

Diversity, Regeneration Potential, and Natural Restoration of Miombo along an Anthropization Gradient in the Rural Area of Lubumbashi (Upper-Katanga, D.R. Congo)

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Keywords: Anthropogenic pressure; deforestation; forest degradation; floristic diversity; natural regeneration; miombo woodlands.



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Article

Diversity, Regeneration Potential, and Natural Restoration of *Miombo* Along an Anthropization Gradient in the Rural Area of Lubumbashi (Upper-Katanga, 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 the diversity and natural regeneration capacity of *miombo* species through floristic inventories in three different habitats (unexploited forests, degraded forests, and post-cultivation fallows). The results reveal that for the adult's 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 ≤ dbh < 10 cm), the three habitats display nearly 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. To sustain this natural regeneration capacity of *miombo* woody species and promote the restoration of forest mass 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, floristic diversity, natural regeneration, *miombo* woodlands.

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 km² 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 contributing 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, 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 is 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 habitats shows similarities. Higher similarities in floristic composition are expected between unexploited and degraded forests compared to post-cultivation fallows, due to the lower disturbances in these habitats compared to post-cultivation fallows.

2. Materials and Methods

2.1. Study area

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

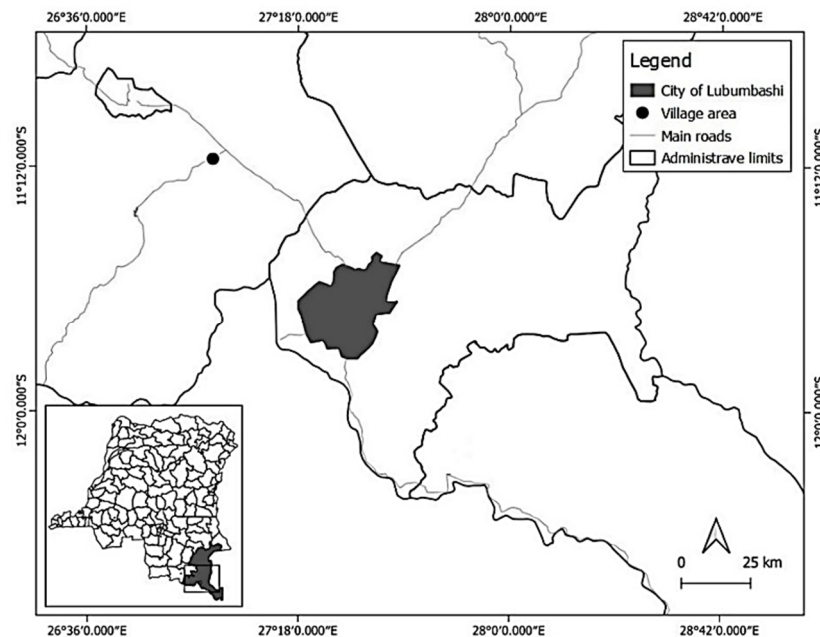


Figure 1. City of Lubumbashi (grey polygon) and its rural area (white space surrounding Lubumbashi). The black dot indicates the village area of Lwisha, located approximately 80 km northwest of Lubumbashi. The geographical coordinates used for this mapping were obtained using a GPS device within the 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 meters, 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 ferrallitic 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



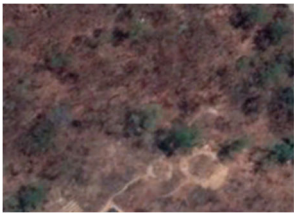
anthropized forest habitats, specifically those affected by charcoal production (degraded forests) and agriculture (post-cultivation fallows). Moreover, the village demonstrates weak implementation of the existing simple forest management plan, contributing to deforestation and forest degradation.

2.2. Methods

2.2.1. Sampling and data collection

To study the composition and floral diversity, three habitat types were chosen: unexploited forests (AUF), degraded forests (DFO), and post-cultivation fallows (FAL). 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
<div>Unexploited miombo forests</div> <div></div>	Are those 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 cover extends over at least 10-30% of the area, which spans between 0.05-1 hectares [15].
<div>Degraded forests</div> <div></div>	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.
<div>Post-cultivation fallows</div> <div></div>	Fallows are habitats abandoned after subsistence farming. Referring to habitats 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 meters long, were established along the four cardinal points (north, south, east, west) of the village. On each transect, four floristic inventory plots measuring 50 m x 20 m, spaced 100 meters apart, were set up [6]. Additionally, to assess the regeneration of *miombo* woody species and thus the restoration of this forest ecosystem in anthropized habitats, 80 subplots of 10 m x 5 m each were installed in each habitat [14]. This represents 20 subplots per transect and 5 subplots per inventory plot. The dimensions of the plots and subplots were determined based on previous studies ([6,14] indicating that 50 m x 20 m and 10 m x 5 m are adequate dimensions for floristic and forest regeneration studies in the *miombo* woodlands, respectively.

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 a forestry tape [31]. Additionally, in these subplots, juvenile individuals (dbh < 10 cm) were inventoried, and their diameters measured. The inventory considered three groups: seedlings (dbh < 1 cm), saplings (1 cm ≤ dbh < 10 cm), and adults (dbh ≥ 10 cm) [47]. 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 March 25 to June 29, 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 [7,48,49].

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, indicator species identification, 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 floral diversity was tested at a 5% significance level [50]. 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 (N ; Equation 1), quadratic diameter (DQ ; Equation 2), and basal area (G/ha ; Equation 3) of the inventoried adult individuals were calculated [6,31,51]. Density expresses the number of individuals inventoried per unit area (ha), while basal area represents the surface area occupied by woody individuals on this surface [31]. Additionally, the averages of woody plant species, genera, and families were calculated for these habitats [50].

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

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

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

where n is the total number of measurements taken, and x_i^2 is each measurement squared.

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

with FE , the correction factor related to the plot area (m^2), m , the number of woody individuals inventoried in the plot, and gi the basal area of each measured individual, calculated using the equation below (Equation 4) [31]:

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

with D , the diameter at breast height (DBH) of an individual, measured at 1.30 meters 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 where 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 [52]. When $NRI < 1$, the regeneration of the species in question is low, while when $NRI \geq 1$, the regeneration is high [53]. Furthermore, to determine indicator species for the habitats in these first two strata, the Indicator Species Identification (IndVal) method [50] was used. It has the advantage of combining the frequency and abundance of a species to determine its indicative nature. Thus, a plant species is considered indicative of a group of plots when it is specific (absent or relatively less frequent in other plot groups) and faithful to that group (present in all or the majority of plots). This index is calculated for each species i in each group j using the following relationship (Equation 8); [54].

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100 \quad (8)$$

with A_{ij} being the ratio between the number of individuals ij and the number of individuals j , while B_{ij} is the ratio between the number of plots ij and the number of plots j . In this regard, A_{ij} is the average abundance of species i within the surveys of group j compared to all groups (a measure of specificity), while B_{ij} is the number of surveys where species i was inventoried within the surveys of group j (a measure of fidelity or constancy).

To compare the abundance and specific diversity of habitat regeneration, the Fisher alpha index (α ; Equation 9) [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].

$$\alpha = \frac{(\sum_{i=1}^S Ni(Ni-1))}{(\sum_{i=1}^S ni)(\sum_{i=1}^S Ni) - \sum_{i=1}^S Ni^2} \quad (9)$$

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, the non-parametric Kruskal-Wallis test was applied to the results related to density, species richness, and types of disturbances. This test was chosen due to the non-normality of the data, confirmed by the Shapiro test [56]. In case of significant differences, the Dunn-Bonferroni post-hoc test was used for pairwise comparison of means of strata or habitats [57,58].

Finally, to compare the similarity of floristic lists among different habitats, non-metric multidimensional scaling analysis (NMDS) [59] was conducted and complemented by the Jaccard index (J ; equation 9) [60].

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

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. Characterization of the Three Habitats Along an Anthropization Gradient

A total of 1,099 adult individuals were inventoried in the three habitats: 500 individuals in the unexploited forests, 456 individuals in the degraded forests, and 143 individuals in the post-cultivation fallows. These individuals belong to 60 species (unexploited forests: 36; degraded forests: 48; post-cultivation fallows: 32), 40 genera (unexploited forests: 27; degraded forests: 33; post-cultivation fallows: 25), and 25 families (unexploited forests: 17; degraded forests: 21; post-cultivation fallows: 16, Table 2).

Furthermore, in the unexploited forests, the families Fabaceae, Phyllanthaceae, and Dipterocarpaceae alone represent 57.77% of the inventoried species, accounting for 33.33%, 11.11%, and 8.33%, respectively. These families represent 89.00% of the inventoried individuals, with the Fabaceae family alone representing 76% of individuals. Among the individuals inventoried in the unexploited forests, 54.00% belong to the species *Brachystegia wangermeeana* (32.60%) and *B. spiciformis* (21.40%). Additionally, in the degraded forests, 62.50% of species belong to the families Fabaceae (33.33%), Phyllanthaceae (10.42%), Clusiaceae, Combretaceae, and Lamiaceae (6.25% each). The Fabaceae family is the most represented with 59.87% of inventoried individuals. In these degraded forests, 58.33% of individuals belong to the species *B. wangermeeana* (18.20%), *B. spiciformis* (12.28%), *Albizia adianthifolia* (10.53%), *Diplorhynchus condylocarpon* (6.58%), *Uapaca kirkiana* (6.14%), and *Baphia bequaertii* (4.61%). Finally, in the post-cultivation fallows, 65.63% of species belong to the families Fabaceae (34.38%), Phyllanthaceae (12.50%), Combretaceae, Loganiaceae, and Malvaceae (6.25% each). The Fabaceae family represents 67.83% of inventoried individuals in the post-cultivation fallows. 44.06% of inventoried individuals in the post-cultivation fallows belong to the species *B. wangermeeana* (21.68%), *B. spiciformis*, and *A. adianthifolia* (11.19% each). From these results, it is evident that the families Fabaceae and Phyllanthaceae are the most represented in the adult populations of these three habitats.

Table 2. Families, genera, and species of inventoried adult individuals in different habitats. AUF: unexploited forests, DFO: Degraded forests, FAL: Post-cultivation fallows. Letters indicate statistical differences between strata, -: the family was not represented during floristic inventories, n: sample size.

Families	AUF (%)			DFO (%)			FAL (%)		
	Genera	Species	Individuals	Genera	Species	Individuals	Genera	Species	Individuals
	n=27	n=36	n=500	n=33	n=48	n=456	n=25	n=32	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

In general, the results regarding dendrometric and floristic parameters reveal significant differences between habitats. Specifically, the mean values of these dendrometric parameters are higher in the unexploited forests (Density: 312.50 individuals/ha; Mean diameter: 40.75 cm; Basal area: 16.78 m²/ha) and degraded forests (Density: 285.00 individuals/ha; Mean diameter: 32.57 cm; Basal area: 9.98 m²/ha) compared to the post-cultivation fallows (Density: 89.38 individuals/ha; Mean diameter: 28.84 cm; Basal area: 1.92 m²/ha). Moreover, floristic diversity is higher in the unexploited forests (10 species; 8 genera; 5 families) and degraded forests (12 species; 10 genera; 6 families) particularly (Table 3). These results suggest a significant influence of anthropization on dendrometric parameters of individuals and floristic diversity in these habitats.

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. AUF: Unexploited forests, DFO: Degraded forests, FAL: Post-cultivation fallows.

Parameters	AUF	DFO	FAL
Dendrometric parameters			
Density (individuals/ha)	312.50±126.36a	285.00±126.97a	89.38±96.02b
Mean square diameter (cm)	40.75±15.83a	32.57±6.78b	28.84±11.18b
Basal area (m2/ha)	16.78±7.25a	9.98±7.14a	1.92±2.07b
Floristic parameters			
Taxa_S/plot	10.25±2.86a	12.44±4.46a	4.81±4.28b
Genera/plot	8.44±2.16a	9.88±3.36a	3.94±3.17b
Families/plot	4.67±1.96a	5.88±1.86a	2.69±2.06b

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

A total of 23,052 regeneration individuals, comprising 7,576 juveniles in unexploited forests, 9,044 juveniles in degraded forests, and 6,432 juveniles in post-cultivation fallows, were inventoried. The juveniles were distributed among 82 species (unexploited forests: 59; degraded forests: 69; post-cultivation fallows: 70), 59 genera (unexploited forests: 43; degraded forests: 48; post-cultivation fallows: 53), and 30 families (unexploited forests: 25; degraded forests: 25; post-cultivation fallows: 27).

In unexploited forests, seedlings (dbh<1 cm) were distributed among 54 species, 40 genera, and 25 families, while saplings (1 cm≤dbh<10 cm) were distributed among 43 species, 32 genera, and 19 families. Moreover, in degraded forests, seedlings belonged to 63 species, 43 genera, and 25 families, while saplings grouped into 44 species, 32 genera, and 19 families. In post-cultivation fallows, seedlings were grouped into 58 species, 44 genera, and 25 families, while saplings grouped into 53

species, 41 genera, and 21 families. Additionally, in unexploited forests, seedlings represented 87.49%, while saplings represented only 12.51%. In degraded forests and post-cultivation fallows, seedlings represented 73.64% and 72.70%, respectively. Furthermore, saplings represented only 14.30%, 35.80%, and 37.55% of seedlings in each habitat.

Moreover, in unexploited forests, 42.37% of inventoried species belonged to the Fabaceae and Phyllanthaceae families, with Fabaceae being the most represented at 30.51% of inventoried species. They represented 42.59% of seedlings and 46.51% of saplings. These two families accounted for 70.80% of inventoried juvenile individuals in unexploited forests, comprising 71.62% of seedlings and 65.40% of saplings. In degraded forests, the Fabaceae and Phyllanthaceae families represented 44.93% of inventoried woody species (dbh<1 cm: 42.86% and 1 cm≤dbh<10 cm: 47.73% of species) and 70.44% of inventoried juvenile individuals (dbh<1 cm: 70.19% and 1 cm≤dbh<10 cm: 71.14% of individuals). Furthermore, in post-cultivation fallows, the Fabaceae and Phyllanthaceae families represented 38.57% of inventoried species (dbh<1 cm: 37.93% and 1 cm≤dbh<10 cm: 43.40% of species) and 70.15% of inventoried juvenile individuals (dbh<1 cm: 69.25% and 1 cm≤dbh<10 cm: 72.52% of individuals).

Furthermore, for seedlings (dbh<1 cm), the relative frequency of woody species ranged from 0.35% to 5.56% (mean: 1.85 ± 1.55) in unexploited forests, while the relative density of these juvenile individuals varied from 0.06% to 12.61% (mean: 1.85 ± 2.91). The natural regeneration index ranged from 0.29 to 296.00 (mean: 25.48 ± 51.45). Regarding degraded forests, the relative frequency of woody species ranged from 0.31% to 4.93% (mean: 1.64 ± 1.33). The relative density of these species in degraded forests ranged from 0.06% to 20.48% (mean: 1.61 ± 3.27), and the natural regeneration index varied from 0.73 to 252.00 (mean: 28.12 ± 43.49). As for post-cultivation fallow lands, the relative frequency ranged from 0.39% to 6.29% (mean: 1.75 ± 1.65), while the relative density varied between 0.09% and 27.89% (mean: 1.75 ± 4.03). The natural regeneration index for these woody species ranged from 1.33 to 152.00 (mean: 33.67 ± 34.04).

In contrast, for saplings (1 cm≤dbh<10 cm), the relative frequency of species ranged from 0.69% to 10.42% (mean: 2.33 ± 2.00), while the relative density ranged from 0.42% to 17.30% (mean: 2.33 ± 3.40) in unexploited forests. The natural regeneration index for species in these unexploited forests varied from 0.87 to 24.00 (mean: 3.66 ± 4.33). In degraded forests, the relative frequency of woody species ranged from 0.52% to 6.71% (mean: 2.27 ± 1.65), while the density varied from 0.17% to 29.53% (mean: 2.27 ± 4.62). The regeneration index for species in these degraded forests ranged from 0.57 to 52.00 (mean: 8.97 ± 10.32). For post-cultivation fallows, the relative frequency ranged from 0.50% to 7.56% (mean: 1.88 ± 1.77), while the density oscillated between 0.23% and 23.46% (mean: 1.89 ± 3.56). The natural regeneration index ranged from 1.33 to 36.00 (mean: 11.57 ± 8.90).

Additionally, for the stratum of seedlings, the species *Brachystegia spiciformis* exhibited high frequencies across different habitats. This species showed similar relative frequencies to the species *Baphia bequaertii* and *B. wangermeeana*, respectively, in unexploited forests and degraded forests. Furthermore, the species *Albizia adianthifolia*, *Baphia bequaertii*, *B. spiciformis*, *B. wangermeeana*, and *Isoberlinia angolensis* represented 49.12% of seedlings inventoried in unexploited forests. In degraded forests, *A. adianthifolia*, *B. spiciformis*, and *B. wangermeeana* represented 42.82% of these juveniles, while these species represented 45.00% of juvenile individuals in post-cultivation fallows. In this stratum of seedlings, the species *Psorospermum febrifugum*, *Ochna schweinfurthiana*, and *Rothmannia engleriana* exhibited the highest natural regeneration index in unexploited forests, degraded forests, and post-cultivation fallows, respectively.

Moreover, for saplings, the species *B. spiciformis* exhibited a high relative frequency in unexploited forests and degraded forests, while the species *B. wangermeeana* showed a high relative frequency in post-cultivation fallows. Additionally, *B. wangermeeana* was the most represented species in all three habitats. The species *B. spiciformis*, *B. wangermeeana*, *Diplorhynchus condylocarpon*, and *Pterocarpus angolensis* represented 43.88% of inventoried juvenile individuals in unexploited forests. The species *A. adianthifolia*, *B. bequaertii*, *B. spiciformis*, *B. wangermeeana*, and *D. condylocarpon* represented 55.87% of juveniles inventoried in degraded forests. Furthermore, *A. adianthifolia*, *Albizia antunesiana*, *B. bequaertii*, *B. spiciformis*, *B. wangermeeana*, and *Isoberlinia angolensis* represented 56.72% of inventoried juveniles in post-cultivation fallows. Additionally, *Olax obtusifolia*, *O. schweinfurthiana*,

and *Albizia antunesiana* exhibited the highest natural regeneration index in unexploited forests, degraded forests, and post-cultivation fallows, respectively.

Furthermore, in the seedlings' stratum, *miombo* characteristic woody species (from the genera *Brachystegia*, *Julbernardia*, and *Isobertia*) represent 14.8% of total species in unexploited forests, 12.70% in degraded forests, and 10.35% in post-cultivation fallows. In the saplings' stratum, these species account for 11.63%, 13.64%, and 15.09%, respectively. In terms of individuals, these species constitute 35.85% of seedlings in unexploited forests, 41.68% in degraded forests, and 43.63% in post-cultivation fallows. For saplings, they represent 36.71%, 44.97%, and 42.14%, respectively. The table below (Table 4) summarizes the top-five woody species for each calculated parameter in each habitat. The entire set of species studied is presented in the appendix (supplementary material 1).

However, other woody species, such as *B. boehmii*, were not inventoried in the adult stands of the different habitats but nevertheless have juveniles in the regeneration. These species represent 33.33% and 33.87% of the total inventoried species in the seedling's stratum of unexploited forests and degraded forests, respectively, while they represent 52.63% in the same stratum of post-cultivation fallows. Additionally, these species represent 27.91%, 15.91%, and 39.62% of inventoried species in the sapling's stratum of the three habitats.

Conversely, other species inventoried in the adult stands of the different habitats, such as *Julbernardia globiflora*, do not have seedlings (dbh < 1 cm). These species, in turn, represent 10.82%, 14.58%, and 15.63% of adult stand species, respectively, in unexploited forests, degraded forests, and post-cultivation fallows. Furthermore, in the stratum of saplings, these species represent 16.22% and 22.92% in unexploited forests and degraded forests, respectively. Specifically, all species inventoried in the adult stratum of post-cultivation fallows have juveniles in the sapling's stratum.

Moreover, in the stratum of seedlings, the species *Garcinia huillensis*, *P. febrifugum*, and *Uapaca kirkiana* are indicative of unexploited forests, while *B. boehmii*, *Harungana madagascariensis*, and *Julbernardia paniculata* are indicative of degraded forests. *Phyllanthus muellerianus* is the only indicative species of this stratum in post-cultivation fallows. In contrast, for saplings, the species *O. obtusifolia* is indicative of unexploited forests, while *Diplorhynchus condylocarpon* and *Isobertia tomentosa* are indicative of degraded forests. The species *Pseudolachnostylis maprouneifolia* is indicative of post-cultivation fallows.

The results related to the dendrometric and floristic parameters of regeneration strata are statistically similar between habitats, except for density per hectare, the number of individuals, species, and genera in seedlings stratum (Table 5), which show particularly low values in post-cultivation fallows. These results suggest that the regeneration potential is inversely proportional to the anthropogenic disturbances experienced by the habitats.

Table 4. Floristic list of the top five regenerative plant species, showing high relative frequency/density and 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. AUF: Unexploited forests, DFO: Degraded forests, FAL: Post-cultivation fallows. NRI: Natural regeneration index (ratio between juveniles and adults), dbh < 1 cm: Seedlings, 1 cm ≤ dbh < 10 cm: Saplings, - : Species not inventoried, n= sample size. RF (Relative Frequency) and RD (Relative Density) values are expressed in percentage. The entire set of species studied is presented in the appendix.

Species	Family	dbh<1cm									1 cm≤dbh<10 cm								
		AUF (n=6628)			DFO (n=6660)			FAL (n=4676)			AUF (n=948)			DFO (n=2384)			FAL (n=1756)		
		RF	RD	NRI	RF	RD	NRI	RF	RD	NRI	RF	RD	NRI	RF	RD	NRI	RF	RD	NRI
<i>Albizia adianthifolia</i> (Schumach.) W. Wight	Fabaceae	4.17	6.76	29.87	4.62	9.01	12.50	5.50	5.39	15.75	4.86	3.38	2.13	5.17	6.71	3.33	5.54	5.47	6.00
<i>Albizia antunesiana</i> Harms	Fabaceae	4.17	4.16	23.00	3.08	2.52	12.92	5.11	3.25	50.67	2.78	1.69	1.33	4.13	1.85	3.38	4.54	6.15	36.00
<i>Anisophyllea boehmii</i> Engl.	Anisophylleaceae	3.13	1.39	18.40	2.77	2.88	48.00	1.97	1.71	40.00	3.47	2.95	5.60	2.07	0.67	4.00	7.06	3.19	28.00
<i>Baphia bequaertii</i> De Wild.	Fabaceae	5.56	7.91	23.82	4.31	5.29	16.76	5.11	6.50	50.67	3.47	3.38	1.45	5.68	5.70	6.48	3.53	7.06	20.67
<i>Brachystegia spiciformis</i> Benth.	Fabaceae	5.56	12.61	7.81	4.93	13.33	15.86	6.29	10.61	31.00	10.42	15.19	1.35	6.71	5.54	2.36	6.05	7.97	8.75
<i>Brachystegia wangermeeana</i> De Wild.	Fabaceae	4.51	10.80	4.39	4.93	20.48	16.43	5.90	27.89	42.06	6.94	17.30	1.01	6.20	29.53	8.48	7.56	23.46	13.29
<i>Combretum molle</i> R. Br ex G. Don	Combretaceae	2.43	1.21	40.00	0.92	0.42	9.33	3.54	3.08	72.00	0.69	0.84	4.00	1.03	0.50	4.00	1.51	1.37	12.00
<i>Combretum zeyheri</i> Sond.	Combretaceae	-	-	-	0.62	0.18	6.00	-	-	0.00	0.69	0.42	-	1.55	2.85	34.00	1.51	0.91	16.00
<i>Diploerhynchus condylocarpon</i> (Müll. Arg.) Pichon	Apocynaceae	2.78	2.96	19.60	4.31	2.46	5.47	1.18	0.86	6.67	3.47	5.91	5.60	5.68	8.39	6.67	2.02	1.82	5.33
<i>Ekebergia benguelensis</i> Welw. ex C.DC.	Meliaceae	2.08	0.54	36.00	1.54	0.36	24.00	2.36	1.45	-	-	-	0.00	1.55	0.50	12.00	2.02	1.14	-
<i>Garcinia huillensis</i> Oliv.	Clusiaceae	3.13	1.15	-	2.16	0.48	16.00	1.57	0.34	16.00	-	-	-	-	-	0.00	0.50	0.23	4.00
<i>Harungana madagascariensis</i> Lam. ex Poir.	Clusiaceae	1.04	0.36	-	2.77	2.04	136.00	1.57	1.28	-	-	-	-	-	-	0.00	1.01	0.46	-
<i>Hymenocardia acida</i> Tul.	Phyllanthaceae	-	-	-	1.23	1.26	42.00	1.18	5.99	-	0.69	0.42	-	1.55	1.34	16.00	1.01	0.46	-
<i>Isoberlinia angolensis</i> (Benth.) Hoyle & Brenan	Fabaceae	3.82	11.04	45.75	4.62	5.23	38.67	3.54	4.53	42.40	4.86	2.95	1.75	2.07	4.53	12.00	3.53	6.61	23.20
<i>Isoberlinia tomentosa</i> (Harms) Craib & Stapf	Fabaceae	0.35	0.18	-	-	-	0.00	-	-	0.00	-	-	-	4.13	4.53	21.60	2.02	2.28	8.00
<i>Julbernardia paniculata</i> (Benth.) Troupin	Fabaceae	0.69	0.12	1.60	1.85	1.44	24.00	-	-	0.00	0.69	0.84	1.60	1.55	0.67	4.00	1.01	1.14	20.00
<i>Markhamia obtusifolia</i> (Boulanger) Sprague	Bignoniaceae	0.35	0.12	2.67	1.23	0.66	44.00	1.97	1.20	-	1.39	0.84	2.67	1.03	1.01	24.00	-	-	-
<i>Mystroxydon aethiopicum</i> (Thunb.) Loes.	Celastraceae	0.69	0.24	16.00	0.92	0.90	60.00	0.39	0.09	-	-	-	0.00	1.03	0.50	12.00	-	-	-
<i>Ochna schweinfurthiana</i> F. Hoffm.	Ochnaceae	4.17	3.02	33.33	3.69	3.78	252.00	3.93	2.65	62.00	4.17	2.53	4.00	3.10	2.18	52.00	1.51	0.91	8.00
<i>Olex obtusifolia</i> De Wild.	Olcaceae	0.69	0.24	16.00	0.92	0.18	-	-	-	-	3.47	2.53	24.00	-	-	-	-	-	-
<i>Parinari curatellifolia</i> Planch. ex Benth.	Chrysobalanaceae	1.74	0.48	5.33	1.85	0.84	3.50	1.57	0.86	10.00	2.08	1.27	2.00	4.13	3.69	5.50	3.53	2.96	13.00
<i>Phyllocosmus lemaireanus</i> (De Wild. & T. Durand) T. Durand & H. Durand	Ixonanthaceae	2.78	2.41	32.00	3.08	2.58	43.00	3.93	1.97	92.00	2.78	2.53	4.80	2.58	1.01	6.00	0.50	0.23	4.00
<i>Pseudolachnostylis maprouneifolia</i> Pax	Phyllanthaceae	2.78	2.35	78.00	3.39	1.80	17.14	3.14	1.80	42.00	2.08	2.53	12.00	2.07	1.01	3.43	5.04	3.19	28.00
<i>Psorospermum febrifugum</i> Spach	Clusiaceae	4.51	4.47	296.00	2.77	2.04	68.00	4.32	1.88	-	-	-	0.00	1.03	0.34	4.00	3.02	1.37	-
<i>Pterocarpus angolensis</i> DC.	Fabaceae	0.35	0.06	0.29	-	-	0.00	0.39	0.17	1.60	5.56	5.49	3.71	3.10	1.17	3.50	3.02	1.59	5.60

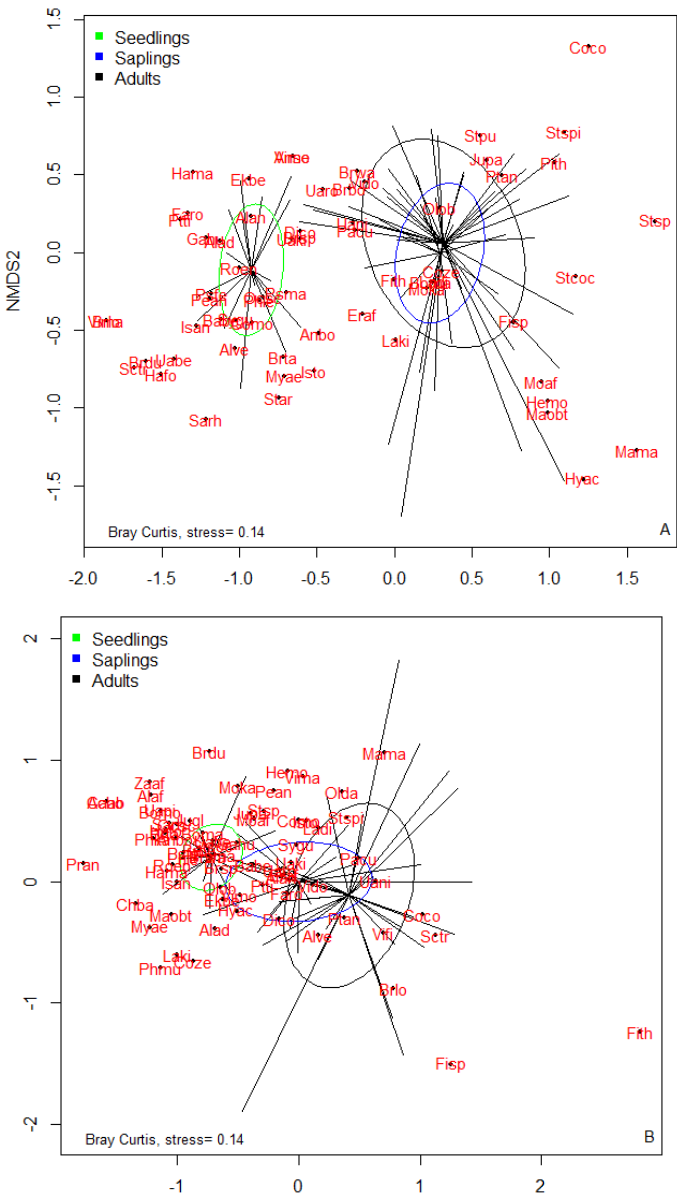
<i>Rothmannia engleriana</i> (K. Schum.) Keay	Rubiaceae	3.82	2.53	-	2.16	1.50		4.72	3.25	152.00	1.39	0.84	-	-	-	-	1.01	0.46	8.00
<i>Schrebera trichoclada</i> Welw.	Oleaceae	0.69	0.12	-	-	-	0.00	1.57	0.60	28.00	-	-	-	-	-	0.00	1.51	1.59	28.00
<i>Strychnos cocculoides</i> Boulanger	Loganiaceae	0.35	0.06	1.33	1.54	0.42	28.00	1.97	1.37	64.00	2.08	1.27	4.00	1.55	0.67	16.00	1.51	0.68	12.00
<i>Strychnos spinosa</i> Lam.	Loganiaceae	-	-	0.00	-	-	-	0.39	0.09	-	0.69	0.42	4.00	1.03	0.50	-	1.51	0.68	-
<i>Syzygium guineense</i> (Willd.) DC. subsp. macrocarpum	Myrtaceae	3.13	1.03	-	1.23	0.48	10.67	2.75	1.97	18.40	1.39	0.84	-	1.55	1.01	8.00	3.53	2.05	7.20
<i>Uapaca kirkiana</i> Müll. Arg.	Phyllanthaceae	4.51	3.14	13.00	2.46	2.70	6.43	0.79	0.34	4.00	4.17	3.80	2.25	3.62	2.35	2.00	2.02	1.37	6.00
<i>Vitex doniana</i> Sweet	Lamiaceae	0.35	0.06	4.00	0.62	0.18	2.40	0.79	0.34	5.33	0.69	0.42	4.00	1.03	0.34	1.60	2.02	1.14	6.67
<i>Vitex mombassae</i> Vatke	Lamiaceae	0.35	0.12	-	0.62	0.12	8.00	1.97	0.77	-	-	-	-	1.55	0.67	16.00	-	-	-

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. AUF: Unexploited forests, DFO: Degraded forests, FAL: 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		
	AUF	DFO	FAL	AUF	DFO	FAL
Dendrometric parameters						
Density (individuals/ha)	4142.50±2176.33ab	4185.00±1544.84a	2935.00±1567.39b	592.50±341.36a	1490.00±1133.21a	1110.00±954.82a
Mean square diameter (cm)	-	-	-	7.52±0.66a	7.16±0.48a	7.06±0.49a
Basal area (m2/ha)	-	-	-	2.49±1.26a	5.76±4.36a	4.25±3.71a
Floristic parameters						
Individuals	103.56±54.41ab	104.63±38.62a	73.38±39.18b	14.81±8.53a	37.25±28.33a	27.75±23.87a
Taxa_S	18.00±3.97ab	20.50±3.41a	16.06±3.99b	16.88±6.91a	19.13±10.83a	19.19±14.62a
Genera	15.25±4.09ab	17.75±3.49a	13.44±3.76b	7.81±3.62a	10.63±5.15a	10.13±6.39a
Families	9.56±2.78a	10.88±2.83a	9.31±2.89a	5.19±2.83a	6.50±3.18a	6.63±3.91a
Chao-1	21.14±5.85a	25.57±4.78a	21.30±8.29a	18.87±11.80a	20.80±11.22a	23.16±17.04a
Taxa_S/Chao-1	0.85	0.80	0.75	0.90	0.92	0.83
Fisher_alpha	6.78±1.66a	8.57±3.13a	6.99±2.11a	10.74±6.17a	9.96±11.91a	8.71±5.79a

3.3. Comparison of specific richness of woody species inventoried in regeneration and adult stands

The comparison of floristic lists among different strata within each habitat reveals that the stratum of seedlings (dbh < 1 cm) notably differs from other strata, except in post-cultivation fallows. Additionally, the floristic list of saplings (1 cm ≤ dbh < 10 cm) is nearly included within that of the adult stratum in each habitat. This situation is particularly observed in unexploited and degraded forests. Conversely, in post-cultivation fallows, the floristic lists of regeneration strata, though largely distinct, are fully encompassed within that of adult individuals. Furthermore, the strata of seedlings and saplings in different habitats are increasingly similar to each other, respectively (Figure 2).



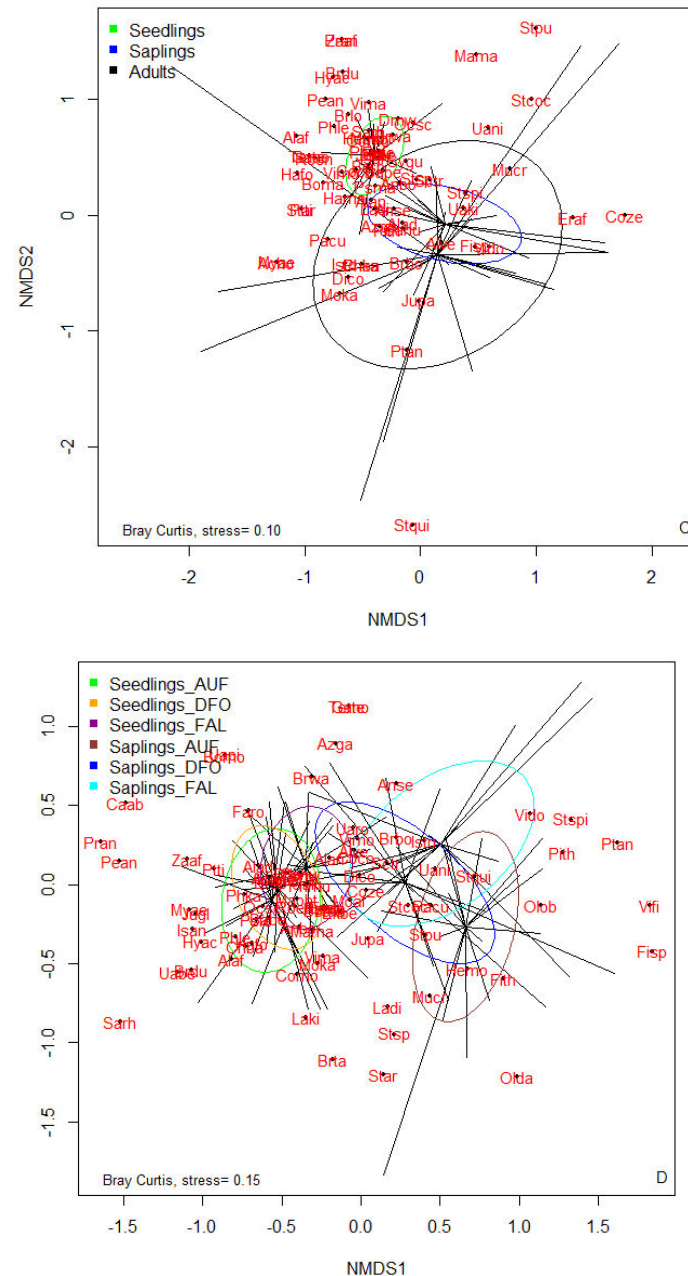


Figure 2. Comparison of floristic richness among different habitats and diameter classes of inventoried individuals. A: Unexploited forests, B: Degraded forests, C: Post-cultivation fallows, D: comparison of Seedlings-Saplings strata. Acho : *Acacia hockii*, Acpo : *Acacia polyacantha*, Alad : *Albizia adianthifolia*, Alaf : *Allophylus africanus*, Alan : *Albizia antunesiana*, Alve : *Albizia versicolor*, Anbo : *Anisophyllea boehmii*, Anse : *Annona senegalensis*, Azga : *Azanza garckeana*, Babe : *Baphia bequaertii*, Boma : *Bobgunnia madagascariensis*, Bomo : *Boscia mossambicensis*, Brbo : *Brachystegia boehmii*, Brdu : *Bridelia duvigneaudii*, Brlo : *Brachystegia longifolia*, Brsp : *Brachystegia spiciformis*, Brta : *Brachystegia taxifolia*, Brwa : *Brachystegia wangermeeana*, Caab : *Cassia abbreviata*, Chba : *Chrysophyllum bangweolense*, Coco : *Combretum collinum*, Como : *Combretum molle*, Coze : *Combretum zeyheri*, Dico : *Diplorhynchus condylocarpon*, Dimw : *Diospyros mweruensis*, Ekbe : *Ekebergia benguelensis*, Eraf : *Erythrophleum africanum*, Faro : *Faurea rochetiana*, Fisp : *Ficus* sp, Fith : *Ficus thonningii*, Gahu : *Garcinia huillensis*, Gate : *Gardenia ternifolia*, Hafo : *Haplocoelum foliolosum*, Hama : *Harungana madagascariensis*, Hemo : *Hexalobus monopetalus*, Hyac : *Hymenocardia acida*, Isan : *Isoberlinia angolensis*, Isto : *Isoberlinia tomentosa*, Jugl : *Julbernardia globiflora*, Jupa : *Julbernardia paniculata*, Ladi : *Lannea discolor*, Laki : *Landolphia kirkii*, Mama : *Marquesia macroura*, Maob : *Markhamia obtusifolia*, Moaf : *Monotes africanus*, Moka : *Monotes katangensis*, Mucr : *Multidentia crassa*, Myae : *Mystroxydon aethiopicum*, Oesc : *Ochna schweinfurthiana*, Olda : *Oldfieldia dactylophylla*, Olob : *Olax obtusifolia*, Pacu : *Parinari curatellifolia*, Pean : *Pericopsis angolensis*, Phka : *Philenoptera katangensis*, Phle : *Phyllocosmus lemaireanus*, Phmu : *Phyllanthus muellerianus*, Pith : *Piliostigma thonningii*, Pran : *Protea angolensis*.

Psfe : *Psorospermum febrifugum*, Psma : *Pseudolachnostylis maprouneifolia*, Ptan : *Pterocarpus angolensis*, Ptti : *Pterocarpus tinctorius*, Roen : *Rothmannia engleriana*, Sarh : *Salacia rhodesiaca*, Sctr : *Schrebera trichoclada*, Star : *Steganotaenia araliacea*, Stco : *Strychnos cocculoides*, Stpu : *Strychnos pungens*, Stqu : *Sterculia quinqueloba*, Stsp : *Strychnos* sp, Stspi : *Strychnos spinosa*, Sygu : *Syzygium guineense* subsp *macrocarpum*, Temo : *Terminalia mollis*, Uabe : *Uapaca benguelensis*, Uaki : *Uapaca kirkiana*, Uani : *Uapaca nitida*, Uapi : *Uapaca pilosa*, Uaro : *Uapaca robynsii*, Vido : *Vitex doniana*, Vifi : *Vitex fischeri*, Vima : *Vitex madiensis*, Vimo : *Vitex mombassae*, Zaaf : *Zanha africana*. AUF: Unexploited forests, DFO: Degraded forests, FAL.

However, the Jaccard similarity of floristic lists among different strata in the three habitats is depicted in the table below (Table 6). 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%). Nonetheless, 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 6. Jaccard similarity between floristic lists of different strata in the three habitats. AUF: unexploited forests, DFO: degraded forests, FAL: post-cultivation fallows, <1: Seedlings; ≥1: Saplings; ≥10: Adults. Relative values are presented in decimal form.

	AUF<1	DFO<1	FAL<1	AUF≥1	DFO≥1	FAL≥1	AUF≥10	DFO≥10
DFO<1	0.65							
FAL<1	0.68	0.65						
AUF≥1	0.65	0.55	0.50					
DFO≥1	0.71	0.59	0.55	0.92				
FAL≥1	0.67	0.64	0.74	0.63	0.68			
AUF≥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	
FAL≥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 (density) and floristic parameters decrease according to the level of habitat disturbance (Tables 2 and 3). This situation is attributed to both natural and particularly anthropogenic disturbances experienced by the human-modified habitats, primarily agriculture and charcoal production. Indeed, the conversion of forested lands into agroecosystems and charcoal production leads to deforestation and fragmentation of the *miombo* woodlands, particularly in the Lubumbashi region [15]. According to Refs. [18,61], anthropogenic activities, often carried out through rudimentary techniques, disrupt the ecological balance of ecosystems, subsequently affecting the structure and composition of the *miombo* woodlands. These results, found in the present study, corroborate those of other research conducted in the *miombo* ecoregion [2,14,21,35,50,62], showing that habitat floristic composition and diversity decline as anthropogenic disturbances increase.

Furthermore, the results of the present study were obtained through floristic inventories conducted on plots along a transect. This method has the advantage of reducing errors in alignment, angles, and width measurements that may arise when setting up continuous plots. Additionally, other methods, such as random sampling or systematic inventories, can be used and produce reliable results. However, these methods require more time and a larger team to conduct the floristic inventory, despite producing indisputable results [63]. Moreover, a square (rectangular) shape was

used for inventory plots in the present study. This shape, for the same area, has the advantage of enumerating more individuals than other shapes and is most recommended in the open and dense forests of the tropical region [64,65]. However, the challenges of this shape lie in measuring distances, angles, and selecting their orientation when installing the plot. Additionally, this square shape often encounters numerous cases of uncertainty regarding whether border trees belong to the plot or not. Therefore, the circular shape would undoubtedly be more commonly used. This latter shape is the most objective in terms of measurements and results, as its installation does not require a preferred direction, thereby overcoming the challenges of the square shape as long as the circular plot is not too large [31]. Nevertheless, the inventory method, shape, and dimensions of the plots used in the present study have been employed by several authors in regeneration studies in the *miombo* ecoregion [6,14], justifying the choice of this methodology in the present study.

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 and 5). 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 [66]. This resource availability, coupled with low inter- and intraspecific competition, allows woody species, particularly pioneer and resilient species to anthropogenic disturbances (present in the herbaceous stratum and in 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 [67]. 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 [68,69]. These results corroborate previous research [14,51,70,71] 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 [68,72].

However, the impact of anthropogenic disturbances on species diversity in degraded forests is not systematically negative. Indeed, 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 [73]. This situation has already been highlighted in previous studies conducted in the *miombo* ecoregion [34,74], demonstrating that floristic characteristics such as stand structure and species richness of anthropized habitats can reach values higher than those of unexploited mature forests after anthropogenic disturbances cease. Moreover, according to these same authors, these recorded disturbances have a long-term effect on the structure of populations and the specific richness of these habitats, keeping these parameters less similar compared to intact *miombo* woodlands after 20 to 35 years of regeneration [35].

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, particularly in vulnerable anthropized habitats. 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 [75], in anthropized areas near settlements for various needs [6]. In addition to this, late and repetitive bushfires [76] characterizing the *miombo* ecoregion [44,77-79] and particularly the Lubumbashi region [80], 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, in particular, induce the return of local communities to regenerating forest stands. This situation contributes to maintaining a high level of forest degradation [81] 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 basic necessities [45]. This further disrupts the process of woody species regeneration and ongoing *miombo* woodlands reconstitution in post-cultivation fallows [82]. 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 unexploited forests and degraded forests exhibit higher similarities compared to post-cultivation fallows (Figure 2 and Table 6). 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 [50,83],

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 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 [84]. 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 [5,74]. 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 enrichment 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 almost similar to the previously exploited forest. In this regard, these restored habitats would continue to support the survival of both rural and urban populations by providing usual ecosystem services [85]. However, selecting fast-growing native species like *Pterocarpus tinctorius* Welw. and *Combretum collinum* Fresen. is necessary for short-term *miombo* woodlands reconstitution [86]. Nevertheless, similar to ANR habitats, reforested or enriched habitats should be protected from anthropogenic intrusions [6,35] and late, repetitive bushfires [80,87].

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 [21,35,51]. 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 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' number are high in degraded forests. Although 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.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1

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