

Woody vegetation structure and composition along a protection gradient in a miombo ecosystem of western Tanzania

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Abstract

Fully protected areas such as National Parks are often assumed to be the best way to conserve plant diversity and maintain intact forest composition and structure. To evaluate this assertion, we sampled trees in areas with four different levels of protection: a National Park, where the protection level is very high, a Game Controlled Area which allows tourist hunting of big game animals, a Forest Reserve which allows selective harvest of trees, and an Open Area where human populations have unrestricted access to forest resources. All four land management areas had healthy size-class distributions with greater numbers of juvenile trees (2–10 cm DBH) than adults. Surprisingly, mean stem density of trees was highest (947 stems ha⁻¹) in the Game Controlled Area but was lowest (635 stems ha⁻¹) in the National Park. The former had the highest basal area value (24 m² ha⁻¹) while the human-inhabited Open Area had the lowest (11 m² ha⁻¹). Species richness in the Forest Reserve and Game Controlled Area was significantly higher than in the other areas. The total number of plots with unique species not found anywhere else was lowest in the National. Our measures of forest structure and composition therefore show that fully protected National Parks do not necessarily conserve the greatest diversity of tree species or unique species, indicating that a suite of different types of protection strategies may be the key to conservation of trees in these African dry tropical forests.

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1. Introduction

Forest conservation is currently the top agenda for a number of world conservation organizations, authorities and interest groups. Concern over forest conservation generally hinges on anthropogenic activities that lead to depletion forest resources. Forest conversion to farmland, exploitation through selective harvest, seasonally set forest fires, fuelwood removal and charcoal production, woodland grazing of cattle and even hunting of native herbivores are the major mechanisms of forest degradation, habitat change and biodiversity loss (Ramirez-Marcial et al., 2001; Reyers, 2004). Disturbances created by these activities influence forest dynamics and tree density at the local and regional scales (Hubbell et al., 1999) and are important in structuring plant communities (Sumina, 1994), particularly evident in changing size class distributions of the most sought-

after species (Luoga et al., 2004). In the face of these problems, conservation biologists have sought to protect forests using several different strategies from strict protection in National Parks, to sustainable forest management and other integrated conservation and development programs (Bruner et al., 2001; Primack, 2002; Borgerhoff Mulder and Coppolillo, 2005).

The miombo ecoregion is a dominant vegetation type in sub-Saharan Africa (Millington et al., 1986) and Tanzania contains a considerable portion of this ecoregion: miombo accounts for 39.6% of the total forest cover across the country (Rodgers, 1996). Tanzanian miombo is characterized by varying land use (management) schemes (Caro, 1999a) listed here in order of decreasing protection status: from fully protected National Parks (NP); to Game Reserves (GR) and Game Controlled Areas (GCA), where tourist hunting is allowed, and resident hunting in some GCAs; to Forest Reserves (FR), which permit selective logging; to Open Areas (OA), where human settlements flourish with few restrictions on resource use. With these varying levels of protection in mind, one might expect that heavily protected areas would be the best way to

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conserve trees, with moderate protection being next, followed by light protection. Using greenness as a metric, this general pattern has been confirmed at a large scale in Tanzania through analyses of AVHRR satellite imagery (Pelkey et al., 2003). Greenness, however, does not provide detailed analysis of forest stand structure, composition and species diversity that can only be obtained at an ecological scale of investigation.

Here, we describe the composition and structure of woody plant species in the Katavi ecosystem of western Tanzania in order to evaluate the effects of different conservation practices on miombo woodland. Our null hypothesis is that there is no difference among land protection categories in compositional and structural attributes. An alternative hypothesis, and one espoused by conservation practitioners is that forest composition, structure and species richness will be more complex and more diverse under greater protection.

2. Materials and methods

2.1. Study site

Fieldwork took place in the Katavi ecosystem (latitude $6^{\circ}35'$ to $7^{\circ}05'S$, longitude $30^{\circ}45'$ to $31^{\circ}25'E$) at the north end of Rukwa Valley in the Rukwa Region of western Tanzania (Fig. 1). Much of the study area is at a low elevation and is characterized by a flat and undulating terrain, sandy soils and consists largely of miombo woodland, a dry deciduous forest characterized by trees in the genera *Markhamia*, *Grewia*, *Terminalia*, *Syzygium*, *Acacia* and *Combretum*, but it also encompasses seasonally inundated floodplains (Caro, 1999a). Rainfall is approximately 750 mm/year that falls between November and April.

This field site provided a good location to study changes in plant species diversity along a continuum of habitat protection. At the high end of the protection continuum is Katavi National Park (KNP), where no temporary or permanent settlements are allowed, aside from Park headquarters and two outlying ranger posts. In addition, no livestock grazing, beekeeping, hunting, fishing or timber extraction are permitted. KNP rangers enforce these laws by conducting vehicle and foot patrols. At the low end of the continuum is a public use area, called Usevya Open Area (OA), where village based horticultural activities and pastoralism encroach on miombo woodland. Between these extremes are two intermediate habitat protection designations abutting KNP: the Msaginia Forest Reserve (FR) and Mlele Game Controlled Area (GCA). Both the FR and GCA prohibit human settlement, agriculture and grazing. Legally the FR allows selective harvest of trees whereas the GCA allows tourist hunting of big game animals but these areas are not frequently patrolled. The FR is located north while the GCA is located north east of the KNP (Fig. 1). There is a gradient of wild herbivore biomass across these areas. In 1995/1996, KNP was $22,526 \text{ kg/km}^2$; GCA, 7106 kg/km^2 ; FR: 152 kg/km^2 ; OA, 705 kg/km^2 (Caro, 1999a).

2.2. Circular plots

One hundred and thirty-three 15 m radius circular plots (0.07 ha) were used as a rapid assessment protocol for vegetation at each of 38 sampling sites. Between 2 and 3, and occasionally 4 were laid within a 0.5 km radius of each other at sites pre-selected for a parallel bird study, where care was taken to ensure that more dense, open and wetter vegetation was sampled at every site. Plots were distributed in an attempt

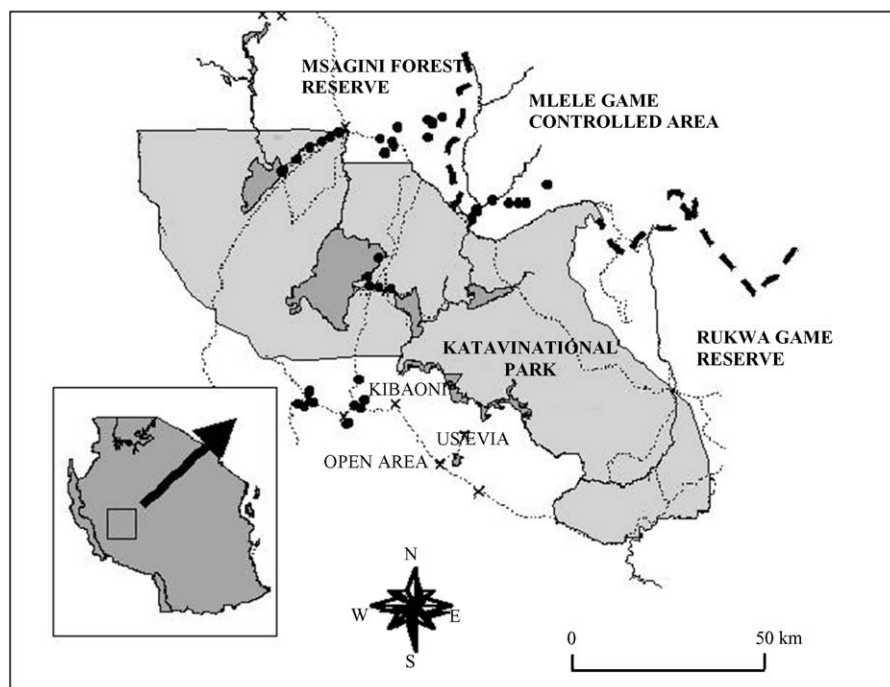


Fig. 1. A map of the Katavi ecosystem in Western Tanzania, showing the four different land protection areas where the study was conducted: Katavi National Park (shaded), Msaginia Forest Reserve, Mlele Game Controlled Area (borders thick dashed lines) and Usevya Open Area with sample sites for circular plots (solid circles); Rukwa Game Reserve is also shown.

to sample a broad range of representative habitats on the Rukwa Valley floor. Exact plot locations were haphazardly located however; KNP had 42, GCA had 17, FR had 24 and OA had 37 individual plots. Circular plots are expeditious in allowing accurate area sampling with minimal effort for plot layout

(a single central marker for permanent location) and they reduce the number of edge decisions because they minimize perimeter to area ratio (McCune and Grace, 2002). Within each plot, we identified every woody individual greater than 1.5 m tall, and then placed them into a corresponding DBH (diameter

Table 1

The 56 most dominant (IV 300) woody plant species of the total 216 species sampled in the miombo ecosystem of western Tanzania

Species	Relative density	Relative basal area	Relative frequency	Importance value (IV300)
<i>Markhamia obtusifolia</i>	12.22	2.66	4.16	19.04
<i>Grewia bicolor</i>	11.92	2.63	2.32	16.87
<i>Terminalia sericea</i>	2.69	6.34	4.16	13.19
<i>Syzygium guineense</i>	1.08	9.87	0.47	11.42
<i>Acacia tortilis</i>	1.37	5.29	2.74	9.40
<i>Combretum purpureiflorum</i>	6.56	0.22	2.21	8.99
<i>Borassus aethiopum</i>	6.56	0.22	2.21	8.99
<i>Combretum adenogonium</i>	0.68	7.36	0.89	8.93
<i>Cordia ovalis</i>	3.01	2.53	2.79	8.33
<i>Friesodielsia obovata</i>	4.41	0.54	3.16	8.11
<i>Diplorhynchus condylocarpon</i>	5.69	0.49	1.89	8.07
<i>Diospyrosfischeri gurke</i>	3.50	2.12	2.37	7.99
<i>Sclerocarya birrea</i>	2.80	1.68	3.16	7.64
<i>Lonchocarpus capassa</i>	0.40	5.20	2.00	7.60
<i>Azanza garckeana</i>	0.90	2.54	2.95	6.39
<i>Zizyphus mucronata</i>	4.29	1.02	1.00	6.30
<i>Combretum collinum</i>	1.08	1.57	3.00	5.64
<i>Grewia flavescens</i>	1.35	2.90	1.32	5.57
<i>Pterocarpus angolensis</i>	4.61	0.33	0.58	5.52
<i>Annona senegalensis</i>	0.77	2.88	1.74	5.38
<i>Harungana madagascariensis</i>	1.56	1.01	2.47	5.04
<i>Erythrophleum africanum</i>	2.61	0.28	1.16	4.04
<i>Pseudolachnostylis maprouneifolia</i>	0.61	1.87	1.42	3.91
<i>Sterculia quinqueloba</i>	0.25	2.14	1.21	3.61
<i>Kigelia africana</i>	0.88	1.19	1.32	3.38
<i>Voacanga africana</i>	0.19	1.88	1.16	3.23
<i>Acacia ataxacantha</i>	1.02	0.26	1.74	3.02
<i>Strychnos heterodoxa</i>	0.48	1.84	0.68	3.00
<i>Schrebera trichoclada</i>	1.17	0.55	1.26	2.98
<i>Tamarindus indica</i>	0.76	0.31	1.68	2.75
<i>Bauhinia petersiana</i>	0.32	1.31	1.05	2.69
<i>Acacia polyacantha</i>	0.45	1.15	0.84	2.45
<i>Burkea africana</i>	0.30	1.51	0.47	2.29
<i>Hymenocardia acida</i>	0.27	0.86	1.16	2.29
<i>Albizia harveyi</i>	0.72	0.19	1.26	2.18
<i>Commiphora africana</i>	0.62	0.82	0.58	2.01
<i>Acacia xanthophloea</i>	0.39	0.16	1.37	1.92
<i>Phyllanthus reticulatus</i>	0.10	1.22	0.53	1.84
<i>Mangifera indica</i>	1.30	0.04	0.42	1.76
<i>Julbernardia globiflora</i>	0.06	1.61	0.05	1.72
<i>Dombeya rotundifolia</i>	0.79	0.42	0.42	1.63
<i>Clerodendrum myricoides</i>	0.36	0.10	1.16	1.62
<i>Pericopsis angolensis</i>	0.95	0.04	0.58	1.57
<i>Combretum psidioides</i>	0.18	0.59	0.74	1.50
<i>Pterocarpus tinctorius</i>	0.15	0.65	0.68	1.49
<i>Piliostigma thomningii</i>	0.33	0.40	0.58	1.31
<i>Combretum molle</i>	0.19	0.23	0.84	1.26
<i>Albizia versicolor</i>	0.12	0.62	0.53	1.26
<i>Lonchocarpus bussei</i>	0.10	0.78	0.37	1.25
<i>Phyllanthus engleri</i>	0.23	0.30	0.68	1.21
<i>Markhamia zanzibarica</i>	0.33	0.22	0.63	1.18
<i>Bridelia cathartica</i>	0.38	0.08	0.68	1.15
<i>Ozoroa insignis</i>	0.53	0.16	0.32	1.01
<i>Brachystegia boehmii</i>	0.48	0.04	0.42	0.94
<i>Acacia nilotica</i>	0.19	0.40	0.32	0.91
<i>Brachystegia spiciformis</i>	0.08	0.55	0.26	0.89

at breast height) category (<2, 2–10, 10–20, 20–30, 30–40, 40–50 and >50 cm) without respect to species identification.

2.3. Rectangular plot data

Depending on the tree density of a plot, one or two 0.1 ha rectangular plots were set up at each sampling site because a separate but related study examining the spatial dispersion of individual trees required the measurement of inter-tree distances and specific DBH values. A total of 75 rectangular plots were sampled, 25 in 2000 and 50 in 2003. A 50 m tape was laid through the plot’s center to demarcate its length while 10 m tapes were used on each side to delineate the 20 m width of the plot. Every woody individual with a DBH of ≥2 cm was measured and identified.

2.4. Data analysis

Plant species identification was achieved by using the “Field guide to trees of Southern Africa” (Van Wyk and Van Wyk, 1997), local names, and taxonomic experts.

The data from both circular and rectangular plots obtained during 2000 (n = 25) and 2003 (n = 183) were combined and used to determine the species basal area, density and distribution of all woody species across the four conservation management areas (Terradas et al., 2004). Some of the 25 plots collected in 2000 had limited taxonomic identification and therefore are only included in those analyses that do not require accurate species identification. Differences in basal area, density and plant community distribution were assessed using JMPIN 4 (Sall et al., 2001) and Microsoft Excel.

3. Results

In 2003, a total of 183 plots were sampled using the circular (0.07 ha) and rectangular (0.1 ha) plots in which 19,721 stems from 216 species, 84 genera and 39 families were recorded (Table 1). The number of plots in which each species occurred ranged from 1 to 79. The number of species ranged from 1 to 28 per plot. The FR and OA had the greatest percentage of plots with high tree density of more than 1000 per hectare (Fig. 2).

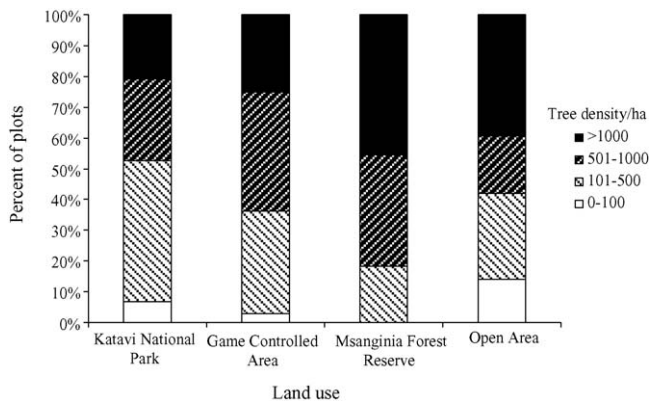


Fig. 2. Distribution of tree densities per hectare in plots sampled along a land protection gradient in the Katavi ecosystem, Tanzania.

Note, the FR had no low density (0–100 trees/ha) plots whereas a majority of plots in the NP contained medium tree densities (101–500 trees/ha).

Forest tree measurements were used for 208 plots sampled in 2000 and 2003 to describe the basal area (Fig. 3a), density (Fig. 3b) and species richness (Fig. 3c) within the different protected area designations. Description of forest structure and composition are arranged from high to low protection gradient. Three of the basic descriptors of forest structure showed significant differences among protection categories (basal area ($p \leq 0.0004$); density ($p \leq 0.025$); species richness ($p \leq 0.0001$)). Comparisons of all paired means of

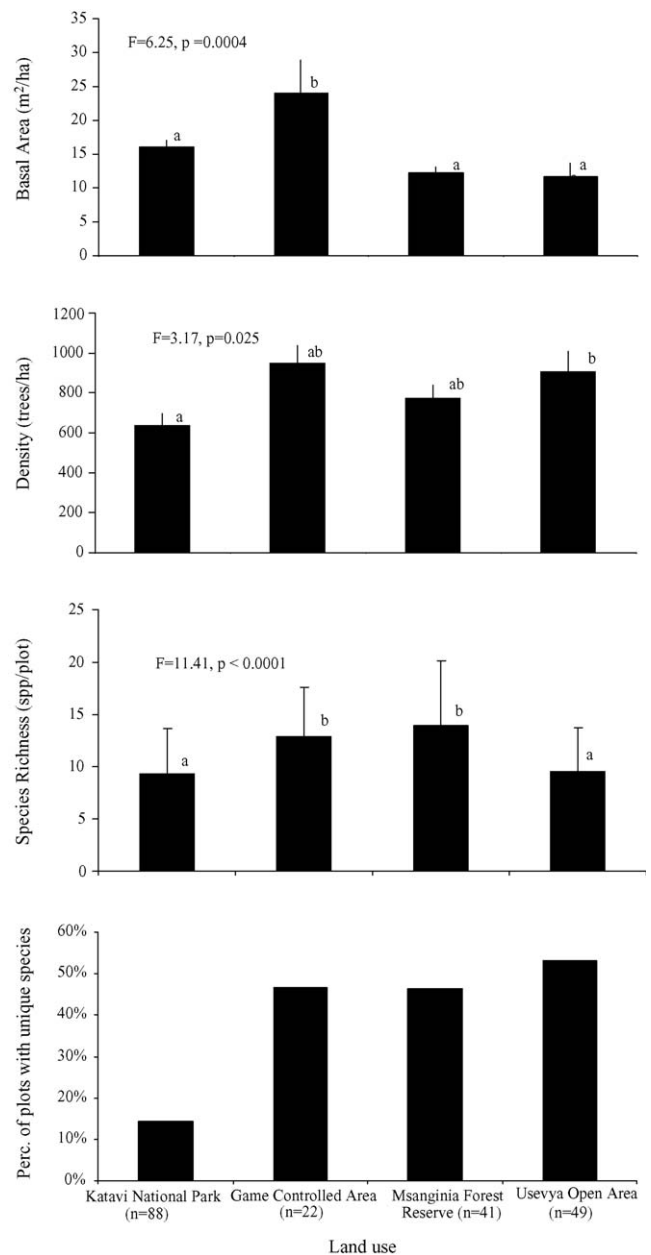


Fig. 3. Distribution of mean (and SD) basal area (a); density (b); species richness (c); number of unique species (d) of woody vegetation in varying land protection types in the Katavi ecosystem, Tanzania. Different letters on top of bars indicate significant differences between those levels of protection.

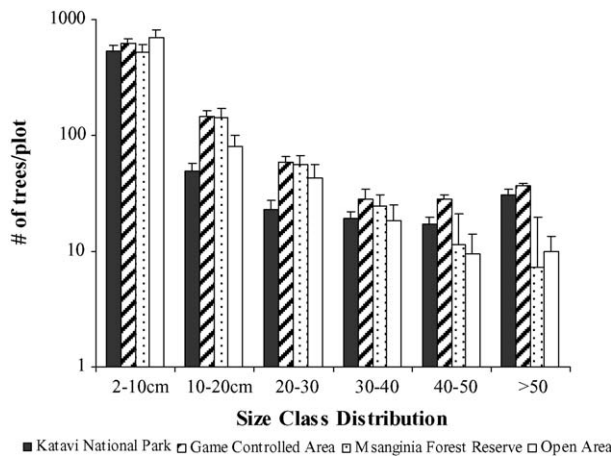


Fig. 4. A size class distribution of woody vegetation along a land protection gradient in the Katavi ecosystem, Tanzania.

basal area using the Tukeys HSD test showed that plots in the GCA had significantly higher tree basal areas than the KNP, FR and OA (Fig. 3a). For density, the KNP was significantly lower than the OA but not significantly different from the FR and GCA (Fig. 3b). The FR and GCA had significantly higher species richness per plot than the KNP and OA (Fig. 3c). The presence of unique species not found in any of the other protected areas varied across each category as shown in Fig. 3d ($X^2 = 0.008$, d.f. = 3, $p < 0.025$). Only 14% of the plots sampled in the KNP contained unique species while the GCA, FR and OA harbored a relatively greater number of unique species in the 46%, 46%, and 54% of their plots respectively.

The size class distribution of all four land protection areas (Fig. 4) is indicative of a healthy population, with populations being dominated by the juvenile classes (Barbour et al., 1999). This trend is especially true in the OA and FR, whereas the GCA and the KNP have more individuals with >50 cm DBH than the preceding classes of 30–40 and 40–50 cm.

4. Discussion

National Parks in East Africa were set up primarily to protect big mammals (Caro, 2003) and although this style of protection maximizes the potential return of National Parks in terms of tourism dollars, it also assumes that protecting big mammals is an appropriate surrogate for conserving all biodiversity—including plants. The main thrust of our investigation was to determine whether this was the case and whether a gradient of protection resulted in a decreasing gradient of miombo forest structure and species richness. First, however, we discuss the species composition of this miombo ecosystem.

Forest composition of miombo has historically been defined by trees of the legume subfamily Caesalpinioideae, particularly three characteristic genera, namely *Brachystegia*, *Julbernardia* and *Isoberlina* (White, 1983; Chidumayo, 1987). In contrast, our results indicate that Katavi ecosystem – which is at the low end of precipitation gradient of all miombo woodland – is dominated by the genera *Markhamia*, *Grewia*, *Terminalia*, *Syzygium*, *Acacia* and *Combretum*. Two

of the renown genera of *Julbernardia* and *Brachystegia* come in fortieth and fifty-fourth positions in frequencies of trees observed, respectively (Table 1). *Grewia bicolor* and *Combretum purpureiflorum* are scrubby species, whose presence suggests disturbance and hydrological influences. These taxa were found in areas that are heavily grazed and browsed by cattle (in the OA) and by large herbivores such as hippopotami (in the KNP). These species are also more frequent along riparian areas. The prevalence of *Syzygium guineense*, a riparian species, reflects that some of our sampling occurred in close proximity to wetter areas. Our results may not therefore be applicable to the entire miombo ecosystem because our sampling locations were limited by constraints of a parallel vertebrate study.

Conservation managers would predict that our measures of forest structure and composition – basal area, species richness and unique species – would be greatest in the strictly protected KNP and would decrease along a gradient of protection to the OA. In addition, we had predicted that the density of trees in the KNP would be lower than in the OA because increased human disturbance such as livestock grazing, cultivation and harvest for timber and firewood in the OA would be greater as a result of regeneration. Our results, summarized in Table 2, show that these measures of woody vegetation in Katavi ecosystem were significantly different along the land protection gradient, but surprisingly, not in the direction that we had expected.

We expected that the KNP would have a higher basal area than the rest of the management areas. On the contrary, the basal area for the KNP, along with the FR and OA were significantly lower than that of the GCA. The density of trees was significantly lower in the KNP than the rest of the management areas (Fig. 3). This might be expected because the KNP is inhabited by high populations of large herbivores (Caro, 1999b), and until recently, the Park contained the second highest densities of large mammals in Tanzania after Serengeti (Caro et al., 1998), so browsing of tree recruits is likely to be higher inside KNP than in the other areas. The density of trees in the largest size class was higher in the GCA than the three other area designations (Fig. 4). This occurrence of high basal area and high density of trees in the largest size class suggests that the GCA is dominated by a more mature forest than the rest of the management areas. The FR had a relatively low proportion of trees in larger size classes, probably due to

Table 2
Summary of findings in this study

	NP	GCA	FR	OA
Level of protection	High	Medium	Medium	Low
Level of human disturbance	Low	Low	Medium	High
Extent of herbivory	High	Medium	Low	High
Outcome measures				
Basal area	Low	High	Low	Low
Stem density	Low	High	High	High
Species richness	Low	High	High	Low
Unique species	Low	High	High	High

selective harvesting of larger trees especially of highly sought after species (Schwartz et al., 2002; Schwartz and Caro, 2003) and its high tree density. Finally, the OA is human inhabited and consequently heavily cut for timber, cultivated for crops, grazed by livestock and harvested for firewood (Holmes, 2003) and thus had trees with low basal area and high density.

Turning to measures of species richness, there was no significant difference in the plant species richness between a fully protected area and a human inhabited OA (Fig. 3c). This is the opposite of the “empty forest” as described for some areas of the tropics whereby the presence of “soaring, buttressed tropical trees do not guarantee the presence of resident fauna (Redford, 1992).” Strictly protected areas in East Africa may be becoming “floral poor” possibly because conservation efforts are geared towards animal species. In our situation “floral poor” symptoms were observed in both the strictly protected and unprotected areas possibly due to herbivory and human activities in the KNP and OA respectively. Note that the KNP is characterized by a significantly lower density of small trees compared to those in the OA (Fig. 4). Possibly herbivore browsing in the Park reduces regeneration, whereas cutting episodes and cattle grazing in the OA reduces the competitive effects of grasses on woody seedlings, or both. A similar trend has been reported in other studies in the miombo ecoregion. For example, in central Zimbabwe, there was no difference in tree species richness between the communal area and a protected area (Vermeulen, 1996). Cumming et al. (1997) has similarly shown that there was low species richness in trees in a protected area with high elephant densities relative to an adjacent open area with low elephant densities but higher human impacts. Interestingly from a conservation standpoint, species richness was high in the lightly protected GCA and FR.

Areas lying outside fully protected zones may be of great importance for conservation of a broad spectrum of biodiversity (Borgerhoff Mulder and Coppolillo, 2005). For instance, our study shows that we were more likely to encounter unique species in the OA than in the KNP (Fig. 3d). In addition, the number of plots harboring unique species was significantly higher in less protected areas (GCA, FR and OA) than the strictly protected KNP. Studies in other human dominated ecosystems (Noble and Dirzo, 1997) have shown that forest disturbance through logging causes an immediate decline in biodiversity followed by a recovery, although not necessarily of the same species. The clearing of forest for cultivation, grazing, fuelwood and other timber purposes that occurs in the OA may allow the recruitment of species that are not found in other management areas. Thus, this increased species richness in the OA may not necessarily be indicative of ecological health. When an area is disturbed over time, species that grow well in the new environment will recruit and establish, increasing the number of species. This may change over time as species that cannot tolerate the new environmental conditions eventually die off. So increased species richness in the OA may simply mean that these areas are in transition between two different vegetation types. This is less likely to apply to the relatively undisturbed GCA and FR, however. It is

not clear why KNP shows low species richness and relatively few unique species compared to the other land protection designations.

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