 105.1 mm, with mean minimum and maximum daily temperatures ranging between 19.5 ± SD 1.3 and 26.3 ± SD 2.4 °C. The Dja forest is situated on the Precambrian plateau; its altitude varies from 400 m to 800 m and relief is characterized by shallow valleys (Fomete & Tchanou, 1998; McGinley, 2008). The research site is officially unprotected and situated within the forest management unit 10 047, one of the numerous forest management units surrounding the DBR. The research site comprises a dense network of watercourses and seasonal swamps. It was partially and selectively logged in the past; further to this old palm trees and pits provide evidence that the site was settled many decades ago (pers. obs.). All this activity has resulted in a patchwork of forest blocks at various stages of stand development, and therefore a mosaic of habitats. For the purpose of this study we targeted all herbaceous species of the understory layer. Abundant herb families in the study site include Marantaceae and Zingiberaceae. They occur in swamps and *terra firma* forests where they can form clumps of more than two meters in height. For a detailed description of these species, see Koechlin (1965).

Habitat types

We adapted previous vegetation classifications in the area (Nguenang & Dupain, 2002; Djoufack, 2003; Dupain et al., 2004) and distinguished six habitat types: 1) Near primary forest (NPF) dominated by large tree species of height > 30 m (e.g. *Omphalocarpum procerum*, *Uapaca* spp., *Polyalthia suaveolens* and *Piptadeniastrum africanum*), with little undergrowth and a closed canopy; 2) Old secondary forest (OSF) with trees of height 25−30 m (e.g. *Terminalia superba*), more pronounced undergrowth than NPF and a discontinuous canopy layer; 3) Young secondary forest (YSF), dominated by early successional trees of < 25 m (e.g. *Tabernaemontana crassa, Myrianthus arboreus*), and a relatively dense undergrowth; 4) Light gaps (LG) which are open-canopied environments resulting from tree and branch fall or elephant activity; 5) Swamps (SW) principally characterized by high densities of *Raphia* spp., few (< 5%) raphia-free open areas (clearings), and a hydromorphic soil; and 6) Riparian forest (RF), located in the transition zone between SW and other forest types, with a mixture of species from all forest types. NPF, OSF, YSF and LG are referred to collectively as *terra firma* habitats. SW and RF are (periodically) flooded habitats.

Sampling design

Stems of all herb species were sampled in 250 4-m^2 square plots placed along 10 6-km transects, at a bearing of 45°. In each transect, 25 plots were set 250 m apart. All plots were set at the right side of transects, at a perpendicular distance of 5 m. For each plot, the habitat type was noted. All species were identified on the ground by the same trained local guides using consistent local names, and scientific names were later confirmed and assigned at the National Herbarium of Yaoundé, Cameroon. In order to compare species richness across habitat types, the sampling process was monitored using rarefaction (individual-based) and first-order Jacknife (Jack1) curves, as recommended in Chapter 1 (see Colwell & Coddington [1994], Chazdon et al. [1998] and Gotelli & Colwell [2001] for detailed descriptions of these estimators). In addition, curves for Chao1, a nonparametric richness estimator, were plotted, as predictions of asymptotic species richness using the multinomial model (see below) were based on this estimator.

Average species richness and evenness

Species richness (total number of species found) and species evenness (relative distribution of species among individuals) were used as diversity indices. Habitats with high indices were considered the most diversity-rich. However, if two habitats had the same number of species (species richness), but differed significantly in evenness, the habitat with high species evenness was considered as having the highest diversity. We used the Diversity module of Ecosim 7.0 software package (Gotelli & Entsminger, 2011), which is a statistical sampling model, to compute average species richness and evenness and associated 95%

confidence intervals (CIs). Statistical differences ($P < 0.05$) between two habitat types occurred only when CIs did not overlap. The Probability of Interspecific Encounters of Hurlbert (Hurlbert's PIE) was used as an index of evenness (Hurlbert, 1971). This index gives the probability that two randomly-sampled individuals from a given habitat type represent two different species. Ecosim 7.0 estimates diversity curves by randomly drawing a specified number of individuals from the data matrix. For each simulation, species diversity indices are determined and the process is repeated several times, thus generating a mean, variance and 95% CIs. We used the Ecosim 7.0 default settings of 1000 iterations and the independent sampling algorithm.

Prediction of asymptotic species richness using the multinomial model

Prediction of species richness beyond the reference sample size (number of individuals inventoried) is done using the multinomial model (Colwell et al., 2012). This model extrapolates the rarefaction curve (observed species richness) to estimate the expected number of species that can be found in a habitat type for additional levels of sampling effort. After an initial survey, n is the total number of individuals inventoried, S_{obs} is the observed species richness (total number of species found), f_1 is the number of species represented by one individual (Singletons), and f_2 is the number of species represented by two individuals (Doubletons). For m additional individuals sampled, the multinomial model predicts species richness $S(n + m)$ as

$$S(n+m) = S_{obs} + \hat{f}_0 \left[1 \; - \; exp \left(\; -\frac{m}{n}\frac{f_1}{\hat{f}_0} \right) \right] \text{(Equation 1)}$$

where $\hat{f}_0$ is the Chao1 estimate of the number of species present in the habitat, but not detected in the initial survey, calculated as follows:

$$\hat{f}_0 = \frac{f_1^2}{2f_2} \quad \text{for } f_2 > 0 \quad \text{or} \quad \hat{f}_0 = \frac{f_1(f_1 - 1)}{2(f_2 + 1)} \quad \text{for } f_2 = 0.$$

To reach asymptotic species richness estimates, the extra number of individuals to sample m is calculated as $m = nx$, where x is the solution to the equation

$$2f_1(1+x) = exp\left[x\left(\frac{2f_2}{f_1}\right)\right],$$

solved using the Newton method (Chao et al., 2009).

Values of m were then used in Equation 1 to estimate the asymptotic species richness for each habitat type. Data were analyzed in SPADE.

Herb community composition across habitats types

We used a Multiple Response Permutation Procedure (MRPP) as a non-parametric method for comparing herb community composition between habitat types (Mielke & Berry, 2001). Data were analyzed in PC-ORD, version 4.0 (McCune & Mefford, 1999), with the Bray-Curtis distance measure. The species matrix measured 250 plots x 36 species. A Nonmetric Multidimensional Scaling ordination (NMDS) was performed to corroborate the results of MRPP analyses.

Indicator species analysis (ISA)

To supplement the MRPP analyses, we used Indicator Species Analysis (ISA) which describes the extent to which each herb species separates among habitat types (Dufrene & Legendre, 1997). This method generates indicator values (I.V.s) for each species in each habitat type by combining information on the species' abundance and frequency in a particular habitat type. The overall I.V. for a given herb species was the highest I.V. of that species across habitat types. I.V.s were tested for statistical significance using a Monte Carlo simulation of 1000 runs with a critical value of 0.05. All analyses were performed in PC-ORD.

RESULTS

Herb density and diversity

We inventoried 36 herb species, belonging to 15 families. Average herb density was 5.98 stems/m^2, and stem density did not significantly vary across habitat types (Median test: $\chi^2 = 4.76$; df = 4; $P = 0.315$). Similar patterns emerged while comparing species richness (Table 2.1).

Table 2.1 Herb species abundance and diversity in different habitat types. Species diversity indices are estimated for 184 individuals, the smallest number of individuals among all habitat types. Significant differences ($P < 0.05$) occur when confidence intervals do not overlap. NPF: Near primary forest; OSF: Old secondary forest; YSF: Young secondary forest; LG: Light gaps; RF: Riparian forest; SW: Swamps.

Parameter	NPF	OSF	YSF	LG	RF	SW
Number of plots	36	93	55	21	9	36
Average stem density (stems/m^2)	5.99	5.74	6.09	5.57	5.11	6.88
Average species richness	**19.92**	**21.79**	**22.48**	**20.40**	**20.00**	**19.33**
95% CI lower bound	17.00	19.00	20.00	18.00	20.00	16.00
95% CI upper bound	23.00	25.00	25.00	23.00	20.00	23.00
Average species evenness	**0.88**	**0.91**	**0.91**	**0.90**	**0.91**	**0.85**
95% CI lower bound	0.86	0.90	0.90	0.88	0.91	0.82
95% CI upper bound	0.90	0.92	0.93	0.91	0.91	0.87

Table 2.2 Estimated herb species richness in different habitat types. n is the total number of individuals inventoried; f_1 is the number of Singletons (species represented by one individual); f_2 is the number of Doubletons (species represented by two individuals); S_{obs} is the observed species richness; q_0 is the probability that the next individual inventoried represents a new species ($q_0 = f_1 / n$); S_{est} is the estimated asymptotic species richness (Chao1 estimator); m is the number of additional individuals required to detect 100% of S_{est}; $S_{est95\%CIlow}$ is the 95% confidence interval lower bound of S_{est}; and $S_{est95\%CIupp}$ is the 95% confidence interval upper bound of S_{est}. Significant differences ($P < 0.05$) occur when confidence intervals do not overlap.

Habitat	n	f_1	f_2	S_{obs}	q_0	S_{est}	m	$S_{est95\%CIlow}$	$S_{est95\%CIupp}$
Near primary forest	863	1	2	25	0.0012	25.3	0	25.0	29.7
Old secondary forest	2134	0	1	26	0.0000	26.0	0	26.0	26.0
Young secondary forest	1339	1	0	27	0.0007	27.0	0	27.0	27.0
Light gaps	468	2	2	23	0.0043	24.0	493	23.1	34.1
Riparian forest	184	2	3	20	0.0109	20.7	115	20.1	27.8
Swamps	990	1	2	26	0.0010	26.3	0	26.0	30.7

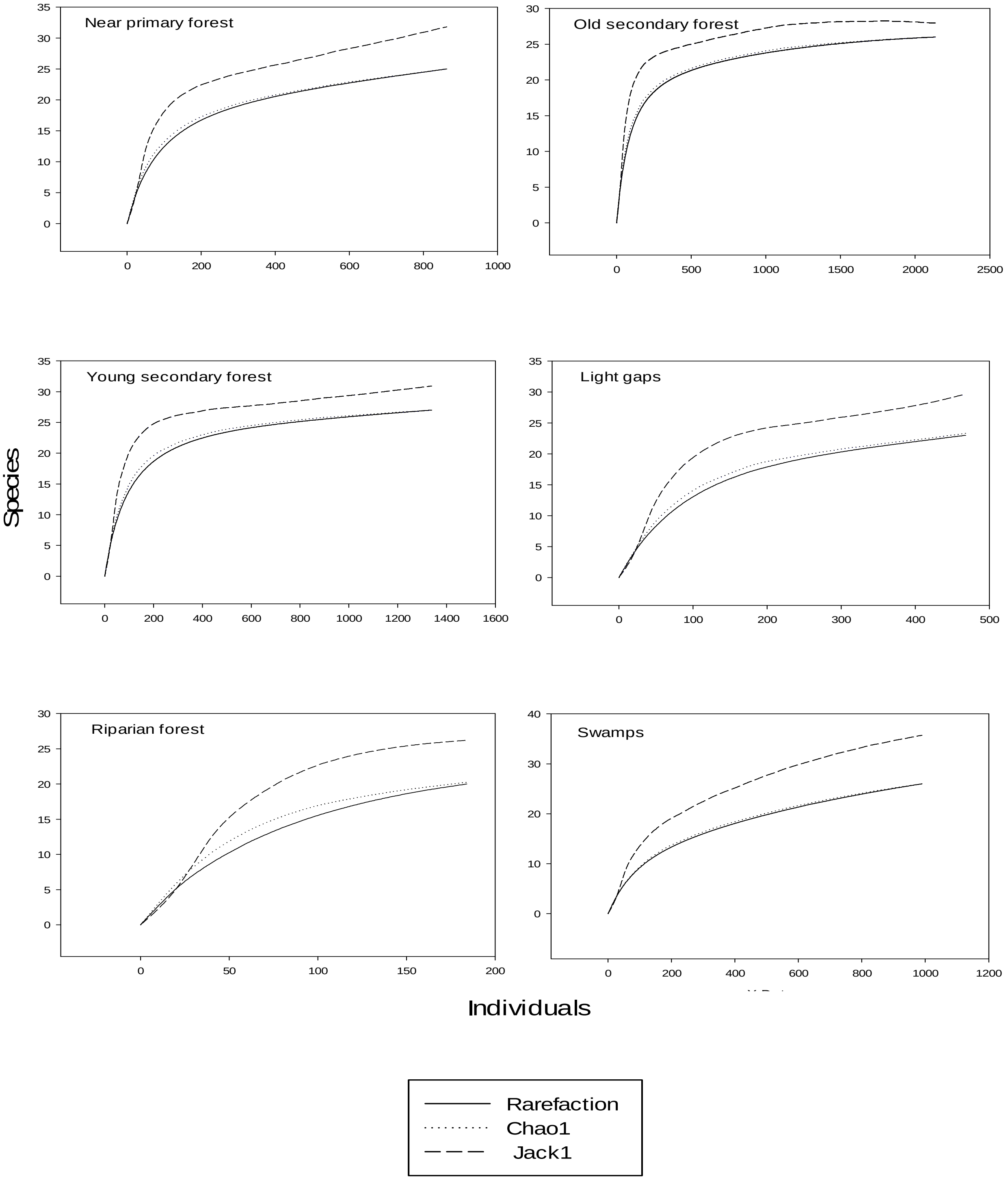


Fig. 2.1 Rarefaction and species richness estimator curves for each habitat.

However, relatively low values of species evenness were found in near primary forest and swamps (Table 2.1). Species richness estimator curves for most habitat types were still increasing (Fig.2.1). However, the probability to discover new species in a further survey was low in all habitat types, usually below 0.005, and no additional sampling effort was needed in most cases (Table 2.2). Predictions using the multinomial model revealed no statistical difference in asymptotic species richness across habitat types (Table 2.2). Estimated and observed values of richness were similar for all habitat types.

Herb community composition

The global MRPP test indicated significant differences in herb composition between all habitat types, but this trend reflected strong differences between swamps and *terra firma* habitats (Table 2.3). This trend would remain unchanged even after adjusting *P* values using a Bonferroni correction (original *P* value x number of tests). Significant differences in herb community composition were also detected between light gaps and late successional forests (old secondary and near primary forest), though separations were not strong. Other pairwise comparisons were statistically non-significant.

The Nonmetric Multidimensional Scaling ordination performed in R using the Euclidian distance on log transformed abundances resulted in a two dimensional solution, and the final stress was 0.24. Although plots from all habitat types considerably overlapped, plots in swamps and light gaps tended to form distinct groups (Fig. 2.2); a trend supporting the results of MRPP. Among *terra firma* plots, young secondary, old secondary and near primary forest plots formed a large cluster, in contrast to plots in light gaps. However, there were considerable differences among young secondary forest plots, and they featured at the edge of this cluster. Riparian forest plots also formed a group next to this large cluster, and they showed a great degree of similarity with both swamp and *terra firma* plots.

Table 2.3 Results of MRPP showing all pairwise comparisons in herb species composition. The separation between habitats is measured by the test statistic *T*. The more negative is *T*, the stronger the separation. Original *P*-values are presented. Asterisks indicate significant differences ($P < 0.05$).

Comparison	*T*	*P*-value
All habitat types	−16.04	0.00001 *
Near primary vs. Old secondary	−1.74	0.0554
Near primary vs. Young secondary	−1.58	0.0690
Near primary vs Light gaps	−2.14	0.0302 *
Near primary vs. Riparian	−1.71	0.0593
Near primary vs. Swamps	−19.39	0.00001 *
Old secondary vs. Young secondary	−0.60	0.2524
Old secondary vs. Light gaps	−3.04	0.0062 *
Old secondary vs. Riparian	−2.02	0.0373
Old secondary vs. Swamps	−23.75	0.00001 *
Young secondary vs. Light gaps	−1.12	0.1335
Young secondary vs. Riparian	−0.98	0.1590
Young secondary vs. Swamps	−19.71	0.00001 *
Light gaps vs. Riparian	−0.27	0.3575
Light gaps vs. Swamps	−11.45	0.00001 *
Riparian vs. Swamps	−4.58	0.0007 *

Indicator species

Of the 36 herb species inventoried, only nine were significant indicators (Table 2.4). For the other species, highest indicator values did not greatly exceed the mean value, implying that they did not have any clear pattern of occurrence in the study site. A similar analysis at family level using pooled data revealed seven significant indicators (Table 2.5). Other herb families were generalists (Fig. 2.3).

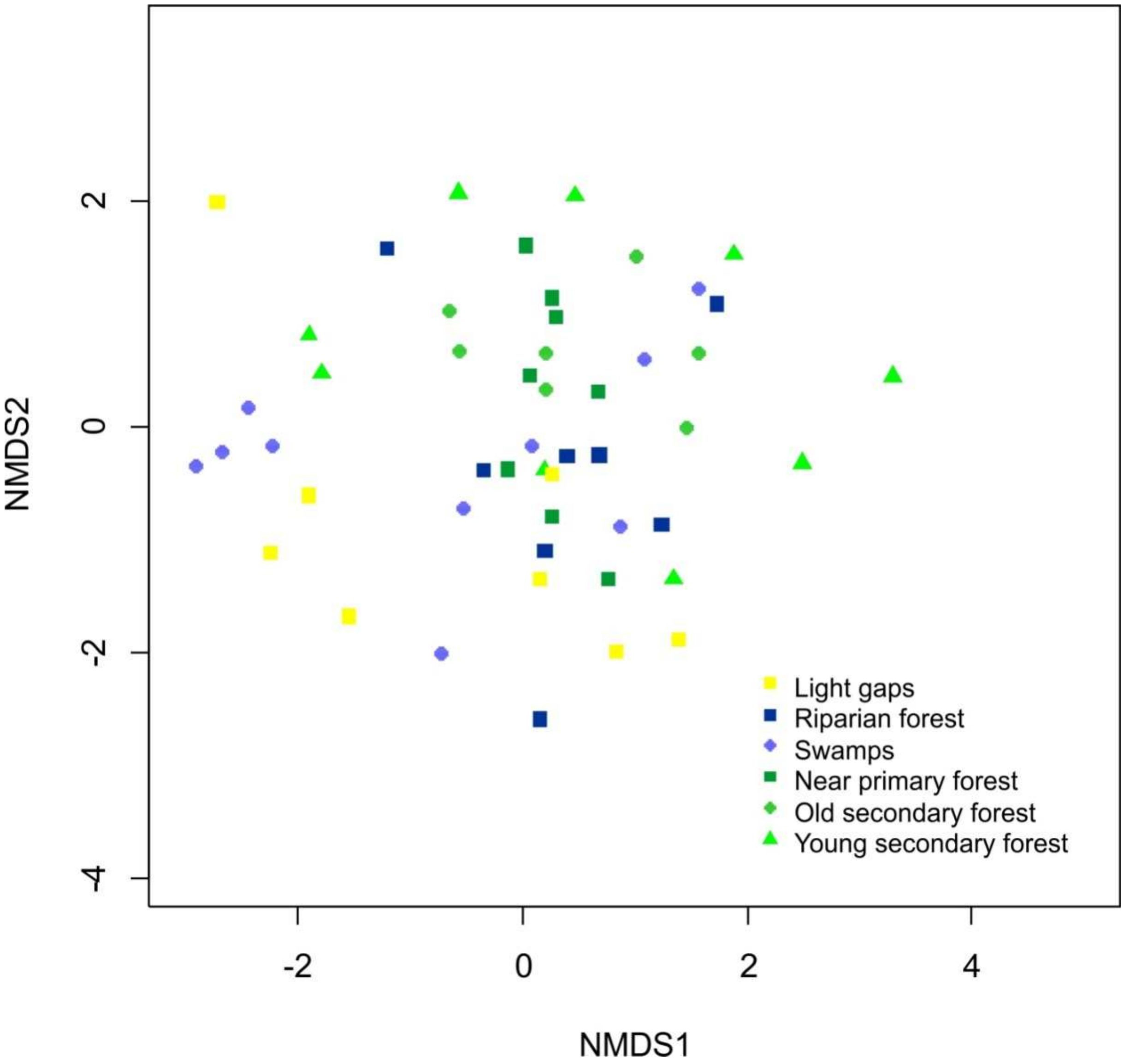


Fig. 2.2 Nonmetric Multidimensional Scaling ordination showing overlap in herbaceous plant community composition across six habitat types. A subset of 50 plots distributed within all habitat types was used to produce the graph. Plots that are close to each other are more similar in species composition.

.

Table 2.4 Indicator herb species for each habitat type. I.V. is the highest indicator value for a given herb species across all habitat types. Observed I.V.s were tested for statistical significance using a Monte Carlo simulation of 1000 runs. The mean of randomized indicator values are presented in each case. *Significant indicators ($P < 0.05$).

Habitat	Scientific name	Family	I.V.	Mean	*P*-value
Near primary forest	*Puelia schumanniana* Pilg.	Poaceae	21.8	13.5	0.039*
	Cercestis dinklagei Engl.	Araceae	12.6	8.8	0.116
	Nephthytis poissonii (Engl.) N.E.Br.	Araceae	6.8	6.4	0.310
	Marantochloa filipes (Benth. & Hook.f.) Hutchinson	Marantaceae	1.0	3.0	0.979
Old secondary forest	*Geophila flaviflora* Aké Assi	Rubiaceae	15.0	8.1	0.039*
	Aframomum arundinaceum K.Schum.	Zingiberaceae	7.3	7.3	0.357
Young secondary forest	*Haumania danckelmaniana* (J.Braun & K.Schum.) MilneRedhead	Marantaceae	13.3	13.3	0.374
	Pityrogramma calomelanos (L.) Link	Pteridaceae	10.8	10.0	0.303
	Pollia condensata C.B.Clarke	Commelinaceae	8.2	6.7	0.215
	Streptogyna crinita P.Beauv.	Poaceae	7.5	4.5	0.101
	Hypselodelphys scandens Louis & Mullend.	Marantaceae	5.9	4.2	0.153
	Palisota barteri Hook.	Commelinaceae	5.7	7.6	0.733
	Aframomum sp.	Zingiberaceae	3.4	4.7	0.590
	Olyra latifolia L.	Poaceae	2.0	3.7	0.793
	Thonningia sanguinea Vahl	Balanophorace	1.8	2.3	0.609

Table 2.4 (continued)

Light gaps	*Aframomum sulcatum* (Oliv. & D.Hanb. ex Baker) K.Schum	Zingiberaceae	17.1	5.5	0.011*
	Selaginella sp.	Selaginellaceae	4.8	2.4	0.119
	Marantochloa leucantha (K.Schum.) Milne-Redhead	Marantaceae	4.7	6.2	0.639
	Renealmia cincinnata Baker	Zingiberaceae	2.8	3.0	0.376
Riparian forest	*Palisota ambigua* (P.Beauv.) C.B.Clarke	Commelinaceae	32.0	11.1	0.002*
	Megaphrynium macrostachyum (Benth.) Milne-Redhead	Marantaceae	12.5	8.1	0.105
	Trachyphrynium braunianum Baker	Marantaceae	11.1	2.4	0.039*
	Asplenium sp.	Aspleniaceae	8.2	9.9	0.662
	Tristemma sp.	Melastomatace	6.9	3.3	0.073
	Geophila repens (L.) I.M.Johnst.	Rubiaceae	6.8	6.4	0.323
	Renealmia africana Benth.	Zingiberaceae	6.0	4.1	0.142
Swamps	*Marantochloa purpurea* (Ridley) Milne-Redhead	Marantaceae	52.2	5.5	0.001*
	Halopegia azurea K.Schum.	Marantaceae	33.3	4.6	0.001*
	Costus afer Ker Gawl.	Costaceae	30.6	5.1	0.001*
	Scleria verrucosa Willd.	Cyperaceae	9.6	4.1	0.038*
	Megaphrynium velutinum (Baker) Koechl.	Marantaceae	8.8	9.5	0.459
	Sarcophrynium brachystachyum K.Schum.	Marantaceae	8.4	11.3	0.863
	Cyclosorus afer Ching	Thelypteridace	5.4	9.8	0.982
	Pilea sp.	Urticaceae	2.8	2.4	0.419
	Sarcophrynium prionogonium K.Schum.	Marantaceae	2.8	2.4	0.410
	Ataenidia conferta (Benth.) Milne-Redh	Marantaceae	2.8	2.5	0.429

Table 2.5 Indicator herb families for each habitat type. I.V. is the highest indicator value for a given herb species across all habitat types. Observed I.V.s were tested for statistical significance using a Monte Carlo simulation of 1000 runs. The mean of randomized indicator values are presented in each case. *Significant indicators ($P < 0.05$).

Habitat	Family	I.V.	Mean	*P*-value
Near primary forest	Poaceae	22.2	13.9	0.033*
	Araceae	17.4	10.8	0.047*
	Rubiaceae	12.5	10.3	0.193
Young secondary forest	Pteridaceae	10.8	10.0	0.287
	Balanophoraceae	1.8	2.3	0.632
Light gaps	Zingiberaceae	17.4	10.7	0.046*
	Selaginellaceae	4.8	2.4	0.129
Riparian forest	Commelinaceae	27.5	13.7	0.004*
	Aspleniaceae	8.2	10.1	0.665
	Melastomataceae	6.9	3.4	0.078
Swamps	Costaceae	30.6	5.1	0.002*
	Marantaceae	24.6	18.8	0.025*
	Cyperaceae	9.6	4.2	0.048*
	Thelypteridaceae	5.4	9.9	0.976
	Urticaceae	2.8	2.5	0.430

DISCUSSION

Sampling thoroughness and species diversity

The survey helped to detect most species with some certainty. The sampling curves did not stabilize in most cases (Fig. 2.1), suggesting that sampling effort was insufficient, and that other species could be detected in further surveys (Colwell & Coddington, 1994; Gotelli & Colwell, 2001; Williams et al., 2007). However, extrapolations at larger sample size using the multinomial model did not indicate important differences between observed and predicted values of species richness (Table 2.2). For example, in light gaps, predictions showed that

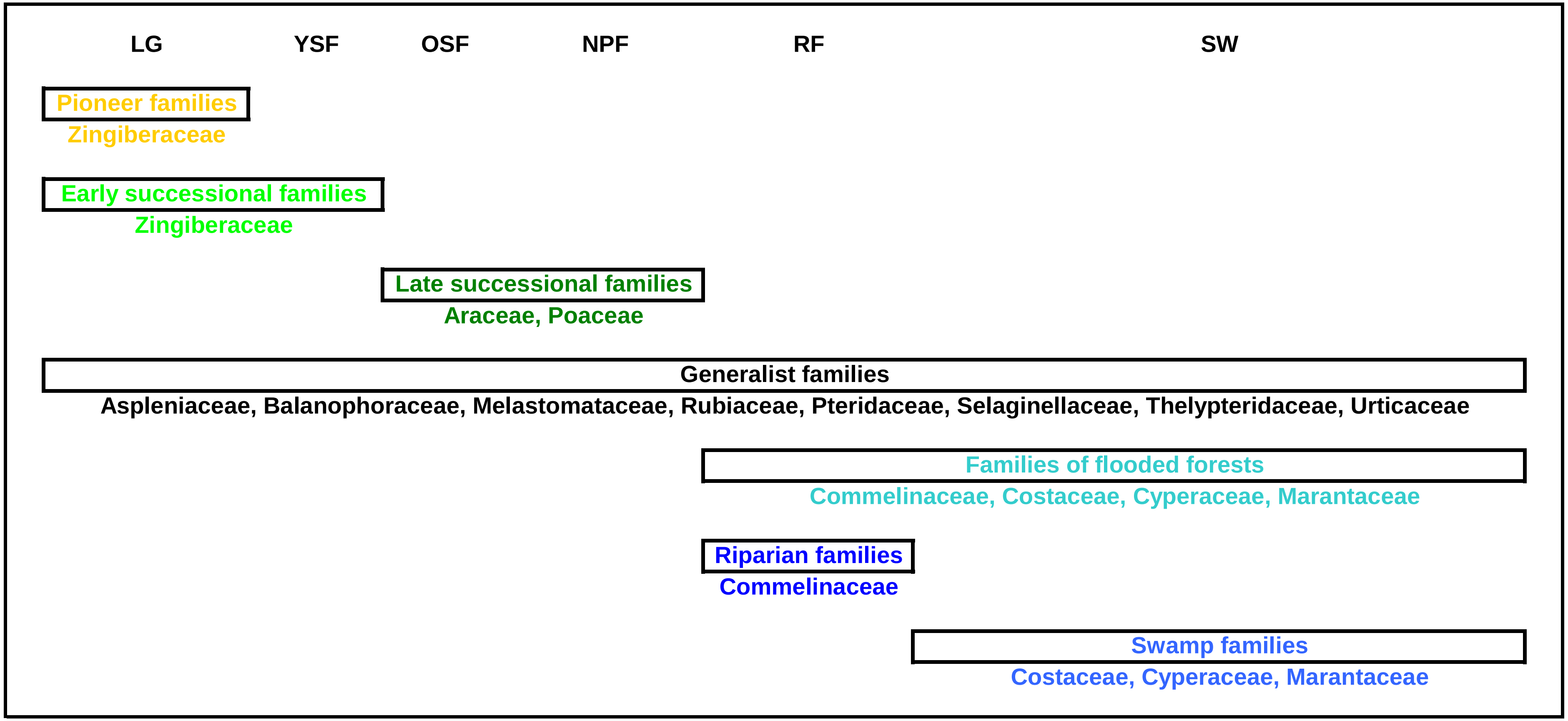


Fig. 2.3 Floristic differentiation graph depicting indicator herb families in six habitat types. LG: light gaps; YSF: young secondary forest; OSF: old secondary forest; NPF: near primary forest; RF: riparian forest; SW: swamps.

493 additional individuals (more than 100% of the initial sampling effort) needed to be inventoried in order to detect one additional species (Table 2.2). It was previously observed that despite the substantial number of additional plots in light gaps and old secondary forest (about 100–200% of the initial number), no species new to the survey was discovered in these habitats (Chapter 1). In most cases species richness estimators did not stabilize at initial sampling effort due to the patchy nature of species distributions (Palmer, 1995; Chazdon et al., 1998). Thus, the observed values of herb species richness for the various habitat types can be considered as 'accurate' estimates, closely matching the predicted values, given that the probability of finding new species was very low in all cases. Moreover, comparison of species richness across habitat types based on observed values did not reveal any significant differences (Table 2.1), and predicted values displayed a similar pattern (Table 2.2). Our results therefore suggest that all habitat types had similar levels of herb species richness.

Herb community composition and indicator species

There was a great overlap in herb community composition across habitat types despite the presence of some indicator species. The test statistic *T* was consistently highly negative in all pairwise comparisons of swamps with all other habitat types (Table 2.3), thus emphasizing the peculiarity of herb community composition in this habitat. As a transition zone between permanently flooded swamps and *terra firma* forests, riparian forest is periodically flooded and presents more heterogeneous features than do other habitats. This heterogeneity may partly account for the considerable overlap in herb species composition between this habitat and all other habitat types, as habitat heterogeneity partly determines species diversity (Spies et al., 2006). Many more herb species and families were indicative of swamps than other habitats (Tables 2.4 and 2.5; Fig. 2.2), and this resulted in strong differences in herb community composition, as shown by the MRPP results. Generalists (e.g. species of fern: *Asplenium* sp., *Cyclosorus afer* and *Pityrogramma calomelanos*) occurred everywhere, but indicators such as Marantaceae and Zingiberaceae species were more localized. Other generalists and indicators of late successional forests (species of Araceae and Poaceae) were small-sized herb species compared to indicators of early successional forest stages and flooded habitats which had relatively large stems, sometimes reaching more than 2 m in height. These results suggest that the vertical structure of herbaceous plant communities changes across habitat types, though stem density seems to be similar. This is consistent with the fact that horizontal visibility decreases from light gaps to near primary forest (Chapter 5).

Given that most tropical herb species thrive in light gaps compared to late successional forests where shade conditions predominate (Wright, 1992), one would expect the highest stem density and/or species diversity in light gaps, as observed by Fay (1997). However, our results do not support this hypothesis. This is probably due to the fact that generalist species, including ferns, can also persist in shade conditions through coping mechanisms that enable them to thrive despite the limited amount of light (Crawley, 1997). Nevertheless, pioneer herbs such as Zingiberaceae species attain their highest densities in light gaps and then decline as succession progresses (Chapter 5), in conformity with the "intermediate disturbance" hypothesis (Sheil, 1999). Decreases in abundance and frequency of occurrence of pioneer herb species led to differences in species composition between light gaps and old successional forests.

Our study has provided insights on diversity patterns and biotic composition of forest understory herbs. Pioneer species featured highly in light gaps and young secondary forest, while other species were common in old secondary and near primary forest. Such variation in the proportion of species resulted in changes to the vertical structure of herbaceous plant communities. Although the separation between swamps and other habitat types was strong, no clear distinction in herbaceous plant community composition was detected among other habitats, as most herb species were generalists. Contrary to our predictions, species diversity and stem density did not appear to decrease with forest succession. The additional description criteria emerging from this work complement the forest stage descriptors of Djoufack (2003), and improve knowledge of herb community composition and indicator species of forest patches in the study area.

ACKNOWLEDGEMENTS

Funding for this research was provided by the Centre for Research and Conservation of the Royal Zoological Society of Antwerp (Belgium), core funded by the Flemish Government. We are grateful to the Ministry of Forestry and Wildlife and the Ministry of Scientific Research and Innovation for permission to conduct this research. Thanks are also extended to Jean Tongo and John Carlos Nguinlong, who provided invaluable help during the field work and to Fulbert Tadjouteu of the National Herbarium of Yaoundé for his contribution in plant specimen identification.

REFERENCES

Chao, A. Colwell, R.K., Lin, C.W. & Gotelli, N.J. (2009). Sufficient sampling for asymptotic minimum species richness estimators *Ecology* 90(4): 1125–1133.

Chazdon, R.L., Colwell, R.K., Denslow, J.S. & Guariguata, M.R. (1998). Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of Northeastern Costa Rica. In: *Forest biodiversity research, monitoring and modeling: Conceptual background and old world case studies* (Eds. F. Dallmeier & J.A. Comiskey). UNESCO Paris and The Parthenon Publishing Group, Paris.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.Y, Mao, C.X., Chazdon, R.L. & Longino, J.T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5(1): 3–21.

Colwell, R.K. & Coddington, J.A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 345: 101–118.

Crawley, M.J. (1997). Life history and environment. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Djoufack, S.D. (2003). *Végétation et distribution des nids de gorilles (Gorilla gorilla gorilla) dans la périphérie Nord de la Réserve de Biosphère du Dja*. Mémoire de DEA, Université de Yaoundé I, Yaoundé.

Dufrene, M. & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366*.*

Dupain, J., Guislain, P., Nguenang, G.M., De Vleeschouwer, K. & Van Elsacker, L. (2004). High chimpanzee and gorilla densities in a non-protected area of the northern periphery of the Dja Faunal Reserve, Cameroon. *Oryx* 38(2), 1–8.

Dupuy, B. (1998). *Bases pour une sylviculture en forêt dense tropicale humide africaine* (Série FORAFRI, document 4). CIRAD, Montpellier.

Fay, J.M. (1997). *The ecology, social organization, populations, habitat and history of the western lowland gorilla (Gorilla gorilla gorilla Savage and Wyman 1847).* Ph. D. thesis. Washington University, St. Louis.

Fomete, N.T. & Tchanou, Z. (1998). *La gestion des écosystèmes forestiers du Cameroun à l'aube de l'an 2000*. UICN, Gland and Cambridge.

Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379–391.

Gotelli, N.J. & Entsminger, G.L. (2011). *EcoSim: Null models software for ecology*. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim.htm.

Hurlbert, S.H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577–585.

Koechlin, J. (1965). *Flore du Cameroun* (Vol.4). Muséum National d'Histoire Naturelle, Paris.

Kollmann, J. (2000). Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in Plant Ecology, Evolution and Systematics* 3(1): 29–51.

Letouzey, R. (1985). *Notice de la carte phytogéographique du Cameroun au 1 / 500 000. Domaine de forêt dense humide toujours verte*. Institut de la Carte Internationale de la Végétation, Toulouse.

Loya, D.T. & Jules, E.S. (2008). Use of species richness estimators improves evaluation of understory plant response to logging: a study of redwood forests. *Plant Ecology* 194: 179–194.

Martinez-Ramos, M., Alvarez-Buylla, E. & Sarukhan, J. (1989). Tree demography and gap dynamics in a tropical rain forest. *Ecology*: 70(3): 555–558.

McCune, B. & Grace, J.B. (2002). *Analysis of ecological communities*. MjM software design, Oregon.

McCune B. & Mefford M.J. (1999). PC-ORD. *Multivariate analysis of ecological data*. Version 4.01. Gleneden Beach: MjM software, Oregon.

McGinley, M. (2008). Dja Faunal Reserve. In: *Encyclopedia of Earth*. (Ed. C.J. Cleveland). United Nations Environment Programme–World Conservation Monitoring Centre. http://www/eoearth.org/article/Dja_Faunal_Reserve,_Cameroon.

Mielke, P.W. & Berry, K.J. (2001). *Permutation Methods: a Distance Function Approach*. Springer, New York.

Moffatt, S.F. & McLachlan, S.M. (2004). Understorey indicators of disturbance for riparian forests along an urban–rural gradient in Manitoba. *Ecological Indicators* 4: 1–16.

Nguenang, G. M. & Dupain, J. (2002). *Typologie et description morpho-structurale de la mosaïque forestière du Dja : Cas du site d'étude sur la socio-écologie des grands singes dans les villages Malen V, Doumo-pierre et Mimpala (Est-Cameroun)*. Rapport interne. SRZA.

Palmer, M.W. (1995). How should one count species? *Natural Areas Journal* 15: 124–135.

Sheil, D. (1999). Tropical forest diversity, environmental change and species augmentation: after the intermediate disturbance hypothesis. *Journal of Vegetation Science* 10: 851–860.

Spies, T.A., Hemstrom, M.A., Youngblood, A. & Hummel, S. (2006). Conserving old-growth forest diversity in disturbance-prone landscapes. *Conservation Biology* 20: 351–362.

Tchouto, M.G.P., De Boer, W.F., De Wilde, J.J.F.E. & Van Der Maesen, L.J.G. (2006). Diversity patterns in the flora of the Campo-Ma'an rain forest, Cameroon: do tree species tell it all? *Biodiversity and Conservation* 15: 1353–1374.

Tutin, C.E.G. and Fernandez, M. (1984). Nationwide census of gorilla (Gorilla g. gorilla) and chimpanzee (Pan t. troglodytes) populations in Gabon. *American Journal of Primatology* 6: 313–336.

White, F. (1986). *La végétation de l'Afrique – Mémoire accompagnant la carte de la végétation de l'Afrique*. UNESCO, Paris.

White, L.J.T. & Edwards, A. (2000). Vegetation inventory and description. In: *Conservation research in the African rain forests: a technical handbook* (Eds. L.J.T. White & A. Edwards)*.* Wildlife Conservation Society, New York.

Williams, V. L., Witkowski, E. T. F. & Balkwill, K. (2007). The use of incidence-based species richness estimators, species accumulation curves and similarity measures to appraise ethnobotanical inventories from South Africa. *Biodiversity and Conservation* 16: 2495–2513.

Wright, S.J. (1992). Seasonal drought, soil fertility and the species density of tropical forest plant communities. *Trends in Ecology and Evolution* 6: 159–152.

Ferns and other herbaceous species occurring at high densities in a swamp clearing.
© Jacob Willie, PGS

Chapter 3

Influence of ecological variables on herbaceous plant community structure in south-east Cameroon

Jacob Willie, Eduardo de la Peña, Nikki Tagg and Luc Lens

ABSTRACT

Abiotic factors significantly influence the structure of plant communities, with the effects varying in both space and time. Herbaceous plants belonging to 15 families were monitored in 250 4-m^2 plots distributed in six habitat types in order to assess the effects of abiotic factors on the abundance of this resource. In each plot, we counted herb stems and determined the total number of species, the total number of normal stems and the total number of dwarf stems. In addition, we determined soil fertility and other environmental variables. Elevation and soil texture varied, but similar levels of chemical fertility were seen across different habitat types. Herb abundance varied within and between patches, reflecting changes in environmental conditions. Stem biomass was highest in light gaps, and decreased in late successional forests. Light seemed to be the most important factor influencing the abundance of Marantaceae and Zingiberaceae. Despite the hydromorphic nature of the soil in swamps, stem biomass did not exceed that of *terra firma* forests. At the temporal scale, rainfall did not seem to influence stem density as herbaceous plants were available year-round. These results suggest that light might limit the abundance of some herbaceous plants in the study site. However, a long-term investigation is needed to draw firm conclusions on the effects of abiotic and climatic factors on herbaceous plant communities in African rain forests.

INTRODUCTION

Abiotic variables, among other factors, significantly shape the structure of plant communities (Tilman, 1983; Wright, 1992; Malenky et al., 1993; Crawley, 1997a; Van Andel, 2005; Bonnefille, 2010; Matías et al., 2012). Plant productivity depends on abiotic resources such as light, water and nutrients. Light is needed to catalyze chemical reactions that result in accumulation of plant biomass (Leuschner, 2005; Mooney & Ehleringer, 1997). In turn, these reactions require water, and plants use available water in the air and soil to compensate the associated loss (Mooney & Ehleringer, 1997). In addition, nitrogen, phosphorus and other nutrients are needed to enhance plant chemical reactions (Fitter, 1997; Mooney & Ehleringer, 1997). For example, under high light conditions, there is a positive correlation between leaf nitrogen content and net photosynthesis (Mooney & Ehleringer, 1997). Tropical herbaceous plant communities are very sensitive to shortages in water, nutrients and light (Wright, 1992).

Across tropical Africa, studies on herbaceous plant community structure have revealed variations in diversity, density and biomass within and across sites (Watts, 1984; Rogers & Williamson, 1987; White et al., 1995; Fay, 1997; Brugiere & Sakom, 2001; Doran et al., 2002; Ganas et al., 2004; Harrison & Marshall, 2011). It has been suggested that such variations might result from differences in land use history and forest structure and composition, as well as variations in light and soil conditions and other environmental constraints (Brugiere & Sakom, 2001; Baeten et al., 2011). For example, human disturbance of natural habitats may deplete soil resources and negatively affect the recruitment of plant species (Martin et al., 2004). Describing abiotic factors and assessing their relationship with plant communities may therefore provide information on species which are effective indicators of habitat quality and diversity (Moffatt & McLachlan, 2004).

The majority of studies focusing on herbaceous plants have not investigated the influence of environmental factors on the diversity, density and biomass of these plants (e.g. Rogers & Williamson, 1987; Malenky et al., 1993; Furuichi et al., 1997; Brugiere & Sakom, 2001). In some rare cases, the influence of a few abiotic factors was assessed (e.g. Rogers et al., 1988; but see also Chapter 5). However, the trends that emerged from such studies were incomplete because the performance of understory plants is a response to the combined effect of a set of environmental factors which vary in magnitude (Ticktin & Nantel, 2004). As a result, other important factors which were not previously explored can affect the performance of these herbs. A more complete evaluation of the relationships between herbaceous plant communities and environmental parameters is therefore needed. Such investigations may help to highlight the abiotic factors that determine herb availability to potential users such as gorillas, and relate these factors to the ecology of these herbivores.

The objective of this study is to assess the influence of abiotic factors on the growth of forest understory herbaceous plants, and provide insights on the causes of gradients in the availability of herbs that are used by gorillas. We hypothesize that spatial changes in the magnitude of ecological variables translate to variations in density, diversity and biomass of herbaceous plants. We predict that soil fertility and light and water availability will be the variables that have the greatest influence on herbaceous plant community structure, and will correlate positively with plant abundance and diversity. Such an investigation can improve knowledge of ecology and conservation of gorillas. For instance, it is likely that certain herb species are highly preferred by gorillas for nest building (Chapter 4). A detailed assessment of density, diversity and growth performance of herbs in relation to abiotic factors might help to describe the environmental features which confer suitability of some species for nest building and consumption. Such descriptions may also provide more clues regarding the environmental characteristics of habitats which are more suitable to gorillas, thus allowing a more accurate assessment of their quality.

MATERIAL AND METHODS

Study site and species

Data were collected in 'La Belgique' research site of *Projet Grands Singes* (PGS), of the Centre for Research and Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), located between 013°07'–013°11' E and 03°23'–03°27' N. The site is situated in the northern buffer zone of the Dja Biosphere Reserve (Cameroon), and is located in the transition zone between the semi-deciduous forests of Equatorial Guinea and the evergreen forests of the Congo basin (Letouzey, 1985). The climate is equatorial and humid and is characterized by seasonal rainfall. During a two-year period (April 2009–March 2011), average rainfall was 1637.9 ± SD 105.1 mm, and mean minimum and maximum daily temperatures ranged between 19.5 ± SD 1.3°C and 26.3 ± SD 2.4°C. The study subjects were herbaceous species belonging to 15 families, namely Araceae, Aspleniaceae, Balanophoraceae, Commelinaceae, Costaceae, Cyperaceae, Marantaceae, Melastomataceae, Poaceae, Pteridaceae, Rubiaceae, Selaginellaceae, Thelypteridaceae, Urticaceae and Zingiberaceae. It is noteworthy that Marantaceae and Zingiberaceae density in the study site is about 3 stems/m^2 (Chapter 5), whereas overall herb density is estimated at 6 stems/m^2 (Chapter 2), therefore meaning that herbs from these two families are an important component of the herbaceous layer in the study site.

Habitat types

In line with previous vegetation classifications in the area (Nguenang & Dupain, 2002; Djoufack, 2003; Dupain et al., 2004), we distinguished six habitat types: 1) Near primary forest (NPF), where large tree species of height > 30 m predominate (e.g. *Polyalthia suaveolens*, *Omphalocarpum procerum*, *Uapaca* spp.

and *Piptadeniastrum africanum*), and there is little undergrowth and a closed canopy; 2) Old secondary forest (OSF), with dominant canopy trees of height 25−30 m (e.g. *Terminalia superba*), a more dense understory than NPF, and a discontinuous canopy layer; 3) Young secondary forest (YSF), characterized by a canopy height of < 25 m dominated by early successional trees (e.g. *Myrianthus arboreus*, *Tabernaemontana crassa*), and a relatively dense undergrowth; 4) Light gaps (LG), with completely open canopies resulting from elephant activity or tree and branch fall; 5) Swamps (SW), with high densities of *Raphia* spp., rare (< 5%) raphia-free open areas (clearings), and a hydromorphic soil; and 6) Riparian forest (RF), growing in the transition zone between SW and other habitat types, with a highly heterogeneous floristic composition comprising species from all habitat types. NPF, OSF, YSF and LG are referred to collectively as *terra firma* habitats. SW and RF are (periodically) flooded habitats.

Sampling design and characterization of plots

Stems of all ground-rooted herb species were surveyed in 250 2 x 2plots placed along 10 transects. Each transect was 6 km long and set at a bearing of 45°. Along each transect, 25 plots were set 250 m apart, at the right side of transects, and at a perpendicular distance of 5 m. Habitat type for each plot was noted. Percentage canopy cover above each plot was visually described (Loya & Jules, 2008) by assigning cover classes and light scores as follows: closed (0), half-open (50) and open (100). Soil humidity scores were determined in a 100–300 scale (100 = *terra firma* habitats on well-drained soils; 200 = riparian forest in the transition zone between *terra firma* habitats and swamps; 300 = swamps on hydromorphic soils). Geographic coordinates and elevation for each plot were also recorded using a GPS Map60cx. Soil samples were collected in 50 plots (7–10 randomly selected plots per habitat type) in 10 x 10 x 15 cm (depth) volumes and analyzed in the lab to determine the pH and the content of organic matter, sand, clay and nutrients (e.g. nitrogen, phosphorus, potassium).

To assess spatial the spatial structure of the herbaceous plant community, we identified and counted herb stems in 4-m^2 contiguous square plots along a 1.5-km transect traversing all habitat types at a bearing of 45°. Average stem density for each habitat patch encountered along the transect was calculated, and results were graphically portrayed to highlight the patterns of variation.

Phenological monitoring of herbaceous plants

Herb stems were monitored in all plots (250) along the 10 6-km transects. In each plot, the total number of herb stems and species were determined. Each stem was examined, and only old stems were classified as “dwarf” or “normal” because they had already completed their developmental cycle. Classification was based on size, which affects vegetative propagation (Ticktin & Nantel, 2004). Old stems were distinguished by signs of age, such as the occurrence of many yellow or brown leaves (entirely or partially), sometimes with holes and a dull color. Dwarf and normal stem dimensions were mutually exclusive. In all cases, dwarf stems were less than half the potential plant height. We collected and weighed ten stems of each species (five normal and five dwarf), and only one overlap in weight was found out of 600 measures. Each stem was assessed based on these chosen limits using a small decameter (with millimeter precision). For each species, we recorded the following information: 1) total number of stems; 2) number of dwarf stems; 3) number of normal stems; 4) number of stems with flowers; 5) number of stems with fruits and 6) number of growing shoots. These data alongside rainfall, humidity and temperature data were collected each month, from August 2011 to July 2012.

Effects of environmental factors on herbaceous plants

To assess the effects of abiotic factors on herbaceous plant community structure, we ran a nonmetric multidimensional scaling (NMDS) ordination in R using the Euclidian distance on log transformed abundances. The data matrix was composed of herb and environmental data collected on a subset of 50 randomly-chosen plots (7–10 per habitat type). Analyses were done using the Euclidian distance on log-transformed abundances. A preliminary principal component analysis (PCA) was performed in XLSTAT in order to assess autocorrelations among environmental variables (Fig 3.1). For final analyses, four non correlated variables were chosen. Component scores for each plot in the original data matrix were calculated, and correlations between dependent variables and principal axes were assessed using Spearman tests of correlation.

Statistical analyses

Nonparametric statistics (which compare medians and not means) were used as data did not meet the assumptions of normality (see Siegel & Castellan, 1988). Moreover, frequency distributions were different. Therefore, Median tests (two-tailed) were used for global comparisons of habitat types, and two-sample Kolmogorov-Smirnov tests (two-tailed) were used for pairwise comparisons. We did not apply the Bonferonni correction for pairwise comparisons as sample sizes were too small ($7 \leq N \leq 60$ in most cases; Garamszegi, 2006). Proportions were compared using Chi-squared tests. Statistical analyses were run in SPSS.

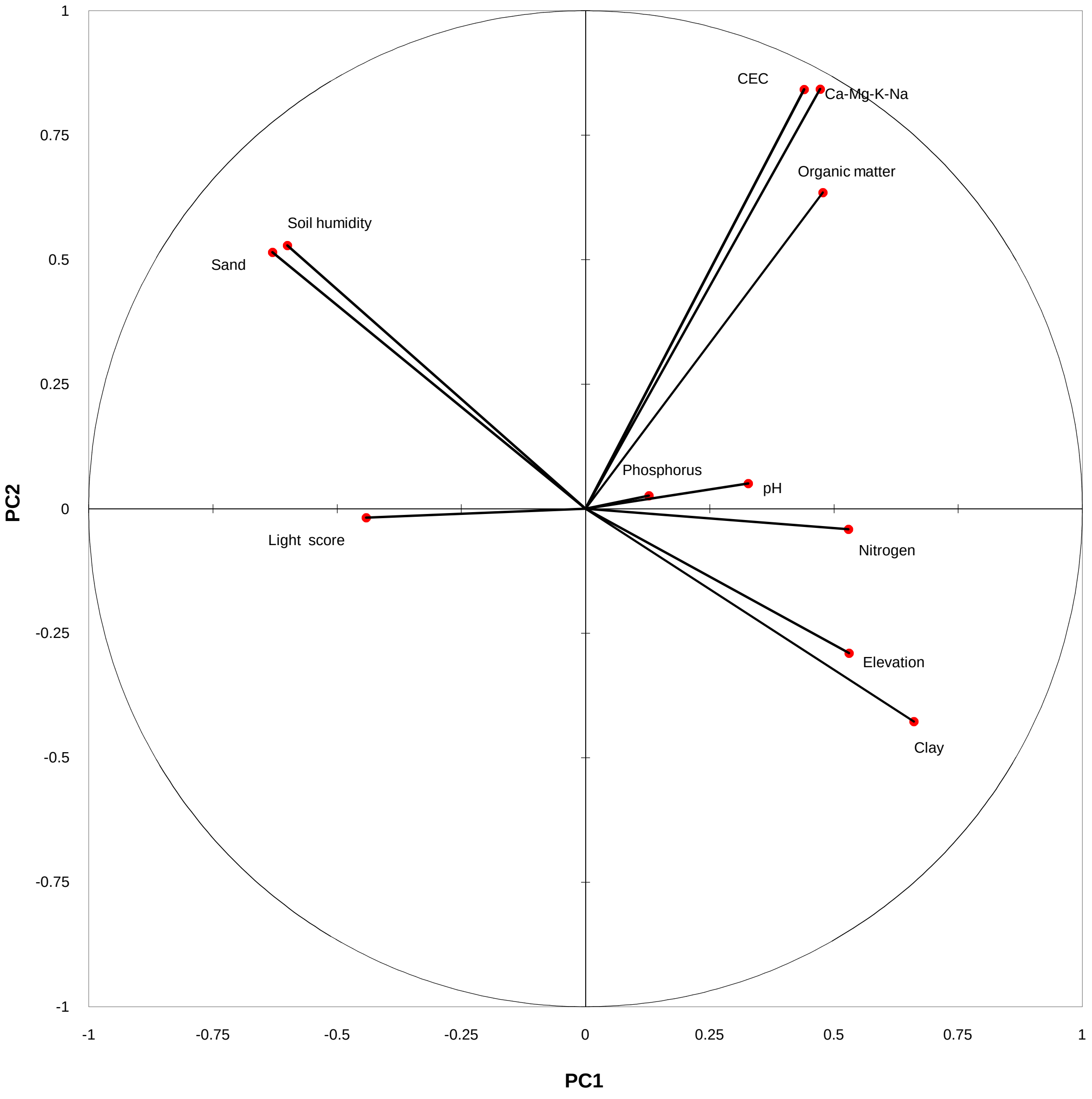


Fig. 3.1 Preliminary principal component analysis (PCA) of environmental variables. Highly autocorrelated variables are more close to each other.

RESULTS

Characteristics of habitat types

There was little variation in plot elevation across habitat types, though differences in medians were statistically significant (Table 3.1). No significant difference in elevation was found among *terra firma* habitat plots or among flooded habitat plots; whereas plots in all *terra firma* habitats, except in young secondary forest, had significantly different elevations compared to plots in swamps (two-sample Kolmogorov-Smirnov tests, $P < 0.01$ in all cases). Sand and clay content of the soil (proxies for soil texture) globally differed across habitat types (Table 3.1). However, no significant difference was found among *terra firma* habitats and among flooded habitats, and all *terra firma* habitat soils had significantly different sand and clay content compared to swamps (two-sample Kolmogorov-Smirnov tests, $P < 0.05$ in all cases). Levels of soil fertility, estimated using measures of pH, organic matter, cation exchange capacity (CEC) and availability of phosphorus and nitrogen did not significantly differ across habitat types (Table 3.1).

Spatial variation in herb availability

Along the 1.5 km transect, a mosaic of small-sized patches of various habitat types was encountered. The highest herb densities occurred in light gaps, young secondary forest and swamp patches. Furthermore, there was considerable variation in herb density among patches within each habitat type (Fig. 3.2 and 3.3).

Table 3.1 Soil characteristics by habitat type. Displayed figures for all measured parameters are average values and corresponding standard deviations (in parentheses); soil parameters were measured in 50 plots selected in all habitat types. All global comparisons were done using Median tests; df = 5 in all cases; ns: non significant; **significant at $P < 0.01$; *significant at $P < 0.05$.

Variable	**Near primary forest**	**Old secondary forest**	**Young secondary forest**	**Light gaps**	**Riparian forest**	**Swamps**	Significant differences
Number of plots	8	7	9	8	8	10	
Elevation (m)	675.25 (17.65)	682.86 (26.30)	674.78 (24.57)	674.63 (12.19)	663.13 (19.25)	650.00 (8.00)	**
Sand content (%)	11.75 (2.05)	10.43 (0.98)	10.56 (2.74)	12.50 (1.60)	25.13 (15.97)	24.40 (8.69)	*
Clay content (%)	66.25 (3.49)	66.00 (3.27)	66.00 (4.15)	67.25 (1.58)	53.00 (15.29)	52.70 (10.30)	*
pH	4.35 (0.43)	4.14 (0.62)	4.54 (0.41)	4.10 (0.30)	4.08 (0.17)	4.13 (0.26)	ns
Organic matter (%)	5.71 (0.93)	5.80 (1.44)	5.56 (1.35)	4.75 (1.67)	6.55 (1.51)	5.22 (0.82)	ns
Cation exchange capacity (milliequivalents/100g)	3.07 (0.66)	3.11 (0.57)	3.11 (0.68)	2.63 (0.61)	3.29 (0.26)	3.08 (0.33)	ns
Assimilable phosphorus (mg/kg)	3.83 (1.01)	3.05 (0.70)	3.65 (0.90)	3.78 (0.87)	3.93 (1.73)	3.45 (0.55)	ns
Total nitrogen (g/kg)	1.99 (0.77)	1.81 (0.31)	1.94 (0.40)	1.75 (0.63)	1.76 (0.44)	1.59 (0.42)	ns

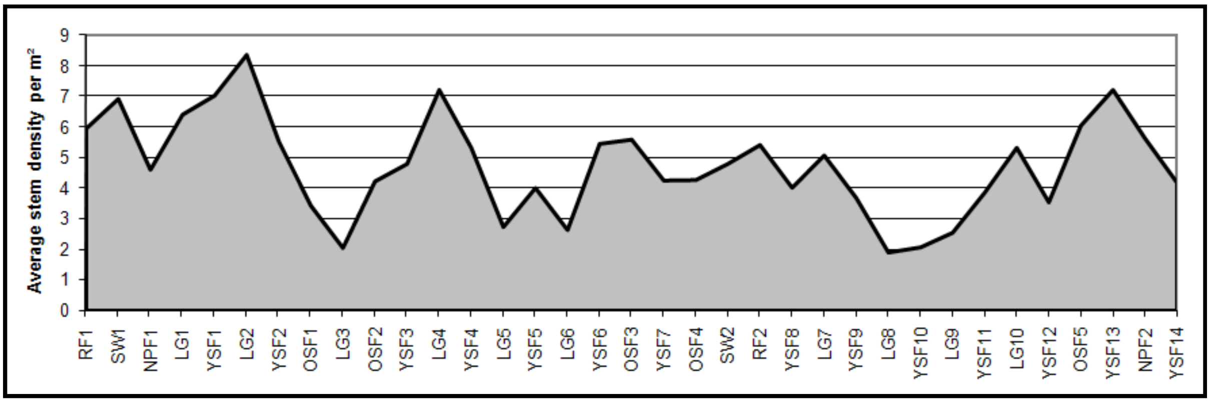


Fig. 3.2 Habitat type sequence and spatial variation of herb stems along a 1.5 km transect (RF: Riparian forest; SW: Swamp; NPF: Near primary forest; LG: Light gap; YSF: Young secondary forest; OSF: Old secondary forest).

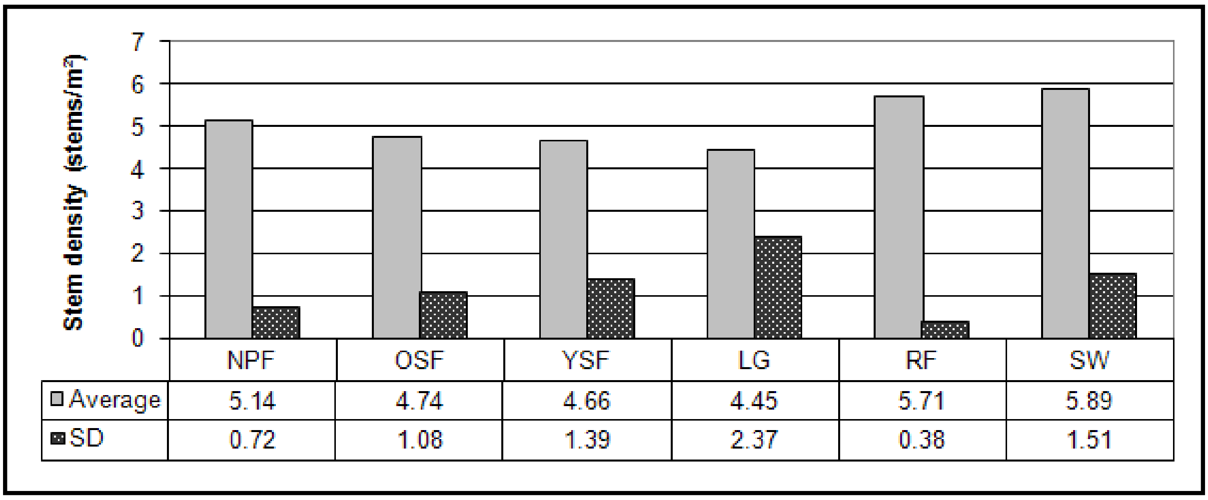


Fig. 3.3 Average values of herb stem density among habitat patches along the 1.5 km transect (NPF: Near primary forest; OSF: Old secondary forest; YSF: Young secondary forest; LG: Light gaps; RF= Riparian forest; SW: Swamps).

Abiotic factors and herb community structure

A preliminary synthesis of environmental parameters using a principal component analysis (PCA) indicated high levels of autocorrelation among variables (Fig.3.1). To facilitate the interpretation of results, we clustered correlated variables into four groups. Each group was represented by the most meaningful variable, namely clay, organic matter, canopy cover and soil humidity. The NMDS ordination of the herbaceous plant community structure in 50 plots resulted in a two dimensional solution, and the final stress was 0.24. As shown in Fig. 3.4, no clear relationship between predictors (clay, organic matter, light score and soil humidity) and dependent variables (stem density, stem biomass and species diversity) was detected. Plots from light gaps, riparian forest and swamps were separated from the others along the second axis. The first axis was roughly related to dependent variables while the second axis was mainly related to the predictors. Correlations with ordination scores were significant only between stem density and axis 1 ($r_S = -0.31$; $P = 0.027$). To corroborate these results, we assessed the relationship between measured environmental variables, namely sand, clay, pH, organic matter, nitrogen, phosphorus, CEC, light score, soil humidity, and elevation, and dependent variables using the Spearman test of correlation: correlation was significant only between species diversity and elevation ($r_S = 0.31$; $P = 0.029$).

At the temporal scale, abiotic factors such as rainfall, temperature and air humidity showed variations throughout the year. We used a Spearman test of correlation to assess possible relationships between herbaceous plant density and climatic variables. No significant correlation was detected between the total number of stems recorded each month and rainfall ($r_S = -0.182$; $P = 0.410$; N = 12) or average temperature ($r_S = 0.152$; $P = 0.493$; N = 12). However, there was a negative correlation with average air humidity ($r_S = -0.697$; $P = 0.002$; N = 12).

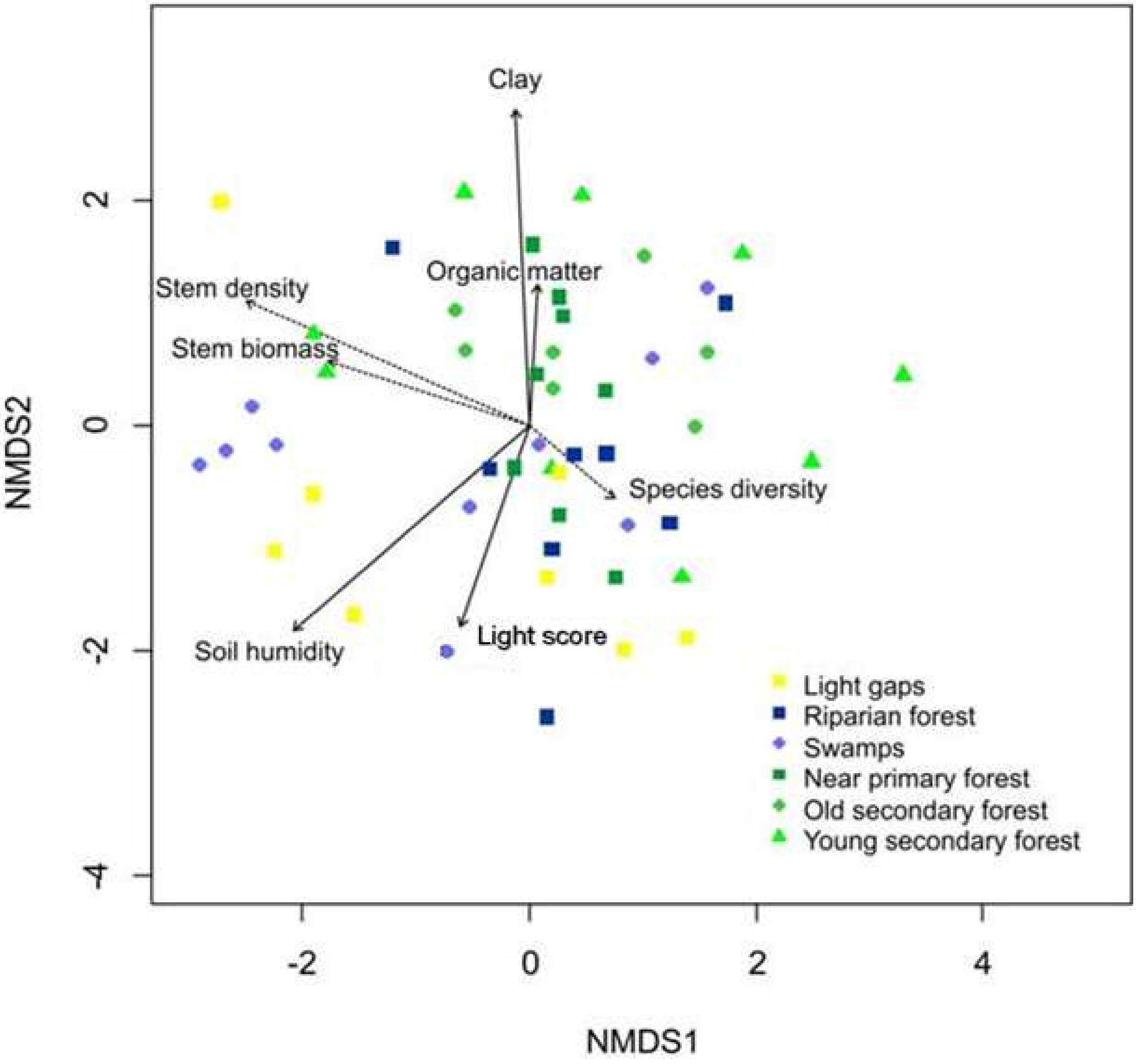


Fig. 3.4 Nonmetric Multidimensional Scaling ordination showing the relationship between habitat type, abiotic factors and herbaceous plant community structure. The symbols represent plots in each habitat type grouped relative to the floristic similarity. The arrows indicate strength and direction of correlations among habitat characteristics and ordination scores (r^2 ranged between 0.02 and 0.2).

Herb size categories

There was a significant difference in the proportion of dwarf and normal stems between habitat types (Chi-squared test: $\chi^2 = 119.6$, df = 5, $P < 0.0001$). These proportions significantly differed while only considering herbs from Marantaceae and Zingiberaceae families (Chi-squared test: $\chi^2 = 89.23$, df = 5, $P < 0.0001$; Table 3.2). The global chi-square value was partitioned to investigate specific differences. For all herbs, detailed results indicated significantly different proportions only in young secondary forest and light gaps ($\chi^2 = 22.14$ and 92.77, df = 1, $P < 0.001$ in all cases). For Marantaceae and Zingiberaceae, significant differences occurred in young secondary forest, light gaps and riparian forest (Chi-squared test: $\chi^2 = 9.65$; 38.07 and 40.38, respectively; df = 1 in all cases; $P <$ 0.001 in all cases).

Table 3.2 Frequencies of herb stem categories in different habitat types.

Stem size	Near primary forest	Old secondary forest	Young secondary forest	Light gaps	Riparian forest	Swamps
Marantaceae and Zingiberaceae only						
Dwarf	152	415	257	66	55	289
Normal	154	461	363	184	10	287
% dwarf	49.67	47.37	41.45	26.40	84.62	50.17
All herb species						
Dwarf	300	696	494	116	259	361
Normal	392	897	559	249	114	384
% dwarf	43.35	43.69	46.91	31.78	69.44	48.46

DISCUSSION

Flooded habitats were located in small depressions, and this resulted in lower elevations as compared to *terra firma* habitats (Table 3.1). Although soil texture varied between these major groups, the chemical characteristics of soils were similar in all habitat types, as also observed by Peh (2009) inside the Dja Reserve (Cameroon). This may be an indication that litter accumulation and decomposition rates and litter nutrient release do not significantly vary across habitat types, despite textural and hydromorphic differences. However, the values of standard deviations of the measured environmental variables were sometimes high (Table 3.1), highlighting spatial variability in the magnitude of these factors. As a result, variations in stem density between and within habitat types (Fig. 3.2 and 3.3) probably resulted from the observed environmental variability, especially as tropical terrestrial herbs are very sensitive to such variations (Wright, 1992). This is consistent with the fact that plant germination, recruitment and mortality across forest patches are likely to be affected by variability in environmental conditions (Martinez-Ramos et al., 1989). Our results highlight that while idiosyncratic differences between habitat types or sites may explain observed differences in levels of ecological factors (Brugiere & Sakom, 2001; Loya & Jules, 2008; Baeten et al., 2011), within-habitat variation in abiotic factors results in uneven biological patterns.

However, no clear relationship was detected between abiotic variables and herb abundance and diversity (Fig. 3.4). Hydromorphic and textural differences between flooded and *terra firma* habitats did not seem to result in variations in herbaceous plant community structure. Furthermore, no relationship existed between light score and herbaceous plant density, diversity and biomass. This may be an indication that light did not affect the structure of herbaceous plant community. However, while only considering herbs from Marantaceae and Zingiberaceae families, the proportion of dwarf stems was lowest in light gaps, and consistently increased from young secondary to near primary forest (Table 3.2). Given that the amount of light drastically decreases as the forest progresses from early to late successional stage (Chapter 5), and that soil fertility did not vary as shown by the analyses, it is possible that light strongly limits the growth and development of Marantaceae and Zingiberaceae herb species in the study site. It is shown that the stem density of herbs of these two families peaks in light gaps, with minimal values in near primary forest (Chapter 5). These trends are consistent with the observations of White et al. (1995) who found differences in growth forms of *Haumania liebrechtsiana* between Marantaceae and mature forest, with shorter stems occurring in the latter habitat type where shade conditions predominate in the understory. Stems of other plant life-forms such as saplings have displayed similar negative correlations between ‘slenderness’ and light availability (Van Breugel et al., 2012). In the ecological literature, it is well established that light is a major determinant of plant growth (Mooney & Ehleringer, 1997; Leuschner, 2005). Our analyses, however, did not reveal a clear effect probably because some of the studied herb species are generalists (Chapter 2), meaning that they can thrive in a range of habitat conditions. For example ferns, an important group of herbs in the study site, can adapt and persist in shade conditions (Crawley, 1997b). Hence, we can suggest that although light had no major influence on the herbaceous plant community as a whole, some species appeared to be more dependent.

Water availability did not seem to limit herbaceous plant growth in the study site. One would have expected high stem density and biomass in flooded habitats if water was a liming factor to herbs in *terra firma* habitats. Stem density seemed to be highest in swamp patches (Fig. 3.3), but differences in stem density between this habitat and others are not significant (Chapter 2). In addition, riparian forest and swamps had high proportions of dwarf stems compared to other habitats (Table 3.2), implying that other factors may be important. Moreover, at the temporal scale, no clear pattern was detected between rainfall and density of herbaceous plants. This result must be interpreted with caution because between consecutive surveys, other factors such as herbivory, trampling by animals and humans and other biotic influences might have removed some stems, including shoots, fruits and flowers, thus biasing the results. Nevertheless, these results suggest that herbs are available year round. It has been noted that tropical herbaceous plants are very sensitive to water shortage which can cause mortality and inhibit the germination of some species (Wright, 1992; Crawley, 1997b). It is therefore possible that seasonal rainfall had no influence on the abundance of herbaceous plants in the study site. However, further investigation is needed to draw firm conclusions.

Following this discussion, it appears that soil nutrients for plant growth are randomly distributed across habitats. Contrary to our predictions, abiotic resources were not limiting factors to the herbaceous plant community of the study site, though light seemed to be the most important factor influencing the abundance of some species. The effect of climatic variables was unclear, although it is suggested that rainfall is a major limiting factor to plant growth in the tropics (Bonnefille, 2010), and that herbaceous plants are very sensitive to climatic stress (Wright, 1992). Further investigations over a longer period are needed to provide a more accurate assessment of the impact of climatic variability on herbaceous plant communities in African forests.

ACKNOWLEDGEMENTS

Financial and logistic support were provided by the Centre for Research and Conservation of the Royal Zoological Society of Antwerp (Belgium), core-funded by the Flemish Government. We thank the Ministry of Forestry and Wildlife and the Ministry of Scientific Research and Innovation, Cameroon, for permission to carry out this research. We deeply appreciate the assistance of John Carlos Nguinlong, Luc Tedonzong and Charles Yem Bamo during data collection and processing. We acknowledge with much gratitude the help of Jean Tongo and his team during data collection. Thanks are also extended to Dr. Antoine Mvondo Ze for soil sample analyses, and to Dr. Lander Baeten for assistance in multivariate analyses.

REFERENCES

Baeten, L., Verstraeten, G., De Frenne, P., Vanhellemont, M., Wuyts, K., Hermy, M. & Verheyen, K. (2011). Former land use affects the nitrogen and phosphorus concentrations and biomass of forest herbs. *Plant Ecology* 212(5): 901–909.

Bonnefille, R. (2010). Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change* 72: 390–411.

Brugiere, D. & Sakom, D. (2001). Population density and nesting behaviour of lowland gorillas (Gorilla gorilla gorilla) in the Ngotto forest, Central African Republic. *Zoologial Journal London* 255: 251–259.

Crawley, M.J. (1997a). The structure of plant communities. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Crawley, M.J. (1997b). Life history and environment. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Djoufack, S.D. (2003). *Végétation et distribution des nids de gorilles (Gorilla gorilla gorilla) dans la périphérie Nord de la Réserve de Biosphère du Dja*. Mémoire de DEA, Université de Yaoundé I, Yaoundé.

Doran, D.M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. & Shah, N. (2002). Western lowland gorilla diet and resource availability: New evidence, cross-Site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology* 58: 91–116.

Dupain, J., Guislain, P., Nguenang, G.M., De Vleeschouwer, K. & Van Elsacker, L. (2004). High chimpanzee and gorilla densities in a non-protected area of the northern periphery of the Dja Faunal Reserve, Cameroon. *Oryx* 38: 1–8.

Fay, J.M. (1997). *The ecology, social organization, populations, habitat and history of the western lowland gorilla (Gorilla gorilla gorilla Savage and Wyman 1847).* Ph. D. thesis. Washington University, St. Louis.

Fitter, A. (1997). Nutrient acquisition. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Furuichi, T., Inagaki, H. & Angoue-Ovono, S. (1997). Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: employing a new method to distinguish between nests of the two species. *International Journal of Primatology* 18(6): 1029–1046.

Ganas, J., Robbins, M.M., Nkurunungi, J.B., Kaplin, B.A. & McNeilage, A. (2004). Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology* 25(5): 1043–1072.

Garamszegi, L. (2006). Comparing effect sizes across variables: generalization without the need for Bonferroni correction. *Behavioral ecology* 17(4): 682–687.

Harrison, M.E. & Marshall, A.J. (2011). Strategies for the use of fallback foods in apes. *International Journal of Primatology* 32: 531–565.

Letouzey, R. (1985)*. Notice de la carte phytogéographique du Cameroun au 1 / 500 000. Domaine de forêt dense humide toujours verte*. Institut de la Carte Internationale de la Végétation, Toulouse.

Leuschner, C. (2005). Vegetation and ecosystems. In: *Vegetation Ecology* (Ed. E. van der Maarel). Blackwell Publishing, Oxford.

Loya, D.T. & Jules, E.S. (2008). Use of species richness estimators improves evaluation of understory plant response to logging: a study of redwood forests. *Plant Ecology* 194: 179–194.

Malenky, R., Wrangham R., Chapman, C. & Vineberg, E. (1993). Measuring chimpanzee food abundance. *Tropics* 2: 231–244.

Martin, P.H., Sherman, R.E. & Fahey, T.J. (2004). Forty years of tropical forest recovery from agriculture: structure and floristics of secondary and old-growth riparian forests in the Dominican Republic. *Biotropica* 36(3): 297–317.

Martinez-Ramos, M., Alvarez-Buylla, E. & Sarukhan, J. (1989). Tree demography and gap dynamics in a tropical rain forest. *Ecology* 70(3): 555–558.

Matías, L. Quero, J.L., Zamora, R. & Castro, J. (2012). Evidence for plant traits driving specific drought resistance. A community field experiment. *Environmental and Experimental Botany* 81: 55–61.

Moffatt, S.F. & McLachlan, S.M. (2004). Understorey indicators of disturbance for riparian forests along an urban–rural gradient in Manitoba. *Ecological Indicators* 4: 1–16.

Mooney, H.A. & Ehleringer, J.R. (1997). Photosynthesis. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Nguenang, G. M. & Dupain, J. (2002). *Typologie et description morpho-structurale de la mosaïque forestière du Dja : Cas du site d'étude sur la socio-écologie des grands singes dans les villages Malen V, Doumo-pierre et Mimpala (Est-Cameroun).* Rapport interne. SRZA.

Peh, K.S.H (2009). *The relationship between species diversity and ecosystem function in low- and high-diversity tropical African forests*. PhD Thesis. University of Leeds.

Rogers, M.E. & Williamson, E.A. (1987). Density of herbaceous plants eaten by gorillas in Gabon: Some preliminary data. *Biotropica* 19: 278–281.

Rogers, M.E., Williamson, E.A., Tutin, C.E.G. & Fernandez, M. (1988). Effects of the dry season on gorilla diet in Gabon. *Primates* 22: 25–33.

Siegel, S. & Castellan, N.J. (1988). *Nonparametric Statistics for the Behavioral Sciences* (2nd ed.). McGraw-Hill Book Co., New York.

Ticktin, T. & Nantel, P. (2004). Dynamics of harvested populations of the tropical understory herb *Aechmea magdalenae* in old-growth versus secondary forests. *Biological Conservation* 120: 461–470.

Tilman, D. (1983). Plant succession and gopher disturbance along an experimental gradient. *Oecologia* 60: 285 –292.

Van Andel, J. (2005). Species interactions structuring plant communities. In: *Vegetation Ecology* (Ed. E. van der Maarel). Blackwell Publishing, Oxford.

Van Breugel, M., Van Breugel, P. Jansen, P.A., Martínez-Ramos, M. & Bongers, F. (2012). The relative importance of above- versus belowground competition for tree growth during early succession of a tropical moist forest. *Plant Ecology* 213:25–34.

Watts, D.P. (1984). Composition and variability of mountain gorilla diets in the central virungas. *American Journal of Primatology* 7: 323–356.

White, L.J.T., Rogers, M.E., Tutin, C.E.G., Williamson, E. & Fernandez, M. (1995). Herbaceous vegetation in different forest types in the Lopé Forest Reserve, Gabon: implications for keystone food availability. *African Journal of Ecology* 33: 124–141.

Wright, S.J. (1992). Seasonal drought, soil fertility and the species density of tropical forest plant communities. *Trends in Ecology and Evolution* 6: 159–152.

Gorilla nests built on the ground with plant material. (A) Fresh nest with green leaves © André Itotoué, PGS; (B) Old nest with brown leaves. © Jacob Willie, PGS

Chapter 4

Plant selection for nest building by western lowland gorillas in south-east Cameroon

Jacob Willie, Nikki Tagg, Charles-Albert Petre, Zjef Pereboom and Luc Lens

Second revision submitted in *Primates*

ABSTRACT

We examined 834 nests built by western lowland gorillas in Cameroon between July 2008 and July 2011 to identify the plant species used in their construction. Preference for each plant species for nesting was evaluated using a 'preference index' calculated by combining information on the occurrence of each species in the forest and in the nests. Forty-six species representing about 15% of the total number of species in the forest and 26% of species used for nest building were frequently used by gorillas. Preference levels significantly varied among these species. Nests were mostly built with herbs of the families Marantaceae and Zingiberaceae and woody species such as *Manniophyton fulvum* (liana) and *Alchornea floribunda* (shrub). As observed in other gorilla populations, suitability for nest building and availability of gorilla food in stems were the likely determinants of plant selection. The total number of species used per nest ranged from 1–11, with an average of 4.9. This is high compared to other sites, emphasizing variability in the availability of nest building materials and habitat differences across the range of the western gorilla. Seasonal changes in the use of different habitat types for nesting did not appear to influence plant use for nest building as variation in plant selection across seasons was not strong enough to result in important changes in the composition of nests. Our findings suggest that gorillas non-randomly select plant species to build nests, and use a particular set of species combined at varying proportions, with no clear seasonal or spatial patterns.

INTRODUCTION

Nesting is of great importance to primates as they spend approximately half their lives at nesting sites which provide protection from predators and are used for sleeping, feeding, socializing, mating, giving birth and dying (Fruth & Hohmann, 1996; Anderson, 1998; 2000; Yamagiwa, 2001). The study of nesting in wild gorilla populations enables a description of behavior at sleeping sites and an assessment of the influence of ecological factors on their use, thus helping to understand how gorillas adapt to their environment (Anderson, 1998). Such topics have been the focus of considerable scientific attention for more than three decades across the range of *Gorilla* spp., which has resulted in improved knowledge of: nest group size; nest size, shape, height, construction type and life-span; nest and nest site reuse; nesting habitat types; age and sex-related variations in nest construction; nest site dimensions, topography, orientation, spatial arrangement, construction and abandonment timing; and ape group size, sympatric mammals, food availability, climate and human influences on nest building (Casimir, 1979; Tutin & Fernandez, 1984; Groves & Sabater Pi, 1985; Remis, 1993; Tutin et al., 1995; Fay, 1997; Yamagiwa, 2001; Mehlman & Doran, 2002; Poulsen & Clark, 2004; Rothman et al., 2006; Iwata & Ando, 2007; Sunderland-Groves et al., 2009).

However, there has been less focus on identifying gorilla nesting materials, and studies that assess plant selection for nest building in relation to plant availability in the forest are rare (Tutin et al., 1995; Rothman et al., 2006). Furthermore, detailed evaluation of the effect of seasonality on plant selection for nest building is lacking. Such investigations can further knowledge of nesting in great apes and provide additional information on the plant preference of gorillas, which is important for conservation management. For instance, it has been suggested that identifying trees that are important to gorillas and should consequently be protected may be a practical approach for reducing the negative impact of commercial logging on great apes (Morgan & Sanz, 2007). Knowledge of preferred plant species for nesting may help to describe gorilla resource distribution and identify their most suitable habitats (Rogers et al., 2004), therefore helping to improve *in-situ* primate conservation efforts.

In this study, we identify plant species used by western gorillas to build nests, classify them in terms of preference, and assess seasonal usage of these plants and habitat types for nest building. Previous studies have documented seasonal changes in habitat use for nesting (Groves & Sabater Pi, 1985; Tutin et al., 1995). Based on the trend described therein, we hypothesize that seasonal distribution of gorilla nests will show non-random patterns with respect to habitat type and as a result, materials used in nest construction will depend on seasonal changes in climate. We discuss plant selection for nest building and nest construction patterns in relation to plant availability and we compare the trends with other western gorilla study sites.

MATERIAL AND METHODS

Study area

The study area is situated in the northern buffer zone of the Dja Biosphere Reserve (Cameroon), specifically in 'La Belgique' research site of *Projet Grands Singes* (PGS), of the Centre for Research and Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), located between 013°07'–013°11' E and 03°23'–03°27' N. This area is located in the transition zone between the semi-deciduous forests of Equatorial Guinea and the evergreen forests of the Congo basin (Letouzey, 1985), with an equatorial and humid climate characterized by seasonal rainfall. Climatic data collected in the site during a two-year period (April 2009–March 2011) showed > 1500 mm of rainfall each year, with an annual mean of 1637.9 ± SD 105.1 mm. Mean minimum and maximum daily temperatures (°C) were 19.5 ± SD 1.3 °C and 26.3 ± SD 2.4. We defined dry-season periods as those with less than 100 mm of rain per month. Rainfall data collected each month during a 28-month period (April 2009– July 2011) in the research site revealed nine alternating rainy and dry season periods (Fig. 4.1). However, temperature data were missing in April 2010 and in February 2011, thus resulting in a 26-month temperature dataset.

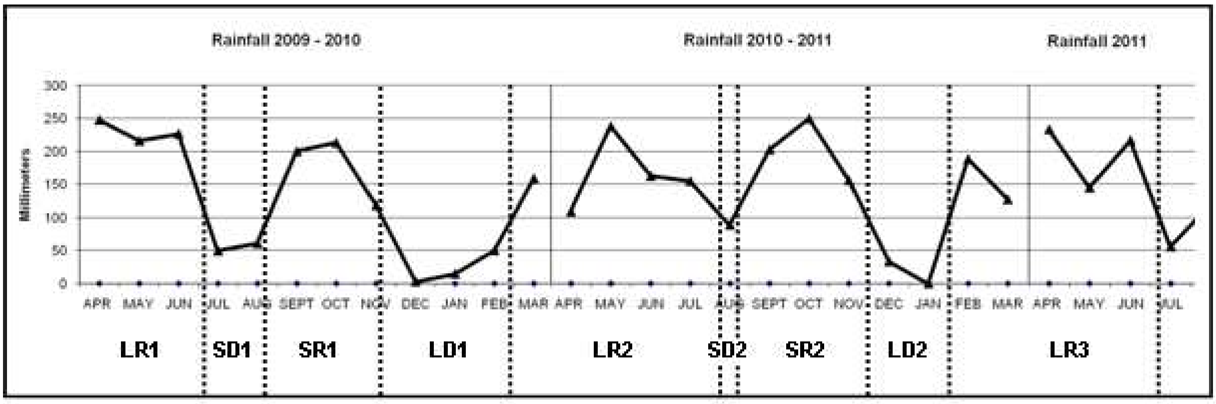


Fig. 4.1 Temporal variation in rainfall patterns between April 2009 and July 2011. LR: Long rainy season (> 4 months); SD: Short dry season (< 1.5 month); SR: Short rainy season (< 4 months); LD: Long dry season (> 1.5 month). Although in the graph LR1 is < 4 months, it occurred during the long rainy period of 2009.

Habitat types

Based on previous vegetation classifications in the area (Nguenang & Dupain, 2002; Djoufack, 2003; Dupain et al., 2004), we distinguished six habitat types: Near primary forest (NPF) dominated by large tree species of height > 30 m (e.g. *Omphalocarpum procerum* and *and Polyalthia suaveolens*), with little undergrowth and a closed canopy; Old secondary forest (OSF) with trees of height 25—30 m (e.g. *Terminalia superba*), more pronounced undergrowth than NPF and a discontinuous canopy layer; Young secondary forest (YSF), dominated by early successional trees of < 25 m (e.g. *Tabernaemontana crassa, Myrianthus arboreus*), and a relatively dense undergrowth; Light gaps which are open-canopied environments resulting from tree and branch fall, with dense tangles of ground herbs; Riparian forest, which are periodically flooded; and Swamps, characterized by high densities of *Raphia* spp., few (< 5%) raphia-free open areas (clearings), and a hydromorphic soil.

Monitoring of gorilla nests

During July, August, October and November 2008, and every month from April 2009 to July 2011, gorilla nest sites were located by trackers who followed trails and recorded additional evidence such as vocalizations or feces. Gorilla trails traversed all habitat types found in the site and reflected habitat preference of gorillas for nest building. Each nest was examined to determine the species of herb, liana and tree used in its construction, and the habitat type of its location was noted. In addition, each nest was assigned to one of five construction types: (i) nest with no vegetative construction, (ii) nest exclusively built with herbs, (iii) mixed nest with both herbs and woody material, (iv) nest exclusively built with woody material, and (v) nest built in tree, according to the definitions of Tutin et al. (1995). Given that sympatric populations of gorillas and chimpanzees live in the area, nest height, nest type, habitat type, sleeping habits and evidence such as hairs, feces, odor and footprints helped to distinguish between chimpanzee and gorilla nests (Sanz et al., 2007).

Availability of gorilla nest construction materials

All trees of $D_{1.30} \geq 10$ cm were identified and counted in 130 plots of 25 x 40 m each, totaling 13 ha. Plots were 250 m apart and were positioned along ten 6-km transects set at a constant bearing of 45° and 600 m apart. *Terra firma* and flooded habitats were represented in plots. Shrubs were counted in 4-m^2 subplots placed in the center of each plot; the average number of stems per subplot was multiplied by the total plot area (13 ha) to estimate the total number of stems in the plots. Further contiguous plots of 2 x 4 m each set along a 1.5-km transect traversing *terra firma* and flooded habitats at a bearing of 45° were used to survey herbs and lianas. A total of 375 contiguous plots were surveyed. The frequency of occurrence in plots was used as a proxy for abundance (Loya &

Jules, 2008) for one species of herb, *Selaginella* sp., because the stems of this species are interconnected and form dense networks. Tree and shrub species were collectively referred to as 'trees', resulting in three main plant groups (trees, lianas and herbs). All plant species were sampled for identification at the National Herbarium of Yaoundé, Cameroon.

Plant preferences for nest building

We calculated an 'importance value' in nest building for each herb as the ratio between the total number of nests in which the herb occurred and the total number of herb species surveyed in the forest. A similar method was applied to lianas and trees. To assess whether some herb species were favored, comparisons among herb species were made using a 'preference index' for each species (adapted from Jacobs, 1974) calculated as the total number of occurrences of each herb species in nests minus the expected number of occurrences. The expected number of occurrences of any herb species in nests depended on its abundance in the site and was calculated as: $\text{expN} = X_i \times Y/100$, where X_i is the relative abundance of stems of species i in the forest and Y is the total number of occurrences of species i in nests. The same approach was used to classify lianas and trees, but the abundance of each tree species in the forest was determined as $AB = RDo + RD + RF$, where RDo, RD and RF represent relative dominance, relative density and relative frequency, respectively (see Hamann et al. [1999] for details). Preference indexes were either positive or negative, and the sum of values for all species of a group equaled zero.

Seasonal composition and diversity of plants in gorilla nests

Gorilla nest composition data collected from March 2009 to July 2011 were grouped into nine seasons as defined above. Data of 2008 were excluded from all analyses of seasonality because no rainfall data were collected that year. A species abundance data matrix was constituted by the frequency of occurrence of each species in nests each month (total number of nests in which a species was found). Data from the same season were pooled and the plant species composition of nests was compared between seasons using a Multiple Response Permutation Procedure (MRPP). This multivariate testing method assesses whether or not the composition of two or more groups differs significantly (see McCune & Grace [2002] for details). For each season, the total number of species found in each nest was used to compare the diversity of nesting materials.

RESULTS

Plants used for nest building by gorillas

A total of 834 gorilla nests were examined between July 2008 and July 2011. Fifty-one had no vegetative construction. Among the 783 nests with vegetative construction, 174 species of tree, shrub, liana and herb were identified, representing 129 genera and 64 families. Gorillas used 55%, 66% and 79% of the number of species, genera and families present in the research site, estimated from our botanical datasets at 314, 196 and 81, respectively. Trees, lianas and herbs were used in nest construction, with importance values of 8.2, 17.1 and 61.8, respectively. Herbs were 7.5 times more important than trees and 3.6 times more important than lianas. Only 3.8% of nests were built in trees. The monthly average number of nests built in trees was 0.3 ± SD 0.8 (range: 0–3), and no correlation was found between the number of nests built in trees each month and rainfall (Spearman rank correlation; $r_S = 0.109$, $P = 0.581$, $N = 28$) or temperature ($r_S = 0.211$, $P = 0.300$, $N = 26$). Forty-six species (14.6% of the total number of species found in the research site) occurred in at least 10 gorilla nests, and were considered as frequently-used species. Herbs displayed the highest proportion of frequently-used plants, comprising nearly half of all species used (Table 4.1). Within each plant group, the preference index varied among species, with standard deviations of 192.7 (herbs), 168.3 (lianas) and 34.4 (trees). Among herbs, *Aframomum* spp. (Zingiberaceae), and other species such as *Hypselodelphys scandens, Haumania danckelmaniana*, *Megaphrynium*

Table 4.1 Classification of plants used by gorillas for nest building. Figures in brackets represent preference index. Most preferred species have more positive preference index. Tree and shrub species are collectively referred to as ‘trees’.

Herbs	**Lianas**	**Trees**
Aframomum sulcatum (+221.7)	*Manniophyton fulvum* (+109.4)	*Alchornea floribunda* (+93.6)
Aframomum sp.2 (+134.0)	*Combretum* sp. (+64.3)	*Tricalysia anomala* (–1.5)
Hypselodelphys scandens (+118.4)	*Macaranga bellei* (+55.2)	*Desplatsia subericarpa* (–1.7)
Haumania danckelmaniana (+116.2)	*Dioclea reflexa* (+19.7)	*Uapaca guineensis* (–4.0)
Megaphrynium macrostachyum (+111.5)	*Cissus dinklagei* (+13.1)	*Desplatsia dewevrei* (–4.1)
Aframomum arundinaceum (+98.9)	*Ancistrophyllumsecondiflorum* (+5.7)	*Myrianthus arboreus* (–6.1)
Marantochloa leucantha (+93.3)	*Clerodendron* sp. (–0.8)	*Uapaca paludosa* (–7.7)
Halopegia azurea (+60.1)	*Tetracera alnifolia* (–6.2)	*Uapaca acuminata* (–16.4)
Costus afer (+49.9)	*Oncocalamus* spp. (–8.4)	*Raphia hookeri* (–19.1)
Scleria boivinii (+21.9)	*Landolphia* spp. (–34.8)	*Tabernaemontana crassa* (–33.0)
Selaginella sp. (+20.3)	*Roureopsis obliquifoliolata* (–44.6)	
Aframomum melegueta (+17.4)	*Neuropeltis laxiflora* (–172.7)	
Olyra latifolia (–8.1)		
Palisota barteri (–60.0)		
Palisota ambigua (–68.9)		
Megaphrynium velutinum (–98.8)		
Pityrogramma calomelanos (–127.0)		
Asplenium sp. (–165.7)		
Cyclosorus afer (–211.0)		
Sarcophrynium brachystachyum (–339.7)		

macrostachyum, Marantochloa leucantha, and *Halopegia azurea* (Marantaceae) were highly preferred by gorillas (Table 4.1). *Manniophyton fulvum, Combretum* sp. and *Macaranga bellei* were the most preferred lianas. *Alchornea floribunda* was the only frequently-used shrub and the most preferred species within the group 'trees'.

Seasonal composition and diversity of plants in gorilla nests

Multiple Response Permutation Procedure (MRPP) tests did not reveal significant differences in plant selection across seasons ($P > 0.05$ in all cases) (Table 4.2). To corroborate the MRPP results, a cluster dendogram was constructed based on the similarity of species used by gorillas each month to build nests. No clear pattern of seasonality occurred even (Fig. 4.2) while considering only data from the most preferred plants (herbs).

Table 4.2 Multiple Response Permutation Procedure (MRPP) results comparing seasonal species use for nest building by gorillas. Separation is measured by the test statistic *T*. The more negative is *T*, the stronger the separation between seasons. The *P*-value associated with *T* assesses how likely observed differences between seasons are due to chance.

Comparison	***T***	***P* - value**
Long dry season vs. Long rainy season	0.589	0.699
Long dry season vs. Short rainy season	1.163	0.911
Long dry season vs. Short dry season	1.329	0.925
Short dry season vs. Long rainy season	0.798	0.778
Short dry season vs. Short rainy season	−0.024	0.413
Long rainy season vs. Short rainy season	0.212	0.511

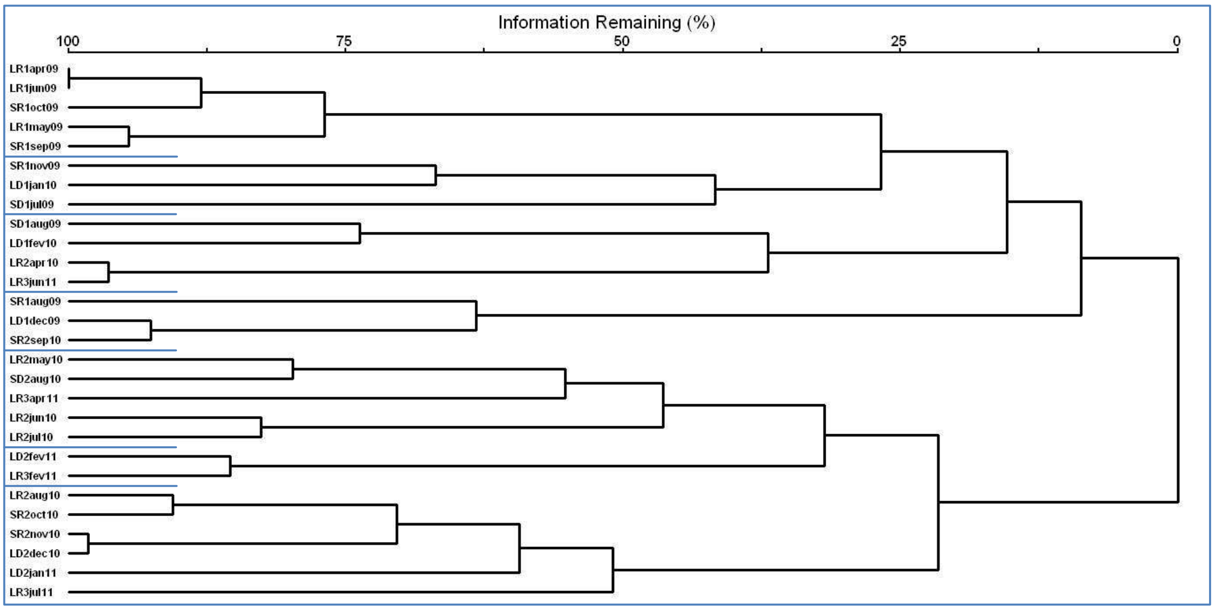


Fig. 4.2 Cluster dendogram depicting seven groups of plant combinations in gorilla nests. The dendogram was constructed using the software PC-ORD, version 4.01 (McCune & Mefford, 1999), with the Bray-Curtis distance.

The total number of plant species per nest for the entire dataset ranged from 1–11, with an average of 4.9 ± SD 2.1. Average values ranged from 4.7 ± SD 2.3 in the long rainy season to 5.3 ± SD 2.1 in the long dry season. Seventy-five percent of nests were constructed using at least four species. Pairwise comparisons of seasons showed weak statistical differences between short rainy and long dry seasons; long rainy and short rainy seasons and long rainy and long dry seasons (two-sample Kolmogorov-Smirnov tests, *P* = 0.045; 0.023 and 0.018 respectively).

Seasonal distribution of gorilla nests in different habitat types

Nest data for each season were pooled together and the total number of nests found in each habitat was computed. Most nests were found in young secondary forest, light gaps and swamps (Table 4.3) and data from these three habitat types were statistically compared. The proportion of nests found in these habitats during the four rainy and dry seasons were significantly different (Chi-squared test: $\chi^2 = 109.601$; df = 6; $P < 0.0001$). Comparable patterns emerged while considering the average number of nests found each month during each season in each habitat type.

Table 4.3 Seasonal distribution of gorilla nests in different habitat types.

Season	Near primary forest	Old secondary forest	Young secondary forest	Light gaps	Riparian forest	Swamps
Long dry season	0	0	85	5	0	39
Long rainy season	2	13	100	136	1	66
Short dry season	0	1	20	18	1	5
Short rainy season	0	0	112	25	2	49

DISCUSSION

The number of plant species and genera identified in gorilla nests in this study constitutes a lower bound estimate of the total number of species and genera used by gorillas during the study period. This is because some plants in nests could not be identified to species or genus level due to the lack of distinctive elements such as flowers or fruits, or because of the state of degradation. Nevertheless, our results reveal that western lowland gorillas used more than half of the species and genera present in their habitat for nest building, though it should be noted that 74% of species used very rarely featured in nests. A similar trend was reported in the Bwindi Impenetrable National Park, Uganda, where mountain gorillas (*Gorilla beringei*) used approximately 60% of plant genera available in their immediate environment to build nests (Rothman et al., 2006).

Table 4.4 Herb availability and use in nest building across the range of western gorillas. CAR: Central African Republic. Herb density includes all herbaceous species, except for Bai Hokou, Lopé, Mondika and Ndoki (herbs commonly consumed by gorillas). WLG: Western lowland gorilla; CRG: Cross River gorilla. 1. [a] Goldsmith (1996) in Doran et al*.* (2002); [b] Remis (1993), longitudinal study; [c] Remis (1993), longitudinal study. 2. This study. 3. [d] White et al. (1995); [e] Tutin et al. (1995); [f] Tutin et al. (1995); [g] Tutin et al. (1995); [h] Tutin et al. (1995). 4. [i] Doran et al. (2002); [j] Mehlman & Doran (2002); [k] Mehlman & Doran (2002). 5. Fay (1997). 6. [l] Malenky et al. (1993); [m] Fay (1997). 7. Brugiere & Sakom (2001). 8. Furuichi et al. (1997). 9. Etiendem et al.(in prep.).

Study site	**Herb density (stems/m^2)**	**Tree nests (%)**	**Bare ground nests (%)**	**Identified number of plant species in nests**	**Number of frequently used plant species**
1. Bai Hokou, CAR (WLG)	0.8 [a]	17.0 [b]	47.0 [c]	–	–
2. Dja, Cameroon (WLG)	4.9	3.8	6.1	174	46
3. Lopé, Gabon (WLG)	2.2 [d]	35.0 [e]	5.1 [f]	98 [g]	14 [h]
4. Mondika, CAR–Congo(WLG)	0.8 [i]	20.7 [j]	46.7 [k]	–	–
5. Ndakan, CAR (WLG)	5.6	15.1	35.4	–	–
6. Ndoki, Congo (WLG)	2.3 [l]	10.9 [m]	–	–	–
7. Ngotto,CAR (WLG)	0.3	61.3	0	–	–
8. Petit Loango, Gabon (WLG)	0.8	92.7	–	–	–
9. Mawambi Hills, Cameroon (CRG)	2.8	38.3	2.7	108	15

The number of species used for each nest was high, with three quarters of nests constructed using at least four species, compared to other studies on plant use by western gorillas where most nests were made with only one or two species (Groves & Sabater Pi, 1985; Tutin et al., 1995). In addition, we identified 174 species in gorilla nests compared to 98 species in the Lopé Reserve (Tutin et al., 1995). This difference reflects the varied availability of herbs in habitats across the range of the western gorilla (Brugiere & Sakom, 2001; Mehlman & Doran, 2002).

However, frequently-used plant species represented only about 15% of all plants present in the forest, indicating selectivity in the use of nesting materials (Fruth & Hohmann, 1996). Only about one quarter of plant species identified in gorilla nests were frequently used, suggesting that gorillas relied more on a restricted range of preferred key species to build nests. Western lowland gorillas in the Lopé Reserve, Gabon, and Cross River gorillas at Mawambi Hills, Cameroon, have also been shown to rely on a restricted range of preferred key species (Table 4.4), probably reflecting relatively limited availability of suitable nesting materials at these two sites. Similarly, mountain gorillas have been observed to select plants for nest building depending on their availability in the habitat (Rothman et al., 2006). The rates at which plant species were used and their importance in nest construction varied across plant groups and between species. Gorillas are large-bodied mammals that usually sleep on the ground, though they may also sleep in trees (Tutin et al., 1995; Furuichi et al., 1997; Mehlman & Doran, 2002; Rothman et al., 2006; Iwata & Ando, 2007). This is confirmed by our nest database which comprised less than 5% of nests built in trees. As such, gorillas mostly rely on forest understory plants and commonly use terrestrial herbaceous vegetation which is an important component of this stratum in the study site, as also observed in the Lopé Reserve where ground nests built with herbaceous material were the most common type, and predominated in habitats with high densities of understory herbs (Tutin et al., 1995). These observations are consistent with the general trend across the range of western gorillas (Table 4.4), which reveals a negative correlation between herb density and the proportion of tree nests (Spearman test: $r_s = -0.700$; $P = 0.036$; N = 9), though this result may be partially affected by differences in survey methodology. As pointed out by Tutin et al. (1995), trees may be avoided because their wood is physically inappropriate or requires excessive effort for nest construction. Furthermore, habitats such as light gaps, young secondary forest and swamps which have poorly-developed tree communities and important densities of herbs constitute about 60% of the study site (Chapter 5). This is a likely explanation as to why the proportion of bare ground nests is small in the study site (Table 4.4), although across the range of western gorillas, this parameter has no clear relationship with herb density (Spearman test: $r_s = 0.107$; $P = 0.819$; N = 7). Lastly, other factors which can influence tree-nest building by gorillas (Remis, 1993; Tutin et al., 1995; Mehlman & Doran, 2002; Sunderland-Groves et al., 2009) had no detectable effect in the present study: no correlation existed between the number of tree nests and rainfall or temperature—perhaps partly as a result of the reduced availability of appropriate woody materials in preferred habitats; and the intermittent presence of elephants in the site had no major influence on gorillas (unpubl. data).

High values of standard deviation of preference indexes within the herb and liana groups reflected a considerable variability in preference for herbs and lianas compared to trees. Some frequently-used species of herb (e.g. *Aframomum* spp., *Haumania danckelmaniana*), liana (e.g. *Landolphia* spp., *Cissus dinklagei*) and tree (e.g. *Uapaca* spp., *Myrianthus arboreus, Desplatsia* spp.) also provide food for gorillas in the form of shoot, pith, leaves and fruit (Remis, 1997; Doran et al., 2002; Salah, 2011; C.A. Petre, unpubl. data). In addition, preferred or frequently-used herb species in the study site tended to have a clumped stem distribution, and in some cases large leaves (*Hypselodelphys scandens*, *Megaphrynium macrostachyum, M. velutinum*; Willie et al., in prep.), thus making them suitable for the construction of mattress-like structures, with or without association of woody material from lianas, shrubs and tree branches. Similarly, in Gabon, marked preference for species of *Haumania*, *Hypselodelphys, Aframomum* and *Megaphrynium* has been noted (Tutin et al., 1995), and *Aframomum* also occurred in many gorilla nests in Equatorial Guinea (Groves & Sabater Pi, 1985). *Megaphrynium macrostachyum* and species of *Aframomum* featured in more than three quarters of ground nests made with herbs in Ndakan, Central African Republic, and Ndoki, Republic of Congo (Fay, 1997). A comparable pattern was observed in Mondika, Central African Republic, where species of *Aframomum, Sarcophrynium, Megaphrynium*, and *Haumania* were commonly used for the construction of ground herb nests (Mehlman & Doran, 2002). It has been suggested that western gorillas prefer these herb genera because of their structural suitability for nest building and the food they provide (Tutin et al., 1995). Mountain gorillas in Uganda showed evidence of preference for *Pteridium* spp. for nest construction, which is a comfortable building material, and *Ipomea* spp., which provides leaves, bark, and flowers for consumption (Rothman et al., 2006). In the Democratic Republic of Congo, the frequency of occurrence of species in eastern gorilla nests significantly varied (Casimir, 1979). Suitability for nest building and simultaneous use of stems as a food supply for gorillas may therefore justify why some species are preferred over others.

Some plant species, such as *Anchomanes difformis* and *Momordica cissoïdes* were avoided by gorillas probably because their physical properties were unsuitable for building comfortable nests (Tutin et al., 1995). Moreover, unlike favorite nesting plants which have a clumped stem distribution and large leaves, some species such as *Geophylla repens* and *Pollia condensata* were not used perhaps due to their patchy stem distribution and/or small leaves. This explanation is consistent with the observations of previous research which demonstrated that gorillas select the densely packed and leafiest plants to make comfortable nests (Groves & Sabater Pi, 1985; Tutin et al., 1995). However, a more thorough investigation of stem properties and spatial distribution of plant species may provide additional evidence as to why some species are preferred and others avoided.

Plant species used for nesting across seasons greatly overlapped, and there were negligible changes in the plant composition of nests. The number of species used per nest showed similar patterns across seasons, and the small variations probably resulted from infrequent species as only 46 species (< 30%) were frequently used. At the temporal scale, utilization of plants by gorillas for nest building might be viewed as nearly stable, with preferred core species being present in the large majority of nests, and a set of intermittent species that are less consistently present. Gorillas principally built nests in young secondary forest, light gaps and swamps, with marked preference for young secondary forest during long dry and short rainy seasons and for light gaps during the long rainy season. These seasonal changes in habitat use did not, however, influence plant composition in gorilla nests. This may be an indication that frequently-used nest-building plants are randomly distributed across habitat types and with no seasonal change in availability. However, more accurate patterns of seasonal plant preference can be investigated by looking at whether or not changes in plant population size and diversity occur across seasons.

Our findings suggest that gorillas do not randomly use plant species to build nests; instead, they are selective and rely on a particular set of species combined at varying proportions, but with no clear seasonal or spatial patterns. The preferred plant species can serve as indicators of suitable nesting habitats and can be considered alongside plants used by gorillas for feeding when devising land-management strategies for the preservation of gorilla habitat. For example, herb species of the families Marantaceae and Zingiberaceae were frequently used for nest building by gorillas, and it has been shown that these plants occur at high density in light gaps, young secondary forest and swamps (Chapter 5), therefore highlighting the suitability of these habitats for nest building and the need to mitigate human influences in such areas for effective conservation of gorillas.

ACKNOWLEDGEMENTS

Funding was provided by the Centre for Research and Conservation of the Royal Zoological Society of Antwerp (Belgium), core-funded by the Flemish Government, and the Flemish Interuniversity Council (VLIR). We thank the Cameroon Ministry of Forestry and Wildlife and the Ministry of Scientific Research and Innovation for kindly providing research permits. We are also grateful to Charles Yem Bamo, John Carlos Nguinlong, Marcel Salah, André Itotoué, Fabrice Ottou, Germain Mbock, all technical and logistical staff of PGS, and all the Badjué guides for their aid in data collection. Plant specimens were identified at the herbarium by Fulbert Tadjouteu and his team. Constructive comments on the manuscript were received from four anonymous reviewers.

REREFENCES

Anderson, J.R. (1998). Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *American Journal of Primatology* 46: 63–75.

Anderson, J.R. (2000). Sleep-related behavioural adaptations in free ranging anthropoid primates. *Sleep Medicine Reviews* 4(4): 355–373.

Brugiere, D. & Sakom, D. (2001). Population density and nesting behaviour of lowland gorillas (*Gorilla gorilla gorilla*) in the Ngotto forest, Central African Republic. *Zoological Journal London* 255: 251–259.

Casimir, M.J. (1979). An analysis of gorilla nesting sites of the Mt. Kahuzi region, (Zaire). *Folia Primatologica* 32: 290–308.

Djoufack, S.D. (2003). *Végétation et distribution des nids de gorilles (Gorilla gorilla gorilla) dans la périphérie Nord de la Réserve de Biosphère du Dja*. Mémoire de DEA, Université de Yaoundé I, Yaoundé.

Doran, D.M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. & Shah, N. (2002). Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology* 58: 91–116.

Dupain, J., Guislain, P., Nguenang, G.M., De Vleeschouwer, K. & Van Elsacker, L. (2004). High chimpanzee and gorilla densities in a non-protected area on the northern periphery of the Dja Faunal Reserve, Cameroon. *Oryx* 38(2): 1–8.

Fay, J.M. (1997). *The ecology, social organization, populations, habitat and history of the western lowland gorilla (Gorilla gorilla gorilla).* PhD thesis. Washington University, Washington.

Fruth, B. & Hohmann, G. (1996). Nest building behavior in the great apes: the great leap forward? In: *Great Ape Societies* (Eds. W.C. McGrew, L.F. Marchant & T. Nishida). Cambridge University Press, London.

Furuichi, T. Inagaki, H. & Angoue-Ovono, S. (1997). Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: employing a new method to distinguish between nests of the two species. *International Journal of Primatology* 18(6): 1029–1046.

Goldsmith, M.L. (1996). *Ecological influences on the ranging and grouping behavior of western lowland gorillas at Bai Hohou, Central African Republic*. PhD thesis. State University of NewYork at Stony Brook, Stony Brook.

Groves, C.P. & Sabater Pi, J. (1985). From ape's nest to human fix-point. *Man* 20:22–47.

Hamann, A., Barbon, E.B., Curio, E. & Madulid, D.A. (1999). A botanical inventory of a submontane tropical rainforest on Negros Island, Philippines. *Biodiversity and Conservation* 8: 1017–1031.

Iwata, Y. & Ando, C. (2007). Bed and bed-site reuse by western lowland gorillas (*Gorilla g. gorilla*) in Moukalaba-Doudou National Park, Gabon. *Primates* 48: 77–80.

Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia* 14: 413–417.

Letouzey, R. (1985). *Notice de la carte phytogéographique du Cameroun au 1 / 500 000. Domaine de forêt dense humide toujours verte*. Institut de la Carte Internationale de la Végétation, Toulouse.

Loya, D.T. & Jules, E.S. (2008). Use of species richness estimators improves evaluation of understory plant response to logging: a study of redwood forests. *Plant Ecology* 194: 179–194.

Malenky, R.K., Wrangham, R., Chapman, C.A. & Vineberg, E.O. (1993). Measuring chimpanzee food abundance. *Tropics* 2(4): 231–244.

McCune, B. & Grace, J.B. (2002). *Analysis of ecological communities*. MjM software design, Oregon.

McCune, B. & Mefford, M.J. (1999). *PC-ORD. Multivariate analysis of ecological data*. Version 4.01. Gleneden Beach: MjM software, Oregon.

Mehlman, P.T. & Doran, D.M. (2002). Influencing western gorilla nest construction at Mondika Research Center. *International Journal of Primatology* 23(6): 1257–1285.

Morgan, D. & Sanz, C. (2007). *Best practice guidelines for reducing the impact of commercial logging on great apes in Western Equatorial Africa*. IUCN SSC Primate Specialist Group (PSG), Gland.

Nguenang, G.M. & Dupain, J. (2002). *Typologie et description morpho-structurale de la mosaïque forestière du Dja: Cas du site d'étude sur la socio-écologie des grands singes dans les villages Malen V, Doumo-pierre et Mimpala (Est-Cameroun)*. Rapport interne, SRZA.

Poulsen, J.R. & Clark, C.J. (2004). Densities, distributions and seasonal movements of gorillas and chimpanzees in swamp forest in Northern Congo. *International Journal of Primatology* 25: 285 –306.

Remis, M.J. (1993). Nesting behavior of lowland gorillas in the Dzanga-Sangha Reserve, Central Africa Republic: implications for population estimates and understanding of group dynamics. *Tropics* 2(4): 245–255.

Remis, M.J. (1997). Western lowland gorillas as seasonal frugivores: use of variable resources. *American Journal of Primatology* 43: 87–109.

Rogers, M.E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., McFarland, K., Nishihara, T., Remis, M. & Tutin, C.E.G. (2004). Western gorilla diet: A synthesis from six sites. *American Journal of Primatology* 64: 173–192.

Rothman, J.M., Pell, A.N., Dierenfeld, E.S. & McCann C.M. (2006). Plant choice in the construction of night nests by gorillas in the Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology* 68: 361–368.

Salah, M.S. (2011). *Contribution des gorilles (Gorilla gorilla gorilla), chimpanzés (Pan troglodytes troglodytes) et élephants (Loxodonta africana cyclotis) à la régénéra-*

tion des forêts dans la périphérie Nord de la Réserve de Biosphère du Dja (Est-Cameroun). Mémoire présenté en vue de l'obtention du diplôme d'Ingénieur des Eaux, Forêts et Chasse. Université de Dschang, Dschang.

Sanz, C., Morgan, D., Strindberg, S. & Onononga, J.R. (2007). Distinguishing between the nests of sympatric chimpanzees and gorillas. *Journal of Applied Ecology* 44: 263–272.

Sunderland-Groves, J.L., Ekinde, A. & Mboh, H. (2009). Nesting behavior of *Gorilla gorilla diehli* at Kagwene Mountain, Cameroon: implications for assessing group size and density. *International Journal of Primatology* 30: 253–266.

Tutin, C.E.G. & Fernandez, M. (1984). Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *American Journal of Primatology* 6: 313–336.

Tutin, C.E.G., Parnell, R.J., White, L.J.T. & Fernandez, M. (1995). Nest building by lowland gorillas in the Lopé Reserve, Gabon: environmental influences and implications for censusing. *International Journal of Primatology* 16(1): 53–76.

White, L.J.T., Rogers, M.E., Tutin, C.E.G., Williamson, E. & Fernandez, M. (1995). Herbaceous vegetation in different forest types in the Lopé Forest Reserve, Gabon: implications for keystone food availability. *African Journal of Ecology* 33: 124–141.

Yamagiwa, J. (2001). Factors influencing the formation of ground nests by eastern lowland gorillas in Kahuzi-Biega National Park: some evolutionary implications of nesting behavior. *Journal of Human Evolution* 40: 99–109.

Herbaceous plant inventory in 1-m^2 plots. © Jacob Willie, PGS

Chapter 5

Density of herbaceous plants and distribution of western lowland gorillas in different habitat types in south-east Cameroon

Jacob Willie, Charles-Albert Petre, Nikki Tagg and Luc Lens

Modified from Willie et al. (2012). *African Journal of Ecology*. doi: 10.1111/aje.12014

ABSTRACT

The study of forest herb availability improves knowledge of ecology and conservation of gorillas that depend on such herbs. Density patterns of herbs and location of western lowland gorilla nest sites were studied in different habitat types at a site in south-east Cameroon to assess their relationship. Herb stems of the families Marantaceae and Zingiberaceae were identified and counted in 10,713 1-m^2 plots distributed within six habitat types. Stem density correlated with light availability and ranged from 2.38 stems/m^2 in near primary forest to 4.66 stems/m^2 in light gaps. Gorillas showed marked preferences for habitats with high herb densities such as light gaps, swamps and young secondary forest. However, no clear relationship exists between terrestrial herbaceous vegetation and gorilla densities across Central Africa. It is suggested that differences in ecological factors and land use history within and between sites may explain differences in herb density and diversity which partly account for variations in the historical and present population distribution and density of western gorillas. Formerly-logged and swamp forests, which are characterized by an abundance of herbs, may prove to be of great value in the conservation of western gorillas given appropriate forest management practices, adequate protection from poaching and limited human encroachment.

INTRODUCTION

Gorillas strongly depend on terrestrial herbaceous vegetation (THV) for nest building and food (Casimir, 1979; Watts, 1984; Tutin et al., 1991; Yamagiwa et al., 1994; Tutin et al., 1995; Mehlman & Doran, 2002; Ganas et al., 2004; Rothman et al., 2006; Doran-Sheehy et al., 2009; Harrison & Marshall, 2011). Eastern gorillas show a high degree of folivory and heavily rely on large quantities of THV year-round (Watts, 1984; Harrison & Marshall, 2011). In comparison, tree fruits are an important component of the diet of western gorillas, but stems, fruits, shoots and young leaves of THV are considered an important fallback food source when fruits are scarce (Tutin et al., 1991); they are still commonly consumed even in times of fruit abundance (Sabater Pi, 1977; Calvert, 1985; Williamson et al., 1990; Groves & Meder, 2001; Doran et al., 2002; Rogers et al., 2004) and are used for nesting (Groves & Sabater Pi, 1985; Tutin et al., 1995). Given their importance, herb availability is thought to be a primary determinant of gorilla distribution and density (Fay, 1997; Brugiere & Sakom, 2001), therefore highlighting the importance of understanding patterns of herb availability and distribution.

Studies that quantify herb resources show large variations in availability across sites throughout the range of gorillas (Watts, 1984; White et al., 1995; Brugiere & Sakom, 2001; Doran et al., 2002; Ganas et al., 2004). These variations reflect changes in gorilla habitats and may translate into shifts in dietary and ranging patterns (Doran-Sheehy et al., 2004; Ganas et al., 2004; Harrison & Marshall, 2011). Additionally, changes in foraging strategies, diet and habitat use within each site are congruent with site-specific variations in the temporal and spatial availability of resources (Yamagiwa et al., 1994; Doran et al., 2002; Doran-Sheehy et al., 2004). A thorough understanding of such animal-habitat relationships is a prerequisite when drafting future land-management strategies aimed at improving or maintaining habitat suitability for gorillas and sympatric species (Johns, 1985; Clark et al., 2009; Stokes et al., 2010).

Western gorilla surveys have revealed a preference for building nests in habitats such as swamps and young secondary forest (Fay & Agnagna, 1992; Dupain et al., 2004; Matthews & Matthews, 2004; Rainey et al., 2010). An analysis of the factors influencing habitat preference is required to better understand how gorillas adapt to their environment (Anderson, 1998). Across sites of Central Africa, including the present study site in south-east Cameroon, THV species of the families Marantaceae and Zingiberaceae are preferred nest-building materials and herb food plants for western lowland gorillas (Groves & Sabater Pi, 1985; Tutin et al., 1995; Rogers et al., 2004; Chapter 4). The objective of this study is to compare THV density in different habitats found in the site and relate this to the distribution of gorilla nest sites. Our hypotheses are twofold: 1) that THV is nonrandomly distributed with respect to habitat type, 2) that gorillas prefer specific habitats to build nests. Also in this paper, we present data for comparison of resource availability with other sites across the range of the western lowland gorilla.

MATERIAL AND METHODS

Study site

All data were collected in the research site called 'La Belgique' (about 40 km^2), which is located between 013°07'-013°11' E and 03°23'-03°27' N in the northern periphery of the Dja Biosphere Reserve (DBR). This area is located in the transition zone between the semi-deciduous forests of Equatorial Guinea and the evergreen forests of the Congo basin (Letouzey, 1985). Rainfall in the site reaches > 1500 mm per year (Chapter 4). The research site is situated within forest management unit 10 047. The site was partially and selectively logged more than 30 years ago, and old pits and oil palm trees provide evidence that the site was settled and cultivated in the past (Sowunmi, 1999; White & Edwards, 2000). Tree and branch falls are frequent in the site resulting in considerable light gaps. These events have resulted in a dense patchwork of various sized forest at various stages of stand development, and therefore a mosaic of habitats. The site is traversed by human-made trails used for hunting and research and comprises a dense network of watercourses and seasonal swamps.

Habitat types

We adapted previous vegetation classifications in the area (Nguenang & Dupain, 2002; Djoufack, 2003; Dupain et al., 2004) and distinguished six habitat types: 1) Near primary forest (NPF) dominated by large tree species of height > 30 m (e.g. *Omphalocarpum procerum*, *Uapaca* spp., *Polyalthia suaveolens* and *Piptadeniastrum africanum*), with little undergrowth and a closed canopy; 2) Old secondary forest (OSF) with trees of height 25−30 m (e.g. *Terminalia superba*), more pronounced undergrowth than NPF and a discontinuous canopy layer; 3) Young secondary forest (YSF), dominated by early successional trees of < 25 m (e.g. *Tabernaemontana crassa, Myrianthus arboreus*), and a relatively dense undergrowth; 4) Light gaps (LG) which are open-canopied environments resulting from tree and branch fall or elephant activity; 5) Swamps (SW) principally characterized by high densities of *Raphia* spp., few (< 5%) raphia-free open areas (clearings), and a hydromorphic soil; and 6) Riparian forest (RF), located in the transition zone between SW and other forest types, with a mixture of species from all forest types. NPF, OSF, YSF and LG are referred to collectively as *terra firma* habitats. SW and RF are (periodically) flooded habitats.

To determine the proportion of each habitat type in the study site, we surveyed ten 6-km transects set 600 m apart at a constant bearing of 45°. In December 2009, the habitat type was determined at 50 m points along each transect based on the above criteria and horizontal visibility at 1.7 m above the floor was assessed in a random direction. The proportion of each habitat type was determined as the relative frequency of occurrence of each habitat type in all transects (see Fig. 5.1 for illustration).

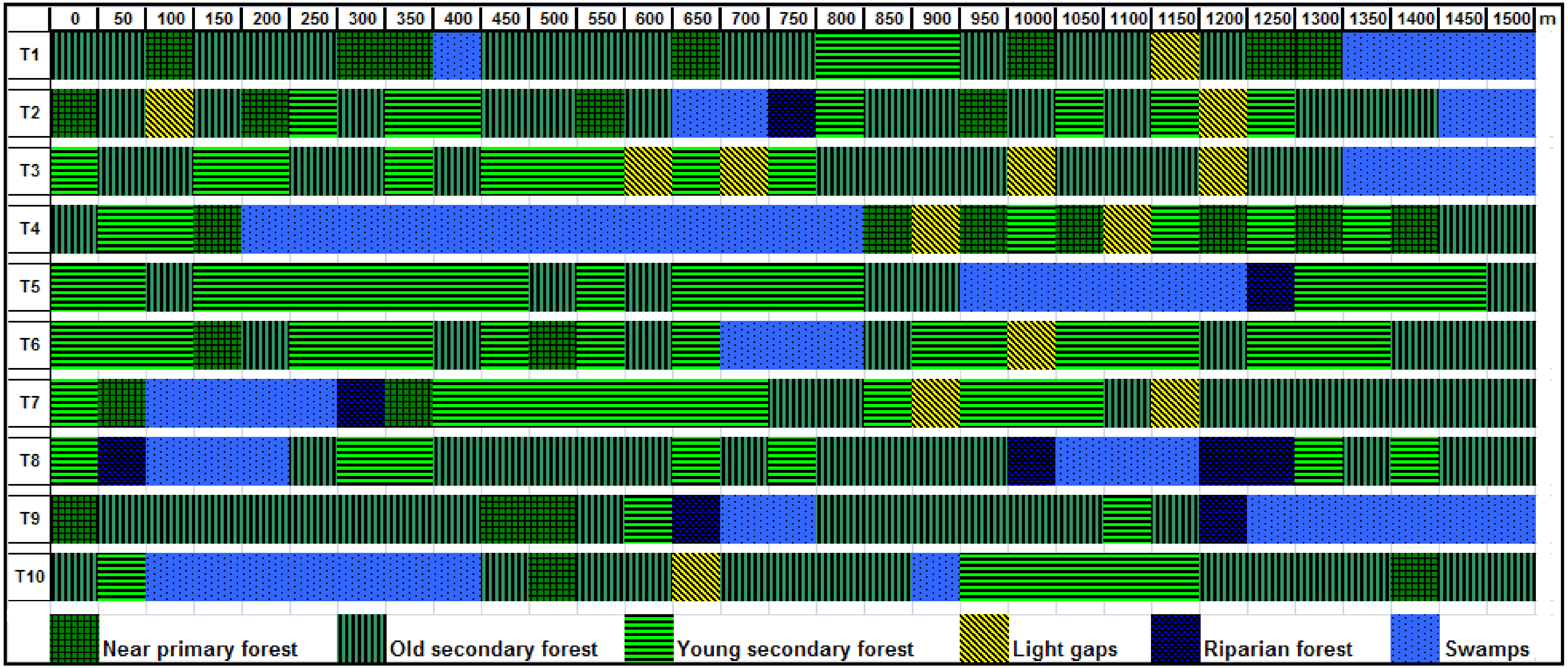


Fig. 5.1 Graph depicting the mosaic of habitat types of various sizes which occurred in the first 1.5 km along the ten 6-km transects. Transects were 600 m apart and opened at a bearing of 45°. Habitat types were identified using a set of criteria (see text for details). In each habitat, THV was surveyed in 1-m^2 contiguous plots.

Density of terrestrial herbaceous vegetation (THV)

For the purpose of this study, we sampled THV species of the families Marantaceae and Zingiberaceae because herbaceous species of other families are relatively less important to gorillas as food or nest-building materials in the study site (Chapter 4). A stratified sampling design with disproportionate allocation was used to sample these herbs because the study site is a dense mosaic of habitat types (strata; Fig. 5.1), and adequate sample size for measuring understory herbs is difficult to estimate and can be approximated only when the plot of cumulative means of herb density against number of plots sampled tends to stabilize (Malenky et al., 1993; Doran et al., 2002). Within each surveyed habitat patch, we identified and counted THV stems in a linear series of 1-m^2 contiguous square plots. In each case, plot direction avoided trails. For each habitat type, we continued to add more plots in new patches until mean densities tended to stabilize. The total area sampled across all habitat types was 1.07 ha. THV species were identified in the field by experienced and trained local botanists and the lead author using consistent local names, and a sample specimen species collected for identification at the National Herbarium of Yaoundé, Cameroon. Raw data for each habitat type were used to calculate a mean THV density (stems/m^2) and associated variance. Mean stem density and variance for each species in the study site was calculated using the total number of plots sampled across all habitats. To investigate a correlation between THV clumping and habitat/species use for nest building, we calculated a coefficient of dispersion (CD) as the variance-to-mean ratio. As discussed by Doran et al. (2002, and references therein), variance-to-mean ratios whenever greater than one indicate significantly clumped distributions ($P < 0.001$).

Canopy openness

In each habitat type, degree of canopy openness above the plot was quantified visually (Loya & Jules, 2008) and an arbitrary 'light score' (0−100) assigned: Open (100), when there was no tree branch or foliage above the 1-m^2 plot, Half-open (50) when the plot was partially covered, and Closed (0) when it was totally covered. The sum of light scores for each set of five consecutive plots in each habitat type was regarded as a single observation, therefore resulting in light score values ranging from 0—500 with a higher light score representing a more open canopy.

Distribution of gorilla nest sites

Gorilla nest sites were located by trackers who followed gorilla trails and recorded information on nests, vocalizations, footprints and feces. Additional data (fresh gorilla nests) were also collected along transects during marked-nest-count (MNC) surveys. Gorilla nest sites and individual nests were counted and a note made of the habitat type in which the nest site was located. Gorilla trails and transects traversed all habitat types found in the site. Data were collected every month from April 2009 to July 2011. Using the method of Dupain et al. (2004), a preference index for nesting in a particular habitat type was calculated as the difference between the actual number and the expected number of nest sites found in that habitat type. For each habitat type, the expected number of nest sites was calculated as X*Y/100 where X is the proportion of the habitat type in the study site, and Y is the total number of nest sites found in the study site.

Statistical analyses

Our data did not meet the assumptions of normality (see Siegel & Castellan, 1988). Therefore nonparametric statistical tests were applied using SPSS. For global comparisons of visibility and light score across habitat types, Median tests (two-tailed) were used. All pairwise comparisons were done using two-sample Kolmogorov-Smirnov tests (two-tailed), and the Bonferroni correction (0.05/number of pairwise comparisons) was applied to control the error rate, therefore maintaining a test-wide significance of $\alpha = 0.05$. Correlations were assessed using the Spearman test of correlation (two-tailed). Because there was a natural *a priori* ordering of the *terra firma* habitat types that represented decreasing light conditions, a Jonckheere-Terpstra test (one-tailed) for ordered alternatives was used to compare stem densities among these habitats (Siegel & Castellan, 1988).

RESULTS

Characteristics of habitat types

OSF, YSF, SW, RF, LG and NPF represented 35%, 31%, 20%, 6%, 5% and 3% of the total forest cover, respectively. Habitat types contrasted in terms of visibility, light score and THV density (Table 5.1). There was global significance in differences in visibility among *terra firma* habitats (Median test: $\chi^2 = 107.35$; df = 3; $P < 0.001$) and all pairwise comparisons (two-sample Kolmogorov-Smirnov tests: $P < 0.001$ in all cases). LG, YSF, OSF and NPF presented increasing values of visibility. Of all habitats, LG and YSF had the lowest visibility. Differences in visibility among flooded habitats were also significant (two-sample Kolmogorov-Smirnov test: Z = 2.14; $P < 0.001$). Both global and pairwise comparisons showed statistically significant differences in light scores among *terra firma* habitats (Median test: $\chi^2 = 324.87$; df = 3; $P < 0.001$; two-sample Kolmogorov-Smirnov tests: $P < 0.05$ in all cases), but no difference was evident among flooded habitats (two-sample Kolmogorov-Smirnov test: Z = 0.97; $P > 0.05$). Of all habitats, LG, YSF and SW had the highest light scores. LG, YSF, OSF and NPF presented a pattern of significantly decreasing light scores. The same pattern was observed for all THV stem density (Jonckheere-Terpstra test, $P < 0.001$; Fig. 5.2). Difference in stem density among flooded habitats was significant (two-sample Kolmogorov-Smirnov test: Z = 1.53; $P < 0.01$). THV density correlated positively with light score (Spearman test: $r_s = 0.943$; $P < 0.01$; N = 6).

Table 5.1 Characteristics of each habitat type and preference index for nesting. NPF: Near primary forest; OSF: Old secondary forest; YSF: Young secondary forest; LG: Light gaps; RF: Riparian forest; SW: Swamps. NPF, OSF, YSF and LG are referred to collectively as '*terra firma*' habitats. RF and SW are collectively called 'flooded' habitats. [a] The sum of light scores for each 5-m stretch along transects in each habitat type was regarded as a single observation. The displayed results represent average values per stretch. Habitat types with more open canopies have higher light scores. [b] The coefficient of dispersion (CD) was calculated as the variance-to-mean ratio; as shown in Doran et al. (2002), CD > 1 indicates significantly clumped distributions ($P < 0.001$). [c] Calculated using data from nest surveys along transects and from trail follows.

Parameter	**NPF**	**OSF**	**YSF**	**LG**	**RF**	**SW**	**FLOODED habitats**	**TERRA FIRMA habitats**
Number of plots	4408	1582	1170	1023	776	1754	2530	8183
Average visibility (m) ±SE	13.56 ±0.82	9.75 ±0.23	7.10 ±0.22	4.57 ±0.37	7.32 ±0.74	13.18 ±0.56	12.20 ±0.50	8.70 ±0.17
Average light score [a] ±SE	85.75 ±4.09	132.75 ±7.65	181.41 ±10.66	423.04 ±8.44	147.10 ±11.78	166.14 ±7.64	160.30 ±6.41	150.61 ±4.20
Percentage of plots with stems	48.68	55.31	60.43	67.45	53.09	59.69	57.67	53.99
Coefficient of dispersion [b]	6.04	6.47	6.54	7.86	7.26	6.59	6.79	6.76
Average THV density (stems/m^2) ±SE	2.38 ±0.06	2.99 ±0.11	3.29 ±0.14	4.66 ±0.19	3.18 ±0.17	3.41 ±0.11	3.34 ±0.09	2.91 ±0.05
Preference index for nesting [c]	–3.75	–40.75	18.25	19.75	–5.50	12.00	6.50	–6.50

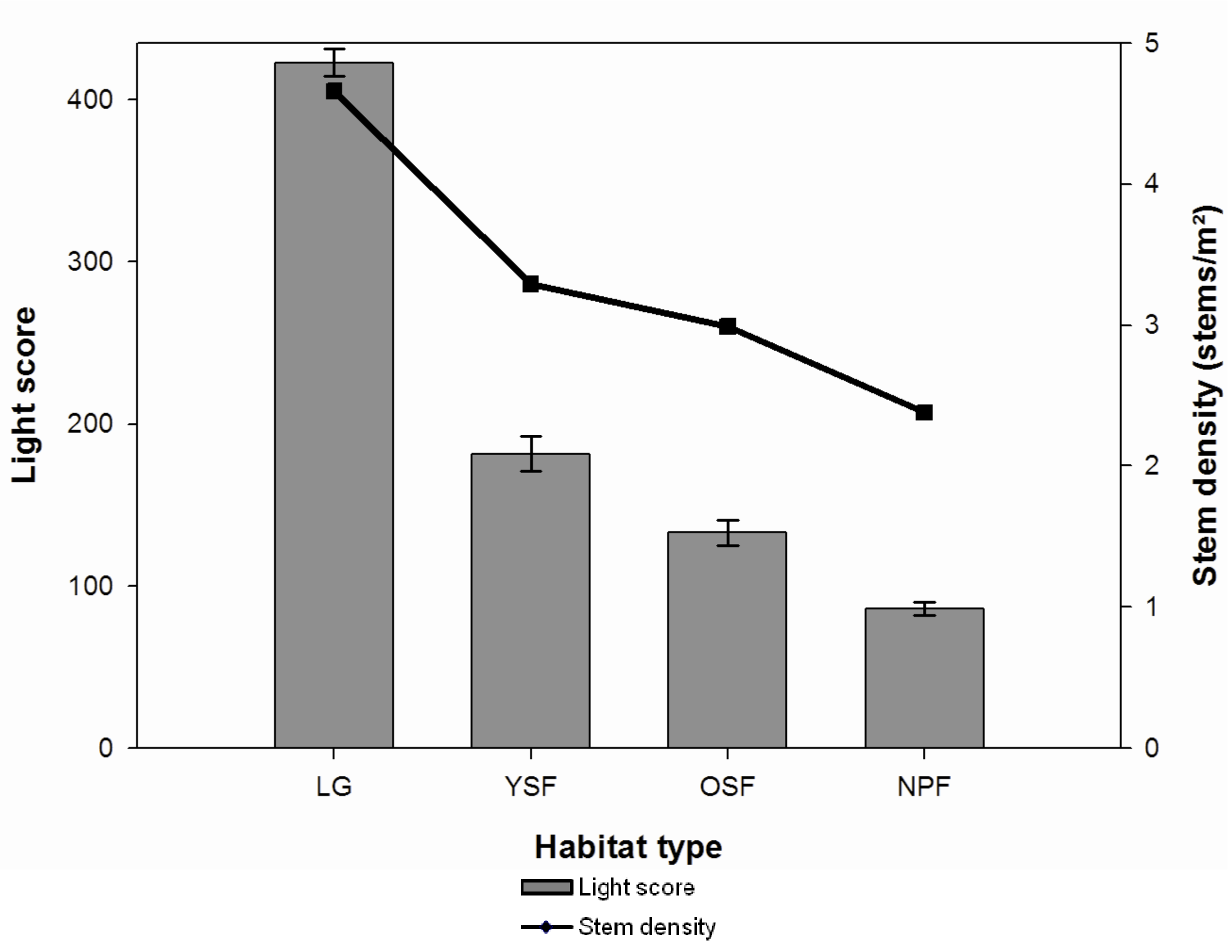


Fig.5.2 Light score (left y-axis, bar plot) and stem density (right y-axis, line graph) among *terra firma* habitats. LG: Light gaps; YSF: Young secondary forest; OSF: Old secondary forest; NPF: Near primary forest.

In terms of major habitat types, pairwise comparisons indicated greater visibility, light score and stem density in flooded compared to *terra firma* habitats (two-sample Kolmogorov-Smirnov tests: Z = 2.87, 2.09 and 1.98, respectively and $P < 0.001$ in all cases). Though THV followed a clumped distribution in all habitats (coefficient of dispersion [CD] > 1 in all cases), clumps were most common in LG, RF and SW.

Stem densities and distribution of THV species

A total of 10,713 plots distributed within six habitat types were surveyed (Table 5.1). Overall THV density was > 3 stems/m^2 (Table 5.2). *Haumania* *danckelmaniana* was the most abundant species whereas *Afrocalathea rhizantha* was the rarest species. *Marantochloa congensis* occured only in open raphia-free swamps and showed the most pronounced clumped distribution of all THV species, with a coefficient of dispersion of 24.78 and a local density of up to 48 stems/m^2. Similar patterns were displayed by *Sarcophrynium prionogonium*, *S. brachystachyum*, *Aframomum polyanthum* and *Trachyphrynium braunianum.* All species exhibited a clumped distribution, but not to the same extent. Marantaceae occurred at the greatest density and comprised 89.72% of stems. Marantaceae and Zingiberaceae occurred in 49.07% and 10.79% of all plots surveyed, respectively. Marantaceae tended to form bigger clumps than Zingiberaceae, with coefficients of dispersion of 6.98 and 4.44, respectively. Of the 22 THV species surveyed, six (*Ataenidia conferta, Halopegia azurea, Aframomum* sp.3*, A. polyanthum, M. congensis* and *T. braunianum*) were exclusively found in flooded forests and one (*A. rhizantha*) in *terra firma* forests. Other species of *Aframomum* (Zingiberaceae) as well as *Megaphrynium macrostachyum* (Marantaceae) were abundant and formed bigger clumps in LG and YSF.

Distribution of gorilla nest sites and preference index for nesting

A total of 125 gorilla nest sites were found, with 57, 37, 26, 3, 2 and 0 nest sites in YSF, SW, LG, OSF, RF and NPF, respectively. Of all habitats, LG, YSF and SW presented higher values of preference index (Table 5.1). Gorillas seemed to avoid NPF, OSF and RF while seeking sleeping sites. Within SW, no gorilla nest site occurred in clearings. Globally, gorillas preferred to build nests in flooded habitats.

Table 5.2 Densities of THV species in four gorilla study sites of Central Africa (stems/m^2). [a] No density data is displayed when the species was not surveyed at a given site. [b] M = Marantaceae; Z = Zingiberaceae. [c] Present study; CMR = Cameroon. [d] Data from White et al. (1995). [e] Doran et al. (2002), mixed forest only; CAR = Central African Republic. [f] Fay (1997); excluding *Costus lucanusianus* (Costaceae). [g] *M. macrostachyum* and *M. velutinum* (Dja and Lopé); *M. macrostachyum/trichogynum* (Mondika); *M. macrostachyum* (Ndakan). [h] *S. prionogonium* and *S. brachystachyum* (Dja); *S. schweinfurthii/brachystachys* (Mondika); *S. prionogonium* and *S. schweinfurthianum* (Ndakan). [i] *A. sulcatum*, *A. arundinaceum*, *A. melegueta*, *A. polyanthum*, *A.* sp.2 and *A.* sp.3 (Dja); two undetermined species (Lopé); at least *A. limbatum* and *A. subsericium* (Mondika).

Species [a]	**Family** [b]	**Dja** [c] (CMR)	**Lopé** [d] (Gabon)	**Mondika** [e] (CAR-Congo)	**Ndakan** [f] (CAR)
Afrocalathea rhizantha	M	0.0002	–	–	–
Ataenidia conferta	M	0.02	0.08	–	1.88
Halopegia azurea	M	0.08	0.14	–	–
Haumania danckelmaniana	M	0.69	–	0.33	0.68
Haumania liebrechtsiana	M	–	0.89	–	–
Hypselodelphys scandens	M	0.04	–	–	0.05
Hyselodelphys violacea	M	–	0.07	–	–
Marantochloa congensis	M	0.02	–	–	–
Marantochloa cordifolia	M	–	0.12	–	–
Marantochloa filipes	M	0.01	0.05	–	0.21
Marantochloa holostachya	M	–	–	–	0.23
Marantochloa leucantha	M	0.09	–	–	–
Marantochloa purpurea	M	0.18	0.01	–	–
Megaphrynium spp. [g]	M	0.87	0.66	0.20	1.11
Sarcophrynium spp.[h]	M	0.64	–	0.07	0.81
Trachyphrynium braunianum	M	0.06	–	–	–
Aframomum spp. [i]	Z	0.29	0.13	0.07	0.16
Renealmia africana	Z	0.02	–	–	–
Renealmia cincinnata	Z	0.004	0.02	–	–
Renealmia macrocolea	Z	–	0.04	–	–
All THV	M & Z	3.01	2.21	0.67	5.13

Table 5.3 Terrestrial herbaceous vegetation and gorilla densities across Central Africa. [a] weaned individuals only; [b] Goldsmith (1996) in Doran et al. (2002); [c] Remis (2000); [d] central and northern sectors; [e] this study; [f] Latour (2010); [g] White et al. (1995); [h] White (1994); [i] Malenky et al. (1993); [j] Fay (1997); [k] Brugiere & Sakom (2001); [l] Brugiere & Sakom (2001); [m] open-canopy Marantaceae forest only; [n] Brugiere, Bougras & Gautier-Hion (2000) in Brugiere & Sakom (2001); [o] Bermejo (1999); [p] Furuichi et al. (1997); [q] Furuichi et al. (1997).

Density	**Bai Hokou** (Central African Republic)	**Dja** [d] (Cameroon)	**Lopé** (Gabon)	**Ndoki** (Congo)	**Ngotto** (Central African Republic)	**Odzala** [m] (Congo)	**Petit Loango** (Gabon)
Herbs (stems/m^2)	0.82 [b]	3.01 [e]	2.21 [g]	2.25 [i]	0.34 [k]	20 [n]	0.51 – 1.01 [p]
Gorillas [a] (ind./km^2)	0.84 [c]	2.08 [f]	0.30 – 1.00 [h]	0.20 [j]	0.34 – 0.40 [l]	11.30 [o]	0.21 [q]

DISCUSSION

The site mostly comprised old and young secondary forests and THV occurred in every habitat type. THV presented a more pronounced clumping in riparian forest and swamps compared to *terra firma* habitats, except light gaps (Table 5.1), because species with high CD such as *M. congensis*, *S. brachystachyum, S. prionogonium*, *A. polyanthum* and *T. braunianum* are more abundant or exclusive to flooded habitats. Of all habitat types, light gaps had the highest value of CD, meaning that the majority of species, including those that presented more patchy distributions (e.g. *Aframomum* spp. and *Megaphrynium macrostachyum*) had relatively clumped distributions in light gaps. When considering *terra firma* habitat types representing vegetation from early stages to near primary forest, canopy cover increased in continuity and the understory vegetation (THV, seedlings, saplings, shrubs and lianas) became less thick; as a result, light scores decreased significantly and visibility increased significantly (Table 5.1). Similar patterns of visibility among *terra firma* habitats were described by Dupain et al. (2004). Stem density significantly decreased with decreasing light scores among *terra firma* habitats (Fig. 5.2). It is worth noting that nitrogen content in leaf-litter and litter decomposition rate are high in late successional forests where old-growth tree leaves predominate (Vasconcelos & Laurance, 2005). An increase in light intensity following large tree or branch falls enables photophilic species to rapidly exploit that fertility and this contributes to high THV densities. These arguments suggest that stem density is greatest in light gaps due to greater use of energy and nutrient resources, and concur with the well-supported conclusion that light and resource availability are the most important limiting factors to plant growth in tropical forests (Dupuy, 1998; White & Edwards, 2000; Costa & Magnusson, 2002).

Gorillas showed a marked preference for light gaps, young secondary forest and swamps for nesting, reflecting the results of other studies (e.g. Fay & Agnagna, 1992; Dupain et al., 2004; Matthews & Matthews, 2004; Rainey et al., 2010). Preference for light gaps and young secondary forest is probably due to the high density and clumped distribution of *Aframomum* spp. and *Megaphrynium macrostachyum* which are the preferred nest-building materials and food herbs for western gorillas (Sabater Pi, 1977; Calvert, 1985; Groves & Sabater Pi, 1985; Carroll, 1988; Nishihara, 1995; Tutin et al., 1995; Kingdom, 1997; Tutin, 1998; Goldsmith, 1999; Mehlman & Doran, 2002; Doran-Sheehy et al., 2009). In preferred habitats, canopy was more open and light scores were correspondingly high (Table 5.1). Visibility was low, except in swamps where the maximum height of dense understory vegetation, essentially Marantaceae and Cyperaceae species, was usually less than that at which visibility was estimated (1.7 m). It should also be noted that hunting pressure is high in the study site; although we did not assess its impact on nesting behavior, it is possible that gorillas preferred dense and low-accessibility habitats types to avoid hunters (Dupain et al., 2004), likely affecting their ranging behavior (Cipolletta, 2003). The higher global value of preference index in flooded habitats suggests that gorillas may prefer swamps. However, this result must be interpreted cautiously as some gorilla groups may avoid nesting in flooded habitats during wet seasons, although they are attracted during the driest months (authors' obs.). Furthermore, sympatric populations of chimpanzees are observed to build ground nests in swamps, which could lead to mis-identification of nest-builder (authors' obs.). However, because only fresh nest sites were included in the present analyses, ancillary evidence such as footprints, dung, urine and hairs will have minimized nest-builder confusion. In addition, previous studies in the site showed that swamp was the second most frequently used habitat for nesting (Maja & Dupain, unpubl.). Swamps may be preferred because they provide natural protection from hunters, abundant and clumped THV species, year-round mineral- and protein-rich aquatic herbs, and at a certain time of the year, succulent fruits in high quantity (e.g., *Grewia* sp. and *Nauclea* sp.; Nishihara, 1995; Kuroda et al., 1996; Magliocca & Gautier-Hion, 2002; Doran-Sheehy et al., 2004; Rainey et al., 2010). Echoing previous findings (e.g. Poulsen & Clark, 2004; Rainey et al., 2010), our results indicate that swamps might be an important gorilla habitat and can potentially serve as a refuge especially during intense logging and hunting activities, thus supporting the relevance of swamps in gorilla conservation.

Overall herb densities displayed in Table 5.2 are higher than those estimated in other sites within the range of western lowland gorillas, such as Mondika, Central African Republic (CAR) and Republic of Congo (Doran et al., 2002), and Lopé, Gabon (White et al., 1995), but lower than the figure reported for Ndakan, CAR (Fay, 1997). Although 54% of plots contained Marantaceae stems at Mondika, slightly higher compared to Dja (49%), THV stems were patchier at Mondika (Doran et al., 2002). Furthermore, herb diversity patterns vary across sites: the highest number of species of both Marantaceae and Zingiberaceae occurred in the Dja, and many species were not surveyed at Mondika (Table 5.2). Inter-site variability in forest structure and composition, light and soil conditions, land use history and other environmental constraints may contribute to the variation in stem density, diversity and frequency observed between sites. For example, it has been shown that changes in herb composition across sites may result in different species' responses to past land use and therefore to different colonization potential of forest herbs (Baeten et al., 2011); that soil texture and structure can influence soil water retention capacity which affects herbaceous vegetation growth (Brugiere & Sakom, 2001); and that nutrient concentrations and biomass of forest herbs are influenced by previous land use (Baeten et al., 2011). Additionally, because survey methodologies are not standardized, differences in sampling methods and/or surveyed species between sites may lead to some of these observed density and diversity differences. However, stem densities of the genera that were surveyed at all sites such as *Haumania*, *Megaphrynium* and *Aframomum* were high at Ndakan (Fay, 1997) and in the Dja and were consistent with the general patterns of THV density (Table 5.2). Most species in the Dja had highly clumped stem distributions and THV displayed a continuous distribution at Ndakan. This seems to indicate that THV is more abundant and forms bigger clumps in these two sites. Across sites of Central Africa, the density and occurrence of *Haumania,* a protein-dense plant that gorillas widely consume (Calvert, 1985; Nishihara, 1995; Tutin, 1998; Goldsmith, 1999; Doran et al., 2002; Doran-Sheehy et al., 2009), and other important gorilla herbs, vary considerably (Table 5.2). These variations in herb density and diversity imply that western lowland gorillas face variable nutritional, nest-building and habitat conditions throughout their range (Head et al., 2011), which may explain variation in their historical and present population distribution and density (Tutin & Fernandez, 1984; Fay, 1997; Bermejo, 1999; Brugiere & Sakom, 2001; Dupain et al., 2004; Matthews & Matthews, 2004; Devos et al., 2008; Rainey et al., 2010). However, other factors such as carrying capacity of habitats, disease epidemics, poaching, human encroachment and survey methodology may lead to such variation (Brugiere & Sakom, 2001; Rogers et al., 2004; Devos et al., 2008; Rainey et al., 2010), and THV availability does not always affect gorilla density (Head et al., 2011). This argument is supported by the data presented in Table 5.3, which showed no clear relationship between maximal and minimal values of THV and gorilla densities across sites of Central Africa (Spearman tests: $r_S = 0.464$ and 0.536; $P > 0.05$ in all cases; N = 7). Although more investigation is needed to draw firm conclusions on the relative effect of each factor on ape density, our data show that gorillas prefer habitats with high THV density for nesting, as observed elsewhere (e.g. Tutin & Fernandez, 1984; White, 1994; Fay, 1997; Furuichi et al., 1997; Bermejo, 1999; Dupain et al., 2004) and support the idea that ape density is best predicted by habitat or THV density (Oates, 1996; Brugiere & Sakom, 2001; Poulsen & Clark, 2004).

To summarize, it appears that forest herb density is positively affected by light regime which is a major limiting factor to plant growth in tropical forests. Abiotic and human-induced factors show temporal and spatial variation, and herb density across habitat types and sites varies accordingly. Gorillas nest in specific habitats with more open canopies, limited visibility and clumps of forest herbs which are used for both feeding and nest building. The present study site had been selectively logged and contained areas with dense clumps of herbs; it may thus be inferred that inevitable canopy opening following future logging operations is likely to result in an increase in the amount of nest-building material (or preferred nesting habitat) and herb food that is available for gorillas. Gorillas can thrive in logged forests given the right conditions (Johns, 1985; Oates, 1996; Tutin et al., 1997; Arnhem et al., 2008; Clark et al., 2009; Stokes et al., 2010). However, this must be regarded with caution. Malenky et al. (1993) reported higher herb densities in lightly logged compared to heavily logged forest in Kibale, Uganda, an indication that logging damage or high light levels may not necessarily increase the density of herbs (Wrangham et al., 1993; Costa & Magnusson, 2002). This shows that selective logging with less canopy opening should be favored. Further investigation is needed to determine the logging intensities and light levels that may become detrimental to herbs in African rainforests and the potential knock-on effects on gorilla density and distribution. However, it is suggested that logged forests and areas with abundant herbs, such as swamp forests, may be of great value in the conservation of western gorillas given appropriate forest management practices, adequate protection from poaching and limited human encroachment.

ACKNOWLEDGEMENTS

We thank the Centre for Research and Conservation of the Royal Zoological Society of Antwerp and VLIR-UOS for financial, logistic and technical support. We are grateful to the Ministry of Forestry and Wildlife and the Ministry of Scientific Research and Innovation for permission to conduct this research. Thanks are also extended to all scientific, technical and logistical staff of PGS and to Guillaume Djang Djang, Jean Tongo, Laurent Tiné, Jean Assimentsien, Anicet Mabom, Patrick Ondji and others who provided invaluable help during field work, and to Fulbert

Tadjouteu of the National Herbarium of Yaoundé for his contribution to plant specimen identification. Constructive comments on the manuscript were received from Dr. Zjef Pereboom and three reviewers.

REFERENCES

Anderson, J.R. (1998). Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *American Journal of Primatology* 46: 63–75.

Arnhem, E., Dupain, J., Vercauteren, D.R., Devos, C. & Vercauteren, M. (2008). Selective logging, habitat quality and home range use by sympatric gorillas and chimpanzees: a case study from an active logging concession in southeast Cameroon. *Folia primatologica* 79: 1–14.

Baeten, L., Verstraeten, G., De Frenne, P., Vanhellemont, M., Wuyts, K., Hermy, M. & Verheyen, K. (2011). Former land use affects the nitrogen and phosphorus concentrations and biomass of forest herbs. *Plant Ecology* 212(5): 901–909.

Bermejo, M. (1999). Status and conservation of primates in Odzala National Park. *Oryx* 33(4): 323–331.

Brugiere, D., Bougras, S. & Gautier-Hion, A. (2000). *Dynamique forestière à processus de colonisation - extinction: relations faune flore dans les forêts à Marantacées du Parc National d'Odzala*. Rapport ECOFAC, Bruxelles.

Brugiere, D. & Sakom, D. (2001). Population density and nesting behaviour of lowland gorillas (*Gorilla gorilla gorilla*) in the Ngotto forest, Central African Republic. *Zoological Journal London* 255: 251–259.

Calvert, J.J. (1985). Food seclection by western Gorillas (*G.g. gorilla*) in relation to food chemistry. *Oecologia* 65: 236–246.

Carroll, R.W. (1988). Relative density, range extension, and conservation potential of the lowland gorilla (*Gorilla gorilla gorilla*) in the Dzanga-Sangha region of southwestern Central African Republic. *Mammalia* 52(3): 309–323.

Casimir, M.J. (1979). An analysis of gorilla nesting sites of the Mt. Kahuzi region, (Zaire). *Folia Primatologica* 32: 290–308.

Cipolletta, C. (2003). Ranging patterns of a western gorilla group (*Gorilla gorilla gorilla*) during habituation to humans in the Dzanga-Ndoki National Park, Central African Republic. *International Journal of Primatology* 24(6): 1207–1226.

Clark, C.J., Poulsen, J.R., Malonga, R. & Elkan JR, P.W. (2009). Logging concessions can extend the conservation estate for Central African tropical forests. *Conservation Biology* 23(5): 1281–1293.

Costa, F. & Magnusson, W. (2002). Selective logging effects on abundance, diversity, and composition of tropical understorey herbs. *Ecological Applications* 12: 807–819.

Devos, C., Sanz, C., Morgan, D., Onononga, J.R., Laporte, N. & Huynen, M.C. (2008). Comparing ape densities and habitats in northern Congo: surveys of sympatric gorillas and chimpanzees in the Odzala and Ndoki Regions. *American Journal of Primatology* 70: 439–451.

Djoufack, S.D. (2003). *Végétation et distribution des nids de gorilles (Gorilla gorilla gorilla) dans la périphérie Nord de la Réserve de Biosphère du Dja*. Mémoire de DEA, Université de Yaoundé I, Yaoundé.

Doran, D.M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. & Shah, N. (2002). Western lowland gorilla diet and resource availability: New evidence, cross-site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology* 58: 91–116.

Doran-Sheehy, D.M., Greer, D., Mongo, P. & Schwindt, D. (2004). Impact of ecological and social factors on ranging in western gorillas. *American Journal of Primatology* 64: 207–222.

Doran-Sheehy, D., Mongo, P., Lodwick, J. & Conklin-Brittain, N.L. (2009). Male and female western gorilla diet: preferred foods, use of fallback resources and implications for ape versus old world foraging strategies. *American Journal of Physical Anthropology* 140: 727–738.

Dupain, J., Guislain, P., Nguenang, G.M., DE Vleeschouwer, K. & VAN Elsacker, L. (2004). High chimpanzee and gorilla densities in a non-protected area of the northern periphery of the Dja Faunal Reserve, Cameroon. *Oryx* 38(2): 1–8.

Dupuy, B. (1998). *Bases pour une sylviculture en forêt dense tropicale humide africaine* (Série FORAFRI, document 4). CIRAD, Montpellier.

Fay, J.M. (1997). *The ecology, social organization, populations, habitat and history of the western lowland gorilla (Gorilla gorilla gorilla).* PhD thesis, Washington University.

Fay, J.M. & Agnagna, M. (1992). Census of gorillas in northern Republic of Congo. *American Journal of Primatology* 27: 275–284.

Furuichi, T., Inagaki, H. & Angoue-Ovono, S. (1997). Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: employing a new method to distinguish between nests of the two species. *International Journal of Primatolology* 18(6): 1029–1046.

Ganas, J., Robbins, M.M., Nkurunungi, J.B., Kaplin, B.A. & McNeilage, A. (2004). Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatolology* 25(5): 1043–1072.

Goldsmith, M.L. (1996). *Ecological influences on the ranging and grouping behavior of western lowland gorillas at Bai Hohou, Central African Republic*. PhD thesis, State University of NewYork at Stony Brook, Stony Brook.

Goldsmith, M.L. (1999). Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *International Journal of Primatolology* 20(1): 1–23.

Groves, C. & Meder, A. (2001). A model of gorilla life history. *Australian Primatology* 15: 2–15.

Groves, C.P. & Sabater Pi, J. (1985). From ape's nest to human fix-point. *Man* 20: 22–47.

Harrison, M.E. & Marshall, A.J. (2011). Strategies for the use of fallback foods in apes. *International Journal of Primatolology* 32: 531–565.

Head, J.S., Boesch, C., Makaga, L. & Robbins, M.M. (2011). Sympatric chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: dietary composition, seasonality, and intersite comparisons. *International Journal of Primatolology* 32: 755–775.

Johns, A.D. (1985). Selective logging and wildlife conservation in tropical rain-forest: problems and recommendations. *Biological Conservation* 31: 355–375.

Kingdon, J. (1997). *The Kingdon field guide to African mammals.* Academic Press, London.

Kollmann, J. (2000). Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in Plant Ecology, Evolution and Systematics* 3(1): 29–51.

Kuroda, S., Nishihara, T., Suzuki, S. & oko, R.A. (1996). Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In: *Great ape societies* (Eds. W.C. McGrew, L.F. Marchant & T. Nishida). Cambridge University, Cambridge.

Latour, S. (2010). *Reserve de faune du Dja-Evaluation du statut des grands singes.* Report to Ecofac 4. Groupement BLR Ingénierie – SECA/GFA/DFS.

Letouzey, R. (1985). *Notice de la carte phytogéographique du Cameroun au 1 / 500 000. Domaine de forêt dense humide toujours verte*. Institut de la Carte Internationale de la Végétation, Toulouse.

Loya, D.T. & Jules, E.S. (2008). Use of species richness estimators improves evaluation of understory plant response to logging: a study of redwood forests. *Plant Ecology* 194: 179–194.

Magliocca, F. & Gautier-Hion, A. (2002). Mineral content as a basis for food selection by western lowland gorillas in a forest clearing. *American Journal of Primatology* 57: 67–77.

Malenky, R.K., Wrangham, R., Chapman, C.A. & Vineberg, E.O. (1993). Measuring chimpanzee food abundance. *Tropics* 2(4): 231–244.

Matthews, A. & Matthews, A. (2004). Survey of gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes troglodytes*) in southwestern Cameroon. *Primates* 45: 15–24.

Mehlman, P.T. & Doran, D.M. (2002). Influencing western gorilla nest construction at Mondika Research Center. *International Journal of Primatolology* 23(6): 1257–1285.

Nguenang, G. M. & Dupain, J. (2002). *Typologie et description morpho-structurale de la mosaïque forestière du Dja : Cas du site d'étude sur la socio-écologie des grands singes dans les villages Malen V, Doumo-pierre et Mimpala (Est-Cameroun)*. Rapport interne. SRZA.

Nishihara, T. (1995). Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. *Primates* 36: 151–168.

Oates, J.F. (1996). Habitat alteration, hunting and the conservation of folivorus primates in African forests. *Australian Journal of Ecology* 21: 1– 9.

Poulsen, J.R. & Clark, C.J. (2004). Densities, distributions and seasonal movements of gorillas and chimpanzees in swamp forest in Northern Congo. *International Journal of Primatolology* 25: 285–306.

Rainey, H.J., Iyenguet, F.C., Malanda, G.A.F., Madzoke, B., Dos Santos, D., Stokes, E.J., Maisels, F. & Strindberg, S. (2010). Survey of raphia swamp forest, Republic of Congo, indicates high densities of critically endangered western lowland gorillas *Gorilla gorilla gorilla*. *Oryx* 44(1): 124–132.

Remis, M.J. (2000). A preliminary assessment of the impacts of human activities on gorillas Gorilla gorilla gorilla and other wildlife at Dzanga-Sangha Reserve, Central African Republic. *Oryx* 34(1): 56–65.

Rogers, M.E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., McFarland, K., Nishihara, T., Remis, M. & Tutin, C.E.G. (2004). Western gorilla diet: a synthesis from six sites. *American Journal of Primatology* 64: 173–192.

Rothman, J.M., Pell, A.N., Dierenfeld, E.S. & McCann, C.M. (2006). Plant choice in the construction of night nests by gorillas in the Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology* 68: 361–368.

Sabater Pi, J. (1977). Contribution to the study of alimentation of lowland gorillas in the natural state, in Rio Muni, Republic of Equatorial Guinea (West Africa). *Primates* 18: 183– 204.

Siegel, S. & Castellan, N.J. (1988). *Nonparametric Statistics for the Behavioral Sciences* (2nd ed.). McGraw-Hill Book Co., New York.

Sowunmi, M.A. (1999). The significance of the oil palm *(Elaeis guineensis* Jacq.) in the late Holocene environments of west and west central Africa: a further consideration. *Vegetation History and Archaeobotany* 8: 199–210.

Stokes, E.J., Strindberg, S., Bakabana, P.C., Elkan, P.W., Iyenguet, F.C., Madzoke, B., Malanda, G.A.F., Mowawa, B.S, Moukoumbou, C., Ouakabadio, F.K. & Rainey, H.J. (2010). Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. *PLoS ONE* 5(4): 1–18.

Tutin, C.E.G. (1998). Gorillas and their food plants in the Lopé Reserve, Gabon. In: *Chorology, Taxonomy and Ecology of the floras of Africa and Madagascar* (Eds. C.R. Huxley, J.M. Lock & D.F. Cutler). Royal Botanic Gardens, Kew.

Tutin, C.E.G. & Fernandez, M. (1984). Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *American Journal of Primatology* 6: 313–336.

Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E.A. & McGrew, W.C. (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philosophical Transactions of the Royal Society of London, Series B* 334: 179–186.

Tutin, C.E.G., Ham, R.M., White, L.J.T. & Harrison, M.J.S. (1997). The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42: 1–24.

Tutin, C.E.G., Parnell, R.J., White, L.J.T. & Fernandez, M. (1995). Nest building by lowland gorillas in the Lopé Reserve, Gabon: environmental influences and implications for censusing. *International Journal of Primatolology* 16(1): 53–76.

Vasconcelos, H.L. & Laurance, W.F. (2005). Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. *Oecologia* 144: 456–462.

Watts, D.P. (1984). Composition and variability of mountain gorilla diets in the central virungas. *American Journal of Primatology* 7: 323–356.

White, L.J.T. (1994). Biomass of rain forest mammals in the Lopé Reserve, Gabon. *Journal of Animal Ecology* 63: 499–512.

White, L.J.T. & Edwards, A. (2000). Vegetation inventory and description. In: *Conservation research in the African rain forests: a technical handbook* (Eds. L.J.T. White & A. Edwards). Wildlife Conservation Society, New York.

White, L.J.T., Rogers, M.E., Tutin, C.E.G., Williamson, E. & Fernandez, M. (1995). Herbaceous vegetation in different forest types in the Lopé Forest Reserve, Gabon: implications for keystone food availability. *African Journal of Ecology* 33: 124–141.

Williamson, E.A., Tutin, C.E.G., Rogers, M.E. & Fernandez, M. (1990). Composition of the diet of lowland gorillas at Lope in Gabon. *American Journal of Primatology* 21: 265–277.

Wrangham, R.W., Rogers, M.E. & Basuta, G.I. (1993). Ape food density in the ground layer in Kibale forest, Uganda. *African Journal of Ecology* 31: 49–57.

Yamagiwa, J., Mwanza, M., Yumoto, T. & Maruhashi, T. (1994). Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates* 35(1): 1–14.

In “La Belgique” research site, terrestrial herbaceous plants occur at high densities in habitats such as swamps, which are characterized by a hydromorphic soil (A), and light gaps (B). © Charles Yem, PGS

General discussion

In this last section, I summarize the main findings of the five chapters and integrate the results in order to describe the relationship between understory herbaceous vegetation and forest stage. I also discuss the influence of ecological factors on herbaceous plant community structure and the resulting consequences on the ecology of western lowland gorillas. Lastly, I suggest relevant ideas for conservation-applied research to address the questions that were not examined in this thesis.

OVERVIEW OF THE MAIN RESULTS

All *terra firma* habitats had comparable levels of Marantaceae and Zingiberaceae species richness, but patchiness differed. As a result, more effort was needed to capture herb diversity in patchy late successional forest stages compared to habitats with more random (not patchy) species distributions (**Chapter 1**). However, while sampling all herbaceous species, the results indicated that most were generalists as they occurred in all habitat types. Although herb species composition greatly overlapped in *terra firma* habitats, shared species highly featured in young secondary forest and light gaps. Differences in the floristic composition between light gaps and other *terra firma* habitats were relatively marked. This variation resulted in changes in the vertical structure of herbaceous plant communities as succession progressed from light gaps to near primary forest. Strong differences in herb species composition between *terra firma* habitats and swamps were noted because species of Costaceae and most species of Marantaceae were indicative of or restricted to flooded habitats (**Chapter 2**).

The relationship between abiotic resource and herb abundance and diversity was unclear. Moreover, herbaceous plants were available year-round, and their density was not correlated with rainfall. However, while considering species of Marantaceae and Zingiberaceae separately, the results showed that the proportion of dwarf stems was lowest in light gaps, and consistently increased from young secondary to near primary forest where shaded conditions predominate, suggesting that light is probably the most important factor influencing abundance of species in these families (**Chapter 3**). Consequently, herb materials preferred by gorillas for nest building—species of Marantaceae and Zingiberaceae—were of lower quality in late successional forests. There was some seasonal variation in the numbers of species selected by gorillas to build nests, and negligible seasonal changes in the plant composition of nests, as a result of intermittent use of some plant species. There were also seasonal changes in habitat use, with marked preference for young secondary forest during long dry and short rainy seasons, and for light gaps during the long rainy season (**Chapter 4**). However, the global pattern of habitat use showed that gorillas preferred to sleep in habitats such as light gaps, young secondary forest and swamps because of the abundant supply of herbs (**Chapter 5**).

RELATIONSHIP BETWEEN HERBACEOUS VEGETATION AND FOREST STAGE

In the study site, the understory vegetation layer and the upper vegetation strata show different patterns of association as the forest represents progression from earlier to mature stages. Previous disturbance events such as logging and the creation of human settlements have resulted in various-sized forest types at various stages of stand development, collectively referred to as *terra firma* forests. Canopy modification occurred frequently due to tree and branch falls, and this resulted in considerable light gaps. In addition, flooded habitats such as swamps and riparian forest also occurred because the site was traversed by an important network of watercourses. This dense patchwork of habitat types therefore resulted in a forest mosaic (Chapter 5). In light gaps, herb species, especially those belonging to the families Marantaceae and Zingiberaceae, were less patchily distributed, and herb stems were of large size, formed big clumps and occurred at high densities (Chapters 1, 3, 5). Although generalists featured in light gaps, such recently disturbed areas were primarily characterized by a high occurrence of Zingiberaceae as well as other species of Marantaceae (Chapters 2, 5). The abundance of these indicator species slightly decreased in young secondary forest, but there was a considerable overlap with light gaps. Martinez-Ramos et al. (1989) and White & Edwards (2000) point out that as the vegetation gradually regenerates after logging or other disturbance events, species composition and structure of the forest are progressively modified. Early successional stages of tropical forest development are characterized by an abundance of light-loving and fast-growing shrubs and thin trees. These pioneer species grow in association with dense understory vegetation. In late successional forest stages, the dominant canopy is composed of large and old shade-tolerant climax tree species, and there is little undergrowth. However, the species composition of herbaceous plants—at least Marantaceae and Zingiberaceae species—does not seem to change with forest succession as light gaps and *terra firma* forests harbored the same species. This finding agrees with the results of Sarmiento et al. (2003) who found a decrease in the abundance and little change in the composition of vascular plants along different stages of tropical alpine vegetation succession. Species of Marantaceae and Zingiberaceae therefore followed patterns of 'auto-succession', in which species composition remains the same throughout all stages of succession (Muller, 1952).

In late successional forests, the limited abundance and frequency of pioneer species was counterbalanced by the presence of generalists (e.g. ferns) and late successional species of the family Araceae and Poaceae. As a result, stem density and species diversity of herbaceous plants did not change with forest succession. However, the vertical structure of herbaceous plant communities changed at least because of the increasing proportions of dwarf stems, as also observed by Fay (1997). Furthermore, indicators of early successional forest stages and flooded habitats had relatively large stems, sometimes reaching more than 2 m in height, compared to some generalists and indicators of late successional forests which were small-sized herb species. Stronger separations in floristic composition existed between swamps and other habitats because, in addition to generalist herb species, this habitat had the highest number of indicators species. These included species of Marantaceae (e.g. *Halopegia azurea*) and other species such as *Costus afer* (Costaceae) (Chapter 2). A species of Commelinaceae, *Palisota ambigua* was indicative of riparian forest; and the herbaceous plant community composition in this habitat and other habitats greatly overlapped, probably due to its heterogeneity (Spies et al., 2006).

ABIOTIC FACTORS AND HERB COMMUNITY STRUCTURE

Although there was no global correlation between abiotic resources and herbaceous plant community structure, light seemed to be the limiting factor to herbs of the families Marantaceae and Zingiberaceae. Soils in all habitat types had comparable levels of fertility despite global variations in elevation, moisture and texture between *terra firma* and flooded habitats (Chapter 3). *Terra firma* habitats were slightly more elevated and the soil contained more clay, whereas flooded habitats held more sand. Light availability considerably varied among habitat types, with lower levels in late successional forests (Chapter 5). The lack of correlation between abiotic resources and herb community structure may be due to the fact that many species were generalists (Chapter 2), meaning that they persisted in many habitats despite possible variations in ecological factors. For example, generalists such as ferns can adapt and persist in shaded conditions (Crawley, 1997). However, there was spatial variation in herb stem density and biomass (Chapter 3), probably reflecting spatial variability in the magnitude of abiotic factors. This observation concurs with the fact that spatial variability in environmental conditions affects the fecundity, germination, recruitment, growth and mortality of plants (Martinez-Ramos et al., 1989). However, variation in herb responses was probably explained by the availability of light. For example, high proportions of dwarf stems of pioneer herb species, as well as other species, occurred in late successional forests where light availability is minimal (Chapters 3, 5). It has been observed that plants occur as dwarf or produce slender stems when light is limited (White et al., 1995; Van Breugel et al., 2012), and that plants grow faster when more light is available (Ticktin & Nantel, 2004). The findings of this thesis concur with these observations and support the idea that light is a major determinant of plant growth (Leuschner, 2005; Mooney & Ehleringer, 1997).

HABITAT AND PLANT USE BY GORILLAS IN RELATION TO HERB AVAILABILITY

Patterns of herb availability influenced habitat- and plant-use by gorillas for nest building. A qualitative evaluation of gorilla herb-resource availability was made by determining herb species richness and patchiness, and by monitoring the sampling process across habitat types (Chapter 1). Species richness indicates how many different resource items can potentially be found in a given habitat type. Patchiness refers to the relative distribution of species among individuals; this parameter assesses the likelihood of finding a variety of resources within herb patches in each habitat type. Also, in each habitat type, the rate of rarefaction and species richness estimator curves during the sampling process are a proxy for the effort that might be expended (by gorillas) to access all the resources. For example, although all *terra firma* habitats had comparable levels of Marantaceae and Zingiberaceae richness, patchiness was higher in late successional forest stages, and higher sampling efforts were required to produce asymptotic species richness estimator curves. This therefore shows that in these habitats, individual herb patches of these particular families are relatively species-poor, and that only a few resources may be available at any given location. Moreover, in late successional forest stages, stems of Marantaceae and Zingiberaceae were relatively few and far between (Chapter 5), with high proportions of dwarf stems (Chapter 3); suggesting that they were structurally less suitable for nest building. Thus, it may be that gorillas have to travel long distances in late successional forest stages to find relatively few herb resources of lower quality. Therefore, there was a general avoidance of these habitats by gorillas, at least for nesting, thus explaining why only three nest sites (2.4%) where found in old secondary and near primary forests (Chapter 5). As observed in other studies (e.g. Fay & Agnagna, 1992; Dupain et al., 2004; Matthews & Matthews, 2004; Rainey et al., 2010), gorillas in the study site preferentially built nests in light gaps, young secondary forest and swamps because their most preferred herbs (species of Marantaceae and Zingiberaceae) were readily available in these habitats with high species diversity (Chapters 1, 2), many large-size herb stems (Chapter 3), more pronounced herb clumps and high herb stem density (Chapter 5). This resulted in an increased diversity of plant species in gorilla nests (Chapter 5) compared to other sites (Groves & Sabater Pi, 1985; Tutin et al., 1995); probably because of their lower levels of herb diversity. As temporal fluctuations in herb population density were not marked (Chapter 3), herb selection for nest building by gorillas did not display great variation across seasons (Chapter 5). This trend was previously observed by Rothman et al. (2006) who found negligible seasonal changes of plant species in mountain gorilla nests. Seasonal variations in the frequency of use of light gaps and young secondary forest for nest building did not result in changes in the plant composition of gorilla nests due to the considerable overlap in herb composition between these habitats (Chapter 2), and possibly to a constant availability of preferred nest-building materials in preferred nesting habitats.

Similarly, herbaceous plant availability also influenced gorilla foraging behavior. Gorilla trail-follow data collected in the study site from 2009 through 2012 show that near primary forest was less visited, and data of feeding remains indicate that dwarf stems were usually avoided (Petre, unpublished data). Gorillas probably avoided dwarf stems as a result of limited supply of edible biomass. These observations suggest that gorillas harvested most of their herb foods in herb patches or habitats with high amounts of large stems, consistent with the fact that gorillas concentrate their foraging efforts in habitats with high-quality and abundant herbaceous vegetation when tree fruits are scare (Remis, 1997), as well as when they are available (Nishihara, 1995). Given the considerable effort required to access herb resources and the relatively high number of dwarf stems in near primary forest (Chapters 1, 3), the energy-cost ratio for feeding on herbs in this habitat is smaller, which makes it less attractive to gorillas that minimize efforts during food acquisition (Doran-Sheehy et al., 2004). Moreover, gorillas may be less attracted to near primary forest because the high proportion of dwarf stems and the patchy distribution of herbaceous foods in this habitat (Chapters 1, 3) negatively affects group cohesion and limits the time spent foraging on herb patches (see Goldsmith [1999] and references therein). Conversely, the highly-clumped nature of herbaceous food distribution and the high proportion of large-sized stems in some habitats (e.g. light gaps; Chapters 3, 5), may result in more cohesive feeding groups in these habitats. In addition, gorillas may have less incentive to move to habitats with low-quality herbs, or they may spend less time there (Goldsmith, 1999) and more time feeding in patches or habitats with high-quality herbs (Nishihara, 1995). Fruiting trees in late successional forests provide food to gorillas in periods of fruit abundance (Nishihara, 1995), but nesting in such habitats may only occasionally occur, probably as a strategy of dietary opportunism (sleeping close to fruiting trees), as food availability influences the choice of nesting sites (Groves & Sabater Pi, 1985). This further supports the observation that only 2.4% of gorilla nest sites were found in old secondary and near primary forest (Chapter 5), and concurs with the results of Rothman et al. (2006) who observed that though mountain gorillas visited closed canopy forest, they seldom nested there; rather, they frequently nested in open forest gaps and secondary forest. It has been shown that western lowland gorillas have longer daily path lengths (DPLs) when they feed on fruits due to the patchy distribution of fruiting trees, and shorter DPLs when they feed on herbs (Goldsmith, 1999; Doran-Sheehy et al., 2004). Patterns of herb availability in the study site suggest that habitats such as light gaps, young secondary forest and swamps provide high-quality clumped herbs in larger quantities (Chapters 2, 3, 5), implying that less effort is needed to obtain herb foods in these habitats, and justifying the observed small foraging efforts exerted by gorillas to feed on herbs. In some sites, it has been documented that there is no seasonal difference in the consumption of pith and fruit of herbaceous plants by gorillas (e.g. Goldsmith, 1999); it seems likely for this to be due to there being no seasonal difference in herbaceous food availability. In most cases however, gorillas consume herb foods at varying proportions throughout the year (Rogers et al., 1988; Williamson et al., 1990; Tutin et al., 1991; White et al., 1995; Doran et al., 2002), and these food items have been termed ‘staple fallback foods’ (Marshall & Wrangham, 2007). Documented changes in the proportion of fallback foods in gorilla diet are likely the result of fluctuations in the availability of preferred food (Harrison & Marshall, 2011), rather than a limit to the availability of fallback foods. This argument is supported by the hypothesis of Doran-Sheehy et al. (2004) who suggested that the availability of important tree fruits in specific habitats (e.g. swamps) is the primary driver of gorilla presence in these habitats during fruiting seasons. Recently-disturbed areas appear to be suitable environments for gorillas, at least partly because they offer a greater diversity of nest-building materials and important food items. Although western lowland gorillas preferentially feed on fruits when available, herbs are important components of their diet (Sabater, Pi 1977; Calvert, 1985; Kingdon, 1997), and spatial and temporal activities of primates are strongly influenced by the need to search for these foods (Oates, 1987). It is therefore possible that recently-disturbed areas play a crucial role in gorilla feeding ecology. This can help to explain why gorilla abundance is not reduced as a result of moderate logging (Groves & Meder, 2001). In addition, swamps are also important habitats for western lowland gorillas because the high availability of herbs and other resources in these habitats promotes a strategy of dietary opportunism.

CONCLUSION AND RECOMMENDATIONS FOR FUTURE RESEARCH

As I hypothesized, the vertical structure of herbaceous plant community was influenced by the spatial variation in the magnitude of abiotic factors. However, this variation primarily reflected fluctuations in the abundance of species of Marantaceae and Zingiberaceae in response to changes in the availability of light. Contrary to my predictions, there were negligible spatial variations in soil fertility, and soil humidity, soil fertility and rainfall did not appear to limit herbaceous plant productivity. The preceding arguments show that light is the major determinant of gorilla herb-resource availability; hence this abiotic factor strongly influences gorilla distribution. However, in some sites, soil property has been suggested to be the likely determinant of herb availability (see Brugiere & Sakom, 2001). Herb availability is therefore determined by a set of abiotic and biotic factors which vary in magnitude within and between sites. Although light appears to be an important factor, other abiotic factors potentially represent important drivers of herb availability, and as such they can also influence gorilla distribution. Even in common cases where light determines the availability of herbs, this factor might not always explain gorilla distribution because high herb availability does not always result in high gorilla density. Moreover, other factors such as climatic variables may be influential. Climate-induced disturbance on gorilla plant-food phenology may significantly reduce resource availability and affect gorilla populations (Tutin et al., 1997). Food consumption by gorillas depends on food availability, which is influenced by temperature and the amount of rainfall (e.g. Remis, 1997; Tutin et al., 1997). Rainfall ultimately limits plant distribution in the tropics (Bonnefille, 2010). Modeling population dynamics and phenology of gorilla herbs and fruit trees based on data collected over an extended period of climatic variability is suggested to be an important research topic that can help to anticipate changes in resource availability and the potential knock-on effects for gorillas. It is generally believed that logging leads to increased herb supply for gorillas as a result of increased light availability. However, it is worth mentioning that large canopy openings may decrease photosynthesis and inhibit the growth and development of some forest plants (Costa & Magnuson, 2002; Mitamura et al., 2008). Moreover, in addition to modifying light conditions, logging practices may alter soil properties as pointed out by Jayakumar et al. (2009, and references therein). Within the range of the western lowland gorilla, where logging is a common practice, little is known about the logging-induced alterations of soil properties and the light levels that can become detrimental to gorilla plant resources. Conservation-applied research efforts should focus on such issues. In the area, local people heavily rely on natural resources. For example, many species of Marantaceae and Zingiberaceae which are important to gorillas are also used by humans as spices or for medicinal purposes, food-wrapping, and handicraft, and some are traded (Betti, 2004; Brink, 2010; pers. obs.). Hence, the pressure on gorillas and their habitats is a real threat in the area. Human encroachment, among other factors, influences gorilla distribution and density (Devos et al., 2008). To better inform conservation planning, future studies should aim to assess the extent of encroachment and the overlap in resource use. Habitats such as light gaps, swamps and young secondary forest, with high density of gorilla herbs, represent about half the study site; this highlights the suitability of this site for gorilla survival and its potential value to conservation. Conservation actions are needed in the field to ensure limited human encroachment and effective control of poaching.

REFERENCES

Betti, L. (2004). An ethnobotanical study of medicinal plants among the Baka Pygmies in the Dja Biosphere Reserve, Cameroon. *African Study Monographs* 25(1): 1–27.

Bonnefille, R. (2010). Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change* 72: 390–411.

Brink, M. (2010). *Ataenidia conferta (Benth.) Milne-Redh.* [Internet] Record from Protabase. Brink, M. & Achigan-Dako, E.G. (Editors). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, Netherlands. <http://database.prota.org/search.htm>. Accessed 4 August 2012.

Brugiere, D. & Sakom, D. (2001). Population density and nesting behaviour of lowland gorillas (Gorilla gorilla gorilla) in the Ngotto forest, Central African Republic. *Zoological Journal London* 255: 251–259.

Calvert, J.J. (1985). Food selection by western gorillas (G.g. gorilla) in relation to food chemistry. *Oecologia* 65: 236–246.

Costa, F. & Magnusson, W. (2002). Selective logging effects on abundance, diversity, and composition of tropical understorey herbs. *Ecological Applications* 12: 807–819.

Crawley, M.J. (1997). Life history and environment. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Devos, C., Sanz, C., Morgan, D., Onononga, J.R., Laporte, N. & Huynen, M.C. (2008). Comparing ape densities and habitats in northern Congo: surveys of sympatric gorillas and chimpanzees in the Odzala and Ndoki Regions. *American Journal of Primatolology* 70: 439–451.

Doran, D.M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. & Shah, N. (2002). Western lowland gorilla diet and resource availability: New evidence, cross-Site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology* 58: 91–116.

Doran-Sheehy, D.M., Greer, D., Mongo, P. & Schwindt, D. (2004). Impact of ecological and social factors on ranging in western gorillas. *American Journal of Primatology* 64: 207–222.

Dupain, J., Guislain, P., Nguenang, G.M., De Vleeschouwer, K. & Van Elsacker, L. (2004). High chimpanzee and gorilla densities in a non-protected area of the northern periphery of the Dja Faunal Reserve, Cameroon. *Oryx* 38(2): 1–8.

Fay, J.M. (1997). *The ecology, social organization, populations, habitat and history of the western lowland gorilla (Gorilla gorilla gorilla Savage and Wyman 1847).* Ph. D. thesis. Washington University, St. Louis.

Fay, J.M. & Agnagna, M. (1992). Census of gorillas in northern Republic of Congo. *American Journal of Primatology* 27: 275–284.

Goldsmith, M.L. (1999). Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *International Journal of Primatology* 20(1): 1–23.

Groves, C. & Meder, A. (2001). A model of gorilla life history. *Australian Primatology* 15: 2–15.

Groves, C.P. & Sabater Pi, J. (1985). From ape's nest to human fix-point. *Man* 20: 22–47.

Harrison, M.E. & Marshall, A.J. (2011). Strategies for the use of fallback foods in apes. *International Journal of Primatology* 32: 531–565.

Jayakumar , S., Ramachandran, A. Bhaskaran, G. & Heo, J. (2009). Forest dynamics in the Eastern Ghats of Tamil Nadu, India. *Environmental Management* 43: 326–345.

Kingdon, J. (1997). *The Kingdon field guide to African mammals*. Academic Press, London.

Leuschner, C. (2005). Vegetation and ecosystems. In: *Vegetation Ecology* (Ed. E. van der Maarel). Blackwell Publishing, Oxford.

Marshall, A.J. & Wrangham, R.W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology* 28: 1219–1235.

Martinez-Ramos, M., Alvarez-Buylla, E. & Sarukhan, J. (1989). Tree demography and gap dynamics in a tropical rain forest. *Ecology*: 70(3): 555–558.

Matthews, A. & Matthews, A. (2004). Survey of gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes troglodytes*) in southwestern Cameroon. *Primates* 45: 15–24.

Mitamura, M., Yamamura, Y. & Nakano, T. (2008). Large-scale canopy opening causes decreased photosynthesis in the saplings of shade-tolerant conifer, *Abies veitchii. Tree Physiology* 29: 137–145.

Mooney, H.A. & Ehleringer, J.R. (1997). Photosynthesis. In: *Plant Ecology*, second edition (Ed. M.J. Crawley). Blackwell Science, Oxford, London, Edinburgh, Cambridge, Massachusetts and Victoria.

Muller, C.H. (1952). Plant succession in arctic heath and Tundra in Northern Scandinavia. *Bulletin of the Torrey Botanical Club* 79(4): 296–309.

Nishihara, T. (1995). Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. *Primates* 36: 151–168.

Oates, J.F. (1987). Food distribution and foraging behavior. *In Primate Societies* (Eds. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker). The University of Chicago, Chicago.

Rainey, H.J., Iyenguet, F.C., Malanda, G.A.F., Madzoke, B., Dos Santos, D., Stokes, E.J., Maisels, F. & Strindberg, S. (2010). Survey of raphia swamp forest, Republic of Congo, indicates high densities of critically endangered western lowland gorillas *Gorilla gorilla gorilla*. *Oryx* 44(1): 124–132.

Remis, M.J. (1997). Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *American Journal of Primatology* 43: 87–109.

Rogers, M.E., Williamson, E.A., Tutin, C.E.G. & Fernandez, M. (1988). Effects of the dry season on gorilla diet in Gabon. *Primates* 22: 25–33.

Rothman, J.M., Pell, A.N., Dierenfeld, E.S. & McCann C.M. (2006). Plant choice in the construction of night nests by gorillas in the Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology* 68: 361–368.

Sabater Pi, J. (1977). Contribution to the study of alimentation of lowland gorillas in the natural state, in Rio Muni, Republic of Equatorial Guinea (West Africa). *Primates* 18: 183–204.

Sarmiento, L., Llambí, L.D., Escalona, A. & Marquez, N. (2003). Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes. *Plant Ecology* 166: 63–74.

Spies, T.A., Hemstrom, M.A., Youngblood, A. & Hummel, S. (2006). Conserving old-growth forest diversity in disturbance-prone landscapes. *Conservation Biology* 20: 351–362.

Ticktin, T. & Nantel, P. (2004). Dynamics of harvested populations of the tropical understory herb *Aechmea magdalenae* in old-growth versus secondary forests. *Biological Conservation* 120: 461–470.

Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E.A. & McGrew, W.C. (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philosophical Transactions of the Royal Society of London, Series B* 334: 179–186.

Tutin, C.E.G., Ham, R.M., White L.J.T. & Harrison, M.J.S. (1997). The primate community of the Lopé reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42: 1–24.

Tutin, C.E.G., Parnell, R.J., White, L,J,T. & Fernandez, M. (1995). Nest building by lowland gorillas in the Lopé Reserve, Gabon: environmental influences and implications for censusing. *International Journal of Primatology* 16(1): 53–76.

Van Breugel, M., Van Breugel, P. Jansen, P.A., Martínez-Ramos, M. & Bongers, F. (2012). The relative importance of above- versus belowground competition for tree growth during early succession of a tropical moist forest. *Plant Ecology* 213: 25–34.

White, L.J.T. & Edwards, A. (2000). Vegetation inventory and description. In: *Conservation research in the African rain forests: a technical handbook* (Eds. L.J.T. White & A. Edwards). Wildlife Conservation Society, New York.

White, L.J.T., Rogers, M.E., Tutin, C.E.G., Williamson, E. & Fernandez, M. (1995). Herbaceous vegetation in different forest types in the Lopé Forest Reserve, Gabon: implications for keystone food availability. *African Journal of Ecology* 33: 124–141.

Williamson, E.A., Tutin, C.E.G., Rogers, M.E. & Fernandez, M. (1990). Composition of the diet of lowland gorillas at Lopé in Gabon. *American Journal of Primatology* 21: 265–277.

Semi-deciduous tree species occur in “La Belgique” research site. ©Jacob Willie, PGS

Abstract

Gorillas depend on herbaceous plants that constitute an important of source nest-building materials and food. The ecological patterns and the use of herbaceous plants were studied in a tropical forest site in south-east Cameroon to assess the influence of ecological factors on these resources and establish a link between environmental variables and herbaceous plant availability and use by gorillas. Species diversity and stem density were determined by identifying and counting herb stems in a series of plots distributed in different habitat types. Soil fertility parameters and other abiotic variables were recorded in a set of plots, and herbaceous plants were monitored in these plots to investigate possible influences of environmental factors on their availability. Nests built by gorillas were seasonally monitored during an extended period to identify the plant species used in their construction and classify them in terms of preference. Preferred herb stems and gorilla nest sites were inventoried in different habitat types to describe the relationship between herb availability and gorilla distribution. Herbaceous plants of the families Marantaceae and Zingiberaceae were preferentially used by gorillas, and light seemed to be the limiting factor to herbs of these families. The spatial variability in the magnitude of abiotic factors translated to spatial variations in the community structure of herbaceous plants. These environmental gradients influenced gorilla ranging patterns, as they commonly built nests and harvested their herb foods in habitats with high herb species diversity, many large-sized herb stems, more pronounced herb clumps and high herb stem density. Stem density and species diversity were high in the study site, and gorillas used a high diversity of plant species to build nests compared to other sites, emphasizing variability in the availability of nest building materials and habitat differences across their range. At the temporal scale, climatic variables such as rainfall, temperature and air humidity did not appear to influence total herb density, as there were only little variations in the number of stems recorded throughout the year. As a result, temporal changes in the plant composition of gorilla nests were not important despite seasonal changes in the use of nesting habitats by gorillas. Recently disturbed forest areas and less-accessible swamps which are characterized by a limited visibility and a high density of forest herbs can play a crucial role in the ecology and conservation of gorillas as they provide abundant and clumped nest-building materials, year-round nutrient-rich herbs and natural protection from hunters. Although light appears to be an important factor of herb availability, soil properties and climatic variables potentially represent important drivers. Conservation-applied research efforts should therefore focus on issues such as the effect of climate change on gorilla plant resources and the impact of logging-induced alterations of canopy and forest soil properties on herbaceous plants.

Samenvatting

Gorillas zijn afhankelijk van het voorkomen van kruidachtige planten als voedsel en als materiaal voor nestbouw. Ecologische patronen in het voorkomen van dergelijke kruidachtige planten, en het gebruik ervan door Gorillas,werden bestudeerd in een tropisch bosgebied in zuid-oost Kameroen. Diversiteit en densiteit aan kruidachtige planten werden bepaald aan de hand van gestandaardiseerde tellingen in studieplots gelegen in verschillende habitaten, en beide parameters bleken hoog in vergelijking met andere studiegebieden. Tevens werden in een deel van deze studieplots bodemvruchtbaarheid en andere abiotische variabelen opgemetenen gerelateerd aan het voorkomen van kruidachtige planten. Tenslotte werd seizoenale variatie in het gebruik van kruidachtige planten bij het vervaardigen van gorillanesten opgemetenin verschillende habitaten, werden deze planten ingedeeld in verschillende preferentieklassen, en werd de beschikbaarheid aan kruidachtige planten gerelateerd aan de ruimtelijke verspreiding van gorillas. Gorillas prefereerden kruidachtige planten van de families Marantaceae en Zingiberaceae, waarbij variatie in ruimtelijke beschikbaarheid van deze planten in belangrijke mate door abiotische factorenzoals licht werd verklaard. Gorillas maakten gebruik van een grote diversiteit aan kruidachtige planten bij hun nestbouw, en bouwden deze nesten het meest frekwent in gebieden met een hoge diversiteit aan kruidachtige planten, een hoog voorkomen van planten met grote stamdiameter, en een hoge stamdensiteit. De gemiddelde stamdensiteit van kruidachtige planten varieerde slechts in beperkte mate doorheen het jaar, en deze temporele variatie werd slechts in zeer beperkte mate verklaard door klimatologische variabelen zoals regenval, temperatuur en luchtvochtigheid.

Ondanks de waargenomen seizoenale variatie in habitaatkeuze bij het bouwen van nesten, werd slechts een beperkte mate van variatie in plantensamenstelling in de onderzochte nesten waargenomen. Recent verstoord bosgebied en weinig toegankelijke moerassen - beiden gekarakteriseerd door een hoge densiteit aan kruidachtige planten -verschaften een belangrijk aanbod aan materiaal voor nestbouw, aan nutriëntrijk voedsel en aan beschutting tegen jacht, en spelen bijgevolg een belangrijke rol in de ecologie en bescherming van Gorillas. Gelet op het grote belang van kruidachtige planten voor Gorillas, dienentoekomstige beheersplannen in voldoende hoge mate rekening tehouden met mogelijke effecten van bosbouw en klimaatsverandering op de beschikbaarheid ervan.

Affiliations of co-authors

Charles-Albert Petre [a, b]
Eduardo de la Peña [c]
Luc Lens [c]
Nikki Tagg [a]
Zjef Pereboom [a, d]

[a] Projet Grands Singes, Centre for Research and Conservation, Royal Zoological Society of Antwerp. Koningin Astridplein 26, 2018 Antwerp (Belgium)
[b] Laboratoire de Foresterie des Régions Tropicales et Subtropicales, Gembloux Agro Bio Tech, Université de Liège. Passage des Déportés 2, B-5030 Gembloux (Belgium)
[c] Terrestrial Ecology Unit, Department of Biology, Ghent University. K.L. Ledeganckstraat 35, B-9000 Gent (Belgium)
[d] University of Antwerp (Belgium)

“La Belgique” research camp in the northern buffer zone of the Dja Reserve ©Jacob Willie, PGS

UNIVERSITEIT GENT

Terrestrische Ecologie

VLIR UOS Vlaamse Interuniversitaire Raad University Development Co-operation

CENTRE FOR RESEARCH AND CONSERVATION

ZOO ANTWERP SINCE 1843

PCS Cameroon

ISBN 978-9-4619708-3-1

9 789461 970831

UNIVERSITY press