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Influence of a disturbance gradient on natural regeneration and understory diversity in semi-deciduous dense forests of Cameroon

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Abstract

This study examines the effects of anthropogenic disturbances on natural regeneration patterns in Angossas Communal Forest (ACF) by conducting a systematic forest inventory of tree species across 40 ha. Disturbance intensity and land-use types were characterised, and woody plants were grouped into diameter-based size classes to evaluate understorey structure and diversity. Tree stumps were inventoried to assess the regeneration capacity of damaged tree species.

The understorey accounted for 80.85% of total stem density, with medium-sized trees as the main component of regeneration (66.14%). Regeneration patterns varied significantly along the disturbance gradient ($p < 0.05$), with the highest density of medium-sized trees observed in highly disturbed areas (875 stems ha^{-1}) and peak densities of small trees in lightly disturbed zones (1467 stems ha^{-1}). Mature secondary forests exhibited the highest understorey density of medium-sized trees (5267 ± 2838 stems ha^{-1}), along with moderate densities of small trees and the greatest species diversity (Shannon-Wiener index: 2.7–2.9), despite low floristic similarity among strata (10%).

Vegetative regeneration was particularly active, with 78.78% of stumps producing an average of 5.00 ± 3.92 sprouts per stump, showing significant correlations with stump diameter and height ($p < 0.05$). These findings suggest partial ecosystem resilience driven by vigorous vegetative regeneration, alongside ongoing limitations in recruitment success.

Our results show that vegetative regeneration is key to post-disturbance recovery in the Angossas Communal Forest, while seed-based recruitment remains limited along the disturbance gradient. These findings suggest a moderate degree of natural regeneration under current disturbance regimes and emphasise the significance of disturbance intensity and land-use context in shaping forest regeneration dynamics.

Keywords Natural regeneration, Understory vegetation, Disturbance effects, Sustainable agricultural practices, Ecological vulnerability, Forest conservation, Ecosystem resilience

1 Introduction

Natural regeneration is crucial for the survival of forest ecosystems amidst global change [1, 2]. It acts as a key indicator of vegetation structure [3] and maintain forest dynamics and stability [4]. The understorey, which harbours 60% of plant diversity [5], supports forest renewal through complex mechanisms, including seed rain, seed banks, and seedling-sapling interactions [6, 7]. Understorey growth relies on light availability and other resources, promoting species conservation and forest recovery [8, 9]. However, ongoing disturbances reduce understorey density [7] and disrupt ecological processes, leading to significant biodiversity loss [10, 11]. Given the escalating land-use pressures and the critical role of forests, the regenerative potential of tropical forests has gained increasing attention [12]. Understanding how disturbance differentially affects the understorey is essential for optimising forest management and conservation strategies.

Studies have highlighted the diversity and ecological significance of the forest understorey [5, 13]. This layer supports the growth of native flora, enhancing ecosystem stability and species heterogeneity [14, 15]. At the landscape level, such diversity reflects vegetation resilience and its ability to maintain biodiversity. Regeneration relies on key mechanisms, including seed rain, seed banks, and seedling–sapling–resprout interactions [6, 7]. However, this critical process is increasingly compromised by ongoing disturbances, threatening ecosystem resilience and functionality.

While disturbances naturally shape forest structure and composition [16, 17], persistent anthropogenic activities, such as fuelwood extraction, overharvesting of non-timber forest products (NTFPs), and slash-and-burn agriculture, lead to biomass loss and disrupt critical ecological processes [18, 19]. These actions drive biodiversity decline [20], alter juvenile banks in ways that conflict with the species' ecological requirements [5] and inhibit natural succession, thereby promoting forest degradation [21] and severely constraining forest regeneration [7, 18]. Their harmful impacts on forest integrity and regeneration dynamics are well-documented in the scientific literature [22–24].

Anthropogenic disturbances significantly damage woody vegetation [25], triggering complex natural regeneration processes. This regeneration represents the most suitable mechanism for restoring ecosystem [26, 27]. It maintains species composition and facilitates post-disturbance recovery [28]. However, disturbances profoundly alter forest structure [9, 29, 30], promoting pioneer species through canopy fragmentation [28, 31, 32]. This dynamic may lead to long-term biomass overcompensation [33], although it follows the ecological path of variables.

Forest ecosystems respond differently to disturbance regimes. Recurrent disturbances favour ruderal species with competitive pioneer traits, while disadvantaging climax species that require stable environmental conditions [34]. For instance, intensive clear-cutting or repeated fires lead to vegetation homogenization, impairing tree recruitment and sapling development [29, 35]. In contrast, moderate disturbances, such as selective logging, can enhance spatial heterogeneity and create ecological niches for specialist species [36–38]. In contrast, minimally disturbed ecosystems exhibit asymmetric competition dominated by mature trees, which significantly suppresses understorey growth and development through shading effects [39, 40]. While anthropogenic disturbances invariably alter forest structure and functioning, their long-term impacts ultimately depend on species' regenerative capacity.

Woody plants regenerate through two pathways: seedling recruitment (sexual) and vegetative resprouting (asexual), both of which are vital for forest dynamics [41, 42]. However, the impacts of disturbance on these mechanisms remain poorly understood. Vegetative regeneration enhances post-disturbance recovery [43] and species persistence [44], but the effect of disturbance on ecosystem services and resilience requires further research [45, 46]. Understanding these processes is critical for conservation [20, 25], particularly in understudied Cameroonian forests.

The Angossas Communal Forest (ACF) exemplifies the current state of Congo Basin forests, characterised by widespread illegal logging, unsustainable resource extraction, and land-use changes [47, 48]. These anthropogenic pressures, exacerbated by population growth, disrupt natural regeneration mechanisms [49, 50], threatening forest stability where regeneration is typically characterised by low density and diversity [7, 51]. Therefore, this study aims to assess the differential effects of anthropogenic disturbances on forest regeneration and the response of damaged trees, with the ultimate goal of developing sustainable management strategies to enhance the resilience of ACF. Specifically, this study will: (1) characterise understorey vegetation diversity and regeneration patterns across disturbance gradients and land-use types; (2) evaluate the vegetative reproduction capacity of damaged trees and the effects of basal diameter and predictive factors on stump resprouting; and (3) identify the morphological characteristics of stumps that influence vegetative regeneration following disturbance.

2 Materials and methods

2.1 Study area

The study was carried out in the Angossas Communal Forest (ACF), a semi-deciduous dense forest within the Guineo-Congolian domain [52]. Located in the Mbaonz municipality (Haut-Nyong Department, East Region of Cameroon), the site extends geographically between 4°4'60"N and 12°58'60"E (Fig. 1) and covers 22,120 ha, divided into two distinct blocks. The topography features gently rolling terrain with an average elevation of 600 m. Slopes ranging from 0% to 5% indicate low erosion susceptibility and favourable plant growth conditions. The equatorial climate exhibits four unevenly distributed seasons, with mean annual rainfall of 1,600 mm and temperatures averaging 22–25 °C. Soils are predominantly ferrallitic and hydromorphic, although their fertility is increasingly compromised by the intensification of slash-and-burn shifting agriculture [53]. Despite this, the area remains a biodiversity hotspot where illegal timber extraction and harvesting of non-timber forest products (NTFPs) constitute major anthropogenic pressures.

2.2 Sampling design and methodology

The sampling unit consisted of linear transects, a method recommended for studies of natural regeneration [54]. This approach allows rapid, straightforward estimation of tree diversity and density while facilitating the assessment of vegetation variation along environmental gradients or across different habitats [55]. Ten straight transects measuring 2,000 m in length and 20 m in width (4 ha per transect) were established using a systematic sampling design. Transects were regularly spaced at 1 km intervals to ensure homogeneous coverage of the study area and to reduce spatial autocorrelation among

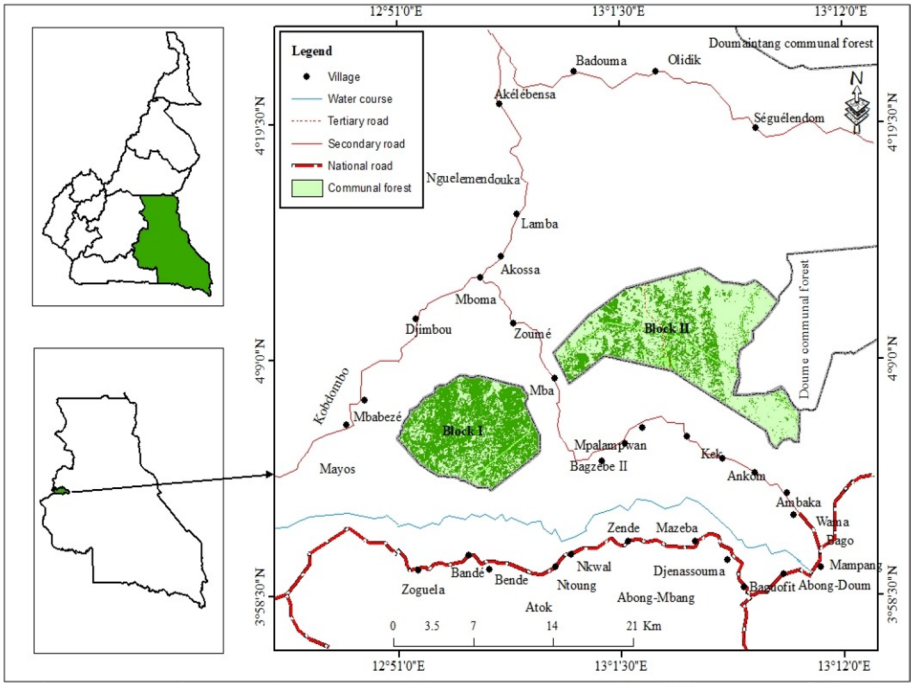

Fig. 1 Location of the study area

sampling units, in accordance with classical parallel-transect approaches in forest ecology [56].

The number of transects was determined based on the total area of Block 1 (8,120 ha), specifically within two annual cutting units, one previously logged and the other relatively intact. This design ensured sufficient replication to allow robust statistical comparisons between logged and unlogged areas. Transects were oriented along a northwest–southeast axis, corresponding to the main geographical gradient extending from the village of Mba. This orientation was selected to capture potential gradients in environmental conditions and anthropogenic pressures, while minimising biases associated with linear landscape features such as roads or streams [57]. Transect starting points were defined systematically using a georeferenced map of the study block, beginning at the northwestern boundary and shifting each successive transect south-eastward by 1 km. All transects were georeferenced using GPS to ensure reproducibility and spatial accuracy of the sampling design. Each transect was subdivided into 100 m segments to improve the recording of individual plants [58]. To accurately evaluate regeneration, nested quadrats of 10 m × 10 m (100 m^2) and 5 m × 5 m (25 m^2) were placed at 100 m intervals along the main transect. These understorey trees were referred to as small and medium-sized. Diameter classes were used as size-based categories and do not necessarily correspond to ontogenetic or life-history stages across species. A total area of 40 ha was surveyed, representing a sampling intensity of 0.18%.

2.3 Disturbance assessment and inventory data collection

Field data on forest structure and disturbance levels were systematically collected along the established transects. At 100 m intervals, forest condition was assessed through physiognomic observations and classified into four disturbance categories following Tchouto et al. [3]: Category A: Severely degraded (> 50% canopy openness); Category

B: Moderately disturbed (25–50% degradation, fragmented canopy with retained forest dominance); Category C: Lightly disturbed (< 25% human-induced canopy gaps) and Category D: Relatively intact (dense canopy, no anthropogenic degradation except hunting and NTFP collection). Land Use Types (LUTs) were characterised using integrated physiognomic and ecological criteria [59], including: dominant species composition, canopy closure status (open/closed), topographic features and understorey vegetation density. The nested plots of 10 m × 10 m and 5 m × 5 m, systematically established within each main plot, inherited the same disturbance class and land-use type as the associated 100 m × 20 m plot, ensuring spatial and hierarchical consistency in disturbance attribution. Tree identification was carried out based on diagnostic characteristics and diameter measurements (DBH). Species identification was performed in the field using standard floristic references and the expertise of experienced botanists; no voucher specimens were collected because the study was based exclusively on non-destructive vegetation inventories. Large trees with a diameter > 10 cm were measured at 1.30 m above ground level [60]. Medium-sized trees (defined as those with 5 cm ≤ DBH < 10 cm) were surveyed in 100 m^2 quadrats, while small trees (DBH < 5 cm) were recorded in 25 m^2 quadrats [61]. For trees with irregular stem shapes, the diameter was measured 30 cm above protrusions [62].

2.4 Stump identification and parameter measurement

Stumps (both dead and living, with or without sprouts) were systematically identified along each transect based on foliage of resprouts, wood characteristics and bark features [38]. The decomposition state of each stump was recorded, and the cause of damage was identified and documented [25]. Basal diameter (BD) was measured at 20 cm below the cutting level, as most stumps were too short to measure at 1.30 m [25]. Conversely, stump height was measured from the root collar to the cutting point. A total of six attributes were recorded: (1) species name (sprouted or non-sprouted stumps); (2) stump diameter; (3) stump height; (4) number of living or dead sprouts; (5) basal diameter and height of the dominant sprout; (6) degree of stump decomposition [43].

2.5 Data analysis

2.5.1 Characterisation of plant diversity and regeneration along disturbance and land-use gradients

The density of small and young trees was estimated for each land-use type along the disturbance gradient. Species richness within a transect was calculated as the total number of distinct species observed in a given stratum. Diversity indices such as the Shannon-Wiener index, Simpson index, Pielou's evenness, and Fisher's alpha were computed based on species presence and abundance. These indices account for species number, relative abundance, and dominance at the given scale [61]. Species similarity between different strata and land-use types was quantified using the Jaccard index (1-Jaccard) [63]. The natural regeneration index (NRI) for each transect was calculated, and a mean value was derived. This index was obtained as the ratio of seedlings (DBH ≤ 10 cm) to large trees [64]. To assess regeneration status, the evenness index (R) was calculated using the following formula [64]:

$$R = \frac{H\prime}{Mmax},$$

where H corresponds to the Shannon–Weaver diversity index (observed diversity), and H_{max} represents the theoretical maximum diversity, calculated under the assumption of equal frequencies of biological traits.

2.5.2 Vegetative reproduction of damaged trees, predictive factors, and relationships between stump characteristics and sprouting potential

The total number of stumps was recorded for each species, with their density extrapolated to a per-hectare basis. The vegetative reproduction (VR) rate was calculated at the species and landscape scales. The stump cross-section was examined to determine the disturbance type (natural or anthropogenic). The mean number of sprouts per stump was used to estimate the VR potential, defined as the ratio of sprouts per stump to the total number of recorded stumps, using the following equation [38].

$$Stump\ sprout\ rate = number\ of\ living\ stumps\ of\ one \frac{species}{total} number\ of\ stumps\ of\ this\ species$$

2.6 Statistical analyses

Several statistical approaches were used to analyse the data. After verifying non-normality of the data using homogeneity tests, an analysis of variance (ANOVA) was performed to assess the effects of land-use types on ecological variables along the disturbance gradient and examine relationships between tree reproductive capacity and biotic factors. A permutational multivariate analysis of variance (PERMANOVA) was applied to evaluate differential disturbance effects on understorey vegetation [65, 66] using the R software with the vegan package (function *adonis2*). This analysis was based on Bray–Curtis similarity and 9,999 permutations.

The structure and distribution of understorey communities, in terms of species composition, across disturbance gradients and land-use types were analysed using non-metric multidimensional scaling (NMDS), performed with the vegan and ggplot2 packages in R (metaMDS function). The NMDS analysis is based on a Bray–Curtis dissimilarity matrix calculated from species abundance data. To visualise intra-group variability, confidence ellipses were plotted for each land-use type, centred on the group centroids and calculated using a standard deviation of the scores along the ordination axes.

In addition, an agglomerative hierarchical classification was performed using the same Bray–Curtis dissimilarity matrix and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA), in accordance with standard approaches in community ecology [67]. Spearman's rank correlations were used to quantify associations between stump attributes and sprouting potential, while linear regression models were applied to analyse the influence of stump parameters on regeneration potential [68]. Spearman's rank correlations were employed to explore non-parametric, monotonic associations between stump attributes and sprouting potential without assuming normality or linearity of the data [69]. In contrast, linear regression models were used to quantify and predict the effect of stump parameters on regeneration potential and to estimate the relative contribution of each predictor, which is appropriate when the objective is explanatory and predictive modelling [68].

3 Results

3.1 Vegetation diversity and regeneration, differential effects of disturbance and land-use types in the understorey

3.1.1 Vegetation diversity and regeneration, differential effects of disturbance

The understorey accounted for 80.85% of total recorded tree density, with a marked predominance of Medium-sized trees (66.14%; 2108 ± 1516.25 stems. ha^{-1}) over small trees (33.86%; 1.08 ± 155 stems. ha^{-1}). For NRI (5.26 ± 1.01), the evenness index (R) was 0.003, approaching zero, confirming strong understorey dominance. PERMANOVA revealed significant variation in vegetation attributes along the disturbance gradient (F = 1,176, $p < 0.001$ for medium-sized trees; F = 89.46, $p < 0.0001$ for small trees). medium-sized trees exhibited significantly higher density in heavily disturbed zones (A: 430.76 ± 14; B: 875.47 ± 39.65 stems. ha^{-1}; F = 2.08, $p = 0.0004$) compared to relatively undisturbed areas (C/D: 3750.99 ± 15.03; 3000 ± 15.13 stems. ha^{-1}). In contrast, small trees reached peak density in less disturbed zones (C: 1466.66 ± 101 stems. ha^{-1}; F = 12.24, $p = 0.005$; Table 1).

Species dominance varied significantly with disturbance intensity (F = 628.1, $p = 0.0011$ for medium-sized trees; F = 628.1, $p = 0.002$ for small trees). Diversity indices peaked in zones C/D for medium-sized trees (Shannon: 2.91/2.74 and Simpson index: 0.91/0.89; F = 327.3, $p < 0.001$), while seedlings showed reduced diversity, though still highest in zone C (Shannon = 0.72; Simpson = 0.45; F = 705.8-248.20, $p < 0.05$; Table 1). Total species richness reached 99 ± 0.38 species, with maximum values in zone D (20.91 ± 10.40 species; $p < 0.001$ Fig. 2a). Medium-sized trees exhibited lower species richness (1.33 ± 0.51 species, $p < 0.000$), but values remained significantly higher in less disturbed C/D zones (Fig. 2b, $p < 0.05$).

For the Pielou evenness index, no significant difference ($p = 0.0652 > 0.05$) was observed between disturbance levels in medium-sized trees, unlike in small trees ($p = 0.003$). In contrast, for the Alpha-Fisher index, variation was significant in medium-sized trees ($p = 0.0003$), with the highest values recorded in relatively undisturbed areas (C: 31.85 ± 12.99; D: 31.14 ± 16.7). In small trees, the Alpha-Fisher index did not vary significantly ($p = 0.052$; Table 1).

3.1.2 Characterisation of understorey diversity and density across land-use types

Results demonstrate significant variations in ecological parameters and understorey diversity (Fig. 3; $p < 0.05$). Small tree density showed marked differences among land-use types (CV = 10.69%, $p = 0.002$), reaching its maximum in Mature Secondary Forests (MSF: 1150 ± 780 trees ha^{-1}), a value significantly higher than in fallows (600 ± 284 trees ha^{-1}; $\chi^2 = 11$, df = 3, $p = 0.005$). This density was strongly influenced by disturbance level (A: $\chi^2 = 14.03$, df = 4, $p = 0.002$). Medium-sized tree density varied considerably and significantly among LUTs (FCC; 55.21%, $p = 0.001$), with higher densities in LUTs with higher disturbance intensity. The highest densities occurred in MSF ($\chi^2 = 11$, df = 4, $p < 0.001$; 5,27 ± 2,84 trees ha^{-1}), which were less disturbed areas (C/D), followed by fallows (733.30 ± 372 trees ha^{-1}). Highly disturbed areas, including croplands (CL), swamps, and Young Secondary Forests (YSF), revealed lower densities for small trees (A, B: 400 trees ha^{-1}; FCC = 10.69; $p = 0.002$) but higher densities for saplings (733.3 ± 372 trees ha^{-1}; $\chi^2 = 12.5$, df = 1, $p < 0.001$).

Table 1 Results of the permutational multivariate analysis of variance (PERMANOVA; $N = 999$ permutations) showing the effects of the disturbance gradient on diversity indices

Variables	Medium-sized trees					Small trees				
	A	B	C	D	*P*-value	A	B	C	D	*p*-value
Density (ind./ha)	430.76 ± 14^{a}	875.47 ± 39.65^{a}	3750.99 ± 15.03^{b}	3000 ± 15.13^{c}	0.0004	933.33 ± 46.88^{a}	600 ± 21.08^{a}	1466.66 ± 101.84^{a}	533.33 ± 21.55^{a}	0.004
Dominance	0.32 ± 0.20^{a}	0.21 ± 0.02^{b}	0.08 ± 0.01^{c}	0.17 ± 0.01^{b}	0.0011	0.70 ± 0.25^{ab}	0.75 ± 0.27^{b}	0.55 ± 0.22^{a}	0.83 ± 0.25^{b}	0.002
Shannon	1.26 ± 0.39^{a}	1.87 ± 0.65^{b}	2.91 ± 0.59^{c}	2.74 ± 0.70^{d}	0.0009	0.42 ± 0.03^{ab}	0.34 ± 0.07^{b}	0.72 ± 0.41^{a}	0.35 ± 0.03^{b}	0.001
Simpson	0.67 ± 0.20^{a}	0.79 ± 0.21^{b}	0.91 ± 0.13^{c}	0.89 ± 0.13^{c}	0.0002	0.29 ± 0.25^{ab}	0.25 ± 0.02^{b}	0.45 ± 0.22^{a}	0.17 ± 0.05^{b}	0.012
Piélou	0.91 ± 0.26^{a}	0.93 ± 0.03^{a}	0.94 ± 0.13^{a}	0.94 ± 0.12^{a}	0.0652	0.61 ± 0.05^{ab}	0.5 ± 0.05^{a}	0.76 ± 0.36^{b}	0.33 ± 0.05^{ab}	0.003
Alpha-Fisher	5.40 ± 6.18^{a}	13.89 ± 4.89^{a}	31.85 ± 12.99^{b}	31.14 ± 16.7^{b}	0.0003	1.75 ± 1.05^{a}	0^{a}	1.73 ± 0.85^{a}	0^{a}	0.052
Total density = 2108 ± 1516.25						Total density = 1079 ± 155				
NRI = 5.26 ± 1.01; R = 0.003										
F = 1176 ; *p*-value = 0.0001 ; $N = 999$						F = 89.46 ; *p*-value = 0.00001; $N = 999$				

Values are presented as mean ± standard deviation. Disturbance level: A: Severely degraded (> 50% canopy openness); Category B: Moderately disturbed (25–50% degradation); Category C: Lightly disturbed (< 25% human-induced canopy gaps) and Category D: Relatively intact

Means followed by the same letter within columns are not significantly different according to the Kruskal–Wallis test at $p < 0.05$. $n = 10$

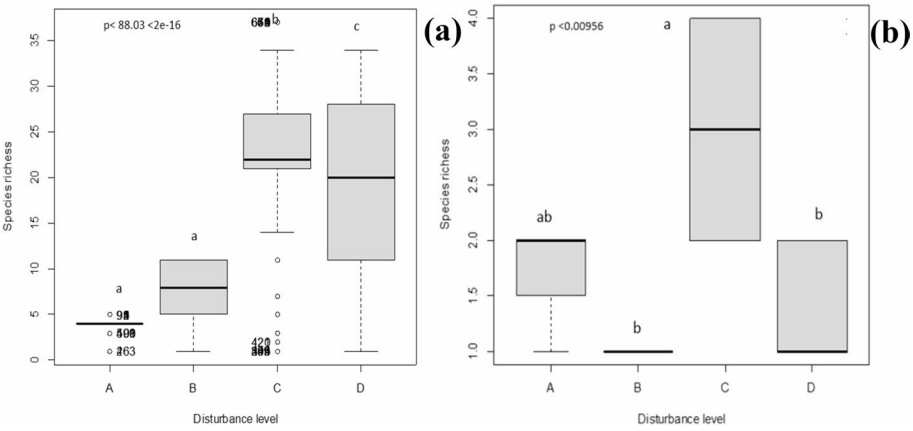

Fig. 2 Species richness within the understorey vegetation according to disturbance intensity level: (**a**) Small trees; (**b**) Medium-sized trees

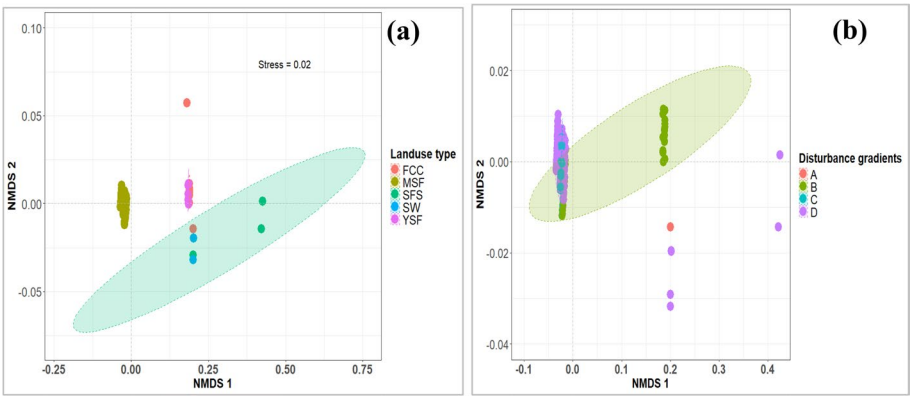

Fig. 3 Non-metric multidimensional scaling (NMDS) ordination showing variations in understorey species composition across land-use types and disturbance gradients. Points represent sampling plots, coloured by land-use type and disturbance level. (**a**). Land-use types; (**b**). Disturbance gradients. Legend. Land-use types: MSF, mature secondary forest; YSF, young secondary forest; SW, swamp; FSF, seasonally flooded swamp; FCC, food crop cultivation. Disturbance gradients: A, severely degraded (> 50% canopy openness); B, moderately disturbed (25–50% degradation); C, lightly disturbed (< 25% human-induced canopy gaps); D, relatively intact. Ellipses represent the dispersion of sampling plots for each disturbance level and land-use type and were drawn using one standard deviation from the group centroid, illustrating within-group variability in species composition. The stress value (0.02) indicates a good fit of the ordination

Species richness varied significantly among LUTs (small trees: FCC = 23.75%, $p < 0.004$; saplings: FCC = 20.74%, $p = 0.007$), consistently peaking in MSF (saplings: 30.75 ± 13.34 species; small trees: 2.5 ± 1.19 species; $p < 0.05$). Species dominance showed contrasting patterns: non-significant for small trees ($p = 0.054$) despite notable variability (CV = 13.25%), but significant for saplings ($p = 0.041$) with high variability (CV = 36.39%) and maximum values in less disturbed MSF (C/D: 30.75 ± 13.34 species; Table 2). The differences in understorey species composition and dominance among land-use types (Fig. 3a) and across the disturbance gradient (Fig. 3b) were confirmed by non-metric multidimensional scaling (NMDS). Species similarity was low between small trees and large trees (Jaccard = 0.10), unlike Medium-sized trees, which showed greater similarity to adults (Jaccard = 0.71 and 0.14 for large trees and Medium-sized trees, respectively; Table 3).

Table 2 Diversity indices and density metrics of understorey vegetation by land-use type and disturbance level

Variables	MSF	YFS	Swamp	FSF	FCC	Fallow	CV (%)	*p*-value
Small trees								
Disturbance level	C	B	C	D	A	A		
Density	1110 ± 78	400	400	160	400	600 ± 184	10.69	**0.002**
Species Richess	2.5 ± 1.19	1	1	2	1	1.50 ± 0.71	23.75	**0.004**
Dominance	0.58 ± 0.29	1	1	0.5	1	0.75 ± 0.35	13.25	0.054
Shannon-index	0.77 ± 0.53	0	0	0.5	0	0.35 ± 0.49	60.35	**0.005**
Simpson-index	0.46 ± 0.30	0	0	0.69	0	0.25 ± 0.35	2.15	**0.001**
Medium-sized trees								
Disturbance	C/D	B	C/D	C	A	A		
Density	5267 ± 28	425 ± 305	200	250 ± 191	733.30 ± 372	400	55.21	**0.001**
Species Richess	30.75 ± 13.34	3.88 ± 2.59	2	2.25 ± 1.5	6.33 ± 2.87	4	20.74	**0.007**
Dominance	5.52 ± 2.60	0.1 ± 0.30	0.5	0.65 ± 0.40	19.70 ± 6.5	0.25	36.39	**0.041**
Shannon-index	3.15 ± 0.47	1.12 ± 0.76	0.69	0.61 ± 0.71	1.73 ± 0.41	1.38	27.04	**0.031**
Simpson-index	0.94 ± 0.02	0.57 ± 0.36	0.7	0.35 ± 0.40	0.81 ± 0.08	0.75	20.87	0.073

land-use type: *MSF* Mature secondary forest, *YFS* Young secondary forest, *FSF* Seasonally flooded swamp, *FCC* Food crop cultivation, *CV* variation of coefficient (%)

Table 3 Jaccard similarity index (%) between regeneration stages (Small trees and medium-sized trees) and the upper canopy layer

	Small trees	Medium-sized trees	Large trees
Seedlings	0		
Saplings	0.14	0	
Larges trees	0.10	0.71	0

Hierarchical clustering distinguished two main groups among land use types (Fig. 3a). Group 1, composed solely of mature secondary forests, was characterised by high species abundance and exhibited unique traits within the study area. Group 2 showed strong homogeneity, with marked similarities between young secondary forests and crop fields, and ecological proximity between swamps and periodically flooded swamps. Fallows, distinguished by high heterogeneity, were predominantly composed of fast-growing pioneer species.

In contrast, the ten most abundant understorey species were divided into four groups (Fig. 3b). Group 1, the largest, included six species: *Afraegle paniculata*, *Enanthia chlorantha*, *Hexalobus crispiflorus*, *Xylopia* sp., and *Nesogordonia papaverifera*. These species are shade-tolerant but require small gaps for growth and are typical of relatively undisturbed mature and young secondary forests. Group 2, represented by *Oddoniodendron normandii*, displayed unique ecological characteristics and high heterogeneity. Its presence indicates a state of mature forest. Groups 3 and 4 shared similar ecological and adaptive traits, including *Annona* sp. and *Coffea* sp. (Group 3), and *Amphimas pterocarpoides* and *Chrysophyllum boukokoense* (Group 4). These species are highly shade-tolerant and require high atmospheric humidity (Fig. 4).

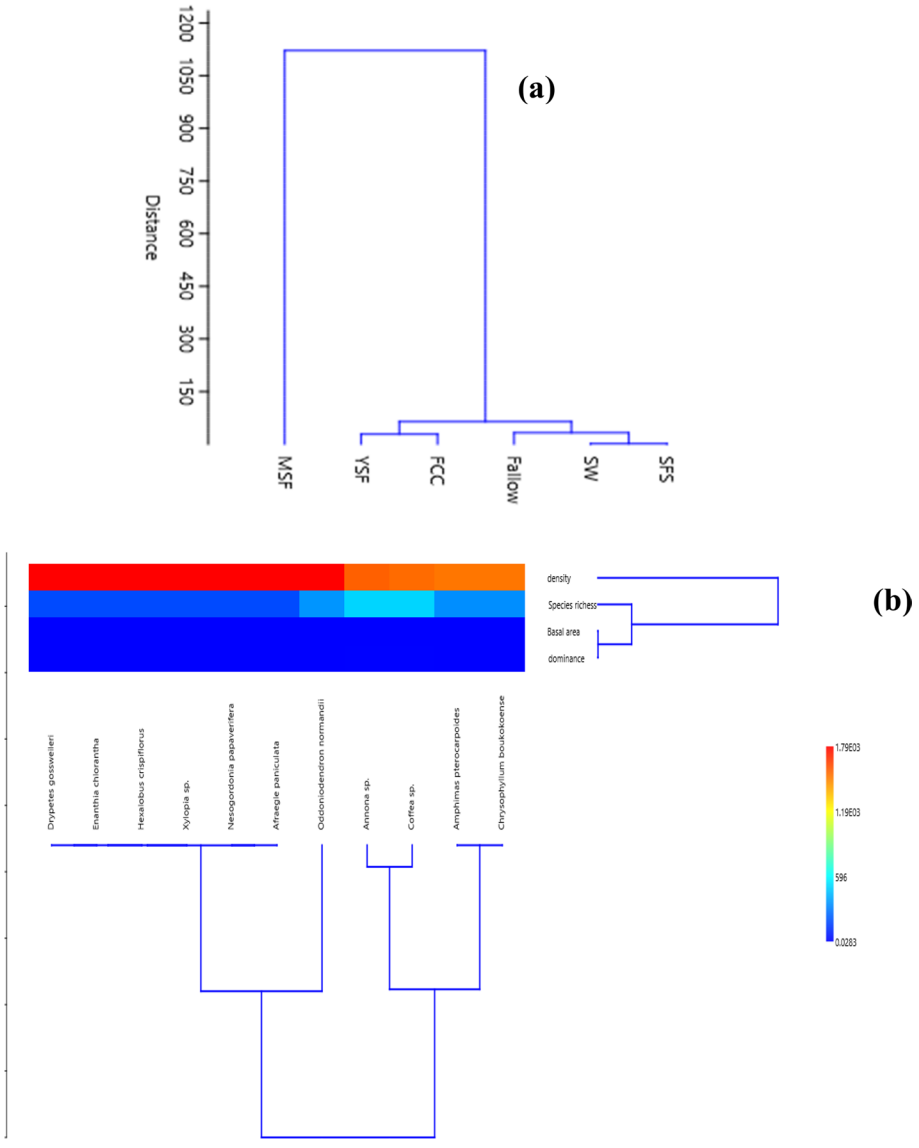

Fig. 4 Hierarchical classification of: (**a**). Land use types; (**b**). Understorey species

3.2 Vegetative reproduction capacity of damaged trees, individual predictive factors, and basal stump diameter effects

3.2.1 Vegetative reproduction capacity of damaged trees

A total of 147 woody stumps were recorded, representing 33 species, 27 genera, and 26 botanical families, with a mean density of 37 stumps. ha^{-1}. Among these, 9.52% could not be identified due to advanced decomposition. Stumps were mainly associated with anthropogenic disturbances (55.88%), followed by natural windthrows (25%). In contrast, relatively undisturbed areas, where damage to trees is limited, exhibited a lower proportion of stumps (22.22%; Appendix 1). Overall vegetative reproduction capacity was high, with 78.79% of individuals producing sprouts versus 21.21% showing no regeneration (predominantly dead and highly decomposed stumps). Mean sprout count per stump was 5.00 ± 3.92, with notable interspecific variation ranging from 6 for *Santiria trimera* to 14 ± 4.22 sprouts for *Uapaca paludosa* (Table 4). Five species demonstrated particularly high vegetative reproduction potential (≥ 5%), collectively representing 43

Table 4 Species with a reproduction potential (≥ 2%), their corresponding numbers of stems and suckers

Familly	Species	Number of stumps	Number of sprouts	Reproduction Potential (%)
Anacardiaceae	*Lannea welwitschii* (Hiern) Engl.	1	10	6.80
	Trichoscypha acuminata Engl.	1	3	2.04
Annonaceae	*Anonidium mannii* (Oliv.) Engl. & Diels	7	3.5 ± 2	2.38
Burseraceae	*Santiria trimera* (Oliv.) Aubrév.	1	6	4.08
Cannabaceae	*Celtis adolfi-friderici* Engl.	2	4	2.72
	Celtis mildbraedii Engl.	2	8.5 ± 2.5	5.78
	Celtis zenkeri Engl.	6	8.75 ± 2.25	5.95
Euphorbiaceae	*Macaranga hurifolia* Beille	7	4.67 ± 1.78	3.17
	Ricinodendron heudelotii (Baill.) Heckel	1	4	2.72
Lecythidaceae	*Petersianthus macrocarpus* (P.Beauv.) Liben	18	6.4 ± 0.78	4.35
Irvingiaceae	*Desbordesia glaucescens* (Engl.) Tiegh.	5	6.2 ± 1.56	4.22
Meliaceae	*Trichilia dregeana* Sond.	3	3.33 ± 1.78	2.67
	Trichilia welwitschii C.DC.	6	4 ± 1.33	2.72
Myristicaceae	*Pycnanthus angolensis* (Welw.) Exell	23	3.57 ± 0.37	6.80
Olacaceae	*Aptandra zenkeri* Engl.	3	3.5 ± 0.12	2.38
Passifloraceae	*Barteria fistulosa* Mast.	3	3.33 ± 1.55	2.27
Phyllanthaceae	*Uapaca paludosa* Aubrév. & Leandri	4	14 ± 4.22	9.75
Urticaceae	*Myrianthus arboreus* P.Beauv.	2	5 ± 1.52	3.40

Table 5 Relationships between biotic variables and the reproductive capacity of damaged tree stumps

Dependent variable	Predictive variables	Coefficient	df	*p*-value
Number of sprouts	Species	33	33	0.47
	Familly	22.34	33	0.44
	Stump condition	13.90	3	0.003
	Disturbance	11.12	8	0.19

stumps (29.25%). These high-capacity reproducers were primarily shade-tolerant taxa affected by anthropogenic disturbances, with a particular concentration in food-crop areas and young fallows (Table 3). The species were: *Uapaca paludosa* (9.75%; Phyllanthaceae), *Lannea welwitschii* (6.80%; Anacardiaceae), *Pycnanthus angolensis* (Myristicaceae), *Celtis zenkeri* (5.95%; Cannabaceae), *Celtis mildbraedii* (5.78%; Cannabaceae), and *Anonidium mannii* (5.44%; Annonaceae; NT; Appendix A1).

3.2.2 Predictive factors and effect of basal diameter of damaged tree stumps

The analysis of variance (ANOVA) revealed the influence of biotic variables on sprout number (Table 5). Sprout number differed significantly with stump condition (coefficient = 13.90; $p = 0.003$). The distribution of physiological states showed that 50% of stumps were in good vitality, 26.47% were in an intermediate state (alive and/or partially decomposed), and 17.64% were in an advanced state of decay. In contrast to the physiological condition, the other biotic variables studied showed no significant influence on sprout production ($p > 0.05$). No notable differences were observed regarding taxonomic affiliation (families: coefficient = 22.34; df = 33; $p > 0.05$; species: coefficient = 33; df = 33; $p > 0.05$) or disturbance origin ($p > 0.05$).

Spearman correlation analysis revealed significant relationships between stump attributes and regeneration performance ($p < 0.05$; Fig. 5). The number of sprouts showed significant positive correlations with both sprout diameter ($r = 0.24$; $p = 0.03$) and stump

height ($r = 0.65$; $p = 0.01$; Appendix A2). Reproduction potential was strongly correlated with the diameter ($r = 0.45$; $p = 0.02$) and height ($r = 0.32$; $p = 0.02$) of the most developed sprout (Appendix 2). While no overall correlation was found with stump diameter ($p > 0.05$), a complete reproduction failure in large-diameter stumps (≥ 40 cm: *Dichostemma glaucescens*, *Mitragyna ciliata*, *Musanga cecropioides*) was observed. Optimal reproduction occurred in intermediate-diameter stumps (8–28 cm), particularly in *Uapaca paludosa* (16.75 cm; 14 sprouts), *Celtis mildbraedii* (18 cm; 8.5 sprouts), *Celtis zenkeiri* (27.83 cm; 8.75 sprouts), *Lannea welwitschii* (25 cm; 10 sprouts), and *Santiria trimera* (8 cm; 6 sprouts) (Appendix 3). Stump density showed no significant correlation with regeneration potential ($p > 0.05$). Notably, species with fewer stumps (*L. welwitschii*; $n = 1$, *C. mildbraedii*; $n = 2$, *C. zenkeri*; $n = 6$, *U. paludosa*; $n = 4$) produced the highest sprout counts, while those with abundant stumps (*Petersianthus macrocarpus*; $n = 18$ and *Pycnanthus angolensis*; $n = 23$) showed limited regeneration (6 and 5 sprouts, respectively; Appendix A1).

3.3 Effects of stump morphological characteristics on post-disturbance vegetative regeneration

Statistical modelling revealed significant effects of stump characteristics on total sprout production ($p < 0.05$). The analysis revealed that the number of sprouts increased significantly with stump diameter (adj. $R^2 = 0.05$, slope = 0.441; $p = 0.04$; Fig. 6a). In contrast, the number of sprouts did not increase significantly with the height of the most

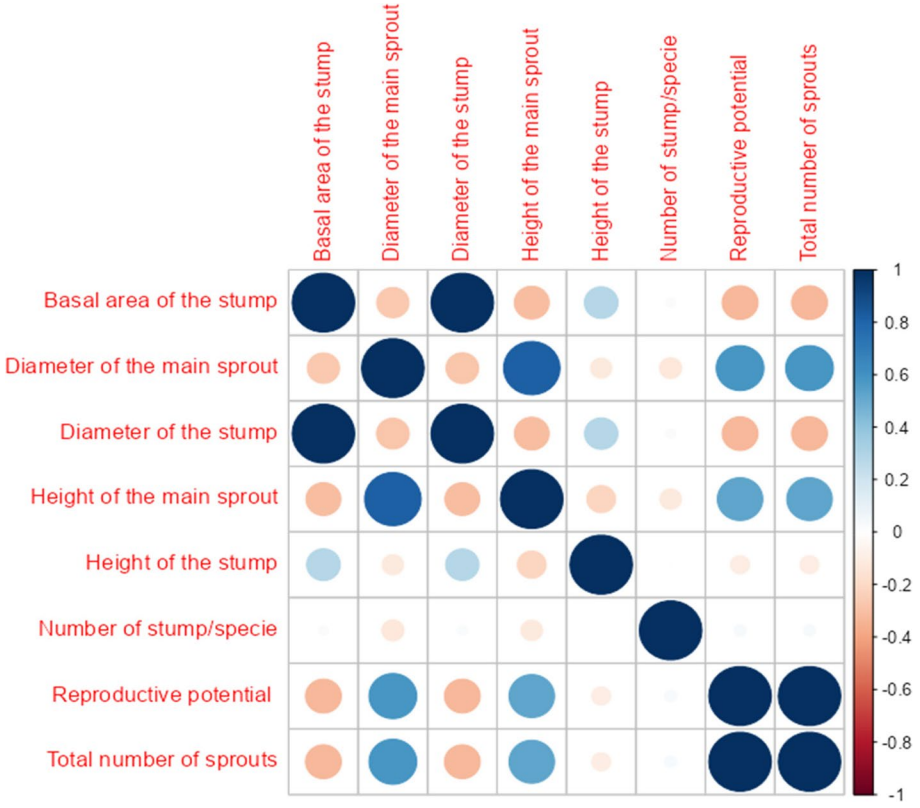

Fig. 5 Spearman correlation ($p < 0.05$) between sprouting potential and stump attributes. Positive correlations are shown in blue, and negative correlations in red. Colour intensity and circle size are proportional to the correlation coefficient. On the right side of the matrix, the legend shows the correlation coefficient and its corresponding colours

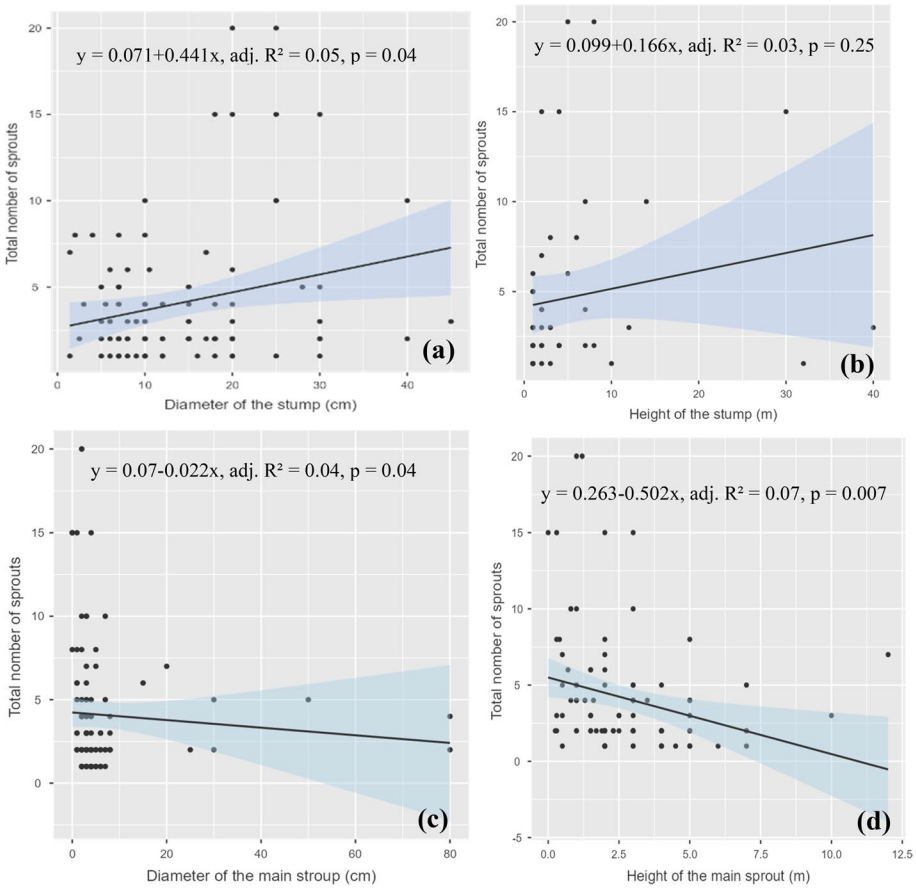

Fig. 6 Regression analysis between stump attributes and sprout production: (**a**) stump diameter, (**b**) height of the tallest sprout, (**c**) stump height, (**d**) height of the main sprout

developed sprout (adj. R^2 = 0.09, slope = 0.17; p = 0.25; Fig. 6b). However, a significant decrease in the total number of sprouts was observed with increasing diameter of the most developed sprout (adj. R^2 = 0.04; slope = – 0.02; p = 0.04; Fig. 6c), and an even stronger negative relationship was found with the height of the most developed sprout (adj. R^2 = 0.07; slope = – 0.50; p = 0.007; Fig. 6d).

4 Discussion

4.1 Vegetation diversity and regeneration, differential effects of disturbance and land-use types in the understorey

Semi-deciduous tropical forests exhibit significant understorey dominance [5]. In the study area, this stratum constituted the predominant component of the forest structure, accounting for 80.85% of all trees, even though this proportion remains lower than values reported for other humid forests [5, 70, 71]. Indeed, biotic and abiotic factors can influence the distribution, survival, recruitment, and mortality of Saplings [5, 7], which may explain the observed variations.

The predominance of Medium-sized trees (66.14%) underscores their critical role in forest regeneration dynamics [5]. However, the relatively low proportion of small trees (33.86%) highlights the adverse effects of anthropogenic and natural disturbances [24] raising concerns about the long-term sustainability of forest regeneration mechanisms. Implementing adaptive management strategies, such as restricting agricultural burning

and promoting agroforestry systems, is essential to preserve understorey biodiversity. Such approaches should integrate ecological conservation with restoration efforts [24, 72, 73].

The results indicated a high understorey density in both highly and moderately disturbed areas. According to Watson et al. [32], disturbances alter forest structure by increasing light penetration and the availability of mineral elements and other nutrients, which stimulate understorey regeneration and facilitate the establishment of pioneer species [33, 61]. Their impacts on biodiversity vary depending on type and frequency [36], which explains why small trees in the region exhibit maximum density in less disturbed areas (1,466.66 ± 101.84 stems. ha-1). Indeed, understorey density and composition are correlated with canopy openness, mediated by environmental variables [74, 75]. These modifications may lead to a selection effect, thereby altering the original diversity [76].

4.2 Effects of land-use types on understorey diversity and density

The analysis of understorey vegetation in this study revealed greater species variation along a disturbance gradient. Species diversity was very low in highly disturbed, stressed vegetation compared to intermediate vegetation (Shannon = 2.91 for Medium-sized trees; 0.72 for small stems), highlighting the link between ecological stability and biodiversity [15]. These findings align with those of Mounmemi et al. [77], who emphasised that low-intensity logging has little negative impact on species diversity and richness. Furthermore, secondary succession is more favourable for the recovery of forests that have undergone low-intensity logging [77]. This is supported by the number of understorey species in low-disturbance environments (20.91 species) compared to 15 species in highly disturbed environments, confirming that intact forests act as biodiversity reservoirs [22]. These differences observed across the disturbance gradient reflect the mechanisms described by Matula et al. [78], notably the post-disturbance explosion of sapling regeneration and the difficulty of establishing small trees. Differential management is essential, aiming to protect intact areas and implement assisted regeneration in degraded zones [6].

Results reveal significant variations in stem density and species richness across land-use types, confirming the impact of anthropogenic disturbances on forest regeneration [2, 7]. Less disturbed mature secondary forests exhibited a higher density of small stems (5,267 ± 2,838 stems/ha) than medium-sized trees (1,150 ± 780 stems/ha), reflecting optimal regeneration under a stable canopy [5, 6]. This stability provides favourable microclimatic conditions for recruitment [8].

In contrast, highly disturbed young secondary forests showed low tree species density (400 stems/ha), confirming the impact of anthropogenic disturbances on forest regeneration [2, 7]. These findings align with similar studies, which reported that the structure and diversity of the understorey in degraded tropical areas are strongly shaped by human activities [24, 79]. Bentsi-Enchill et al. [80] attributed similar patterns to disturbance factors such as logging, fuelwood extraction, and slash-and-burn agriculture in a similar context. Fuelwood extraction and slash-and-burn agriculture are common in the study area and are likely contributing to reduced understorey vegetation density. This explains why fallows and subsistence crop fields exhibited limited regeneration (600 – 400 stems/ha), characterised by a depleted soil seed bank and substantial competition with ruderal species [7]. These results are consistent with previous studies highlighting the detrimental effects of unsustainable agricultural practices on natural regeneration [5, 51, 81],

where human activities reduce seed availability through land clearance [32]. Furthermore, human-induced bushfires exacerbate this trend by reducing the survival of small trees [50].

Species richness was highest in mature secondary forests (30 species) compared to 6 species in croplands, where disturbances promote the dominance of a few generalist species [51]. While degraded croplands have been shown to favour certain pioneer species [5], their expansion risks impairing forest succession [17]. The pronounced species richness for small stems in subsistence crop fields (19.70) aligns with heavily exploited areas, where overall diversity is impoverished. This phenomenon has been observed in other studies [51, 82], which have highlighted that repeated disturbances disproportionately benefit a limited number of generalist species at the expense of specialists. Repeated disturbances disproportionately benefit a few generalists at the expense of specialists. Thus, balanced management (e.g., selective harvesting) and targeted restoration are critical to sustaining ecological resilience.

4.3 Vegetative reproduction capacity of damaged trees, individual predictive factors, and basal stump diameter effects

The study of stump sprouting reveals a major adaptive mechanism in response to environmental disturbances, representing a recurrent biological phenomenon in woody plants [83]. Results indicated that 78.79% of recorded tree stumps produced sprouts, demonstrating a remarkable capacity for post-disturbance reproduction in the Semi-Deciduous Forest [7]. Although this phenomenon primarily constitutes a survival strategy rather than true regeneration [38], it plays a major ecological role in tropical forest ecosystems. These results can be explained by several interdependent factors, including local edapho-climatic conditions, particularly the rainfall regime characteristic of tropical zones [84]; post-disturbance micro-environmental modifications, such as increased light availability [8]; and thermal fluctuations that promote meristem activation [85]. Our findings are consistent with the 79% recorded in the semi-deciduous forests of South-West Cameroon and 75% in Asia [38], but lower than the 97.5% observed in Ugandan forests [25]. The high reproductive capacity recorded in the tropical zone confirms the universality of this adaptive mechanism, providing forest ecosystems with two key strategies: (1) enhanced competition through rapid recolonisation of ecological niches, and (2) improved resilience to anthropogenic disturbances [43]. However, while this regeneration mode maintains forest cover effectiveness, it leads to a depletion of the original species diversity and increased dominance of pioneer species [86]. These findings underscore the need for differentiated management that combines protecting natural sprouts, conserving stumps of climax species, and assisted regeneration for species with low sprouting capacity. This integrated approach would reconcile ecological resilience and biodiversity maintenance in disturbed ecosystems.

4.4 Relationship between stump attributes and regeneration potential

The study reveals a positive correlation between the number of sprouts, stump height, and sprout diameter. Consistent with previous studies [25, 43], our analysis revealed a significant relationship between stump diameter and the number of sprouts. However, for some species, very large stumps (≥ 40 cm, *Dichostemma glaucescens*, *Mitragyna ciliata*, *Musanga cecropioides*). showed low regeneration, whereas intermediate diameters

performed best. This result may be explained by the poor state of decomposition for most of these species. Furthermore, certain species (*Musanga cecropioides*) preferentially regenerate via seeds [87], while others (*Uapaca paludosa*) favour vegetative reproduction.

Although seed regeneration dominates after a disturbance [87], our study confirms the complementary importance of stump sprouts, particularly under recurrent anthropogenic pressures. The low stump mortality rate (9.52%) indicates a regenerative capacity that ensures the partial replacement of felled individuals. Furthermore, the number of sprouts increases with stump height and the height of the dominant sprout, consistent with the findings of Mwavu & Witkowski [25]. This underscores the activation of dormant buds, maximising their chances of survival. This morphological plasticity enables the rapid reconstitution of the photosynthetic apparatus after cutting or mechanical damage [88]. The growth and survival of sprouts are crucial for the resilience of disturbed forests [79]. However, excessive disturbance (e.g., logging, shifting cultivation) that exceeds a critical threshold could compromise this regeneration [24]. Sustainable management should therefore limit the frequency and intensity of cutting to preserve this potential.

4.5 Implications for sustainable management and conservation

The findings highlight the need for adaptive, differentiated forest management strategies that enhance natural regeneration while minimising the impacts of disturbance. Protecting less disturbed stands as biodiversity reservoirs and promoting assisted regeneration in degraded zones are essential to maintain ecological resilience [6, 24]. Integrating agroforestry and restricting slash-and-burn agriculture could reduce pressure on forest resources [51]. Furthermore, conserving stumps of climax species and managing natural sprouts can sustain forest structure and genetic diversity [51]. Furthermore, conserving stumps of climax species and managing natural sprouts can sustain forest structure and genetic diversity [86]. Such measures support a landscape-level approach linking conservation, restoration, and community-based management, ensuring the long-term sustainability of semi-deciduous tropical forests.

5 Conclusion

This study assessed the differential effects of anthropogenic disturbances on forest regeneration and the response of damaged trees. It highlights the complexity of natural regeneration dynamics in the Angossas forest and emphasises several key findings. The results show a strong understorey dominance (80.85% of total tree density), with seedlings accounting for 33.86% of individuals, and regeneration patterns vary with disturbance intensity. Saplings thrive in disturbed areas (875 stems·ha^{-1}) with relatively high diversity (Shannon-Wiener index = 2.9), while maximum pole diversity is observed in intact zones. Land-use types significantly influence the structure and composition of the understorey, with a 60% reduction in seedlings in disturbed areas. Although resilient, mature secondary forests remain vulnerable to fragmentation, confirming that anthropogenic disturbances substantially reduce understorey density and diversity.

The low floristic similarity between strata (only 10% of species shared) confirms an ecological discontinuity between the understorey and the canopy, highlighting the increased vulnerability of juvenile trees to anthropogenic pressures and indicating an

urgent need for targeted conservation measures. Damaged trees exhibit a high capacity for vegetative reproduction at the individual level (78.8% of stumps producing sprouts), with variability among species and micro-environmental conditions. The abundance and rapid growth of sprouts indicate that vegetative regeneration constitutes an important resilience mechanism for individual trees and the understorey community.

These results demonstrate that tropical forest regeneration relies on both reproductive modes (sexual and vegetative), with a notable contribution of vegetative regeneration in disturbed areas. They also highlight the vulnerability of juvenile trees to anthropogenic disturbances and provide essential guidance for targeted conservation measures, particularly the preservation of mature secondary forests and the restoration of disturbed areas.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s44415-026-00103-x.

Supplementary Material 1: Appendix A1. Thirty-two recorded species across corresponding families exhibited varying attributes and disturbance responses within the 40-ha study area. Appendix A2. Spearman's Rank Correlation Analysis Between Tree Stump Attributes and Vegetative Reproduction Potential.

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Authors' contributions

Conceptualisation : APE, CDC, CJZ; Methodology : APE, CDC, JCZ; Formal analysis and investigation: APE; Writing - original draft preparation : APE, CDC, KLM, GY, LFME; Writing - review and editing : APE, CDC, JCZ, RLN, KLM, JLF, MMM; Funding acquisition : APE, CDC, JCZ; Resources: APE, CDC, JCZ; Supervision : JLF, MMM.

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Data availability

The data supporting the findings of this study will be made available by the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

This study was conducted in strict compliance with relevant national (Cameroon) and international guidelines governing the use of plant resources for scientific research, including the Convention on Biological Diversity (CBD) and Cameroonian regulations relating to the sustainable management of forests. In accordance with these guidelines, the study was designed according to a non-destructive approach: no plant specimens (stems, leaves, bark, fruits, seeds, or tissues) were collected from the trees inventoried. Species identification was carried out exclusively through visual observation of external diagnostic characteristics and by measuring diameters at breast height (DBH), without compromising the integrity of the trees. Official authorizations for the surveys were obtained prior to the start of fieldwork from the Regional Delegation of the Ministry of Forestry and Wildlife (MINFOF), the Angossas Council, and the Senior Divisional Officer of the Angossas Subdivision. No threatened or protected plant species listed on the IUCN Red List or in Cameroonian legislation were collected, disturbed, or damaged during this study.
Not applicable. No human participants were involved in this study.

Consent for publication

All authors consent to the publication of this manuscript.

Competing interests

The authors declare no competing interests.

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