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Impacts of Diffuse Land-Use on Plant Diversity Patterns in the Miombo Woodlands of Western Zambia

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Abstract: Land use is known to influence the diversity of vascular plants in the Miombo woodlands. However, little is known about the interaction between soil and land use in herbaceous and woody species. We compared the diversity of vascular plants at the plot level (20 m × 50 m) and site level for three sites in the Miombo woodlands of western Zambia subject to different levels of intensity classes of diffuse land use (e.g., livestock herbivory and selective timber harvesting). For each of the sites, twenty plots were randomly selected for assessment of species composition of vascular plant species, indicators of land-use intensity, and soil chemistry per plot. We hypothesized that the site with the lowest human impact would have the highest richness and diversity of woody and herbaceous species. At the site level, we found that richness and diversity of woody species were unaffected by land-use intensity, whereas herbaceous species richness was higher for the protected site (28 species on average per 1000 m^2) than the two other sites (23 and 21 species on average per 1000 m^2). At the plot level, herbaceous species richness was positively associated with woodcutting and soil pH. We interpret the positive effect of woodcutting on herbaceous species richness as the effect of lower competition by the woody component for resources such as water, nutrients, and light. With regard to the absence of any effect of land-use intensity on the richness of woody species, we conclude that in our study areas selective timber harvesting may be at a sustainable level and might even have a positive effect on the diversity of the herbaceous layer.

Keywords: species richness; Shannon diversity; herbaceous species; woody species; soil variables; Miombo woodlands

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1. Introduction

The Miombo woodlands form a widespread dry woodland belt covering large parts of southern and eastern Africa, encompassing Angola, Botswana, the Democratic Republic of Congo, Malawi, Mozambique, Tanzania, Zambia, and Zimbabwe [1]. While the flora of the Miombo woodlands is characterised by high species richness, the diversity of canopy trees is low [2]. The natural resources of the Miombo woodlands strongly contribute to the wealth of the social and economic systems in their distribution area [3]. This ecosystem and its resources, however, are prone to habitat transformation and biodiversity loss [4]. Anthropogenic activities such as fuel combustion, commercial selective harvesting of valuable timber, grazing, crop production, and complete deforestation threaten the woodland system [5–7]. With a deforestation rate of 1.5% per year, Zambia is even classified as one of the countries with the highest deforestation rates in the world [8]. Complete habitat conversion from forest to cropland inevitably decreases both herbaceous and woody species richness [9,10].

In contrast to deforestation, with its complete transformation of land cover, diffuse disturbance is characterised by relatively small patches of change distributed over a large area [11]. In woodlands, scattered, small-scale land use through grazing, selective timber harvesting, or small-scale cropping has a diffuse but continuous negative impact on the vegetation and woody and herbaceous forest biodiversity, as has been shown by studies of (sub)tropical forest ecosystems in southern Africa [12], Brazil [13], the mountains of Mexico [14], and the tropical rainforests of Madagascar [15]. Yet, the extent of the impact appears to vary from low to high [16,17]. Revermann et al. [12] showed how plant species richness and evenness respond to the diverging land-use patterns of spatially diffuse versus intense land use in the dry woodlands along the Kunene in Angola and Namibia. They showed that the spatially diffuse land use on unfenced communal land in Namibia has measurable negative effects on the richness of mainly woody plant species. The authors attributed this pattern to selective timber logging. In Zambia, Chidumayo [18] expressed a growing concern countrywide about the negative effects of diffuse disturbance due to the selective harvesting of trees for charcoal production and other uses. Irrespective of the potential impact of diffuse land use on botanical diversity, the effects of spatially-diffuse land use on the vegetation of the Miombo woodland have received little scientific attention in the available literature. Most of the researchers who have investigated the impact of land use on the Miombo woodlands have mainly focused on the effects on the woody component of the vegetation [3,19,20]. However, as has been shown by Revermann et al. [12], the response of forbs and grass species to diffuse disturbance of woodland systems may differ from that of woody species. The herbaceous layer of the Miombo woodlands shows great spatial variation in species composition, and several herbaceous genera contribute to the species richness and local endemism in the system [2]. Irrespective of the reported response of the herbaceous vegetation to diffuse land use in other vegetation types [12] and the strong contribution of herbaceous flora to the overall species richness and endemism, we are not aware of any study on the effect of land use on both the woody and herbaceous vegetation of the Miombo woodlands.

Therefore, in this study we focus on the effect of spatially diffuse land use on the composition and diversity of herbaceous and woody plant species in the western Zambian Miombo woodlands. To this end, we selected three sites in the Miombo woodlands of western Zambia, each representing a different land use type (i.e., national park, national forest, and community forest) related to a different level of spatially diffuse land-use intensity.

National Park (Kafue): no land-use activities are permissible, and only prescribed fires are used as a management intervention tool.

National Forest (Dongwe): a medium level of disturbance; only minimal land-use activities are allowed, and harvesting of timber is only allowed upon issuance of a permit.

Community Forest (Luampa): high level of disturbance with several land-use activities permitted, including the harvest of both timber and non-timber products as well as occasional agricultural activities.

We compared two species diversity measures for woody and herbaceous species at the three sites and analysed the spatially heterogeneous effects of indicators of diffuse land-use intensity and soil chemical variables on the species diversity measures at plot scale (1000 m^2, $n = 60$).

Our hypothesis was that the Kafue site in the National Park would have a higher richness and diversity of woody and herbaceous species at both the plot and site scale than the two sites with higher land-use intensity. We additionally expected that, as observed by Revermann et al. [12], the diffuse disturbances would have a greater negative effect on species richness and biodiversity of trees than on the herbaceous layer.

2. Material and Methods

2.1. Study Area

The study was conducted at three sites in the Miombo woodlands of western Zambia (Figure 1), extending over latitudes S 14°–16° and longitudes E 24°–26° at an elevation ranging from 1068 m to 1210 m a.s.l. (Table 1). The Miombo woodlands are the most extensive tropical seasonal woodland considered part of the African Savannah, covering about 2.4 million km^2 in Africa [21]. Dominant plant families of Fabaceae tree species of the genera *Brachystegia* Benth., *Isoberlina* Craib and Stapf ex. Holland, and *Julbernardia* Pellegr., which are clustered in the subfamily Caesalpinioideae and the tribe Ahmerstieae [22–24], characterise the Miombo woodlands [24]. The area has a tropical sub-humid climate with alternating dry and wet seasons. Rainfall occurs for 5–7 months in summer [25]. The mean annual temperature of the study area is 20.8 °C, and the mean annual rainfall ranges from 875 to 990 mm (Table 1). The soils consist of Kalahari sands from the Tertiary to the recent period which, according to Japan Association for International Collaboration of Agriculture and Forestry [26], cover western and northwestern Zambia. The main soil type is Arenosols, a formation of the parent Basement and Katanga rocks, with the accumulation of Karoo deposits [27].

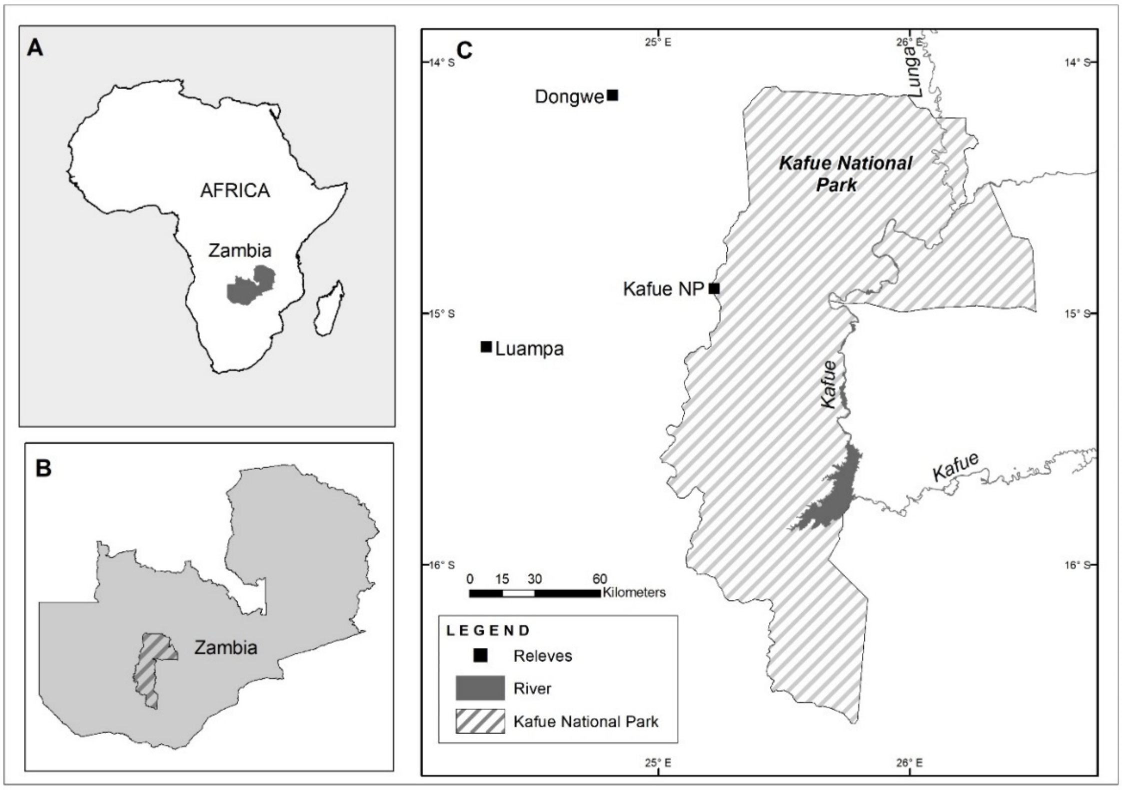

Figure 1. Locations of study sites (**C**) in western Zambia, showing the sites in relation to the continent (**A**) and the country (**B**).

Floristically, the three sites fall within the Sudano-Zambezian Phytoregion [28], whereas the vegetation is classified as Miombo woodlands *sensu* [29], which forms part of the tropical seasonal woodlands [30]. Miombo woodlands are characterized by co-dominance of trees, shrubs, and herbaceous plants, with respective proportions determined by environmental, ecological, and human parameters and adapted to fire [31]. The dominant tree species are those referred to by Phiri [24] as dominant taxa of the Miombo woodlands.

2.2. Study Design and Data Collection

We selected three study sites in Kafue National Park (called Kafue for the rest of the text), Dongwe, and Luampa, approximately 100 km apart (Figure 1), based on literature consultations [29,32] and site visits to the study area of western Zambia in 2014. Classification according to land-use type and intensity was guided by the State of the Environment in Zambia [33]. Each site was characterised by different land-use intensities, from low to medium to high (Table 1). For each study site, we classified the vegetation into open or closed woodland using the most recent Google Earth image [34] at the time of data assessment. Based on habitat stratification, we randomly selected twenty vegetation plots for each of the sites. The plots were 1000 m^2 (20 m $\times$ 50 m) in size and were laid out in an east–west extension.

Table 1. Descriptive attributes of the three study sites.

Site Name	Mean Annual Rainfall [mm/yr]	Mean Annual Temperature [°C]	Land-Use Type	Land-Use Intensity	GPS Coordinates (North West Corner)	Elevation Min–Max [masl]
Luampa	875.5	22.22	Forest Reserve	High	S15.13782, E24.48778	1152–1158
Dongwe	990.6	22.34	Community Forest	Medium	S14.09577, E24.01520	1066–1145
Kafue NP	897.4	21.98	National Park	Low	S14.89830, E25.43676	1091–1210

Sources: [35] for mean annual rainfall and temperature; [36] for land-use type; and [27] for soil type.

For each of the plots, we recorded the presence and identity of all angiosperms as herbaceous or woody species (as defined by Petruzzello [37], with the former being plants that do not have a true woody stem and may be either perennial or annual), estimated cover per species in percent, and counts of individuals per species (see Appendix A, Table A1 for all recorded species identified). Grass species had to be excluded from the analyses because at the time of sampling the majority of grasses did not have inflorescence, which compromised identification of the species. To assess the presence of exotic species and field weeds in the study area, we reviewed the literature sources in Zambia [38–41]. Indicators for land-use intensity, such as signs of recent woodcutting, grazing, and browsing, were recorded semi-quantitatively. The categories of woodcutting were 1–2 stumps per 1000 m^2-plot = 1, 3–5 stumps = 2, 6–8 stumps = 3, and >8 stumps = 4. Signs of browsing from game animals (domestic livestock were not observed in any of the study sites) were graded from 1 (no browsing) to 4 (high abundance of signs of browsing) depending on the frequency of signs of browsing observed. Grazing was not observed on any of the plots. The time from the last fire event on the plot was determined based on consultation with local field assistants as well as our own observations of the age of visible signs. We did not determine the cause of the fire. However, in areas where human activity is frequent, fires caused by human activity are more common than natural causes [42]. The determined time from the last fire was translated to the ordinal scale for the recent occurrence of fire: long ago = 2 (10 or more years since last fire), recent = 1 (5 years), and very recent = 0 (1 or 2 years).

One composite soil sample comprising five subsamples per plot was collected from the topsoil layer (0–10 cm). Soil samples were analysed at the Mt. Makulu Research Centre Soil Laboratory, Chilanga, Zambia for the variables of pH, nitrogen (N), phosphorus (P), organic carbon (Org C), calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), zinc (Zn), manganese (Mn), iron (Fe), and cation exchange capacity (CEC). For the soil analytical methods, see Appendix A, Table A2.

Within the plots, vegetation data were collected during the rainy seasons (March–May) of 2014 and 2015. The data obtained from the Zambia Meteorology Department (ZMD) indicated that the annual rainfall in these years was at 50–70% of the mean annual rainfall, which ranges between 875 and 990 mm for the study area (Table 1). Mean annual rainfall per site was available for the period from 1950 to 2010 from the Global Land Data Assimilation System site [35].

Plant species identification in the field was carried out using field guides [43–46] and later confirmed at the herbarium of the University of Zambia. Plant nomenclature followed Phiri [24] for the majority of the identifications; in cases of ambiguity, the Flora of Zambia [39], the JSTOR Global Plants database [47], and the Plant List [48] were used for verification. Voucher specimens were lodged at the Herbarium Hamburgense of the Universität Hamburg (HBG) and the herbarium of the University of Zambia (UZL).

2.3. Data Analysis

Species inventories were analysed for richness (S) and Shannon index per plot [49]. The sites differed in the degree of exposure to human activities (Table 1). We tested the semi-quantitative land-use variables (browsing, grazing, woodcutting, and time from last fire) for differences among the three land-use intensities by applying a Kruskal–Wallis test and then running a pairwise comparison of the land-use variables.

We tested the normal distribution of the diversity data. For the non-normally distributed Shannon diversity values, which are already on a log scale, we used the exponential of the Shannon, which is a common way to transform Shannon entropy into Shannon diversity values [50]. The diversity values were then expressed as the effective number of species. We applied one-way ANOVA to test for differences between the species richness values and the exponential of the Shannon under different land-use intensities followed by a Tukey HSD post hoc test.

We were interested in how well land-use intensity and soil chemistry can explain variation in richness and Shannon diversity of woody and herbaceous plants at the plot scale across the three study sites. We screened all soil variables visually for skewed distributions, which are common for these kinds of data. Of the twelve measured soil variables, we had to log-transform eight (P, Ca, Mg, K, Na, Zn, Mn, Fe). We tested the environmental variables for pairwise correlation to exclude multicollinearity, and only maintained the relevant variables of fire, woodcutting, browsing, soil pH, and above-mentioned eight soil variables. We employed generalised linear models (GLM) using the Poisson distribution, as the data were discrete and had a lower boundary (zero) for richness. A Gaussian distribution was used for the exponential of the Shannon diversity values. For the four response variables in the GLM (i.e., the richness and the diversity of woody and herbaceous species, respectively), we created a full model including soil and land-use variables as predictors. We used a heuristic approach that compared all 2100 possible models (not using interactions) and identified a final best model. All models were fitted using the R package *glmulti* [51]. Because we were using GLMs, we used a 'pseudo'-R^2 measure, which behaves like R^2 and measures the improvement of a fitted model compared to a null model calculated as the ratio [52]. Here, we used Cragg and Uhler's R^2 available from the R package *pscl* [53].

3. Results

3.1. Indicators for Land-Use Intensities at the Three Sites

We compared the indicator values for diffuse land-use intensity among the three sites. Table 2 shows that the two sites which were subject to diffuse anthropogenic disturbance, Dongwe National Forest and Luampa Community Forest, showed more frequent signs of woodcutting and shorter time from the last fire along with a lower frequency of signs of browsing compared to the Kafue site.

3.2. Diversity Patterns at the Different Land-Use Intensities

Due to our pre-classification of the sites into three different land-use types (Table 1) and the higher frequency of recorded signs of anthropogenic disturbances at the two sites under human land use (Luampa and Dongwe) compared with the National Park site (Kafue, Table 2), we expected strong differences between the diversity indicators in the sites. For all three sites, a cumulative total of 624 vascular plant species from 51 plant families was recorded. Of these species, 239 were woody and 385 were herbaceous. The mean species richness of the twenty plots (1000 m^2) per site for woody species was 27 (Luampa), 25 (Dongwe), and 27 (Kafue), while for herbaceous species it was 23 (Luampa), 21 (Dongwe), and 28 (Kafue) (Figure 2). In contrast to our expectations, species richness and Shannon diversity at the plot level only differed in terms of herbaceous species (Figure 2). Kafue had on average eight more herbaceous species per 1000 m^2 plot than the other two sites. The mean richness of woody species per plot was about 26 species, and the mean diversity was at about 13 effective species at all three sites. Very little research has been published on exotic and invasive plant species in woodland habitats [38–41]. Of the herbaceous species observed in the semi-disturbed sites of our study (Luampa and Dongwe), the following herbaceous species have been classified as weeds in the literature: *Crassocephalum rubens*, *Striga asiatica*, *Vernonia petersii*, and *Crotalaria* spp. *Dichrostachys cineria*, a species reported by Blaser-Hart et al. [40] to cause bush encroachment in Zambia, was observed in the woody vegetation of all the sites, though with low density.

Table 2. Pairwise comparisons using the Wilcoxon Rank Sum Test. Median values for the levels of the land-use variables. Figures in brackets = the range of the observed intensity of the respective land-use variables; hyperscripts indicate differences between sites at a significance level of $p < 0.05$.

Land-Use	Luampa (High Land-Use Intensity) [Median Values and (in Brackets) Min–Max Values]	Dongwe (Medium Land-Use Intensity) [Median Values and (in Brackets) Min–Max Values]	Kafue (No Land-Use) [Median Values and (in Brackets) Min–Max Values]
Woodcutting	1^{a} (0–3)	1^{a} (0–3)	0^{b} (0–1)
Browsing	0^{a} (0–1)	0^{a} (0–1)	1^{b} (0–2)
Time since last fire	0^{a} (0–2)	1^{a} (0–2)	2^{b} (1–2)

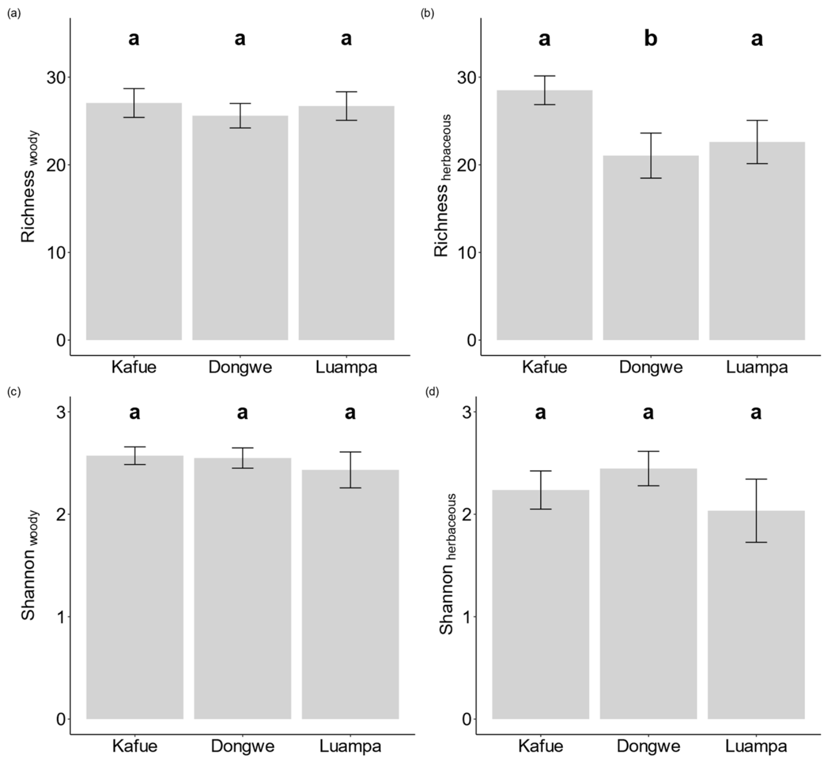

Figure 2. Bar plots of the diversity indices of the 1000 m^2 plots for species richness and Shannon index as follows (**a**) Richness for the woody species; (**b**) Richness for the herbaceous species; (**c**) Shannon index for the woody species and; (**d**) Shannon index for the herbaceous species. Different groups (based on Tukey's HSD test) are indicated by superscripts.

3.3. Environmental Drivers of Diversity at Plot Level

Although the recorded disturbance variables of woodcutting, browsing, and fire events differed between Kafue and the other two sites, their distribution varied within each of the sites as well (Table 2). We were therefore interested in the effects of the plot-based land-use intensities on the diversity measures per plot. We related the observed signs of disturbance per plot to the species richness and Shannon diversity of woody and herbaceous plant species for the respective plots. To discriminate between the disturbance effects and those of other abiotic habitat variables, we included plot-based soil variables in the analyses as well. For each of the four response variables (i.e., richness and diversity of woody and herbaceous species), we did not find any significant variation in richness or diversity of the woody component in response to any of the disturbance or soil variables (Table 3). We did, however, find a positive response of the species richness in the herbaceous layer to an increase in soil pH and to woodcutting at the plot level. The Shannon diversity of herbaceous species solely responded to organic carbon (positively) and iron (negatively). Overall, the models were rather weak, with low pseudo-R^2 values except for the richness of the herbaceous layer.

Table 3. Generalised linear models for species richness (S) and the exponential of the Shannon diversity (H′) of woody and herbaceous species after multi-model inference. The values for the logarithm of iron (logFe) and woodcutting are chi-square statistics, indicating an overall significant effect of the parameters. pR^2 is Cragg and Uhler's pseudo r-squared [51] measure based on the differences between best model and null model. SOC = soil organic carbon.

Diversity Model	Distribution and Link	n	Intercept	$_{log}$Mg	SOC	pH	$_{log}$Fe ‡	Wood Cutting ‡	pR^2
S_{woody}	Poisson (log)	60	3.275 ***						0.00
S_{herbs}	Poisson (log)	60	2.593 ***			0.151 **		9.432 *	0.36
H'_{woody}	Gaussian (id)	60	11.880 ***	0.935	−5.970				0.07
H'_{herbs}	Gaussian (id)	60	2.773 ***	2.506	−12.952 *		−2.141 *		0.18

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ ‡ Chi-square statistic.

4. Discussion

4.1. Effect of Land Use on Plant Species Diversity

Our study showed that the two sites under medium and high land-use-intensity, namely, Dongwe Forest Reserve and Luampa Community Forest, indeed had higher frequency of woodcutting and a shorter time from the last fire than Kafue (Table 2). Selective woodcutting in the Miombo woodlands in Zambia targets valuable timber species. The most harvested species according to the Forest Department are *Baikiaea plurijuga* and *Pterocarpus angolensis* [54], which are used for both domestic and commercial purposes. Selective harvesting of valuable timber species could lead to overharvesting and even local extinction, as has been shown by De Cauwer et al. [55] for *Pterocarpus angolensis* in Namibia. Therefore, we expected woodcutting for selective timber harvesting to have a negative effect on woody species richness and diversity. Even though intensity of woodcutting intensity differed between Kafue and the other two sites, woody species richness and diversity were not significantly different among the three sites. One possible reason for this might be that the observed woodcutting intensity at Dongwe Forest Reserve and Luampa Community Forest, with 0–3 tree stumps per 1000 m^2, while significantly higher than in Kafue (Table 2), was too low to have a measurable negative effect on the tested diversity measures. In previous studies, very moderate land-use intensity did not show any negative effect on species richness and abundance of woody species in the Miombo woodlands of Tanzania [56] and in the West African savannah of Burkina Faso [57], and even showed an increase in the tree species diversity of the Miombo woodlands in Angola [12]. It appears that in the present study the impact of land use on woody species diversity was below the threshold, in contrast to that observed in other studies [56,57]. This observation shows that the offtake of woody species through woodcutting and destruction by fire can be considered sustainable if the impact remains on a small spatial scale.

In contrast to the woody species richness and diversity, we found the richness of herbaceous species to be lower at Luampa and Dongwe than at the Kafue National Park site, suggesting a negative impact of land use on the herbaceous layer. Nacoulma et al. [57] compared the herbaceous species richness of sites under land use and in protected areas for savannah woodlands in Burkina Faso. They found that sites under higher land-use intensity to have lower herbaceous species richness, which they explained by the effect of higher grazing intensity in the unprotected area. Unsustainable grazing pressure from livestock reduces the number of palatable herbaceous species in woodlands [58]. The impact of grazing livestock (i.e., livestock that predominantly consume the herbaceous layer of the vegetation) on biodiversity has been addressed by previous studies on savannah ecosystems [59–61], showing that grazing may, depending on its intensity, have either a positive or negative effect on species richness. In our study, however, we did not find any signs of grazing in either Kafue, where one might expect game to graze, or at either of the other two sites, where grazing domestic cattle could be expected. The observed absence of grazing signs at the Miombo woodland site in Kafue supports reports that the grazers of the national park prefer the open grasslands (called *dambos*) [62]. Similarly, at Luampa and Dongwe, where grazing is also absent, the livestock farmers prefer to graze their cattle in the open grasslands (*dambos*), where the quality of forage is better.

Although we did not find any signs of grazing (consumption of the vegetation of the herbaceous layer), we did find signs of browsing (consumption of the leaves on twigs and branches of shrubs and trees), which was significantly less at the two sites under land use (Luampa and Dongwe) than at Kafue. At Luampa and Dongwe, browsing livestock such as goats have been restricted to areas close to land users' homesteads, and are kept away from the distant woodlands, according to personal communication with local farmers. At Kafue, we found signs of browsing, even though no presence or signs of large mammals were observed. The browsing signs could be attributed to the presence of insects known to browse on woody species [62]. However, increased density of browsing insect species in the woodlands of Kafue National Park is unlikely to have a negative effect on the woody component of the vegetation. This means that the low density of woody species at the Kafue site cannot be explained by grazing. Reduced woody cover facilitates the abundance of herbaceous species by reducing the competition with woody components for resources such as light, water, and nutrients [30].

Field weeds and invasive species such as *Crassocephalum rubens*, *Striga asiatica*, *Vernonia petersii*, and *Crotalaria* spp. were recorded only occasionally or even rarely in the plots of the semi-disturbed study sites. *Dichrostachys cineria* was only rarely observed at all three sites. Owing to the very limited information available in the literature on exotic and invasive plant species in the woodlands of Zambia, very few species in our study were identified as exotic or invasive, and these had very low densities. Therefore, our data suggest that the influence of synanthropic plants on the diversity patterns is likely to be low.

4.2. Drivers of Diversity at Plot Level

The range of land-use variables per site (Table 2) revealed within-site variability of land-use effects within the three study sites. Therefore, we tested for the effect of land-use intensity on species richness and diversity per plot. Because soil characteristics show interplay with biotic drivers and drive vascular plant diversity in the Miombo woodlands [25], we tested the effect of both land-use indicators and soil variables on diversity and richness at plot level irrespective of the land-use type they were exposed to. Land-use (woodcutting) and soil variables (soil pH) showed effects on the diversity patterns of herbaceous species, whereas woody species diversity and richness were not affected. The absence of land-use effects on woody species diversity and richness is in contrast to other studies showing that selective harvesting of valuable timber species can lead to local extinction [55]. The patchy nature of diffuse disturbance of woodlands referred to by Asefa et al. [63] is defined by the absence of settlements and crop cultivation as well as relatively low-level logging and grazing, and had positive effects on woody species richness in Ethiopia. In turn, we found the herbaceous species richness to increase with woodcutting. As discussed earlier, this positive effect might have been a result of better light conditions for the herbaceous species coupled with reduced competition for space, water, and nutrient resources [4,30]. Reduction of competition for resources in combination with the release of organic nutrients through decaying tree stumps have previously been shown to increase herbaceous biomass in the Miombo woodlands [64]. At the site level, Kafue had the highest herbaceous species richness as well as the highest density in terms of signs of browsing (Table 2). Browsing, as discussed earlier, may already have a positive effect on herbaceous species and species diversity. Our study showed a positive effect of diffuse disturbance caused by woodcutting (plot level) and browsing (site level in Kafue) on herbaceous species richness and diversity.

We further found a positive relationship between richness of herbaceous species and an increase in soil pH at the plot level. Soils in humid subtropical regions are typically acidic [65]. In our study area, the dominant soil type (Arenosols) is leached under high rainfall conditions, resulting in low pH [66], with soil pH ranging from 3.7 to 5.4 (Appendix A, Table A3). Acidity in soils slows down the rate of decomposition of soil organic material, and thereby reduces the availability of nutrients for plant uptake [67]. Thus, highly acidic soils may provide a low nutrient supply, which limits the range of plant species that can cope with these conditions [68]. Therefore, very low soil pH has previously been found to be negatively associated with species diversity of herbaceous species in the Miombo woodlands [2,69,70] and the tropical montane forests of Cameroon [71].

We further found SOC at the plot level to be negatively associated with the Shannon diversity of herbaceous species. Generally, SOC content increases with precipitation and with optimal levels in humid and cold climates and decreases with soil pH; beyond that, SOC storage links to biophysical factors and management practices [72]. A study in Ghana by Quaye et al. [73] revealed unsuitably low SOC in strongly acidic soils in the western African Savannah woodlands. In the Miombo Woodlands of our study area, which are Savannah woodlands, low soil pH might have negatively affected SOC as well. The SOC appeared to be negatively related to the biodiversity of herbaceous species, which could be because herbaceous species have a lower root network than woody species [30].

At the plot level, our study showed that both land use (woodcutting) and soil acidity were drivers of the diversity of herbaceous species, whereas woody species were unaffected. The absence of variance in the richness and diversity of woody species, however, does not exclude the fact that there are differences in other vegetation characteristics, such as species composition. Variances in small-scale species composition in response to fire and herbivory have previously been shown in the Miombo woodlands of Zimbabwe [74]. We expect similar effects in our study area, which we will analyse in a subsequent study.

5. Conclusions

This study revealed that diffuse land use has no influence on woody species richness and diversity in the Miombo woodlands in our study area. The absence of such effects on woody species richness and diversity was consistent across all three of our sites. However, the study showed influence of both diffuse land use and soil acidity on herbaceous species richness at the plot level. Among the land-use parameters, woodcutting (at plot level) and browsing (at site level) showed positive effects on herbaceous species richness; both of these result in opening up of the tree canopy, providing water, nutrients, and sunlight for herbaceous species. Other land-use effects, such as fire and grazing, which have been shown in other studies to influence patterns of richness and diversity of vascular plant species in the region, were not found in our study. We assume that the intensities of these disturbances at all three sites and plots were too low to show any effects.

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Appendix A

Table A1. List of woody and herbaceous plant species with their life form, collection number, and location, arranged according to family: Abundance was assigned according to the frequency of observations of each woody plant species: rare (1 or 2 recordings), occasional (3–5 recordings), frequent (6–10 recordings), and common (>11 recordings). The locations where these species occurred in the study sites are abbreviated as D = Dongwe, K = Kafue National Park, and L = Luampa. The different uses were coded as TI = timber production, PO = posts, pole, and roundwood, WO = fuelwood and charcoal, PU = pulp and paper production, FD = fodder, FO = food, NW = other non-wood products (gums, medicines, dyes, tanning, etc.), AE = aesthetic and ethical values, and TX = toxic to livestock.

Species Name	Life Form	Abundance	Uses	Voucher Number	Location
Acanthaceae					
Duosperma quadrangulare (Klotzsch) Brummitt	Herbaceous	rare	FO	138076	K
Hypoestes forskaolii (Vahl) R.Br.	Herbaceous		TX	132148	K
Amaryllidaceae		rare			
Crinum macowanii Baker	Herbaceous	rare	NW	132141	L, K
Anacardiaceae					
Searsia quartiniana (A. Rich.) A.J. Mill.	Woody	Frequent	FO	131071, 142196	L, D
Sclerocarya birrea (A.Rich.) Hochst.	Woody	rare	FO	132128	K
Annonaceae					
Friesodielsia obovata (Benth.) Verdc.	Woody	occasional	FO, FD	142610	K
Uvariastrum hexaloboides (R.E.Fr.)	Woody	occasional	FO	132107	L, K
Xylopia odoratissima Welw. ex Oiv.	Woody	common	NW	131181	L, D
Apocynaceae					
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	Woody	common	NW	140121	D, L, K
Landolphia parvifolia K. Schum.	Woody	frequent	FO	142505	D, L
Strophanthus welwitschii (Baill.) K. Schum.	Woody	occasional		142649	D

Table A1. *Cont.*

Species Name	Life Form	Abundance	Uses	Voucher Number	Location
Asparagaceae					
Asparagus racemosus Willd.	Herbaceous	occasional		142788	K
Asphodelaceae					
Bulbine abyssinica A.Rich.	Herbaceous	rare	NW	131355, 132214	D, K
Asteraceae					
Conyza gouanii (L.) Willd.	Herbaceous	occasional	NW	132207	K
Crassocephalum rubens (Jacq.) S. Moore	Herbaceous	rare	NW	131301	D
Dicoma anomala Sond.	Herbaceous	occasional		138099	K
Elephantopus scaber L.	Herbaceous	frequent		131119	D, L, K
Erythrocephalum zambesianum Oliv. & Hiern	Herbaceous	frequent	NW	142503	L, K
Felicia welwitschii (Hiern) Grau	Herbaceous	rare		142698	D
Macledium poggei (O.Hoffm.) S.Ortiz	Herbaceous	rare		142660	K
Pleiotaxis eximia O. Hoffm. *Vernonia glabra* ssp. laxa (Seetz) Vatke	Herbaceous	occasional	NW	142665	L, K L, K
Vernonia melleri Oliv. & Hiern	Herbaceous	occasional		131401	L
Vernonia petersii Oliv. & Hiern ex Oliv.	Herbaceous	frequent	FD	142678	D, K
Vernonia poskeana Vatke & Hildebr.	Herbaceous	rare		131157	L
Capparaceae					
Capparis tomentosa Lam.	Herbaceous	frequent	NW, FO, AE	138093	K
Cleome hirta (Klotzsch) Oliv.	Herbaceous	frequent		138076	K
Maerua triphylla ssp. *pubescens* A. Rich. (Klotzsch) DeWolf	Herbaceous	frequent		131358	K
Chrysobalanaceae					
Parinari capensis Harv.	Woody	frequent	NW, FO		L
Parinari curatellifolia Planch. ex Benth.	Woody	frequent	NW, FO, WO	131213	L, K
Combretaceae					
Combretum collinum Fresen.	Woody	occasional	NW, TI	131113	D, L, K
Combretum elaeagnoides Klotzsch	Woody	occasional		131403	D, L
Combretum molle R.Br. ex G.Don	Woody	frequent	NW, TI	142578	D, L, K
Combretum psidioides Welw.	Woody	occasional	NW	131402	D
Combretum zeyheri Sond.	Woody	common	NW, WO	131183	L, K
Pteleopsis anisoptera (Welw. ex M.A.Lawson) Engl. & Diels	Woody	occasional	NW, TI, WO	1320102	D
Terminalia brachystemma Welw. ex Hiern	Woody	occasional	NW, FO, WO	131165	L, K
Commelinaceae					
Cyanotis longifolia Benth.	Herbaceous	frequent		131016	D, L, K
Dipterocarpaceae					
Marquesia macroura Gilg	Woody	occasional		140121	K
Gilg	Woody	occasional		132222	K
Monotes glaber Sprague	Woody	occasional	NW, WO	142639, 141189	L
Ebenaceae					
Diospyros batocana Hiern	Woody	common	NW, FO, PU	140159	D, L, K
Diospyros mespiliformis Hochst. ex A.DC.	Woody	frequent	NW, FO		K
Diospyros virgata (Gürke) Brenan	Woody	common	NW	131054, 131191, 140143	D, L, K
Ericaceae					
Cleistanthus polystachyus Hook. f. ex Planch.	Herbaceous	rare		132122	L
Erythroxylaceae					
Erythroxylum emarginatum Thonn.	Woody	occasional		142649	K

Table A1. *Cont.*

Species Name	Life Form	Abundance	Uses	Voucher Number	Location
Euphorbiaceae					
Acalypha ornata Hochst. ex A. Rich.	Herbaceous	occasional		132101	L
Flueggea virosa (Roxb. ex Willd.) Voigt	Woody	occasional	NW, FO	142566	L, K
Hymenocardia acida Tul.	Woody	common	NW	142526	D, L, K
Maprounea africana Müll.Arg.	Woody	frequent	NW		L
Oldfieldia dactylophylla (Welw. ex Oliv.) Léonard	Woody	frequent		142693	D
Pseudolachnostylis maprouneifolia Pax	Woody	common	NW, FO	140131, 131047	D, L, K
Sclerocroton oblongifolius (Müll. Arg.) Kruijt & Roebers	Herbaceous	rare	NW	131056, 142172, 135679	L, K
Uapaca kirkiana Müll. Arg.	Woody	occasional	NW, FO	142817	D, K
Uapaca nitida ssp. *nitida*	Woody	occasional	NW, FO		L, K
Fabaceae					
Afzelia quanzensis Welw.	Woody	frequent	NW, FO TI, WO	131163	L, K
Albizia antunesiana Harms	Woody	frequent	NW, WO	142766	D, L, K
Albizia versicolor Welw. ex Oliv.	Woody	common	NW, WO	132156	D, K
Anisophyllea boehmii Engl.	Woody	occasional	NW, FO	132216	K
Baphia massaiensis var. obovata Taub.	Woody	common	NW, FO, FD	131007	D, L, K
Bauhinia petersiana Bolle	Woody	frequent	NW, FO, FD	142520	D, L, K
Bobgunnia madagascariensis (Desv.) J.H.Kirkbr. & Wiersema	Woody	common	NW, FO, TI	131191	L, K
Brachystegia boehmii Taub.	Woody	common	TI, WO, PO, NW		D, L, K
Brachystegia spiciformis Benth.	Woody	common	TI, WO, PO, NW	131146	D, L, K
Burkea africana Hook.	Woody	common	WO, PO, NW		D, L, K
Cassia abbreviata Oliv.	Woody	occasional	NW	142622	K
Chamaecrista mimosoides (L.) Greene	Herbaceous	occasional	NW	131025, 142559	D, K
Copaifera baumiana Harms	Woody	common	NW	131085	L, K
Crotalaria alexandri Baker f.	Herbaceous	occasional		142576	L, D
Crotalaria anisophylla (Hiern) Welw. ex Baker f.	Herbaceous	occasional		142774	L
Crotalaria caudata Welw. ex Baker	Herbaceous	occasional		131176	D, L
Crotalaria cephalotes Steud. ex A.Rich.	Herbaceous	occasional	NW	132180	K
Crotalaria laburnifolia L.	Herbaceous	common		142570	D
Crotalaria microcarpa Hochst. ex Benth.	Herbaceous	rare		131099	D, L
Cryptosepalum exfoliatum ssp. *pseudotaxus* De Wild.	Woody	common	TI, NW, PO,	142504	D
Dichrostachys cinerea (L.) Wight & Arn.	Woody	common	NW, WO		D, L, K
Erythrophleum africanum	Woody	common	WO, PO, NW	131124	D, L, K
Guibourtia coleosperma (Benth.) J.Leonard	Woody	common	TI, NW,	140151	D, L
Indigofera demissa Taub.	Herbaceous	occasional		131174	D, L
Indigofera flavicans Baker	Herbaceous	common		131130	L, K

Table A1. *Cont.*

Species Name	Life Form	Abundance	Uses	Voucher Number	Location
Isoberlinia angolensis (Benth.) Hoyle & Brenan	Woody	occasional	TI, NW, AE		K
Julbernardia paniculata (Benth.) Troupin	Woody	common	TI, WO, PO, NW, FD	140155	D, L, K
Keetia venosa (Oliv.) Bridson	Woody	occasional		142561	K
Lannea edulis (Sond.) Engl.	Woody	frequent	NW	131178	L, K
Mucuna poggei Taub.	Woody	occasional	NW	142564	K
Pericopsis angolensis (Baker) Meeuwen	Woody	occasional	TI, WO, NW, FD	138072	L, K
Piliostigma thonningii (Schumach.) Milne-Redh.	Woody	occasional			K
Pterocarpus angolensis DC.	Woody	common	TI, WO, NW		D, L, K
Rhynchosia caribaea (Jacq.) DC.	Woody	occasional	NW	131195	L, K
Flacourtiaceae					
Flacourtia indica (Burm.f.) Merr.	Woody	frequent	NW, FO	131198	K
Hypericaceae					
Psorospermum baumii Engl.	Woody	occasional	NW, FO	131162	D
Lamiaceae					
Ocimum africanum Lour.	Herbaceous	rare			K
Tinnea vestita Baker	Herbaceous	occasional	NW, FO	131021, 142739	L, K
Vitex doniana Sweet	Woody	occasional	TI, FO, NW, FD	140154	L
Vitex madiensis Oliv. subsp. *milanjiensis* (Britten) F. White	Woody	rare		142638	L
Lauraceae					
Cassytha pondoensis ssp. Pondoensis Engl.	Woody	occasional	NW	131134	D, L
Malvaceae					
Abutilon angulatum (Guill. & Perr.) Mast.	Woody	occasional	NW	142504	D
Pavonia senegalensis (Cav.) Leistner	Woody	rare		131268	D, L
Meliaceae					
Bersama abyssinica Fresen.	Woody	rare	NW, AE	142874	K
Trichilia emetica Vahl	Woody	rare	NW, AE		K
Myrtaceae					
Syzygium guineense (Willd.) DC.	Woody	occasional	NW, FO	142200	L
Ochna pulchra Hook.	Woody	common	NW	131059	D, L, K
Olacaceae					
Olax obtusifolia De Wild.	Woody	occasional		142598	L
Ximenia americana L.	Woody	frequent	NW, FO	142523	L, K
Ximenia caffra Sond.	Woody	frequent	NW, FO	131047	K
Oleaceae					
Olea capensis L.	Woody	occasional		138065	K
Schrebera trichoclada Welw.	Woody	rare		144524	L, K
Orobanchaceae					
Striga asiatica (L.) Kuntze	Herbaceous	occasional	NW	138077	L, D
Oxalidaceae					
Biophytum abyssinicum Steud. Ex A. Rich.	Herbaceous	occasional	NW		D
Biophytum umbraculum Welw.	Herbaceous	occasional		131098	D, L
Passifloraceae					
Paropsia brazzeana Baill.	Woody	frequent	NW	131080	D, L, K
Polygalaceae					
Securidaca longepedunculata Fresen.	Woody	occasional	NW	131204	L

Table A1. *Cont.*

Species Name	Life Form	Abundance	Uses	Voucher Number	Location
Proteaceae					
Protea angolensis Welw.	Woody	rare	NW	142795	K
Protea gaguedi J.F. Gmel.	Woody	frequent	NW		K
Ranunculaceae					
Clematis chrysocarpa Welw. ex Oliv.	Herbaceous	occasional		131351, 142755, 142609	L, K
Rhamnaceae					
Ziziphus mucronata Willd.	Woody	occasional	FO, NW		K
Rubiaceae					
Agathisanthemum bojeri Klotzsch	Woody	occasional	NW	142781	L, K
Fadogia cienkowskii Schweinf.	Woody	occasional		142191	L
Gardenia ternifolia Schumach. & Thonn.	Woody	occasional	NW, FO	132132	D
Pavetta schumanniana F. Hoffm ex K. Schum	Woody	frequent		142749	D, K
Rothmannia engleriana (K.Schum.) Keay	Woody	frequent	NW	131196	D, L
Spermacoce pusilla Wall.	Woody	occasional		131100	D, L
Tricalysia longituba De Wild.	Woody	occasional		131255	L, K
Vangueriopsis lanciflora (Hiern) Robyns	Woody	frequent	NW, WO	131180	D, L
Sapindaceae					
Zanha africana (Radlk.) Exell	Woody	occasional	WO	142751	K
Sapotaceae					
Englerophytum magalismontanum (Sond.) T.D.Penn.	Herbaceous	occasional	NW	131079	D, L
Solanaceae					
Solanum mauritianum Scop.	Herbaceous	occasional			K
Strychnaceae					
Strychnos cocculoides Baker	Woody	frequent	NW, FO, AE, PO	131083	D, L, K
Strychnos pungens Soler.	Woody	frequent	NW, FO	140149	D, L, K
Thelypteridaceae					
Christella chaseana (Schelpe) Holttum	Herbaceous	occasional			D
Tiliaceae					
Grewia flavescens Juss.	Herbaceous	occasional	NW, FO	131013	D, L, K
Triumfetta annua L.	Herbaceous	occasional		131109	L, K
Verbenaceae					
Endostemon obtusifolius (E. Mey. ex Benth.) N.E.Br.	Herbaceous	occasional			D, L
Lantana angolensis Moldenke	Herbaceous	occasional	NW, FO, FD	142644	L, K
Vitaceae					
Cyphostemma junceum Wild & R.B. Drumm.	Herbaceous	frequent	NW, FO	132169	D
Cyphostemma princeae Wild & R.B. Drumm	Herbaceous	frequent	NW, FO	131382	D, L, K
Zingiberaceae		occasional			
Aframomum alboviolaceum (Ridl.) K.Schum.	Herbaceous		NW, FO		D

Table A2. Methods of soil sample analysis.

Analysis Variable	Method and Reference	Unit
pH	using the $CaCl_2$ mixture in H_2O [75]	
Nitrogen (N)	Kjeldahl method [76]	percentage per total weight
Phosphorus (P)	Bray I extractant [77]	parts per million
Organic Carbon (Org C)	Walkley Black technique [78]	percentage per total weight
Calcium (Ca)	Ammonia acetate extraction [79]	parts per million
Magnesium (Mg)	Ammonia acetate extraction [79]	parts per million
Sodium (Na)	Ammonia acetate extraction [79]	parts per million
Potassium (K)	Ammonia acetate extraction [79]	parts per million
Zinc (Zn)	DPTA method [80]	parts per million
Manganese (Mn)	DPTA method [80]	parts per million
Iron (Fe)	DPTA method [80]	parts per million
Cation Electronic Exchange (CEC)	Conductivity method [81]	Milli-equivalents

Table A3. Soil variables from the observatory samples analysis.

Variables	Mean and Covariance	Luampa	Dongwe	Kafue National Park
pH	$\bar{x}$	4.4	3.9	4.9
	CV	0.04	0.07	0.08
N	$\bar{x}$	0.016	0.011	0.018
	CV	0.5	0.64	0.66
P	$\bar{x}$	5.0381	3.01	7.73
	CV	0.42	0.39	0.83
Org C	$\bar{x}$	0.25	0.21	0.26
	CV	0.43	0.37	0.5
Ca	$\bar{x}$	40	32	120
	CV	0.71	1.61	0.49
Mg	$\bar{x}$	10.23	11	24.31
	CV	0.58	0.14	0.57
Na	$\bar{x}$	2.23	3.75	6.53
	CV	1.49	0.64	0.65
K	$\bar{x}$	10.91	10.35	42.05
	CV	1.28	1.14	0.48
Zn	$\bar{x}$	0.27	0.05	0.15
	CV	2.19	1.43	1.4
Mn	$\bar{x}$	14.42	12.1	82.05
	CV	1.15	2.6	0.58
Fe	$\bar{x}$	11.23	11.95	28.47
	CV	0.49	0.84	0.51
CEC	$\bar{x}$	3.45	2.4	3.83
	CV	0.35	0.58	0.32

Soil variables with $\bar{x}$ for mean values and CV for covariance.

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