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Floristic Diversity and Natural Regeneration of *Miombo* Woodlands in the Rural Area of Lubumbashi, D.R. Congo

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Abstract: Increased anthropogenic pressure on forest resources leads to deforestation and forest degradation, significantly limiting the regeneration capacity of native woody species and consequently the restoration of *miombo* woodlands in anthropized habitats within the rural area of Lubumbashi. This study assessed miombo species' diversity and natural regeneration capacity through floristic inventories in three different habitats (unexploited forests, degraded forests, and post-cultivation fallows). The results reveal that for the adult stratum, unexploited and degraded forests exhibit higher dendrometric (density, mean square diameter, basal area) and floristic parameter (taxa, genera, families) values compared to post-cultivation fallows. Furthermore, the regeneration of *miombo* woody species is higher in degraded forests (21 taxa; 105 juveniles/plot). However, regarding the sapling's stratum (1 cm $\leq$ dbh < 10 cm), the three habitats display similar situations. Additionally, the floristic composition and diversity of unexploited and degraded forests show a significantly higher similarity (76.50%) among them compared to these habitats and the post-cultivation fallows (56.00%). These findings indicate that *miombo* woodlands have the potential to regenerate and maintain floristic diversity even in anthropized habitats, particularly in degraded forests. To sustain this natural regeneration capacity of *miombo* woody species and promote the restoration of forest cover and its floristic diversity, it is imperative to determine the rotation period after habitat exploitation and regulate anthropogenic activities and late bush fires, particularly in anthropized habitats at the village level.

Keywords: anthropogenic pressure; deforestation; forest degradation; woody species diversity; natural regeneration; *miombo* woodlands

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1. Introduction

Forests constitute one of the most crucial terrestrial biomes on the planet, harboring 80% of terrestrial biodiversity [1,2] across approximately 4.06 billion hectares [3]. In Africa, forests cover 23% of the continent, totaling 675 million hectares [4], with nearly 10% of this area dominated by *miombo* woodlands [5,6]. *Miombo* woodlands are predominantly composed of woody species from the genera *Brachystegia*, *Julbernardia*, and *Isoberlinia* [7]. These woodlands span about 2.8 million km^2 in the Zambezi region [8], supporting the livelihoods of over 100 million rural and urban residents through the ecosystem services they provide [6,9]. Moreover, *miombo* woodlands boast significant biodiversity with high endemism rates, making them a conservation priority [10,11].

However, *miombo* woodlands are experiencing a reduction in area due to natural and particularly anthropogenic factors [12]. The combination of population growth and a deleterious socio-economic and political context, which forces local populations to heavily rely on forest resources for survival [13], leads to deforestation and degradation [14,15]. Furthermore, inadequate and poorly enforced forestry legislation [16] results in unsustainable exploitation of forest resources, exacerbating deforestation and degradation [17].

The direct anthropogenic drivers of this change are primarily agriculture and charcoal production [15,18], both of which are itinerant [19]. Additional factors include the extraction of timber and craft wood, fuelwood, and late and repeated bushfires, all of which contribute to forest loss [20,21]. Consequently, the annual conversion rate of *miombo* woodlands ranges from 2% to 22% within the *miombo* ecoregion [21], with significantly higher rates in countries with intense anthropogenic pressure due to population poverty, such as the Democratic Republic of Congo (D.R. Congo). Despite its high forest potential, the D.R. Congo has the highest annual deforestation rate in the Congo Basin: approximately −0.4% between 2001 and 2019 [22]. Furthermore, in the southeastern D.R. Congo, where *miombo* woodlands are the dominant vegetation unit [23], its coverage dropped from nearly 70% to 43% between 2000 and 2010 [24]. In this region, the *miombo* deforestation rate is even higher in rural areas adjacent to major cities, such as the rural area of Lubumbashi, which has a deforestation rate of 1.51% [15]. This situation contributes to environmental degradation and threatens the livelihoods of rural and urban populations dependent on *miombo* woodlands [2,9].

To address this deforestation and forest degradation, forest cover restoration is one of the recommended solutions [5,25–27]. Restoration involves adaptive processes that implement practices to restore ecological functionality and enhance human survival in deforested or degraded habitats [27]. This can be achieved through reforestation using fast-growing exotic woody species, which allows for the short-term reconstitution of vegetation cover and the availability of ecosystem services [19]. However, these exotic species pose a threat to native biodiversity and alter the original forest functions [28,29]. Therefore, using native woody species remains a viable alternative, ensuring the continuity of ecosystem service production by maintaining floristic composition, structure, and function [1]. This restoration typically involves nursery seedling production or facilitating natural regeneration in habitats. However, combined with logistical complexity management, nursery and the final establishment of seedlings in human-disturbed habitats can be costly, reducing its applicability [5]. In this perspective, promoting natural regeneration is a sustainable and optimal alternative to current forest loss [25]. Natural regeneration allows adult individuals in a plant community to replace themselves by establishing juveniles in the undergrowth (dbh < 10 cm) [30]. This regeneration, which ensures the persistence of woody species [31], is dependent on the disturbance gradient of habitats and the resilience of woody species to these disturbances [14].

Furthermore, several studies on the natural regeneration of forests in anthropized habitats have already been conducted in the *Miombo* ecoregion [2,6,14,21,32–35]. However, these studies have predominantly focused on Southern Africa, while no research on natural regeneration has been initiated in the *miombo* woodlands of Central Africa, whose ecological and floristic characteristics increasingly differ from those of Southern African *miombo* [23]. Additionally, no study has been conducted to analyze the natural regeneration of *miombo* woodlands through forest inventory. This inventory technique remains reliable for assessing the capacity of woody species to regenerate and consequently restore forest cover [31,36]. Moreover, results on the natural regeneration capacity of woody species are valuable for forest management, sustainable biodiversity management [20], and implementing responses to human disturbances to ensure *miombo* woodlands' resilience [14].

In this context, the present study was initiated to evaluate the natural regeneration capacity of *miombo* woody species in the rural area of Lubumbashi. It tests the hypothesis that (i) the density, average diameter, basal area, and floristic diversity differ among habitats due to anthropogenic disturbances. Higher values are expected in unexploited forests and lower values in post-cultivation fallows, with degraded forests in between. (ii) The regeneration capacity of *miombo* species is higher in degraded forests than in unexploited forests and post-cultivation fallows, due to the availability of resources (water, light, space) and lower intra/inter-specific competition and disturbances. (iii) The floristic diversity of strata and habitats shows similarities. Higher similarities in floristic composition are expected between strata of unexploited and degraded forests compared to post-cultivation fallows, due to lower disturbances in these habitats.

2. Materials and Methods

2.1. Study Area

The present study was conducted in the rural area of Lubumbashi, located in south-eastern D.R. Congo (Figure 1).

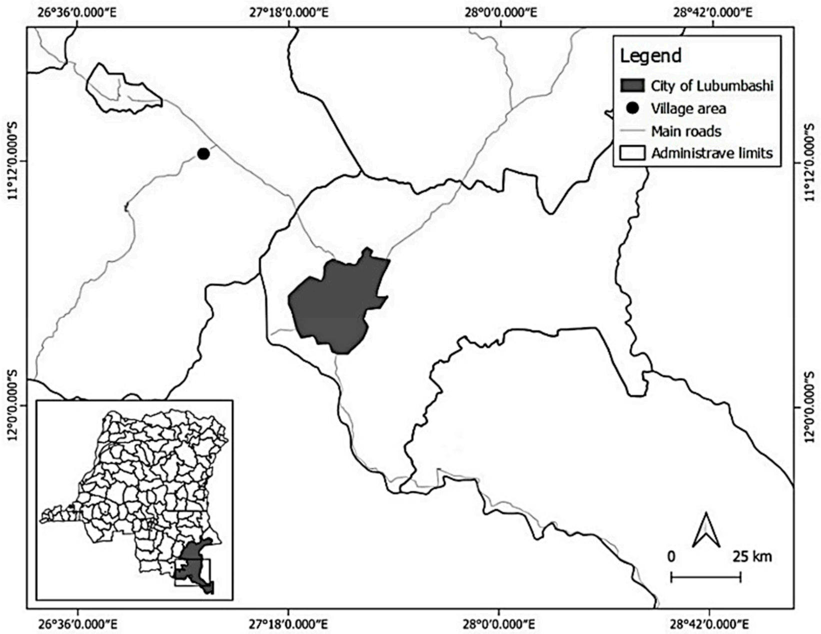

Figure 1. City of Lubumbashi (gray polygon) and its rural area (white space surrounding Lubumbashi). The black dot indicates the village area of Lwisha, located approximately 80 km northwest of Lubumbashi. The geographical coordinates used for this mapping were obtained using a GPS device within the premises of the Lwisha village chief's office. The administrative boundaries on this map mark the borders between the DRC and Zambia, as well as between Kipushi Territory and other territories in Upper-Katanga Province.

Situated at an altitude ranging from 1200 to 1300 m, Lubumbashi and its rural surroundings have a Cw-type climate, characterized by a rainy season (November–March) and a dry season (May–September), separated by two transitional months (April and October) [37]. While the average annual temperatures in the latter half of the 20th century ranged between 17 and 26 °C [7], recent observations indicate a warming trend [38]. Annual total precipitation varies between 1200 and 1300 mm [23]. Typically established on ferralitic soils [39], the *miombo* woodland is the dominant vegetation unit, although its cover is constantly declining primarily due to shifting agriculture, charcoal production, and increasing urbanization [12,15,18]. The population in the Lubumbashi region remains heavily dependent on natural resources, which are increasingly depleted by shifting agriculture and charcoal production (97.9% of the population), art wood carving (1.5%), artisanal timber exploitation (0.4%), and non-timber forest product collection (0.2%) [40]. Moreover, this population predominantly lives on less than USD 1.25 per day, indicating a high level of poverty and food insecurity [41].

Additionally, the village area of Lwisha, located approximately 80 km northwest of Lubumbashi, was selected as the study site. This village area was chosen due to its identification as a site with high anthropogenic activities, particularly agriculture, charcoal production, and mining [40,42]. Furthermore, the selection was guided by the availability of both unexploited and anthropized forest habitats, specifically those affected by charcoal production (degraded forests) and agriculture (post-cultivation fallows). Moreover, the village demonstrates weak implementation of the existing simple forest management plan, contributing to deforestation and forest degradation.

2.2. Methods

2.2.1. Sampling and Data Collection

To study the composition and floral diversity, three habitat types were chosen: unexploited forests (UFO), degraded forests (DFO), and post-cultivation fallows (PCF). These habitats are illustrated and described in the table below (Table 1).

Table 1. Presentation and description of the three surveyed habitats in Lwisha area.

Habitat	Description
Unexploited forests 	These forests are not exploited for charcoal production or cultivated at a human scale [6]. These refer to the land characterized by vegetation dominated by a sparse herbaceous layer under a 10–20 m forest stratum. The canopy covers 0.05 and covers at least 10–30% of the area, spanning between 0.05 and 1 hectare [15].
Degraded forests 	These forests have been exploited for charcoal production [43] and correspond to forests where the capacity to provide ecosystem services has been significantly reduced due to decreased woody plant density and biodiversity.
Post-cultivation follows 	Fallows are habitats that are abandoned after subsistence farming. This refers to habitats that have been severely damaged by excessive land use, degrading soil and vegetation, and delaying woody plant diversity recovery. Vegetation is primarily dominated by grasses [44].

For comparison purposes, the degraded forests and post-cultivation fallows were 4 to 5 years post-exploitation, corresponding to the optimal fallow period in the Lubumbashi region [45]. These anthropized habitats were selected based on a visual analysis of high-resolution Quick Bird images available for free on Google Earth [46]. In each habitat, four transects, each 500 m long, were established along the four cardinal points (north, south, east, and west) of the village. On each transect, four floristic inventory plots measuring 50 m × 20 m, spaced 100 m apart, were set up [6]. This method significantly reduces alignment, angle, and width measurement errors that often occur during the setup of continuous plots. Additionally, it saves time and enhances data reliability, result consistency, and reproducibility [47]. Furthermore, to assess the regeneration of *miombo* woody species and thus the restoration of this forest ecosystem in anthropized habitats, 80 subplots of 10 m × 5 m each were installed in each habitat [14]. This represents 20 subplots per transect and 5 subplots per inventory plot (Figure 2). The dimensions of the plots and subplots were determined based on previous studies ([6,14] indicating that 50 m × 20 m and

10 m × 5 m are adequate dimensions for floristic and forest regeneration studies in the *miombo* woodlands, respectively).

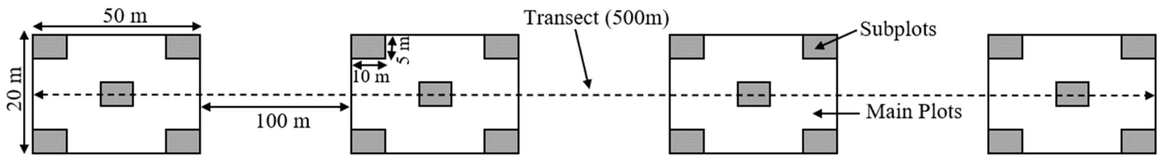

Figure 2. Graphical representation of the floristic inventory plan showing main plots and subplots along a 500 m transect [6].

Furthermore, in each plot, all woody individuals with a diameter at breast height (dbh) ≥ 10 cm were inventoried. The diameter of these individuals was measured using forestry tape [31]. Additionally, in these subplots, juvenile individuals (dbh < 10 cm) were inventoried, and their diameters were measured. The inventory considered three groups: seedlings (dbh < 1 cm), saplings (1 cm ≤ dbh < 10 cm), and adults (dbh ≥ 10 cm) [48]. The first two strata consist of juvenile individuals (regeneration individuals) while the last stratum represents the adult population. It should be noted that seedlings were only counted. Moreover, juveniles from coppicing were not included in the inventory. The floristic inventories for this study were conducted from 25 March to 29 June 2023. During the inventories, the identification of unknown woody species was facilitated by comparing the collected herbarium specimens with existing floras (Flora of Zambia, Flora of Zimbabwe, and World Flora), specialized books, and various identification guides [7,49,50].

2.2.2. Data Analysis

The detailed analyses in this section focused on individuals inventoried in the three strata. However, the mean square diameter and basal area were not calculated for seedlings, as their diameters were not measured during the floristic inventory. Additionally, relative frequency and density, the natural regeneration index, and alpha diversity were only applied to the regeneration strata. To ensure homogeneity among plots of different ages within each habitat, the variability in terms of density and floristic diversity was tested at a 5% significance level [51]. Thus, data collected on regeneration (dbh < 10 cm) in the subplots were extrapolated to the plot level, considering the ratio between the plot area (50 m × 20 m) and the cumulative area of the subplots within each plot (5 × (10 m × 5 m)).

Furthermore, to characterize the three habitats, the density of individuals (N; Equation (1)), quadratic mean diameter (DBH_m; Equation (2)), and basal area of individuals (GBA; Equation (3)) of the inventoried adult individuals were calculated [6,31,52]. Density expresses the number of individuals inventoried per unit area (ha), while the basal area is a common measure in forest management (expressed in m^2/ha), representing the cross-sectional area of tree trunks at breast height (1.3 m) [31]. The quadratic mean diameter is the calculated diameter (expressed in cm) for trees with multiple trunks or branches at 1.3 m above the ground [31]. In this study, this parameter (DBH_m) was used to calculate the average diameter of woody individuals inventoried in each habitat. Additionally, the averages of woody plant species, genera, and families were calculated for these habitats [51].

$$N = \frac{ni}{a} \quad (1)$$

where ni is the number of individuals of a species in a plot, and a is the area of the plot expressed in hectares.

$$DBH_m = \sqrt{\frac{1}{n}\sum_{i=1}^{n} d_i^2} \quad (2)$$

where d_i is the diameter at breast height (*DBH*) of each tree trunk or branch, measured at 1.3 m above the ground, and *n* is the total number of these trunks or branches measured.

$$GBA = FE\sum_{i=1}^{m} gi \quad (3)$$

with gi, the basal area of each measured individual (expressed in m^2/plot area), calculated using the equation below (Equation (4)), *m* is the number of woody individuals inventoried in the plot, and *FE* is the extension factor related to the plot area (m^2), used to extrapolate *gi* values to per hectare [31].

$$gi = \frac{\pi D^2}{4} \quad (4)$$

with *D*, the diameter at breast height (DBH) of an individual, measured at 1.30 m above the ground.

In addition, to assess the regeneration potential (dbh < 10cm) of the habitats, the frequency (*f*; Equation (5)), relative frequency (*RF*; Equation (6)), and relative density (*RD*; Equation (7)) were calculated [6]. Frequency expresses the probability of a woody species being inventoried in each of the floristic inventory plots, while relative frequency is the proportion that a given species represents compared to all inventoried species. Relative density, on the other hand, expresses the proportion that individuals of a given species represent compared to the entire population of individuals in a forest stand [14].

$$f = \frac{n}{Np} \quad (5)$$

with *n* being the total number of plots in which the species has been inventoried and *Np* the total count of plots.

$$RF = \frac{f}{F} \times 100 \quad (6)$$

with *f* being the frequency of a woody species and *F* the sum of all frequencies.

$$RD = \frac{ni}{N} \times 100 \quad (7)$$

where *ni* is the number of individuals of a species and *N* is the total count of all inventoried individuals.

Additionally, the natural regeneration index (NRI), defined as the ratio between the number of juvenile individuals (dbh < 10 cm) and the number of adult individuals (dbh > 10 cm) of a species, was calculated [53]. When NRI < 1, the regeneration of the species in question is low, while when NRI $\geq$ 1, the regeneration is high [54]. Furthermore, to compare the abundance and specific diversity of habitat regeneration, the Fisher alpha index (α; Equation (8)) [2,55] was calculated. Additionally, the sampling effort of woody species in the regeneration was assessed by calculating the proportion between the inventoried species in the understory (Taxa_S) and the number of species according to the floristic richness estimator (Chao 1) [50].

$$\alpha = \frac{\left(\sum_{i=1}^{S} Ni(Ni-1)\right)}{\left(\sum_{i=1}^{S} ni\right)\left(\sum_{i=1}^{S} Ni\right) - \sum_{i=1}^{S} N_i^2} \quad (8)$$

with *S* being the total number of species; *Ni* the total abundance of species *i*, and *ni* the number of sites or plots where species *i* is present.

Furthermore, to identify statistical differences at the 5% significance level among the parameters characterizing the three habitats—unexploited forests, degraded forests, and post-cultivation fallows—the non-parametric Kruskal–Wallis test was applied. This test, which compares group medians, is suitable for datasets that do not meet the normality assumptions required by parametric tests, thus providing robust comparisons across multiple groups. Specifically, dendrometric parameters, including the density of individuals per hectare, quadratic mean diameter, and basal area, as well as floristic parameters such as the number of individuals, taxa, genera, families, Chao-1 estimator, and Fisher alpha index, were analyzed. The non-normal distribution of the data, confirmed by the Shapiro test [56], motivated our choice of the Kruskal–Wallis test. When significant differences were found, the Dunn–Bonferroni post hoc test was employed for pairwise comparisons among strata or habitats [57,58]. Finally, The Jaccard index (J; Equation (9)) [59] was used to compare floristic lists of habitat strata, highlighting the impact of anthropogenic disturbance on species composition.

$$J = \frac{a}{a+b+c} \quad (9)$$

where a is the total number of woody species inventoried in two habitats for comparison; b and c, respectively, represent the number of woody species inventoried in one of the two habitats but absent in the other habitat.

All these analyses were conducted using R software version 4.3.2. Pairwise comparisons of floristic diversity between strata and habitats were performed using Past 4.05 software, while the alpha diversity index was calculated using EstimateS version 9.1 software.

3. Results

3.1. Floristic Characterization of the Three Habitats along an Anthropization Gradient

A total of 1099 adult individuals were inventoried in the three habitats, belonging to 60 species, 40 genera, and 25 families. Additionally, many of these individuals were inventoried in unexploited and degraded forests compared to post-cultivation fallows. Furthermore, the families Fabaceae and Phyllanthaceae are the most represented, particularly in the unexploited forests (Table 2).

Table 2. Families, genera, and species of inventoried adult individuals in different habitats. UFO: unexploited forests, DFO: degraded forests, PCF: post-cultivation fallows. Values are expressed in percentage (frequencies). -: the family was not represented during floristic inventories, n: number of genera, species, or individuals inventoried.

Families	UFO (%)			DFO (%)			PCF (%)		
	Genera n = 27	Species n = 36	Individuals n = 500	Genera n = 33	Species n = 48	Individuals n = 456	Genera n = 25	Species n = 32	Individuals n = 143
Anacardiaceae	3.70	2.78	0.80	3.03	2.08	2.63	-	-	-
Anisophylleaceae	3.70	2.78	1.00	3.03	2.08	0.88	4.00	3.13	1.40
Annonaceae	-	-	-	-	-	-	4.00	3.13	1.40
Apocynaceae	3.70	2.78	2.00	3.03	2.08	6.58	4.00	3.13	4.20
Bignoniaceae	3.70	2.78	0.60	3.03	2.08	0.22	-	-	-
Celastraceae	3.70	2.78	0.20	3.03	2.08	0.22	-	-	-
Chrysobalanaceae	3.70	2.78	1.20	3.03	2.08	3.51	4.00	3.13	2.80
Clusiaceae	3.70	2.78	0.20	9.09	6.25	1.10	4.00	3.13	0.70
Combretaceae	3.70	5.56	0.60	3.03	6.25	2.41	4.00	6.25	2.10
Dipterocarpaceae	7.41	8.33	7.20	6.06	4.17	5.04	-	-	-
Fabaceae	33.33	33.33	76.00	27.27	33.33	59.87	28.00	34.38	67.83
Ixonanthaceae	3.70	2.78	1.00	3.03	2.08	0.88	4.00	3.13	0.70
Lamiaceae	3.70	2.78	0.20	3.03	6.25	2.85	4.00	3.13	2.10
Loganiaceae	3.70	8.33	1.60	3.03	4.17	0.44	4.00	6.25	1.40
Malvaceae	-	-	-	-	-	-	8.00	6.25	3.50
Meliaceae	3.70	2.78	0.20	3.03	2.08	0.22	-	-	-
Moraceae	-	-	-	3.03	4.17	0.66	-	-	-
Myrtaceae	-	-	-	3.03	2.08	0.66	4.00	3.13	3.50
Ochnaceae	3.70	2.78	1.20	3.03	2.08	0.22	4.00	3.13	1.40
Olacaceae	3.70	2.78	0.20	-	-	-	-	-	-
Oleaceae	-	-	-	3.03	2.08	0.22	4.00	3.13	0.70
Phyllanthaceae	7.41	11.11	5.80	9.09	10.42	10.96	12.00	12.50	5.59
Proteaceae	-	-	-	3.03	2.08	0.44	-	-	-
Rubiaceae	-	-	-	-	-	-	4.00	3.13	0.70
Total of frequencies	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

However, the mean values of dendrometric parameters are higher in the unexploited and degraded forests compared to the post-cultivation fallows. Moreover, floristic diversity is higher in the unexploited forests in particular (Table 3). These results highlight the importance of preserving untouched forests to maintain both forest structure and biodiversity. They underscore the potential impacts of logging and degradation on these critical parameters and advocate for sustainable management and conservation strategies to protect these valuable ecosystems.

Table 3. Dendrometric and floristic parameters of inventoried adult individuals in different habitats. Means ± standard deviations. For a given parameter, habitats without common letters differ significantly at $p < 0.05$. UFO: unexploited forests, DFO: degraded forests, PCF: post-cultivation fallows. Taxa_S: number of species.

Parameters	UFO	DFO	PCF
Dendrometric parameters			
Density (individuals/ha)	312.50 ± 126.36 a	285.00 ± 126.97 a	89.38 ± 96.02 b
Quadratic mean diameter (cm)	40.75 ± 15.83 a	32.57 ± 6.78 b	28.84 ± 11.18 b
Basal area (m^2/ha)	16.78 ± 7.25 a	9.98 ± 7.14 a	1.92 ± 2.07 b
Floristic parameters			
Taxa_S/plot	10.25 ± 2.86 a	12.44 ± 4.46 a	4.81 ± 4.28 b
Genera/plot	8.44 ± 2.16 a	9.88 ± 3.36 a	3.94 ± 3.17 b
Families/plot	4.67 ± 1.96 a	5.88 ± 1.86 a	2.69 ± 2.06 b

3.2. Natural Regeneration of Miombo Woody Species in the Three Habitats

The study inventoried 23,052 regenerating individuals across varied forest types: 7576 juveniles in unexploited forests, 9044 in degraded forests, and 6432 in post-cultivation fallows. These juveniles represented 82 species (unexploited: 59, degraded: 69, fallows: 70), 59 genera (unexploited: 43, degraded: 48, fallows: 53), and 30 families (unexploited: 25, degraded: 25, fallows: 27). However, in unexploited forests, seedlings (dbh < 1 cm) spanned 54 species, 40 genera, and 25 families; saplings (1 cm ≤ dbh < 10 cm) were found in 43 species, 32 genera, and 19 families. In degraded forests, seedlings were in 63 species, 43 genera, and 25 families, and saplings in 44 species, 32 genera, and 19 families. Post-cultivation fallows had seedlings in 58 species, 44 genera, and 25 families, and saplings in 53 species, 41 genera, and 21 families. Seedlings predominated: 87.49% in unexploited forests, and 73.64% in degraded forests and 72.70% in fallows, while saplings comprised 12.51%, 26.36%, and 27.30% respectively. In addition, Fabaceae and Phyllanthaceae were predominant, comprising 42.37% to 44.93% of the inventoried species and 70.15% to 70.80% of juvenile individuals across all habitats. Most seedlings were in unexploited and degraded forests; fewer saplings were noted in unexploited forests compared to anthropized habitats. Brachystegia and Albizia species were prominent across regeneration strata (Table 4). Further details on the relative frequency, and relative density of species, can be found in the Supplementary Materials (Table S1).

However, the results indicating similar dendrometric and floristic parameters across habitats highlight surprising uniformity despite environmental differences. Additionally, the low density per hectare, as well as the number of individuals, species, and genera in the seedling stratum of post-cultivation fallows (Table 5), raise questions about these habitats' ability to restore forest cover in optimal time. These observations suggest that fallows require careful management to promote woody species regeneration, diversity, and forest restoration.

Table 4. Floristic list of the top five regenerative plant species, showing high relative frequency/density (values in bold). The species list is presented in alphabetical order, and in case of tied values, the species concerned are counted as one. UFO: unexploited forests, DFO: Degraded forests, PCF: post-cultivation fallows. dbh < 1 cm: seedlings, 1 cm ≤ dbh < 10 cm: saplings, -: species not inventoried, *n* = number of individuals inventoried. RF (relative frequency) and RD (relative density) values are expressed in percentage. The entire set of species studied is presented in the Supplementary Materials (Table S1).

Species	Family	dbh < 1 cm						1 cm ≤ dbh < 10 cm					
		UFO (*n* = 6628)		DFO (*n* = 6660)		PCF (*n* = 4676)		UFO (*n* = 948)		DFO (*n* = 2384)		PCF (*n* = 1756)	
		RF	RD	RF	RD	RF	RD	RF	RD	RF	RD	RF	RD
Albizia adianthifolia (Schumach.) W. Wight	Fabaceae	**4.17**	**6.76**	**4.62**	**9.01**	**5.50**	**5.39**	**4.86**	3.38	**5.17**	**6.71**	**5.54**	5.47
Albizia antunesiana Harms	Fabaceae	**4.17**	4.16	3.08	2.52	**5.11**	3.25	2.78	1.69	**4.13**	1.85	4.54	**6.15**
Anisophyllea boehmii Engl.	Anisophylleaceae	**3.13**	1.39	2.77	2.88	1.97	1.71	3.47	2.95	2.07	0.67	**7.06**	3.19
Baphia bequaertii De Wild.	Fabaceae	**5.56**	**7.91**	**4.31**	**5.29**	**5.11**	**6.50**	3.47	3.38	**5.68**	**5.70**	3.53	**7.06**
Brachystegia spiciformis Benth.	Fabaceae	**5.56**	**12.61**	**4.93**	**13.33**	**6.29**	**10.61**	**10.42**	**15.19**	**6.71**	**5.54**	**6.05**	**7.97**
Brachystegia wangermeeana De Wild.	Fabaceae	**4.51**	**10.80**	**4.93**	**20.48**	**5.90**	**27.89**	**6.94**	**17.30**	**6.20**	**29.53**	**7.56**	**23.46**
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	Apocynaceae	2.78	2.96	**4.31**	2.46	1.18	0.86	3.47	**5.91**	**5.68**	**8.39**	2.02	1.82
Garcinia huillensis Oliv.	Clusiaceae	**3.13**	1.15	**2.16**	0.48	1.57	0.34	-	-	-	-	0.50	0.23
Hymenocardia acida Tul.	Phyllanthaceae	-	-	1.23	1.26	1.18	**5.99**	0.69	0.42	1.55	1.34	1.01	0.46
Isoberlinia angolensis (Benth.) Hoyle & Brenan	Fabaceae	**3.82**	**11.04**	**4.62**	**5.23**	3.54	4.53	**4.86**	2.95	2.07	4.53	3.53	**6.61**
Isoberlinia tomentosa (Harms) Craib & Stapf	Fabaceae	0.35	0.18	-	-	-	-	-	-	**4.13**	4.53	2.02	2.28
Ochna schweinfurthiana F. Hoffm.	Ochnaceae	**4.17**	3.02	**3.69**	3.78	3.93	2.65	**4.17**	2.53	3.10	2.18	1.51	0.91
Parinari curatellifolia Planch. ex Benth.	Chrysobalanaceae	**1.74**	0.48	**1.85**	0.84	1.57	0.86	2.08	1.27	**4.13**	3.69	3.53	2.96
Pseudolachnostylis maprouneifolia Pax	Phyllanthaceae	2.78	2.35	**3.39**	1.80	3.14	1.80	2.08	2.53	2.07	1.01	**5.04**	3.19
Psorospermum febrifugum Spach	Clusiaceae	**4.51**	4.47	2.77	2.04	4.32	1.88	-	-	1.03	0.34	3.02	1.37
Pterocarpus angolensis DC.	Fabaceae	0.35	0.06	-	-	0.39	0.17	**5.56**	**5.49**	3.10	1.17	3.02	1.59
Rothmannia engleriana (K. Schum.) Keay	Rubiaceae	**3.82**	2.53	2.16	1.50	**4.72**	3.25	1.39	0.84	-	-	1.01	0.46
Uapaca kirkiana Müll. Arg.	Phyllanthaceae	**4.51**	3.14	2.46	2.70	0.79	0.34	**4.17**	**3.80**	3.62	2.35	2.02	1.37

Table 5. Comparison of dendrometric parameters and species richness between the two classes of juvenile individuals inventoried in the three habitats. Means ± standard deviations. For a given parameter, habitats without common letters differ significantly at $p < 0.05$. UFO: unexploited forests, DFO: degraded forests, PCF: post-cultivation fallows, dbh < 1 cm: seedlings, 1 cm ≤ dbh < 10 cm: Saplings, -: values were not calculated due to lack of relevant data.

	dbh < 1 cm			**1 cm ≤ dbh < 10 cm**		
	UFO	**DFO**	**PCF**	**UFO**	**DFO**	**PCF**
Dendrometric parameters						
Density (individuals/ha)	4142.50 ± 2176.33 ab	4185.00 ± 1544.84 a	2935.00 ± 1567.39 b	592.50 ± 341.36 a	1490.00 ± 1133.21 a	1110.00 ± 954.82 a
Quadratic mean diameter (cm)	-	-	-	7.52 ± 0.66 a	7.16 ± 0.48 a	7.06 ± 0.49 a
Basal area (m^2/ha)	-	-	-	2.49 ± 1.26 a	5.76 ± 4.36 a	4.25 ± 3.71 a
Floristic parameters						
Individuals	103.56 ± 54.41 ab	104.63 ± 38.62 a	73.38 ± 39.18 b	14.81 ± 8.53 a	37.25 ± 28.33 a	27.75 ± 23.87 a
Taxa_S	18.00 ± 3.97 ab	20.50 ± 3.41 a	16.06 ± 3.99 b	16.88 ± 6.91 a	19.13 ± 10.83 a	19.19 ± 14.62 a
Genera	15.25 ± 4.09 ab	17.75 ± 3.49 a	13.44 ± 3.76 b	7.81 ± 3.62 a	10.63 ± 5.15 a	10.13 ± 6.39 a
Families	9.56 ± 2.78 a	10.88 ± 2.83 a	9.31 ± 2.89 a	5.19 ± 2.83 a	6.50 ± 3.18 a	6.63 ± 3.91 a
Chao-1	21.14 ± 5.85 a	25.57 ± 4.78 a	21.30 ± 8.29 a	18.87 ± 11.80 a	20.80 ± 11.22 a	23.16 ± 17.04 a
Taxa_S/Chao-1	0.85	0.80	0.75	0.90	0.92	0.83
Fisher_alpha	6.78 ± 1.66 a	8.57 ± 3.13 a	6.99 ± 2.11 a	10.74 ± 6.17 a	9.96 ± 11.91 a	8.71 ± 5.79 a

The regeneration potential of species remains high in unexploited forests within the seedling stratum, while it is high in anthropized habitats within the sapling stratum. These results show the capacity of miombo species to regenerate, and subsequently to reconstitute forest cover in anthropized habitats, particularly in degraded forests, which experience lower anthropogenic disturbances compared to fallows. The table below (Table 6) lists the top five species with the highest natural regeneration index. The complete table is provided in the Supplementary Materials (Table S2).

Table 6. Floristic list of the top five regenerative plant species, showing the natural regeneration index for each habitat (values in bold). The species list is presented in alphabetical order, and in case of tied values, the species concerned are counted as one. UFO: unexploited forests, DFO: degraded forests, PCF: post-cultivation fallows. NRI: natural regeneration index (ratio between juveniles and adults), dbh < 1 cm: seedlings, 1 cm ≤ dbh < 10 cm: saplings, 0: species not inventoried in the regeneration stratum but inventoried in the adult individual's stratum of the habitat, -: species inventoried in the regeneration stratum but not in the adult individual's stratum of the habitat. The entire set of species studied is presented in the Supplementary Materials (Table S2).

Species	dbh < 1 cm			1 cm ≤ dbh < 10 cm		
	UFO	DFO	PCF	UFO	DFO	PCF
Albizia antunesiana Harms	23.00	12.92	50.67	1.33	3.38	**36.00**
Anisophyllea boehmii Engl.	18.40	**48.00**	40.00	**5.60**	4.00	**28.00**
Baphia bequaertii De Wild.	23.82	16.76	50.67	1.45	6.48	**20.67**
Combretum molle R.Br ex G. Don	**40.00**	9.33	**72.00**	**4.00**	4.00	12.00
Combretum zeyheri Sond.	0.00	6.00	0.00		**34.00**	16.00
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	19.60	5.47	6.67	**5.60**	6.67	5.33
Ekebergia benguelensis Welw. ex C.DC.	**36.00**	24.00		0.00	12.00	
Harungana madagascariensis Lam. ex Poir.		**136.00**		0.00	0.00	
Hymenocardia acida Tul.	0.00	42.00			**16.00**	
Isoberlinia angolensis (Benth.) Hoyle & Brenan	**45.75**	38.67	42.40	1.75	12.00	**23.20**
Isoberlinia tomentosa (Harms) Craib & Stapf		0.00	0.00	0.00	**21.60**	8.00
Julbernardia paniculata (Benth.) Troupin	1.60	24.00	0.00	1.60	4.00	**20.00**
Markhamia obtusifolia (Boulanger) Sprague	2.67	44.00		2.67	**24.00**	
Mystroxylon aethiopicum (Thunb.) Lœs.	16.00	**60.00**		0.00	12.00	0.00
Ochna schweinfurthiana F. Hoffm.	33.33	**252.00**	**62.00**	**4.00**	**52.00**	8.00
Olax obtusifolia De Wild.	16.00		0.00	**24.00**	0.00	0.00
Phyllocosmus lemaireanus (De Wild. & T. Durand) T. Durand & H. Durand	32.00	43.00	**92.00**	**4.80**	6.00	4.00
Pseudolachnostylis maprouneifolia Pax	**78.00**	17.14	42.00	**12.00**	3.43	**28.00**
Psorospermum febrifugum Spach	**296.00**	**68.00**		0.00	4.00	
Rothmannia engleriana (K. Schum.) Keay			**152.00**		0.00	8.00
Schrebera trichoclada Welw.		0.00	28.00	0.00	0.00	**28.00**
Strychnos cocculoides Boulanger	1.33	28.00	**64.00**	**4.00**	**16.00**	12.00
Strychnos spinosa Lam.	0.00	0.00		**4.00**		
Vitex doniana Sweet	4.00	2.40	5.33	**4.00**	1.60	6.67
Vitex mombassae Vatke		8.00		0.00	**16.00**	0.00

3.3. Comparison of the Specific Richness of Woody Species Inventoried in Regeneration and Adult Stands

However, the Jaccard similarity of floristic lists among different strata in the three habitats is depicted in the table below (Table 7). It is evident from this table that the lowest similarity is between the floristic list of seedlings in degraded forests and that of adults in post-cultivation fallows (42.00%), while the highest similarity is between the floristic lists of installed juveniles in unexploited forests and those in degraded forests (92.00%). Nonetheless, a pairwise comparison of floristic lists of habitats (all strata combined) reveals that the floristic lists of unexploited and degraded forests exhibit a similarity of 76.50%, whereas that of post-cultivation fallows is 56.00% similar to unexploited and degraded forests, respectively. These results indicate that the floristic lists of habitats are influenced by natural factors (intra- and interspecific competition) and, particularly, by the extent of disturbances experienced by the habitats.

Table 7. Jaccard similarity between floristic lists of different strata in the three habitats. UFO: unexploited forests, DFO: degraded forests, PCF: post-cultivation fallows, <1: seedlings; ≥1: saplings; ≥10: adults. Relative values are presented in decimal form.

	UFO < 1	DFO < 1	PCF < 1	UFO ≥ 1	DFO ≥ 1	PCF ≥ 1	UFO ≥ 10	DFO ≥ 10
DFO < 1	0.65							
PCF < 1	0.68	0.65						
UFO ≥ 1	0.65	0.55	0.50					
DFO ≥ 1	0.71	0.59	0.55	0.92				
PCF ≥ 1	0.67	0.64	0.74	0.63	0.68			
UFO ≥ 10	0.65	0.48	0.57	0.71	0.79	0.63		
DFO ≥ 10	0.67	0.57	0.59	0.73	0.80	0.74	0.86	
PCF ≥ 10	0.56	0.42	0.50	0.71	0.67	0.63	0.60	0.63

4. Discussion

4.1. Structure and Floristic Composition of Forest Strata and Stands along the Anthropization Gradient

Dendrometric, particularly the density, and floristic parameters decrease according to the increase in the level of habitat disturbance (Tables 2 and 3). This situation is attributed particularly to anthropogenic disturbances experienced by the anthropized habitats, primarily agriculture and charcoal production. Indeed, cutting trees for dendro-energy (typically targeting larger-diameter trees during selective logging) and agriculture reduces tree density and biomass, thereby affecting both the diversity and distribution of woody species [60]. Thus, the conversion of forested lands into agroecosystems and dendro-energies leads to deforestation and fragmentation of the *miombo* woodlands, particularly in the Lubumbashi region [15]. According to Refs. [18,61], anthropogenic activities disrupt the ecological balance of ecosystems, subsequently affecting the structure and composition of the *miombo* woodlands. However, natural factors such as climate change and natural disasters can also negatively impact the dendrometric and floristic parameters of habitats [62]. These results, found in the present study, corroborate those of other research conducted in the *miombo* ecoregion [2,14,21,35,51,63], showing that the values of dendrometric (number of individuals inventoried, mean quadratic diameter, basal area) and floristic parameters (number of species, genera, and families) of habitats decrease as anthropogenic disturbances increase.

4.2. Regeneration of Miombo Woody Species along the Anthropization Gradient

The regeneration potential (individual number and diversity) of habitats within the two regeneration strata remains higher in degraded forests than in unexploited forests and post-cultivation fallows (Tables 4–6). These results demonstrate that the regeneration of woody species and subsequently the reconstitution of the *miombo* woodlands would be possible in anthropized habitats provided that human activities, especially agriculture, dendro-energy production, wood cutting, and bushfires, are prohibited. Additionally, these measures must be increasingly enforced in heavily disturbed habitats, such as post-cultivation fallows. The similarity in floristic richness between degraded and unexploited forests could be explained by the fact that the anthropogenic disturbances experienced by degraded forests, particularly related to the decrease in individual density through selective harvesting, make resources available in these habitats, such as space, water, and insolation [64]. This resource availability, coupled with low inter- and intraspecific competition, allows woody species, particularly pioneer species and those resilient to anthropogenic disturbances (present in the herbaceous stratum and the soil seed bank), to establish themselves [57]. In contrast to degraded forests, anthropogenic disturbances in agroecosystems are not only related to the loss of woody species density (tree cutting and stump removal) but also to the disruption of soil physicochemical and biological properties [19]. The combination of these disturbances negatively affects the regeneration potential and resilience capacity of woody species, potentially leading to savannization [65]. Furthermore, the regeneration potential in unexploited forests would depend on strong inter-and intraspecific competition for the aforementioned resources, primary factors in the establishment of plant species in habitats [66,67]. These results corroborate previous research [14,51,68,69] indicating that anthropized habitats exhibit high species richness in regeneration strata. These anthropized habitats are characterized by high environmental heterogeneity during early succession stages and high regeneration potential of *miombo* woody species [6]. However, these results do not support the findings of studies conducted, notably in Zimbabwe by [35], indicating that species richness is high in unexploited forests due to the absence of anthropogenic disturbances on a human scale. Nevertheless, the regeneration potential in unexploited forests depends on several factors, including inter/intra-specific competition for resources and minimal anthropogenic disturbances. Additionally, the vigor of adult trees (producing quality and sufficient seeds), the presence of animal species (facilitating seed dispersal), symbiotic interactions, good soil structure, and high nutrient availability also play crucial roles. These factors interact in complex ways, influencing the regeneration process in unexploited forests [66,70].

However, these disturbances could create new environmental conditions that sometimes favor increased plant diversity if these anthropogenic disturbances are of low intensity, limited duration, and characterized by minimal removal [71]. This situation has already been highlighted in previous studies conducted in the *miombo* ecoregion [34,72], demonstrating that floristic characteristics such as stand structure and species richness of habitat with medium anthropization level can reach values higher than those of unexploited mature forests after anthropogenic disturbances cease. Indeed, habitats with intermediate disturbance regimes, such as degraded forests in this study, may exhibit high species diversity through the creation of diverse ecological niches, thereby confirming the widely evoked intermediate disturbance hypothesis in various fields of natural resources management and conservation [73].

Conversely, maintaining human pressure on natural resources even in heavily anthropized habitats compromises the regeneration of woody species and subsequently the reconstitution of the *miombo* woodlands. Indeed, the distance from intact forests over an increasingly extensive radius [12] has led local communities to harvest woody species, furthermore through less sustainable practices [74], in anthropized areas near settlements for various needs [6]. In addition to this, late and repetitive bushfires [75] characterizing the *miombo* ecoregion [44,76–78] and particularly the Lubumbashi region [79], affect the natural regeneration of woody species in habitats. Moreover, the scarcity of species with high calorific value and the increase in charcoal production distance induce the return of local communities to regenerating forest stands. This situation contributes to maintaining a high level of forest degradation [80] and decreases the potential for forest regeneration. Similarly, population growth and increased land pressure resulting from it have led local communities to shorten fallow periods to meet increased demand for necessities [45]. This further disrupts the process of woody species regeneration and ongoing *miombo* woodlands reconstitution in post-cultivation fallows [81]. These results are similar to those of studies conducted in Mozambique [6], showing that ongoing human activities in already anthropized habitats compromise the reconstitution of the *miombo* woodlands in these habitats.

4.3. Similarity between Floristic Lists along the Anthropization Gradient

The floristic lists of strata in unexploited forests and degraded forests exhibit higher similarities compared to post-cultivation fallows (Table 7). This similarity between unexploited forests and degraded forests is also observed among habitats when all strata are merged. This situation is attributed to the fact that during exploitation, agrosystems transitioning into post-cultivation fallows undergo anthropogenic disturbances that negatively impact dendrometric and floristic parameters, particularly. These findings corroborate studies conducted in the dense humid forest region [51,82], and specifically in the *miombo* ecoregion [6,35], demonstrating that anthropogenic activities in agrosystems negatively influence floristic diversity in post-cultivation fallows.

4.4. Implications for Sustainable Miombo Woodlands Restoration in Anthropized Landscapes

Anthropogenic disturbances affect the high potential for natural regeneration and resilience of different *miombo* woody species. To address this, Assisted Natural Regeneration (ANR) could be one solution. ANR involves the deliberate protection of disturbed habitats against anthropogenic pressures and invasive plant species to accelerate natural forest succession processes leading to the reconstitution of a resilient and productive ecosystem [5,26]. It requires legislative reform and rules governing interactions between natural and social dynamics [83]. However, in the D.R. Congo, this reform would focus on access to natural resources, establishing reasonable rotation periods, regulating bushfires, and anthropogenic incursions into habitats at the end of their exploitation. ANR could be effective and less costly than reforestation and other revegetation strategies, provided there are seed sources in the restoration area [5]. This restoration technique has been successfully used in Ethiopia to restore forests over significant areas previously impacted by anthropogenic activities and has been proposed in Mozambique to restore *miombo* woodlands in anthropized habitats [5,73]. However, in regions with rapid population growth like the Lubumbashi region, implementing ANR can be challenging due to increased anthropogenic pressures on land and natural resources. To address this, zoning and defined collaborative restoration options involving local communities actively would be one solution to this situation [27,40].

Furthermore, reforestation and forest enrichment—practice aimed at restoring and enhancing selectively logged forests by introducing valuable woody species (cultural, economic)—would be palliative solutions for anthropized habitats with low *miombo* resilience capacity after exploitation, such as post-cultivation fallows. Utilizing *miombo* woody species for reforestation and habitat enrichment would result in forest ecosystems with a structure, specific composition, and function similar to those of the previously exploited forest. In this regard, these restored habitats would continue to support the survival of both rural and urban populations by providing the usual ecosystem services [84]. However, selecting fast-growing native species like *Pterocarpus tinctorius* Welw. and *Combretum collinum* Fresen. is necessary for short-term *miombo* woodlands reconstitution [85]. Nevertheless, similar to ANR habitats, reforested or enriched habitats should be protected from anthropogenic intrusions [6,35] and late, repetitive bushfires [79,86].

Furthermore, this study shows the current state of anthropized habitats regarding regeneration potential and subsequent forest reconstitution. However, it does not depict the successional dynamics of woody species in these habitats over the years following exploitation [21,35,52]. Additionally, the study does not show the distribution of these woody species based on their functional traits within different strata and habitats [50]. These missing ecological aspects would provide complementary information to the present results and remain important for the establishment of sustainable *miombo* woodlands management strategies.

5. Conclusions

The present study assessed the natural regeneration capacity of *miombo* woody species along a gradient of anthropization through floristic inventories in three different habitats, including one that was unexploited and two with varying levels of anthropization. The results confirm that density, mean diameter, basal area, taxa, genera, and families have high values in both unexploited and degraded forests. Indeed, significant differences were observed among the three habitats, with low values observed in fallows. Furthermore, these results confirm that the regeneration potential of *miombo* species and individuals' numbers are high in degraded forests. However, low regeneration was observed in unexploited forests and post-cultivation fallows, except in the sapling's stratum where regeneration in different habitats is almost equivalent. Additionally, our results indicate that there are similarities and dissimilarities in terms of floristic richness between habitats, as the floristic lists of unexploited forests and degraded forests show higher similarities than post-cultivation fallows. While our study did not characterize variations in dendrometric and floristic parameters according to the age of anthropized habitats, as well as the distribution of species in strata and habitats in terms of functional traits of woody species, our results show that the regeneration potential of *miombo* species depends on the intensity of anthropogenic disturbances experienced by habitats. To contribute to the regeneration of woody species and the reconstitution of *miombo* in anthropized habitats, appropriate legislation determining rotation periods and regulating repetitive bushfires and anthropogenic activities should be established. Additionally, inclusive reforestation and agroforestry activities using *miombo* woody species should be considered.

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