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A comparative study of vegetation in primary and secondary tropical forests on Mount Oku, Cameroon

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Globally, human populations are rapidly converting large blocks of tropical old-growth forests into small forest patches, embedded within human-modified landscapes, consisting mostly of agricultural fields and pasture lands. Mount Oku commonly known as Kilum-Ijim, situated at the North-western Cameroon is recognized as a globally important center of endemism and a hotspot for biodiversity conservation but now undergoes unprecedented degradation. The aim of this study was to compare the diversity between primary and secondary forests in mount Oku (Cameroon) and determine whether species richness and composition are distinguishable in the two forest types. The vegetation was sampled in 102 plots according to a stratified sampling design so as to cover the altitudinal gradient from 1833 to 2772 m. Forty plots were located in primary forest and 62 in secondary forest. A set of 6 plant traits/characteristics associated with dispersal, establishment, and persistence functions were gathered. A total of 385 vascular plant species were present in the 102 plots. 243 species were common to primary and secondary forest plots, 69 were present exclusively in primary forest plots and 73 in secondary forest plots. The Indicator Species Analysis showed that 38 and 28 species were indicator of primary and secondary forests, respectively. The mean species richness per plot was 45.5 and 44.1 in primary and secondary forests, respectively. Only tree species richness was significantly higher ($p < 0.001$) in the primary forest. The maximum height of vegetation and density of trees were respectively 19.42 m, 101 stems/ha in primary forest and 11.93 m, 36 stems/ha in secondary forest and show significant difference ($p < 0.001$). Primary forest plots were characterized by phanerophytes, while secondary forest plots were characterized by geophytes and chamaephytes, able to propagate vegetatively and resist disturbances. Finally, there is need to urgently protect the last remnants of ancient forest for their biological value.

Key words: Afromontane forest, biodiversity, endemism, human activities, mount Oku, species composition, species richness.

INTRODUCTION

Tropical rainforests are vanishing more rapidly than any other biome (Achard et al., 2002; Laurance et al., 2009).

In the last decades, their deforestation has led to an unprecedented loss of old-growth or primary forest

habitats and, concomitantly, to an increase of the proportion of secondary forests (Tabarelli et al., 2012). At a global scale, deforestation of tropical forest leads to biodiversity loss and could cause catastrophic species extinctions (Dent and Wright, 2009). The leading causes of deforestation are well known and vary across continents (Geist and Lambin, 2002): human population increase, conversion of forest to agricultural lands, timber extractions for local or industrial uses and exportation. Faced with the urgent need to save the biodiversity of tropical rain forests, a myriad of studies monitoring forest cover changes, diversity losses and species extinctions bloomed in all the continents (Brancalion et al., 2013, Uddin et al., 2015). In large proportion of them, the rainforest is still considered as a whole ancient, old-growth or primary forest patches and is not distinguished from secondary habitats.

Recently, an increasing attention has been placed on tropical secondary forests (Barlow et al., 2007; Thier and Wesenberg, 2016) since they provide various ecosystem services, host a non-negligible part of the biodiversity, including endemic animals and plants displaced from destroyed primary habitats, and may act as buffer zones protecting primary forests (Brearley et al., 2004). From biodiversity conservation and a sustainable management perspective, it is important to know how much primary and secondary forests diverge in terms of species richness and identities. Our knowledge of the value of the secondary forests for biodiversity conservation remains limited (Barlow et al., 2007) and the roles and value of the secondary forests are still argued (Gibson et al., 2011). Indeed, the responses of the different taxa to land use patterns and the percentages of species restricted to primary forests vary markedly across the world.

In central and west Africa, tracts of tropical rainforest have survived on scattered mountain top in relatively intact conditions (Laurance et al., 2006). This is the case of the Kilum-Ijim forest on Mount Oku (Cameroon), which is the largest remaining tract of the Central African cloud forest. In this paper, there is focus on this cloud forest, which is recognized as a global biodiversity hotspot (Myers et al., 2000). The Kilum-Ijim forest area has continuously decreased during the last century due to land use changes. Today, primary or old-growth forest habitats remain only on the summit of Mount Oku. In the last two decades, new patches of secondary forest appeared on the site, consecutively due to forest protection projects and abandonment of cultivated areas.

The main objective of this study is to compare the diversity of primary and secondary forest types and determine whether species richness and composition are distinguishable between these two forest types. Regarding the intensive agricultural practices and forest

use methods (clear cuttings, wildfires, conversions to cropping areas, grazing of forest interior by cattles and goats, over hunting, bark harvesting of *Prunus africana*, etc) that occurred during the last three decades on Mount Oku, it is hypothesized that primary and secondary forests strongly differ in terms of plant richness. This difference should be *a fortiori* pronounced among dominant plant traits occurring in the two types of forest. The underground question of this paper is to know if the (almost inevitable) loss of primary forest could be partly offsetted by the expansion of secondary habitats encouraged by local nature conservation projects in term of ecosystem services.

MATERIALS AND METHODS

Study area

The study was carried out on the Mount Oku, a mountain area of the Bamenda Highland located in north-west region of Cameroon (6°12'N and 10°32'E). This site hosts the Kilum-Ijim forest, which is the largest tract remaining of Central African cloudy forest, a biodiversity hotspot threatened by contemporary land-use changes. Peaking at 3 011 m, Mount Oku is the second highest peak in the mainland of West Africa (Asanga, 2002). The climate is characterized by a rainy season which extends from May to September and a dry season from October to April (Hawkins, 1965). Rainfall mainly occurs between July and September and varies from 1780 to 2290 mm per year. It peaks at 3050 mm per year on the summit, commonly described as cold, very cloudy and misty. In most parts of the mountain, mean temperatures vary between 13 and 22°C.

A crater lake is present at the centre of the mountain area. The geological substrate mainly consists of Tertiary basaltic and trachytic lava, covering the granitic Basement complex rocks. Locally, superficial deposits of volcanic ash occur (Cheek et al., 2000). The dominant soils are clay (mainly Gibbsite) soils but altitude and climate can generate soils with high organic matter contents (humic soils). Before the spectacular increase of human population and the development of agriculture in the past century, it is believed that the whole of the Bamenda Highland area was covered with forest (Cheek et al., 2000). The forest area covered 20 000 ha in 1978 but, today, it is reduced to about 9 500 ha (Momo et al., 2012).

The vegetation of Mount Oku has been mainly described by conservation project reports, species listing and notes (Hawkins, 1965; Cheek et al., 2000, 2004; Letouzey, 1985; Maisels and Forboseh, 1997; Asanga, 2002; ENGREF, 1987). The Kilum-Ijim forest is a mountain cloudy forest. Its canopy is dominated by upper montane forest species such as: *Podocarpus latifolius*, *Syzygium staudtii*, *Schefflera mannii*, *Carapa grandiflora*, *Nuxia congesta*, *Prunus africana* and *Bersama abyssinica*. In the last decades, post-agricultural forests appeared on fallow lands and are mainly characterised by heliophilous and fire-resistant trees and shrubs (*Gnidia glauca*, *Hypericum revolutum*, *Hypericum roeperianum*, *Maesa lanceolata* and *Erica mannii*), and open habitat herbs (*Hyparrhenia* sp., *Sporobolus africanus* and *Pennisetum clandestinum*).

Since 1987, the Kilum-Ijim forest has been benefited from

biodiversity conservation projects (Maisels and Forboseh, 1997) and the creation of community forests (Gardner, 2001; Nkengla, 1999). Despite these efforts in implying villagers and forest community managers, results are mitigated and forest stands are still cleared, converted to crop land, burned, grazed by domestic animals, overhunted and overexploited for their medicinal plants (Stewart, 2003, 2009; Asanga, 2002). Many species, including large mammals, have been lost on Mount Oku during the last century due to hunting (Maisels et al., 2001).

Sampling design and data collection

Based on the results of an earlier study using remote sensing analyses, the authors distinguished between primary and secondary forest patches on Mount Oku (Momo et al., 2012). Primary forests were defined as forest patches that were already referenced in ancient documents (Hawkins, 1965; ENGREF, 1987; Cheek et al., 2000; Macleod, 1987) and continuously present on a series of Landsat satellite images from 1978 (the oldest image available) till now. Secondary forest patches appeared after 1978 on these same satellite images and/or experienced heavy recent disturbances (clearcuts, fire).

The vegetation was sampled in 102 plots following a stratified sampling design so as to cover the altitudinal gradient from 1833 to 2772 m. 40 plots were located in the primary forest and 62 in the secondary forest, which is representative of the dominance of the secondary forest representing 66% of the Kilum-Ijim forest area. In each plot, vascular plant species were sampled in a system of nested quadrats: trees (> 10 m height) and shrubs (2-10 m) were sampled in a 40 x 40 m area, low shrubs and tall herbs (1 to 2 m) in a 40 x 20 m area and low herbs (<1 m) in a 20 x 20m area located in the corner of large plot. Their cover-abundance was scored using the following scale: i= one individual with very low cover (0.1%); += few individuals with low cover (0.5%); 1= many individuals but cover <5%; 2a = 5-25%; 3 = 25-50%; 4 = 50-75%; 5 = 75-100%. Species nomenclature follows Lebrun and Stork (1991-1997).

The following local environmental variables were measured in each plot: vegetation height (m), trees density (number of stems.ha⁻¹), number of rodent traps, bare soil cover (%), altitude and slope. For this purpose, several Landsat satellite images taken between 1978 and 2007 were integrated in a Geographic Information System (GIS), and changes in land-use types were compare. Forest fragmentation over this period was assessed by comparing the number, the area and the perimeter of forest fragments, and a forest fragmentation index was derived. Finally, the respective effects of natural (altitude, slope) and human (human density, distance to villages) factors on deforestation were quantified using structural equation models (Momo et al., 2012).

An orientation index was calculated following Chabrerie et al. (2013). Landscape elements (forests, savannas, crops) were digitalized from satellite images (Landsat MMS 1978 and ETM+ 2007, freely available at www.landcover.org) using a Geographic Information System (GIS; ArcGis® v.8.3, ESRI). The area of the different landscape elements and the percentage and area of cleared forest between 1978 and 2007 were calculated at a radius of 500 m around each sampling plot. This radius is commonly used to assess the effect of landscape structure on forest plants communities (Jamoneau et al., 2011). The following human population variables were extracted from administrative data (Direction Nationale du Recensement, 1991-1994; Bureau central du recensement de la population, 2010) and completed by field surveys: distance of the nearest house and human population density within a radius of 5 km around the plots.

A set of 6 plant traits/characteristics (including 39 trait categories) associated with dispersal, establishment and persistence functions were gathered and summarized in Appendix 1. Data were extracted from plant databases, thesis, books and completed by field

measures: life forms (Raunkiaer, 1934), diaspore types (Dansereau and Lems, 1957; Doucet, 2003), dispersal modes (Dansereau and Lems, 1957; Guillaumet, 1967), leaf types (Ohsawa, 1995), altitudinal tolerance (Senterre, 2006) and biogeographic history (White, 1978; White, 1979; White, 1983). These plant characteristics are likely to respond to the changing environment that occurred on Mount Oku for decades, that is, an intensification of agriculture practices and deforestation.

Data analysis

To explore gradients of species composition, the species cover-abundance matrix was subjected to a nonmetric multidimensional scaling (NMS) using PC-Ord® v.5 (MjM Software Design, Gleneden Beach, Oregon, USA). NMS used the relative Sørensen's index as distance measured between plots. A three-dimensional solution was found with a maximum of 400 iterations and 50 runs with randomized data (final stress = 21.50; final instability = 0.00001). The NMS was coupled with a Detrended Correspondence Analysis (DCA) according to the recommendations of Økland (2003). In order to align NMS and DCA ordination diagrams to maximise their comparability, the recommendations of McCune and Grace (2002) were followed and a rotation of the NMS and DCA clouds of points by the same elevation variable along the first ordination axes was applied. Rotation rigidly maintains the Euclidean distance among points in the ordination diagrams. Spearman correlation tests were used to assess concordances between NMS and DCA axes and between NMS axes and environmental variables. Multi-response permutation procedures (MRPP) and indicator species analysis (ISA) from Dufrière and Legendre (1997) were used to examine differences in species composition among primary and secondary forest plots. ISA were also run for each trait on the plots x trait category abundance matrices to highlight traits which were filtered by primary and secondary forest environments. Mann-Whitney U-tests ($p < 0.05$) were used to test differences in species richness between primary and secondary forest plots. Finally, the effects of local and landscape variables on total, tree and herb richness were tested using generalized linear models (GLMs) and Poisson error distribution of response variables. Only the most significant models were retained. Univariate analyses and GLMs were built using SPSS (version 17.0).

RESULTS

Species composition

A total of 385 vascular plant species were present in the 102 plots. 243 species were common to primary and secondary forest plots, 69 were present exclusively in primary forest plots and 73 in secondary forest plots. The first DCA axis was highly positively correlated with the first NMS axis ($r = 0.918$; $p < 0.001$) and the second DCA axis was highly negatively correlated with the third NMS axis ($r = -0.925$; $p < 0.001$). The third DCA axis was slightly correlated with the three NMS axes (axis 1: $r = -0.213$; $p = 0.032$; axis 2: $r = 0.278$; $p = 0.005$; axis 3: $r = -0.238$; $p = 0.016$). Consequently, only NMS axes 1 and 3 were retained in subsequent analyses. The NMS ordination diagram (Figure 1) showed that primary and secondary forest plots were clearly separated along the third NMS axis.

The first NMS axis was highly positively correlated with elevation, distance of the nearest case, forest and

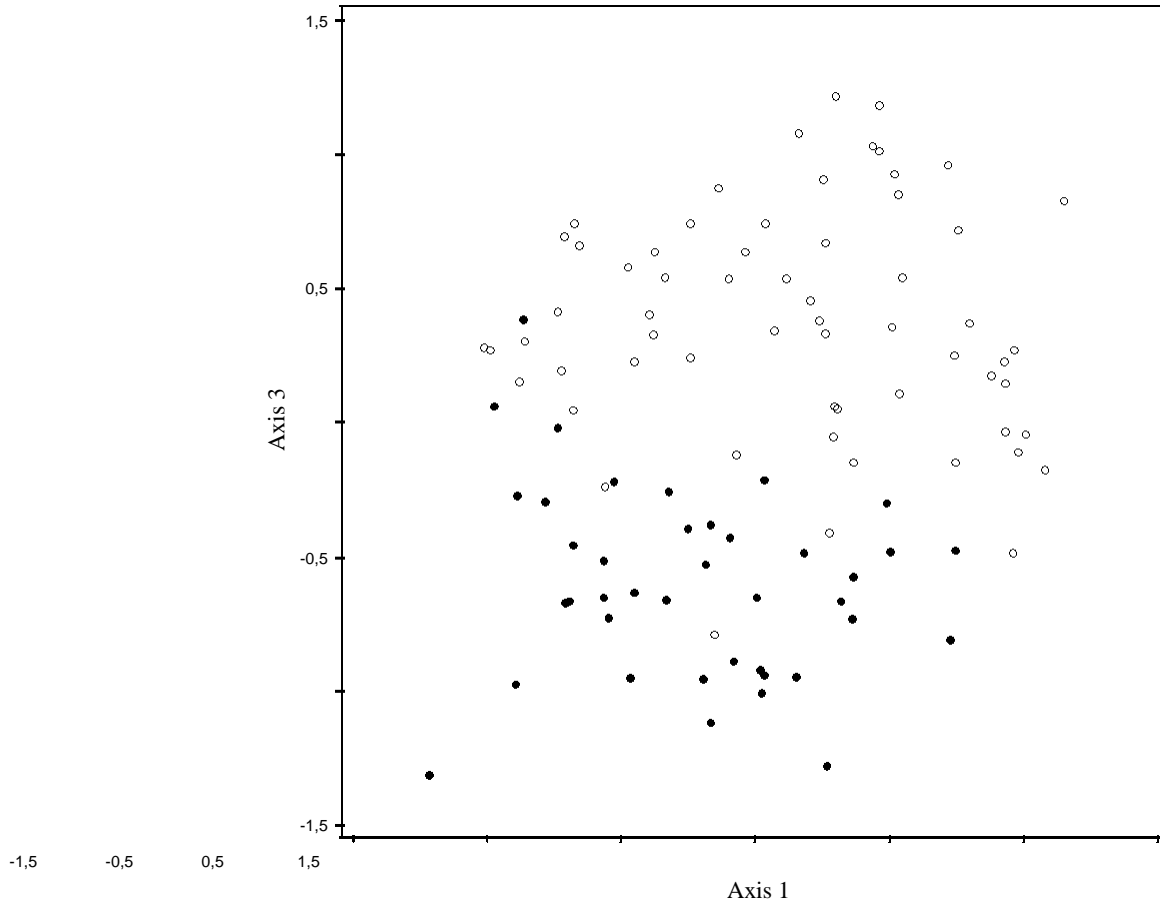


Figure 1. Ordination diagram defined by the first and third axes of the non-metric multidimensional scaling showing the 102 plots; symbols: black circles = plots in primary forest (n=40), white circles = plots in secondary forest (n=62).

secondary forest areas ($p < 0.001$) and negatively with crop and savannas areas, human population density, tree density and number of rodent traps (Table 1). It can therefore be considered that this axis represented an increasing elevation gradient coupled with a decreasing gradient of landscape management intensity. Bare soil cover and distance to the nearest home increased, while vegetation height and tree density decreased along this axis. The ordination diagram of plots separates at first, the oldest forests was inherited from primary formations on one side, and on the other side, secondary forest and shrub recolonization of fallow and savana.

The ISA showed that 38 and 28 species were indicators of primary and secondary forests, respectively (Table 2). The primary forest plots were characterized by afro-montane forest trees (*Carapa grandiflora*, *Nuxia congesta*, *Syzygium staudtii*, *Schefflera mannii*, *Bersama abyssinica* and *Podocarpus latifolius*), shrubs (*Ardisia kivuensis*, *Allophylus bullatus*, *Mimulopsis solmsii*, *Xylamos monospora*, *Rytigynia neglecta*) and herbs (*Commelina cameroonensis*, *Laportea alatipes*, *L. ovalifolia*, *Mimulopsis solmsii*) including ferns (*Asplenium*

friesiorum). Only one species was indicator of the canopy of secondary forests. Secondary forests were dominated by two heliophilous edge species, *Gnidia glauca* and *Hypericum revolutum*.

Plant traits

The ISA performed on the plant trait matrices highlighted trait categories which were filtered whether by primary or secondary forest conditions (Table 3). Primary forest plots were characterized by phanerophytes with large leaves (40 to 200 cm²), reproducing with sarcochorous diaspores (*Syzygium staudtii*, *Carapa grandiflora*, *Schefflera mannii*, *Allophylus bullatus*, *Podocarpus latifolius*, *Pittosporum viridiflorum* and *Pavetta hookeriana*), that is, diaspores with fleshy parts, adapted to endozoochory. The fruits of these species were known to attract birds and/or small rodents. Primary forest hosted mainly submountain and lower mountain species. The spatial distributions of these species were limited to a narrowed geographic area (Cameroon, East Africa,

Table 1. Spearman correlation tests between NMS axes and environmental variables. Only variables showing significant correlations are indicated. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Variables	NMS axis 1		NMS axis 3	
	R	p	R	p
Vegetation height (m)	-0.494	<0.001 ***	-0.569	<0.001 ***
Tree density (n.stem.ha-1)	-0.423	<0.001 ***	-0.605	<0.001 ***
Bare soil cover (%)	0.495	<0.001 ***	-0.017	0.869
Number of rodent traps	-0.237	0.017 *	-0.409	<0.001 ***
Elevation (m)	0.732	<0.001 ***	0.038	0.708
Distance to the nearest village	0.363	<0.001 ***	0.013	0.900
Human population density (r=3 km)	-0.307	0.002 **	-0.065	0.515
Distance to the nearest case	0.399	<0.001 ***	-0.008	0.934
Forest area	0.458	<0.001 ***	-0.121	0.224
Crop area	-0.361	<0.001 ***	0.157	0.115
Savannas area	-0.299	0.002 **	0.122	0.222
Primary forest area	0.086	0.392	-0.373	<0.001 ***
Secondary forest area	0.444	<0.001 ***	0.077	0.445
% deforested area (1978-2007)	0.012	0.908	0.315	0.001 **

Table 2. Results of indicator species analysis (ISA) conducted on plant species in the four vegetation layers in (a) primary (n=40) and (b) secondary forest plots (n=62). Only species with p -values <0.05 are shown. p -values from Monte Carlo tests are based on the proportion of randomized trials with expected IV>observed IV.

Primary forest			Secondary forest		
Species	IV	p	Species	IV	p
Tree layer			Tree layer		
<i>Nuxia congesta</i>	82.2	0.001	<i>Gnidia glauca</i>	25.8	0.002
<i>Syzygium staudtii</i>	76.8	0.001			
<i>Carapa grandiflora</i>	47.4	0.001			
<i>Schefflera mannii</i>	31.6	0.002			
<i>Bersama abyssinica</i>	22.4	0.002			
<i>Allophylus bullatus</i>	19.4	0.008			
<i>Podocarpus latifolius</i>	14.8	0.010			
<i>Pittosporum viridiflorum</i>	13.5	0.013			
<i>Pavetta hookeriana</i> var. <i>hookeriana</i>	10.0	0.021			
<i>Corynanthe pachyceras</i>	7.4	0.045			
Shrub layer			Shrub layer		
<i>Carapa grandiflora</i>	79.3	0.001	<i>Nuxia congesta</i>	66.0	0.006
<i>Ardisia kivuensis</i>	76.0	0.001	<i>Maesa lanceolata</i>	65.4	0.002
<i>Allophylus bullatus</i>	74.6	0.001	<i>Vernonia hymenolepis</i>	60.0	0.001
<i>Rytigynia neglecta</i>	62.3	0.014	<i>Gnidia glauca</i>	58.9	0.001
<i>Clausena anisata</i>	49.1	0.014	<i>Hypericum revolutum</i>	58.8	0.001
<i>Xymalos monospora</i>	48.0	0.006	<i>Rapanea melanophloeos</i>	46.3	0.003
<i>Psydrax dunlapii</i>	37.9	0.001	<i>Schefflera abyssinica</i>	30.4	0.009
<i>Bersama abyssinica</i>	35.4	0.012	<i>Bridelia speciosa</i>	22.1	0.037
<i>Piper capense</i>	28.5	0.005	<i>Erica mannii</i>	11.3	0.044
<i>Cassipourea malosana</i>	27.4	0.001			
<i>Arundinaria alpina</i>	26.8	0.001			
<i>Zanthoxylum rubescens</i>	16.9	0.021			
<i>Rauvolfia vomitoria</i>	14.6	0.018			

Table 2. Contd.

<i>Dracaena fragrans</i>	12.5	0.011			
<i>Corynanthe pachyceras</i>	12.3	0.029			
Under-shrub layer			Under-shrub layer		
<i>Ardisia kivuensis</i>	80.3	0.001	<i>Hypericum revolutum</i>	57.7	0.001
<i>Allophylus bullatus</i>	70.4	0.001	<i>Vernonia hymenolepis</i>	42.9	0.001
<i>Carapa grandiflora</i>	58.6	0.001	<i>Nuxia congesta</i>	38.9	0.008
<i>Rytigynia neglecta</i>	51.6	0.033	<i>Gnidia glauca</i>	37.1	0.001
<i>Mimulopsis solmsii</i>	45.2	0.001	<i>Maesa lanceolata</i>	24.6	0.041
<i>Bersama abyssinica</i>	42.9	0.001	<i>Maytenus undata</i>	13.8	0.047
<i>Psydrax dunlapii</i>	26.8	0.004	<i>Psorospermum aurantiacum</i>	12.9	0.044
<i>Dracaena fragrans</i>	25.0	0.001			
<i>Cassipourea malosana</i>	22.5	0.001			
<i>Piper capense</i>	22.0	0.040			
<i>Rubus pinnatus</i>	10.0	0.024			
<i>Rauvolfia vomitoria</i>	9.6	0.033			
<i>Aframomum</i> sp.	7.5	0.048			
Herb layer			Herb layer		
<i>Commelina cameroonensis</i>	62.5	0.001	<i>Geranium arabicum</i>	58.0	0.001
<i>Achyranthes aspera</i>	48.0	0.018	<i>Cynoglossum amplifolium</i>	44.3	0.001
<i>Laportea alatipes</i>	35.2	0.007	<i>Pteridium aquilinum</i> subsp. <i>aquilinum</i>	42.6	0.003
<i>Laportea ovalifolia</i>	28.9	0.002	<i>Alchemilla cryptantha</i>	40.6	0.014
<i>Impatiens sakeriana</i>	27.3	0.002	<i>Desmodium repandum</i>	38.4	0.032
<i>Piper capense</i>	25.3	0.012	<i>Agrocharis melanantha</i>	31.2	0.018
<i>Momordica foetida</i>	21.3	0.012	<i>Platostoma rotundifolium</i>	28.4	0.007
<i>Sida rhombifolia</i>	19.9	0.010	<i>Rhamnus prinoides</i>	25.5	0.017
<i>Mimulopsis solmsii</i>	15.9	0.027	<i>Cynoglossum coeruleum</i>	22.9	0.012
<i>Psydrax dunlapii</i>	15.2	0.036	<i>Pilea tetraphylla</i>	17.7	0.014
<i>Cyathula cylindrica</i> var. <i>cylindrica</i>	15.0	0.005	<i>Hibiscus noldeae</i>	16.8	0.025
<i>Raphidiocystis phyllocalyx</i>	13.5	0.016	<i>Centrosema pubescens</i>	16.1	0.012
<i>Zehneria minutiflora</i>	13.2	0.049	<i>Crassocephalum biafrae</i>	14.5	0.022
<i>Dovyalis</i> sp.	12.5	0.010	<i>Helichrysum cameroonense</i>	14.5	0.023
<i>Diplazium</i> sp.	10.0	0.016	<i>Laggera crispata</i>	12.9	0.036
<i>Asplenium friesiorum</i>	10.0	0.023	<i>Pentas pubiflora</i>	12.9	0.036
<i>Landolphia</i> sp.	7.5	0.042	<i>Lecanthus peduncularis</i>	12.6	0.049

Table 3. Results of indicator species analysis (ISA) conducted on plant trait and biogeographical categories (see details in Appendix) in (a) primary (n=40) and (b) secondary forest plots (n=62).

Primary forest			Secondary forest		
Trait	IV	p	Trait	IV	p
Life form			Life form		
Phanerophyte	53.4	0.008	Chamephyte	54.2	0.041
			Geophyte	63.0	0.003
Diaspore type			Diaspore type		
Sarcochore	56.6	0.003	Acanthochore	59.7	0.001
			Barochore	59.0	0.003
			Pogonochore	73.2	0.001

Table 3. Contd.

Dispersal type			Dispersal type		
Endozoochory	56.7	0.003	Epizoochory	65.0	0.001
Leaf type			Leaf type		
Mesophyll	61.0	0.001	Notophyll	55.6	0.003
Altitudinal tolerance			Altitudinal tolerance		
Submountain	57.8	0.045	Lower and middle altitudes	62.1	0.009
Submountain to lower mountain	58.1	0.004	Lower mountain	57.7	0.012
			Large latitudinal range	55.4	0.012
Phytogeographic type			Phytogeographic type		
Guineo-Congolian	76.2	0.001	Paleotropical and Afro-Malagasy	65.0	0.001
Common to Cameroon and east African mountain	53.5	0.016	Multiregional African	74.2	0.001
Only in Cameroon mountain	67.8	0.001	Afro-tropical mountain	63.1	0.001

Table 4. Mean (\pm Standard Error) values of species richness in primary (n=40) and secondary (n=62) forest plots. Z is the value of the Mann-Whitney's test. Significant p-values are shown in bold.

Variables	Primary forest		Secondary forest		Mann-Whitney test	
	Mean	S.E.	Mean	S.E.	Z	p
Species richness						
Total	45.5	2.4	44.1	1.5	-0.202	0.840
Tree layer	5.4	0.4	2.4	0.3	-5.307	0.001
Shrub layer	16.8	0.8	15.2	0.7	-1.291	0.197
Under-shrub layer	14.3	1.1	12.4	0.7	-1.194	0.232
Herb layer	22.7	1.8	24.8	1.3	-1.286	0.198

Guineo-Congolian areas).

Secondary forest plots were characterized by geophytes (*Pteridium aquilinum*) and chamaephytes (*Alchemilla* sp.) able to propagate vegetatively and to resist to disturbances (bush fire) or survive under grazing pressure. The tree and shrub layers of the secondary forests were often dominated by the barochorous species, *Gnidia glauca*, explaining this significant trait in the ISA. Other secondary forest species used animal vectors (epizoochory) or wind (pogonochore diaspores producing plumed appendages) to disperse. Species in secondary forest plots were able to occur in a wide range of altitudinal levels and biogeographic areas (multiregional African, afro-tropical mountain species).

Species richness and some variables between primary and secondary forest plots

The mean (\pm 1SE) species richness per plot was 45.5

(\pm 2.4) and 44.1 (\pm 1.5) in primary and secondary forests, respectively (Table 4). Only tree species richness showed significant differences ($Z=-5.307$; $p < 0.001$) between the two types of forests.

The total plot species richness was influenced positively by tree density and human population density and negatively by deforestation (Table 5). The tree species richness decreased along the elevation gradient and increased with the area of primary forest neighbouring plots (Table 5). The herb species richness increased with human population density and secondary forest area in the neighbouring landscape.

Table 6 shows mean values of local and landscape variables in primary (n=40) and secondary (n=62) forest plots. The maximum height of vegetation and density of trees were respectively 19.42 m, 101 stems/ha in primary forest and 11.93 m, 36 stems/ha in secondary forest and show significant difference ($p < 0.001$). Anthropogenic activities were high in primary forest as shown by the number of rodent trap ($p < 0.05$) and the proximity of

Table 5. Generalized linear models the effects of local and landscape variables on species richness. ¹: parameter estimate; ²: standard error; ³: degrees of freedom; ⁴: significant *p*-values are shown in bold. Dependent variables: RTOT: total species richness in plots; Rtree: tree species richness; Rherb: tree species richness; Explanatory variables: DA: Tree density (n. stems.ha⁻¹); ALTI: altitude; HAB: human population within a 5km radius around plots; F7807: deforested area (ha) between 1978 and 2007 within a 500 m radius around plots (=forest area in 1978-forest area in 2007); FP: area of primary forest (ha) within a 500 m radius around plots; FS: area of secondary forest (ha) within a 500 m radius around plots.

Dependent variables	Explanatory variables	Par. est. ¹	S.E. ²	D.F. ³	Khi-2	P -value ⁴
RTOT	Intercept	3.4878	0.0471	1	5491.48	<0.001
	DA	0.0014	0.0003	1	22.34	<0.001
	HAB	0.0009	0.0001	1	45.63	<0.001
	F7807	-5.2E-07	1.1E-07	1	23.68	<0.001
Rtree	Intercept	6.4318	0.6946	1	85.73	<0.001
	ALTI	-0.0024	0.0003	1	54.59	<0.001
	FP	0.0165	0.0040	1	16.81	<0.001
Rherb	Intercept	3.2309	0.0558	1	3347.50	<0.001
	HAB	0.0009	0.0001	1	44.10	<0.001
	FS	0.0034	0.0009	1	13.29	<0.001

Table 6. Mean values of local and landscape variables in primary (n=40) and secondary (n=62) forest plots. Z is the value of the Mann - Whitney's test. * *p*<0.05, ** *p*<0.01, *** *p*<0.001.

Parameter	Code	Primary forest		Secondary forest		Mann-Whitney test	
		Mean	S.E.	Mean	S.E.	Z	p
Local variables							
Maximum height of vegetation (cm)	HMAX	1942.5	72.0	1193.5	56.2	-6.402	0.000 ***
Density of trees (n. stems/ha)	DA	101.0	7.6	36.0	4.7	-6.056	0.000 ***
Bare soil cover (%)	SOL	3.3	1.0	4.4	0.9	-1.339	0.181
Number of domestic bee hives	RUCH	0.6	0.1	0.5	0.1	-0.234	0.815
Number of rodent traps	PIEG	0.9	0.2	0.4	0.2	-3.433	0.001 **
Altitude (m)	ALTIMC	2302.1	23.0	2352.2	27.9	-1.539	0.124
Slope (°)	PENTE	12.9	1.1	12.9	0.7	-0.446	0.656
Orientation index =180°-Absolute value (orientation-180°)	OrientSud	68.5	7.6	74.3	6.0	-0.665	0.506
Landscape variables							
Number of villages in a radius of 5 km	NBVL5KM	4.9	0.2	4.1	0.1	-3.539	0.000 ***
Distance of the nearest village (m)	DVIL	2388.6	85.1	2564.5	113.2	-1.145	0.252
Number of inhabitants in a radius of 5 km	HAB5KM	373.8	24.8	325.7	11.9	-1.395	0.163
Distance of the nearest house (m)	DCASE	1803.2	105.5	1985.6	108.2	-0.898	0.369
Percentage of primary forest loss (ha; 100x(forest 1978-primary forest 2007)/forest 1978) r=500 m	PDEFP7807	64.4	2.9	74.8	2.9	-2.670	0.008 **
Forest area in 2007 (r=500 m)	F2007	42.4512	15.7707	40.707	24.1658	-0.158	0.875
Savanna area in 2007 (r=500 m)	S2007	26.1477	12.9258	27.0103	17.6999	-0.24	0.81
Crop area in 2007 (r=500 m)	C2007	8.1452	13.3525	8.6936	10.7118	-0.786	0.432
Primary forest area in 2007 (r=500m)	FP	23.1	2.0	15.5	2.0	-2.876	0.004 **
Secondary forest area in 2007 (r=500 m)	FS	18.7	1.8	24.9	2.5	-1.083	0.279

villages.

DISCUSSION

Forests generally become fragmented through intensification of human activities. The results of this study suggested cropland and pasture expansion as the major reasons for the observed fragmentation along with high dependence on forest resources such as thinning, bee keeping and hunting (Uddina et al., 2015). In fact, Momo et al. (2012) show that between 1978 and 2007, the number of forest fragments increased from 2627 to 5183, their average area decreased from 7.4 to 1.8 ha, and perimeter from 912 to 446 m, and the forest fragmentation index increased by 285.7%, so despite the recent progression of forest cover (since the year 2001), the proportion of ancient forest has continuously decreased from 1978 to 2007, indicating that deforestation is still ongoing. The loss of forest is particularly serious in this mountainous area, because the landscape is fragile with steep slopes and loss of soil cover can mean that recovery of the ecosystem can be very slow or even impossible as in other mountainous zones (Halada, 2010).

The ordination diagram of plots separates at first, the oldest forests inherited from primary formations on one side, and on the other side, secondary forest and shrub recolonization of fallow and savanna. In the study zone, 63.1% of species are common to the different types of forests while Zapfack et al. (2002) showed that the primary and secondary forests have only 42% of similarity in terms of species composition. Where forest plants are present in secondary as well as primary forests, it can be assumed that they colonised the secondary forest sites from the primary forests and hedgerows that surround most fields. Why have some forest plants been so successful in colonising secondary forests from source populations in primary forests? To answer this question, let us consider the different land-use histories of primary and secondary forests. Clearing of the original forests, combined with the sustained use of a site for agriculture for the better part of a century, would eliminate the forest plants present at the time of clearing. Thus, when a farm field is abandoned, primary forest plants can colonise it only if they can get there from nearby forests (Lôbo et al., 2011). The re-growing secondary forest has significantly altered forest structure and often significantly altered canopy species composition as well, as compared to the original forest. So, there is really no more primary forest on Mount Oku. In fact, the primary nature of tropical forests is also quite debated because many studies show the existence of very ancient human traces in these forests (Denevan, 1992).

Only one species was indicator of the canopy of secondary forests. Secondary forests were dominated by

two heliophilous and pioneer edge species, *Gnidia glauca* and *Hypericum revolutum*. These two species are commonly found in high altitude communities that have been damaged, cleared or burned (Cheek et al., 2000; Asanga, 2002). They characterised the altitude coppices described by Letouzey (1985) and the first stages in the succession back to mountain forest (Asanga, 2002). Common disturbances that give rise to secondary forests include fragmentation of habitats, deforestation and change in land use practices (Chokkalingam and De Jong, 2001). Changes in plant species composition of Mount Oku forests in the last century could be partly related to the drastic reduction of seed disperser mammals (Maisels et al., 2001). Now, 80% of tree species occurring in the Mount Oku forest are adapted to animal dispersal. Out of these, 97.5% are dispersed by birds or monkeys and 2.4% by rodents (Maisels and Forboseh, 1997). Only 20% of the trees are wind-dispersed. Some forest species are much better than others at dispersing seeds to abandoned fields. Thus, one reason secondary forests differ in species from primary forests is that they contain species with better dispersal capabilities. Secondary forests contain herbaceous plants with tiny spores that drift long distances in wind, such as fern plants. But not all forest species capable of dispersing in abandoned farmlands are well represented in secondary forests. Some shade-tolerant forest species are uncommon in secondary forests, perhaps because they cannot tolerate the sunny, open conditions of rundown, abandoned fields.

According to Yongo (2002), tropical forests are characterised by the presence of high phanerophytes. The low percentage of phanerophytes obtained in this study as compared to other sites reinforces our belief that we are in predominantly disturbed forest. Although, disturbed forests of Mount Oku still harbor a flora composed mainly of phanerophytes, with a significant proportion of chamaephyte, this high proportion of chamaephytes results in the exposure of understorey to light rays, following the opening of the canopy. It shows that secondary forests generally with fewer tree species, are dominated by widespread pioneer trees and have a simpler structure (Whitmore, 1998; Aide et al., 2000).

The species richness per plot was slightly higher in primary forests, and it can be assumed that the proximity of many secondary forest plots to primary forest stands will likely result in increased richness in these plots due to potentially high seed input from mature forests (Mesquita et al., 2001; Kennard et al., 2002). Secondary forests contain a subset of the forest plants found in primary forests; plants may be uncommon in secondary forests because of seed size and seed dispersal ability. Small seeds give rise to small seedlings, which compete poorly with the dense vegetation of abandoned farm fields. Generally, these secondary forests regenerate largely through natural processes after partial abandonment of alternative land use (agriculture, pasture, etc.) on

formerly forested lands (Smith et al., 1999).

Conclusion

Finally, this study suggests that expansions of cropland coupled with high dependency on forests by human population are the major drivers of the forest fragmentation and degradation with implications for biodiversity, ecosystem services and people's livelihoods. A total of 385 vascular plant species were present in the 102 plots. 243 species were common to primary and secondary forest plots, 69 were present exclusively in primary forest plots and 73 in secondary forest plots. The Indicator Species Analysis showed that 38 and 28 species were indicator of primary and secondary forests, respectively. The mean species richness per plot was 45.5 and 44.1 in primary and secondary forests, respectively. Only tree species richness was significantly higher ($Z=-5.307$; $p < 0.001$) in primary forest. The maximum height of vegetation and density of trees were respectively 19.42 m, 101 stems/ha in primary forest and 11.93 m, 36 stems/ha in secondary forest and show significant difference ($p < 0.001$). Primary forest plots were characterized by phanerophytes, while secondary forest plots were characterized by geophytes and chamaephytes. This study improves the information base at national scale, and may contribute to understand global change in forest. Such information is required for informed decision making and planning conservation. So, there is need to urgently protect the last remnants of ancient forest for their biological value.

Conflict of Interests

The authors did not declare any conflict of interests.

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Appendix 1. The plant traits and biogeographic characteristics and their categories.

Plant characteristics	Codes	Categories	Functions	References
Life form	B-Ph	Phanerophyte	Holding space and time	Raunkiaer, 1934
	B-Ch	Chamephyte		
	B-L	Liana		
	B-H	Hemicryptophyte		
	B-Th	Therophyte		
	B-G	Geophyte		
Diaspore type	G-Acan	Acanthochore	Ability to disperse, to regenerate and to establish in the ecosystem	Dansereau and Lems, 1957; Doucet, 2003
	G-Ballo	Ballochore		
	G-Baro	Barochore		
	G-Pogo	Pogonochore		
	G-Ptero	Pterochore		
	G-Sarco	Sarcochore		
	G-Sclero	Sclerochore		
G-Sporo	Spore			
Dispersal type	D -Ane	Anemochory	Ability to migrate, to colonize, dispersal distance	Dansereau and Lems, 1957; Guillaumet, 1967
	D-Auto	Autochory		
	D-Endozoo	Endozoochory		
	D-Epizoo	Epizoochory		
Leaf type	F-Mg.Ma	Megaphyll (leaf area > 20 dm ²) and Macrophyll (2-20 dm ²)	Adaptation to macro and microclimatic conditions	Ohsawa, 1995
	F-Me	Mesophyll (40-200 cm ²)		
	F-No	Notophyll (20-40 cm ²)		
	F-Mi	Microphyll (2-20 cm ²)		
	F-Na.Le	Nanophyll (0,2-2 cm ²) and leptophyll (< 0,2 cm ²)		
Altitudinal tolerance	A-lowalti	Lower and middle altitudes	Response to climate and tolerance to altitude	Senterre, 2006
	A-SM	Submountain		
	A-SM+MI	Submountain to lower mountain		
	A-MI	Lower mountain		
	A-MI+MS	Lower mountain to upper mountain		
	A-alpine	Upper mountain to subalpine		
	A-large	Large latitudinal range (> 2 altitudinal levels)		
Phytogeographic type	P-Cos	Cosmopolitan	Flora stability and age, response to natural disturbances and to human presence (species exchanges between continents), response to isolation and forest degradation (endemic species)	White, 1978; White, 1979; White, 1983
	P-Pan	Pantropical		
	P-Pal	Paleotropical and afro-malagasy		
	P-Afr	Afro-tropical		
	P-P-A	Multiregional african		
	P-GC	Guineo-Congolian		
	P-MoAfr	Afro-tropical mountain		
	P-MoCam.EAfr	Common to cameroonian and east African mountain		
	P-MoCam	Only in cameroonian mountain		