ORIGINAL ARTICLE

Land use has little influence on the soil seed bank in a central African moist forest

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Abstract

Regeneration of tropical forest occurs naturally and mainly through early secondary succession by soil seed banks. Here, we analyzed seed bank variation in density and diversity along a degradation gradient. We also explored the relationship (similarity in composition) between the seed and seedling banks and the overstory vegetation. The investigated forests were located at Dja Fauna Reserve and its surroundings, south-eastern Cameroon. We sampled 33 one-ha forest plots scattered in a protected area, in a logging concession and in community forests. Within each plot, we inventoried the seed bank in the litter and in four successive soil layers of 5 cm depth interval, and the standing vegetation. Seed density significantly varied with sampling depth but not between land use types. A total of 181 morphospecies were identified. Trees species accounted for 46% of seeds with pioneer species dispersed by animals dominating the seed bank. Species diversity and composition strongly varied with the sampling depth; the litter seed bank was more similar in composition to the soil seed bank than to the seedling bank, sapling, and forest stands. We highlighted the presence of a dense and diverse seed bank in each land use type. We also showed the differentiation of each sampling depth in terms of species composition, thus revealing their complementarity in the dynamics of natural regeneration. The dominance of pioneers in the seed bank and weak relationship with the overstory are universal for tropical forests and logically follow from forest succession after disturbance.

Abstract in French is available with online material.

KEYWORDS
biodiversity reservoirs, land use types, logging, natural regeneration, soil depth, south-eastern Cameroon

1 | INTRODUCTION

The seed bank is defined as the set of viable seeds present in the soil and/or litter (Martins & Engel, 2007). It is formed by the accumulation of seeds as a result of natural movements such as the percolating action of rain and concealment by animals or by the movement of contractile roots (Christoffoleti & Caetano, 1998; Long et al., 2014). The resulting burial increases seed persistence as soil depth increases, light penetration decreases, and moisture conditions become more stable, thus slowing down the processes of breaking dormancy and aging (Hopkins & Graham, 1987; Long et al., 2014). In tropical forests, the seed bank is mostly made up of pioneer species,

from seed rain or from an earlier stand that once existed on the site (Quintana-Ascencio et al., 1996; Young et al., 1987). Their seeds are mainly persistent or "orthodox seeds", characterized by long viability in the soil (Dalling et al., 1994). Seed bank density is generally higher in disturbed environments because the pioneer seed source is more abundant and competitive (Long et al., 2014; Saulei & Swaine, 1988). The soil seed bank plays a significant role in maintaining biodiversity (Hosogi & Kameyama, 2006; Nicotra et al., 1998), specifically for forest regeneration and resilience (Lemauviel et al., 2005).

Studies in tropical forests have revealed strong spatial and temporal heterogeneity of the seed bank communities (Chen et al., 2013; Mendoza et al., 2009; Young et al., 1987). Biotic and abiotic factors such as forest composition, topography, soil properties, and land use types play an important role in this heterogeneity (Akinyemi et al., 2018; Dupuy & Chazdon, 1998; Hopfensperger, 2007; Hosogi & Kameyama, 2006; Lemauviel et al., 2005). Land use types, for instance, have been expected to influence the litter and the soil seed banks by creating micro-conditions favorable for the development of specific vegetation types (Nicotra et al., 1998).

The forest soil seed bank also varies with soil depth. Previous studies have reported a higher seed density in the first few centimeters (Hall & Swaine, 1980), which then decreases linearly with soil depth. In a 0- to 20-cm soil profile, for instance, Dalling et al. (1997) observed that about half of the viable seeds are concentrated in the first 0–3 cm soil depth. However, the majority of studies conducted on tropical seed banks do not examine soil layers beyond 5 cm (Fenner & Thompson, 2005; Garwood, 1989; Hall & Swaine, 1980; Shen et al., 2014), suggesting that these seeds are less important for forest dynamics. Douh et al. (2018) in the Northern Republic of Congo reported substantial amounts of seeds down to 20 cm depth attesting to a high density and diversity of seeds beyond the soil surface. This latter study confirmed the presence and persistence of small viable seeds of many pioneer species in soils over several decades, as also noted by Dalling and Brown (2009). Therefore, the pattern of seed distribution along soil layers in tropical forests requires further studies that incorporate both litter and deeper soil layers.

Tropical forests are deforested and degraded at an alarming rate (Vancutsem et al., 2021), and regeneration occurs naturally, mainly through secondary succession (Poorter et al., 2016). The regeneration strategies implemented involve different life-forms: (i) the seed bank that is mainly composed of herbaceous species (Daïnou et al., 2011; Hall & Swaine, 1980; Sanou et al., 2019), (ii) dispersal syndromes that promote or limit seed dispersal and survival (Garwood, 1989; Hopfensperger, 2007), and (iii) species regeneration guilds that determine the order of appearance of the seedling in the succession dynamics (Bekker et al., 1998; Leck & Leck, 1998). Because early successional stages are determined by the seed bank (Dalling & Denslow, 1998; Swaine & Hall, 1988), a broader understanding of the ecology of viable seeds present in litter and soil is essential to ensure regeneration and restoration of these forests. In addition, the relationship among seed bank, seedling bank (juveniles plants found in the understory, *sensu* Kitajima & Fenner, 2000), and the

surrounding vegetation has not been sufficiently explored in Central Africa (Hopfensperger, 2007; Lipoma et al., 2019).

In tropical Africa, 11 seed bank studies have been published (Douh et al., 2014, 2018) with only three studies from Central Africa (Daïnou et al., 2011; Douh et al., 2018; Zebaze, 2014). Those studies highlighted: (i) a high density and diversity of seeds both in the litter and in the soil, (ii) a predominance of herbaceous and light-demanding species, (iii) a high spatial variability, and (iv) a low similarity with the overstory vegetation. Nevertheless, most of the related studies considered only the first 5 cm of the topsoil or were performed with a low sampling rate (3.3 and 4.05 m^2 investigated) (Daïnou et al., 2011; Zebaze, 2014). In addition, variation in seed bank characteristics combining different forest management systems and successive sampling depths has never been investigated in Central Africa. Although in West Africa, Sanou et al. (2019) note no interaction between these parameters. The objective of this study was to examine the variation in seed bank diversity and composition along a degradation gradient, represented by the main land use types found in Central Africa: (i) a protected area, (ii) a selectively logged forest, and (iii) disturbed community forests. We also examined the impact of sampling depth on seed bank communities and compared the seed bank with the standing vegetation, including the seedling bank, sapling, and forest stands (small and large trees). The specific questions addressed are as follows:

1. How do the density and diversity of the seed bank vary along the degradation gradient and with soil depth?
2. Which species and traits in terms of life-forms, dispersal syndromes, and regeneration guilds are found in the seed bank?
3. To what extent does the seed bank resemble the surrounding vegetation?

2 | METHODS

2.1 | Study area

The study was conducted in Cameroon where forests cover about 20 million hectares, 19% of them being attributed to protected areas, 32% to logging concessions, and the rest either not assigned or managed by local communities (Mosnier et al., 2016). The forest in these three land use types is managed in different ways, leading to a gradient of forest degradation (Lhoest et al., 2020). The investigated forests were located in south-eastern Cameroon (Figure 1) where the predominant vegetation is lowland semi-deciduous forest (mean elevation of 625 m) dominated by the Malvaceae and Cannabaceae (ex Ulmaceae) (Letouzey, 1985). Because of the relatively flat topography, patches of seasonally flooded forests and evergreen forests are also present (Letouzey, 1985). Annual rainfall ranges from 1500 to 2000 mm and is mainly distributed along two rainy seasons (>100 mm per month) from April to May and September to December. The mean temperature is 24°C, and the relative humidity is about 75% throughout the year (Fick & Hijmans, 2017).
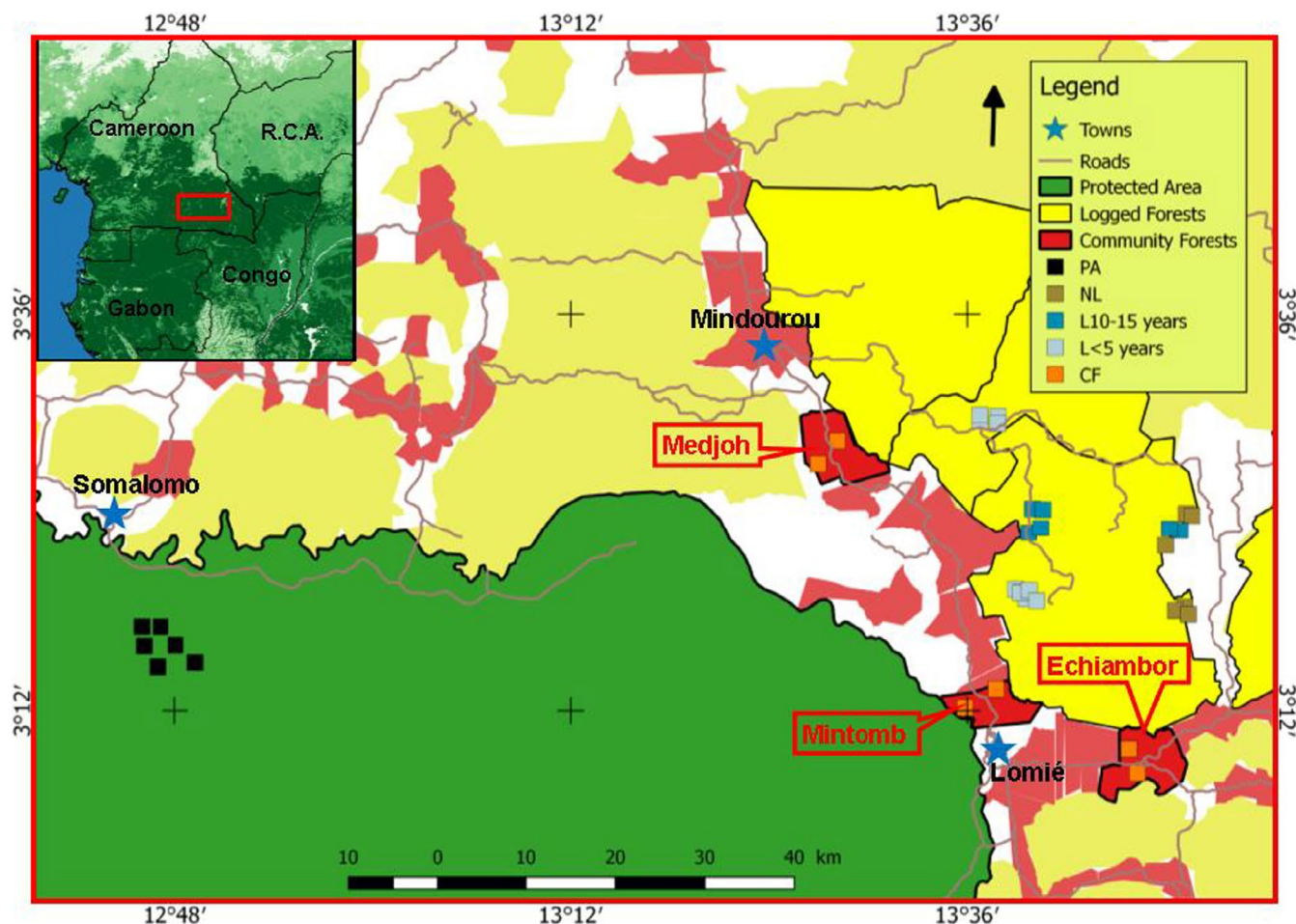
FIGURE 1 Location of the study area in Central Africa (inset) and in the Dja area. The 33 one-ha plots sampled in the different types of land use are indicated (filled squares). Abbreviations for the land use types correspond to the following: PA, protected area (in green); logging concession (in yellow) with NL, never logged; L10-15, logged forest between 10 and 15 years ago; L<5, logged forest less than 5 years ago; and CF, community forest (in red)

Metamorphic rocks form the parent material, and soils are mainly ferralitic (Segalen, 1967).

We sampled the seed bank following the degradation gradient highlighted by Lhoest et al. (2020): (i) a protected area, the Dja Biosphere Reserve (526,000 ha), characterized by an abundant fauna, particularly active in seed dispersal. This area has never been logged, and its distance from the villages makes the collection of other forest products difficult and limits its anthropisation; (ii) a Forest Stewardship Council (FSC)-certified production forest granted to the Pallisco company (341,708 ha). It is subject to selective timber logging (9.6 m³ per ha over a 30-year cutting cycle). Other activities such as hunting and collection of other forest products are limited, and shifting cultivation is prohibited; (iii) three community forests owned by the villages of Echiambor (5069 ha), Medjoh (4964 ha), and Mintomb (3433 ha). They are managed by the local communities under the supervision of the forestry authorities of Cameroon. In those forests, there is a higher intensity of collection of both timber and non-timber forest products. Because the duration after logging may influence the composition of the seed bank and the forest structure, three subdivisions were derived from the production

forest: never logged (NL), logged between 10 and 15 years ago (L10-15), and logged less than 5 years ago (L<5) (Figure 1).

2.2 | Forest sampling

We installed a total of 33 one-ha (100 × 100 m) plots within the different land use types separated by at least 700 m (Figure 1). Because the objective of the sampling was to capture the diversity and composition of the seed bank in different land use types, our 1-ha plots were set up in forest units that were as homogeneous as possible and best represented the physiognomy of each land use. Six 1-ha plots were installed in the protected area, 21 in the FSC-certified production forest (i.e., six each for NL and L10-15 and nine for L<5), and six in the community forests.

Within the 1-ha plot, we collected seed bank samples at three locations: at the center and at two other points located 15 m away from the center along a diagonal. For each location, we used an equilateral triangle of 1-m side (Daïnou et al., 2011) and collected soil samples (15 × 15 cm each) from the three summits and for five

sampling depths: the litter layer and 0–5, 5–10, 10–15, and 15–20 cm deep in the soil. For each triangle, we combined the samples by depth to form five composites samples corresponding to the five layers. All samples were packed in airtight bags and transported to the shade house for germination trials. Thus, for each 1-ha plot, seed bank samples comprised 15 composite samples (i.e., three locations × five layers), corresponding to 0.20 m² of sampled area (0.15 m × 0.15 m × 3 summits ×3 sampling locations) and to 0.04 m³ (40 dm³, excluding the litter) of soil volume. A total of 495 composite samples (33 plots ×3 sampling locations ×5 layers) were brought to the nursery. Sampling was realized between May and June 2017.

Within the same 1-ha plot, we measured, tagged, and identified all trees having a diameter at breast height (dbh) equal/or greater than 10 cm. To assess vegetation with dbh less than 10 cm, a 40 × 40 m area was defined within each plot. Here, trees, shrubs, and lianas with a dbh between 1 and 10 cm were inventoried in 10 randomly selected 16 m² (4 × 4 m) sub-plots. Trees, shrubs, herbs, lianas, and seedlings with dbh below 1 cm were inventoried in six randomly selected 1 m² (1 × 1 m) sub-plots (Figure S1a). Botanical vouchers were collected to confirm field identification at the Plant Systematics and Ecology Laboratory (LaBosystE) of the University of Yaoundé I and at the Herbarium of the Université Libre de Bruxelles (BRLU). Inventories were performed between April 2015 and December 2018.

2.3 | Monitoring seed germination

The 495 seed bank samples were placed in germination beds in two shade houses completely covered with nets of 0.50 mm mesh and equipped with 1.20 m high tables (Figure S1b). Each sample was spread in a germination bed measuring 40 × 30 × 10 cm and containing a 5-cm layer of steamed sand previously sterilized at 90°C for 90 min. Beds were watered daily and were randomly rotated every 10 days. Seed germination was monitored once a week, and emerging seedlings were counted and identified when possible. Unidentified emerged seedlings were carefully transplanted into germination bags (Figure S1c) to enable growth and further identification by experienced botanists. Germination trials lasted 16 weeks, and the last germination occurred around the 14th week. Thus, by continuing the monitoring 2 weeks after the last germination, it was intended to ensure that all viable seeds had germinated, although neglecting dormant seeds. Figure S2 shows the accumulation of new germinations per sample for each soil depth within the different land use types. Unidentified emerged seedlings at the end of the experiment were collected and identified at LaBosystE and BRLU.

Taxonomic nomenclature was checked and standardized following the African Plant Database (http://www.ville-ge.ch/musinfo/bd/cjb/) and The Plant List (http://www.theplantlist.org/tpl/). Using information from the literature supplemented by our field experience, we classified species into four life-forms: tree, shrub, herb, and liana. Three regeneration guilds were determined following Doucet (2003), Hawthorne (1995), and Meunier et al. (2015): pioneer,

non-pioneer light demanding, and shade bearer. Seven dispersal syndromes following Howe and Smallwood (1982) were identified: (i) Acanthochory with spiny, hooked, or hairy diaspores; (ii) Ballochory with seeds ejected by the plant; (iii) Barrochory with diaspores characterized mainly by their large mass and the absence of other dispersal structures; (iv) Pogonochory with diaspores with feathery or silky appendages; (v) Pterochory with diaspores with winged appendages; (vi) Sarcochory with diaspores with a soft, fleshy envelope; and (vii) Sclerochory with diaspores with no particular characteristics and a mass of less than 1 g.

2.4 | Data analysis

The vegetation datasets were organized as follows: (i) soil and litter seed bank from the germination trials, (ii) seedling bank represented by <1 cm dbh trees, (iii) sapling stand represented by 1–9.9 cm dbh trees, (iv) small trees stand represented by trees 10–29.9 cm dbh trees, and (v) larger trees stand represented by ≥30 cm dbh trees.

To evaluate changes in density and diversity of the seed bank along the degradation gradient and according to sampling depth, we computed the absolute seed density (expressed as the number of seeds per meter square) for each sample. Given the large variation in the number of seeds per sample (from 2 to 81 seeds per sample) and the fact that we defined the 1-ha plot as a sampling unit, the values were aggregated by soil depth at the plot scale (the three samples were merged) and $\log_{10}$-transformed to fulfill the condition of normal distribution. We used a linear mixed-effects model to test whether the layers (litter and soil sampled at 0–5, 5–10, 10–15, and 15–20 cm depth) and land use types (protected area, NL, L10-15, L<5, and community forest) were predictors of seed density and also if there was an interaction between them. We used soil layers and land use types as fixed factors and the plot location as random factors to integrate the spatial dependency of land use type. A pairwise post hoc test followed by a Tukey test was used to determine whether there is a difference between the means of all possible pairs.

Given the large variation in the number of species inventoried in the samples (from 1 to 39 species per sample), the seed bank data for the three samples were also aggregated by layer at the plot scale. We assessed sampling completeness with accumulation curves for each land use type and for all the land use types pooled together. To assess the diversity of the seed bank in each layer and in each land use type, the observed species richness (S.obs) was computed, and the number of missing species was estimated using two non-parametric estimators of true species richness: based on abundance (S. Chao1) and based on incidence (S.ACE). The heterogeneity of the seed bank was additionally estimated using Shannon and Simpson indices of diversity, sensitive to the distribution of abundant and rarest species, respectively. A linear mixed-effects model was used to test whether the sampling depth and land use types were predictors of seed bank richness and diversity. The sampling depth and land use types were taken as fixed factors and the plot location as random factors. A pairwise post hoc test followed by a Tukey test was used

to determine whether there was a difference between the means of all possible pairs.

To evaluate the overall dominance of each species in the seed bank community, we computed the relative frequency, expressed as a percentage, which represents the proportion of plot containing a given species, and the relative density, which represents the number of seeds observed in 1 m³ of soil. To identify indicator species, we computed the indicator value index (IndVal) and its significance using a threshold of 5% (Dufrene & Legendre, 1997).

A non-metric multidimensional scaling (NMDS) was performed to compare the floristic composition of the seed bank on data aggregated at horizon levels for each land use. To identify which life-form, regeneration guild, and dispersal syndrome dominated the seed bank community, the proportions were calculated for each life-form, regeneration guild, and dispersal syndrome group. We used a linear mixed-effects model to test whether the sampling depth and land use types could influence life-forms, regeneration guilds, and dispersal syndromes in the seed bank and also if there was an interaction between them.

To compare the composition of the seed bank to the standing vegetation, we restricted our dataset to trees identified at the genus level. We first calculated the proportion of genera specific to the seed bank then the indicator values of trees genera using the IndVal index at a 5% threshold (Dufrene & Legendre, 1997). On data aggregated at plot level, we assessed the similarity between different groups in terms of species presence using the Sorensen similarity index (1-dissimilarity) (Faith et al., 1987) and in terms of relative species abundance using a NMDS.

All analyses were performed in the R open-source environment (R CoreTeam, 2017). We used the following packages: *vegan* for diversity analyses (Oksanen et al., 2019), *lme4* for fitting and analyzing mixed-effect models (Bates, 2016), *labdsv* to compute species indicator value (Roberts & Roberts, 2019), and *MASS* for the NMDS (Ripley et al., 2020).

3 | RESULTS

3.1 | Seed bank density and diversity

A total of 7344 seeds germinated, corresponding to a seed density of 1099 seeds/m² and 5495 seeds/m³ (4660 seeds/m³ excluding the litter) for all land uses combined. The soil seed density decreased with soil depth with the highest seed density of 404 ± 204 seeds/m² or 8080 ± 4080 seeds/m³ observed in the upper soil horizon (i.e., 0–5 cm, Figure 2a). The linear mixed-effects model revealed a significant difference in seed density among layers ($F = 104.93$; $df = 4$; $p < .001$) and a significant interaction between layer and land use type ($F = 2.78$; $df = 16$; $p < .001$). However, no significant differences were recorded between the land use types ($F = 1.67$; $df = 4$; $p = .21$) (Figure 2a; Table S1).

Because of high mortality during germination trials, only 4384 germinated individuals were identified, accounting for 60% identified and 40% unidentified seedlings. Identified emerged seedlings belonged to 181 morphospecies, 117 genera, and 50 families

(Table S2). The S.obs/S. Chao ratio was between 48% and 69% (Table S3). The linear mixed-effects model revealed significant differences of seed richness and diversity between sampling depths, as well as a significant interaction between sampling depth and land use type (Table S1). Species rarefaction revealed that species richness decreased with sampling depth (Figure 2b). The Shannon index but not the Simpson index was significantly different between sampling depths ($F = 8.99$, $df = 4$, $p < .001$). Litter was the most diverse layer and 15–20 cm the least diverse layer.

Observed ($F = 2.74$, $df = 4$, $p < .05$) and estimated species richness ($F = 3.76$, $df = 4$, $p < .001$ and $F = 3.532$, $df = 4$, $p < .01$, respectively, for S. Chao and S.ACE) were significantly different between land use types. This was also the case with diversity ($F = 2.673$, $df = 4$, $p = .05$ and $F = 2.79$, $df = 4$, $p < .05$, respectively, for Shannon and Simpson indices). The most species rich land use type was the Never Logged part of the production forest, and the most diverse land use was the forest logged between 10 and 15 years ago. The Protected Area had the lowest richness and diversity (Table S1).

3.2 | Composition of the seed bank community

The 10 most representative species in the seed bank in terms of relative density and frequency were *Musanga cecropioides*.R. Br. (0.34; 0.85), *Nauclea diderrichii* De Wild. T. Durand. Merr. (0.08; 0.48), *Sabicea* sp1 (0.04; 0.45), *Axonopus compressus* Sw. P. Beauv. (0.04; 0.42), *Eleusine indica* L. Gaertn. (0.02; 0.32), *Phyllanthus amarus* Schumach. Thonn. (0.02; 0.32), *Elytraria marginata* Vahl (0.02; 0.30), *Tristemma albiflorum* G. Don. Benth. (0.02; 0.26), *Tristemma* sp1 (0.02; 0.22), and *Paspalum conjugatum* P. J. Bergius (0.01; 0.22; see Table S2 for the complete list of species). The majority of emerged seedlings were from woody species (46% trees), species dispersed by animals (62% sarcochore), and species requiring high light conditions for their development (87% pioneers) (Figure 3).

The relative frequency of species in the seed bank strongly varied according to sampling depth (Table S2). Over 33% of the species were found only in a single layer while 14% of species were present in all layers. The number of indicator species varied 16-fold across the five layers and decreased with sampling depth (i.e., 7, 16, 1, 1, and 1 for the five consecutive depth, respectively; Table 1). The 5–10 and 10–15 cm layers were characterized by long-lived pioneer herbaceous (*Brachiaria* sp1) and liana species (*Adenia cissampeloides*). The 15–20 cm layer was characterized by short-lived pioneer woody species (*Macaranga* sp2). Depending on the land use, the number of indicator species varied from 1 to 7 (Table 1). The protected area was characterized by herbaceous species while never logged forests were characterized by long-lived pioneer herbaceous and woody species. Forests logged less than 5 years ago were characterized by herbaceous species, and community forest was characterized by typical pre-forest fallow species (*Chromolaena odorata*) and short-lived pioneer woody species characteristic of young fallow (*Trema orientalis*, *Musanga cecropioides*, and *Ficus exasperata*).
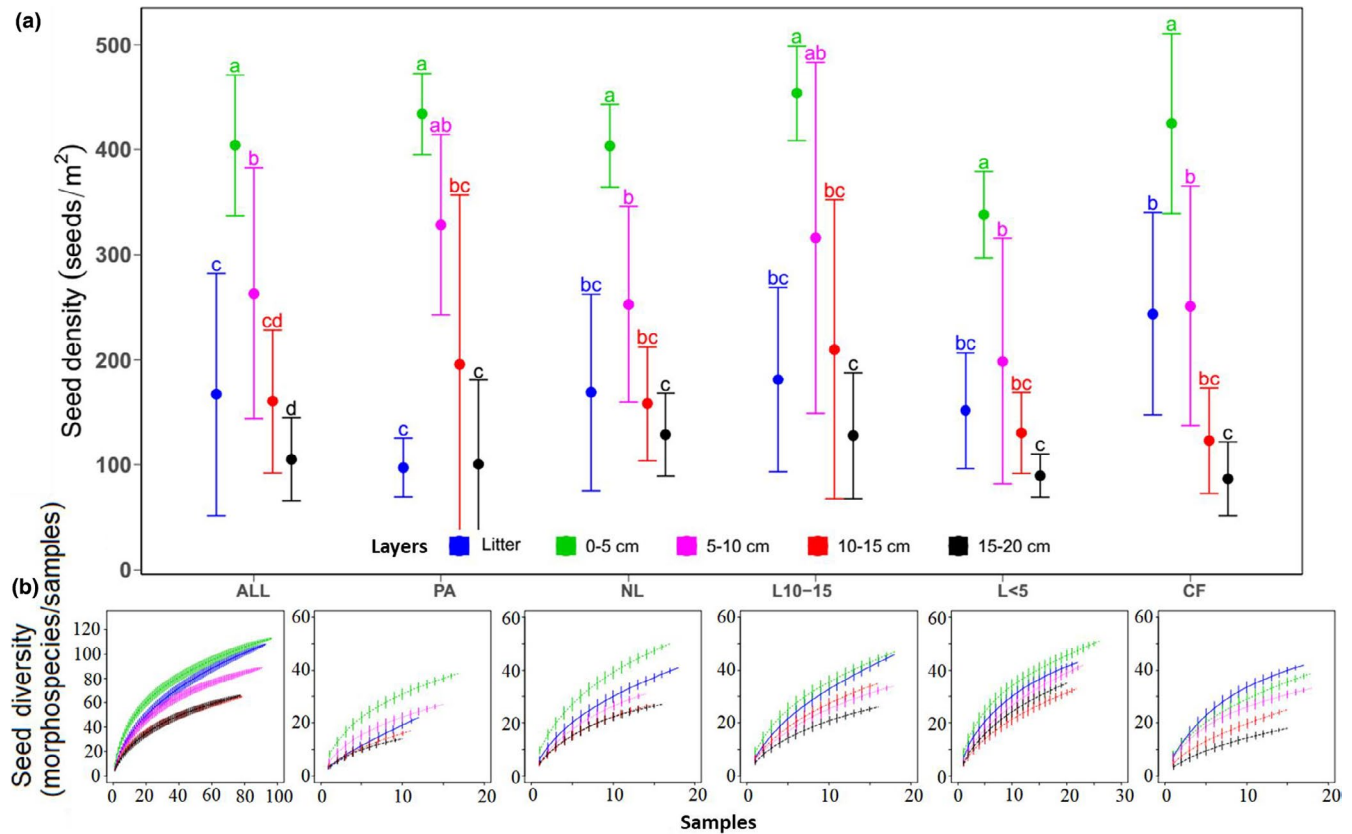
FIGURE 2 (a) Seed bank density and (b) diversity for all the land use types taken together (All) and separately for the land use types (PA, protected area; NL, never logged; L10-15, logged between 10 and 15 years ago; L<5, logged less than 5 years ago; and CF, community forest). The points indicate the means, error bars, standard deviations, and letters as the results of the Tukey post hoc test. (b) Sample-based rarefaction curves showing the accumulation of new taxa with new samples. The colors correspond to the litter and soil layers with the following details: blue, litter; green, 0–5 cm; pink, 5–10 cm; red, 10–15 cm; and black, 15–20 cm

The NMDS ordination showed a dissimilarity in composition between all sampled layers but with a great overlap between the deepest two (Figure 4a). Sampling depth significantly influenced the proportion of life-forms, regeneration guild, and dispersal syndromes within the seed bank. There was a significant effect of sampling depth on the distribution of all the life-forms, pioneer and shade-bearer regeneration guilds, and then for seed dispersal syndromes (except barochores and sclerochores, Table S1). For the land use types, there was a significant effect on life-forms distribution (except for shrubs) and for pioneer regeneration guilds. Distribution of dispersal syndromes was only significant for acanthocore, pogono-chore, and sarcochore seeds (Table S1). The interaction between sampling depths and land use type was only found for the regeneration guilds of pioneers ($F = 1.757$; $df = 16$; $p = .047$) and pogonochore dispersal syndrome ($F = 2.465$; $df = 16$; $p = .003$) (Table S1).

3.3 | Comparisons between the seed bank and the standing vegetation

By considering only the trees in the different vegetation datasets, that is, seed bank in litter and in soils, seedling bank and sapling

stand, and small and large tree stands, no genera were observed to occur exclusively in either the litter or soil seed bank. Significant indicator genera were however observed for the soil seed bank: *Nauclea* (indval = 0.43; $p = .001$), *Musanga* (0.36; 0.001), *Macaranga* (0.13; 0.001), *Maprounea* (0.12; 0.006), and *Ficus* (0.11; 0.018). According to the NMDS, the composition of the soil seed bank was found to be more similar to the litter seed bank than to the over-story vegetation, and the dissimilarity increased with the seedling bank, the sapling stand, and up to the smaller and larger tree stands (Figure 4b). These results were confirmed with the pairwise Sorensen similarity indexes (Table S4). This dissimilarity in composition between the seed bank and the overstory vegetation was observed for all land use types.

4 | DISCUSSION

We investigated how forest degradation and sampling depth affect the characteristics of seed banks in the moist forest of south-eastern Cameroon. For trees at the genus level, we assessed the similarity between the seed bank and the overstory vegetation, with a focus on the seedlings and saplings that are assumed to be more
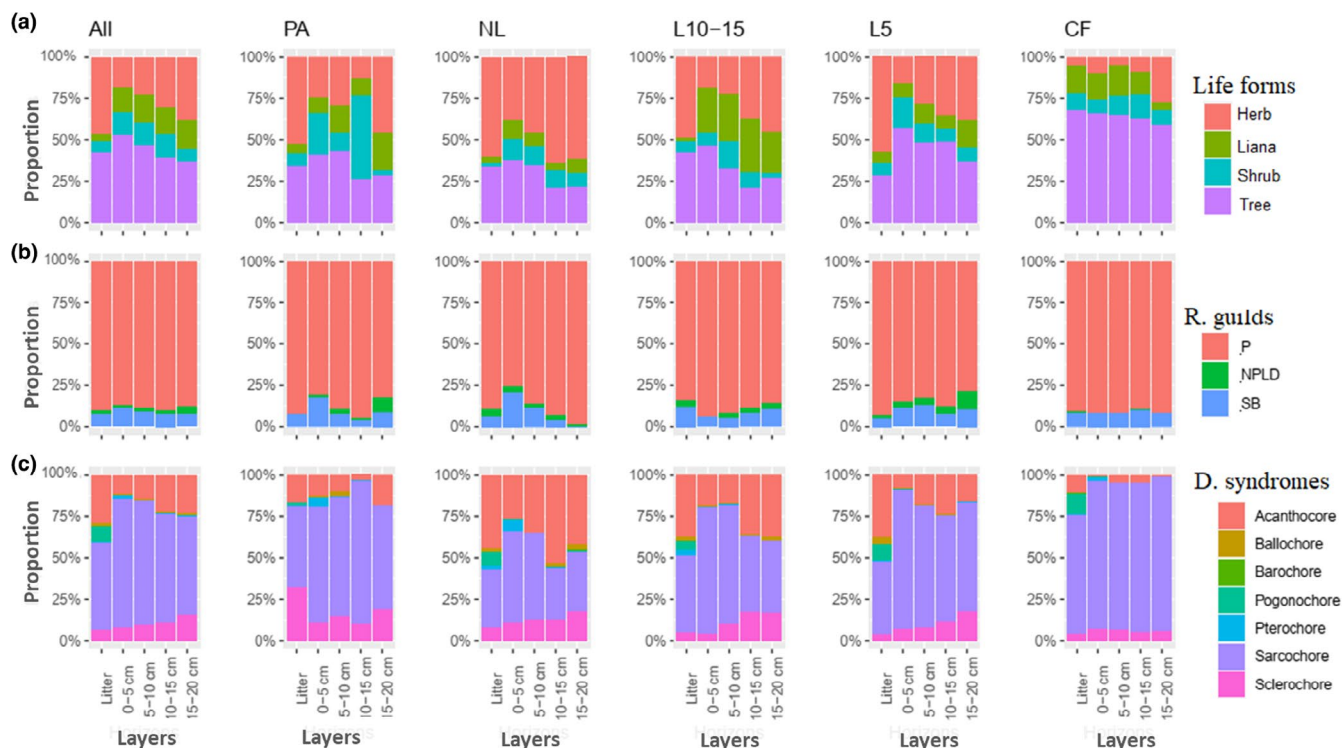
FIGURE 3 Proportions of (a) life-forms, (b) regeneration guilds, and (c) dispersal syndromes across soil depths and land use types. Representation of soil depths: litter (litter layer) and other soil depths (0–5, 5–10, 10–15, and 15–20 cm). Representation of land use types: All, land use types taken together; PA, protected area; NL, never logged; L10-15, logged between 10 and 15 years ago; L<5, logged less than 5 years ago; CF, community forest; SB, shade bearer; NPLD, non-pioneer light demanding; P, pioneer

related to the seed bank. Considering the litter seed bank and soil seed banks separately, we found a strong stratification in seed diversity and composition with soil depth but only a weak impact of forest degradation. We also identified significant indicator species for each soil depth and degradation stage and found an influence of management and soil depth on life-forms, regeneration guilds, and dispersal syndromes.

4.1 | Seed bank characteristics are more strongly influenced by soil depth than by land use types

The observed seed density in this study was 1099 seeds/m², which falls within the 25–3350 seeds/m² range predicted by Garwood (1989) for tropical regions. However, our observed seed density was noticeably higher than the 247–330 seeds/m² range reported by Douh et al. (2018) in northern Republic of Congo. Our study confirms a high spatial heterogeneity of the seed bank in line with previous studies (Daïnou et al., 2011; Hall & Swaine, 1980; Martins & Engel, 2007). No significant difference in seed density between land use types or logging history was observed, as was also reported by Daïnou et al. (2011) in the same region. This finding could be due to the high homogeneity of soils (Segalen, 1967) and forest cover of the region. In contrast, in the northern Republic of Congo, where forest types are contrasted because of the geological substrate

and soils (clay and sandy soils; Fayolle et al., 2014), the seed bank density and composition have been found to strongly differ (Douh et al., 2018). Burial and seed survival may indeed depend on soil texture (Christoffoleti & Caetano, 1998; Long et al., 2014).

Seed density consistently decreased with soil depth regardless of the land use type. Young et al. (1987) observed a similar pattern in old and young tropical forests in Costa Rica. This could be explained by (i) the continuous seed rain responsible for the accumulation of seeds at the soil surface and not at low depths and (ii) the fact that mainly spherical, small, and dormant seeds can be buried and survive at great depths (Schwienbacher et al., 2010). Larger seeds are generally trapped in the litter and soil surface (Bekker et al., 1998). Thus, the number of seeds of a species in the soil, in addition to depending on the size of the seeds, is also influenced by their longevity (Hopkins & Graham, 1987; Long et al., 2014). It is the case for *Musanga cecropioides* and *Nauclea diderrichii* (with a diameter of 1 mm), which lose respectively 20% and 19% of their viability between 0 and 20 cm depth. Within the same depth, seeds of *Trema orientalis* (with a diameter of 2.5–2.8 mm) lose 100% of their viability.

The richness and diversity of the seed bank were more strongly influenced by the depth of soils than by land use types. Our results suggest that soil seed bank characteristics in the 10–15 cm and 15–20 cm layers were similar, so that three layers can be distinguished: 0–5, 5–10, and 10–20 cm. The seed bank is established by progressive accumulation of seeds in the soil, so its vertical structure may

TABLE 1 Number of indicator species for different land use types and soil depths

	PA	NL	L10-15	L<5	CF	All land uses	Indicator species
Litter	3	3	2	4	1	7	*A. conyzoides, C. mundtii, O. barrelieri, M. hirtus, D. sarmentosa, C. odorata,* and *P. umbellatum*
0–5 cm	1	5	2	3	1	16	*M. cecropioides, E. marginata, U. sp., S. sp1, P. sp2, P. sp2, N. diderrichii, C. sp., Z. heitzii, B. sp1, P. macroceras, T. albiflorum, A. umbrosum, I. Guania, P. ambigua,* and *P. hylodendron*
5–10 cm			1			1	*B. sp1*
10–15 cm			0			1	*A. cissampeloides*
15–20 cm				1		1	*M. sp2*
All sampling depths	2	7	5	1	7		
Indicator species	*C. sp., D. sp1*	*D. sarmentosa, B. deflexa, A. sp., C. sp2, P. conjugatum, N. diderrichii,* and *S. alba*	*I. Guania, A. sp., B. sp1, P. notatum,* and *A. umbrosum*	*C. sp5*	*T. orientalis, E. sp1, C. odorata, B. bicarpellata, M. cecropioides, A. conyzoides,* and *F. exasperata*		

Note: CF, community forest; L10-15, logged between 10 and 15 years ago; L<5, logged less than 5 years ago; NL, never logged; PA, protected area.
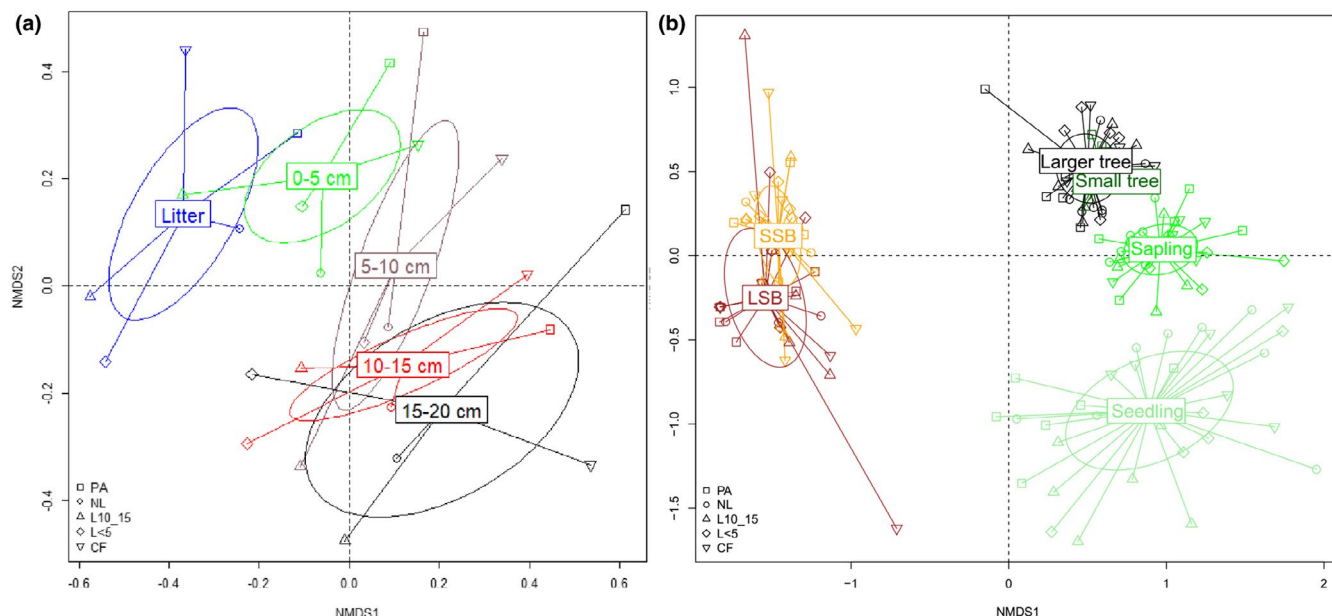
FIGURE 4 Non-metric multidimensional ordination (NMDS) showing (a) differences in the seed bank composition (at the species level) across soil sampling depths. This is materialized by ellipses connecting the centroids of the sampling depths with a 95% confidence interval. (blue, litter; green, 0–5 cm; pink, 5–10 cm; red, 10–15 cm; and black, 15–20 cm) within different land use types; (b) the (dis)similarity between the seed bank in soil (SSB) and litter (LSB) and the different vegetation strata (seedling bank with dbh <1 cm, saplings with dbh between 1 and 10 cm, small trees with dbh between 10 and 30 cm, and larger trees with dbh >30 cm) at the scale of the plot. (PA, protected area; NL, never logged; L10-15, logged between 10 and 15 years ago; L<5, logged less than 5 years ago; CF, community forest)

reflect a time scale from the youngest soil layers (litter and 0–5 cm) to the oldest one (15–20 cm). The presence of species that are exclusive or with higher relative densities in the deepest layers generally indicates higher seed viability and can reflect the history of soil formation (Bekker et al., 1998; Leck & Leck, 1998). The layering observed in the soil seed bank probably influences forest regeneration and recovery after disturbance. Thus, seeds found in the upper layers contribute to the regeneration of some shade-tolerant species while those contained in the deeper layers may contribute to the regeneration of pioneer and light-demanding species.

The distribution of dispersal syndromes in the seed bank was also linked to both land use type and soil depth. The litter layer was characterized by high proportions of species with no particular dispersal structure (barochores), seeds ejected by the plants themselves (ballochore), and seeds dispersed by wind (acanthochores and pogonochores). In the deepest layers (10–20 cm), low-mass and quasi-spherical diaspores (sclerochores) were more abundant, confirming the influence of shape and mass on the burial of seeds (Bekker et al., 1998). Sarchochores, characterized by soft and fleshy-enveloped diaspores and dispersed by animals, were more abundant in disturbed forests.

The seed bank in intact forests generally exhibits lower species richness and diversity than in degraded forests (Dupuy & Chazdon, 1998; Garwood, 1989; Martins & Engel, 2007; De Medeiros-Sarmento et al., 2021). Here, species richness in the seed bank was highest in secondary forests (L10-15) compared with the more degraded community forests and the recently logged forest (L<5). In

the latter, recent human impacts might have induced a reduction of a part of the soil seed bank due to the germination of seeds in canopy gaps. However, once forest degradation has reached a certain level (after repeated clearings of a regenerating forest for instance), the richness of the soil seed bank can be greatly reduced (Alvarez-Aquino et al., 2005; Quintana-Ascencio et al., 1996; Weerasinghe et al., 2019; Young et al., 1987). This probably occurred in the community forests, where land conversion to shifting cultivation is the greatest threat to diversity. The abundance of pioneer species in the seed bank also increased with forest degradation, probably because these light-demanding species were also more frequent in the stands (Calster et al., 2008).

The only clear differences in terms of regeneration strategy among land use types were found in community forests with many trees and few herbs. This suggests that there are many pioneer trees in their canopy. Community forests are small forest areas situated along roads and near villages, and they are used by local communities for timber, non-timber forest products harvesting, and agriculture. This land use and the village's proximity increase its frequency of visitation and the intensity of degradation (Lhoest et al., 2020; Weerasinghe et al., 2019).

It is worth noting that the true richness of the seed banks in this study may have been underestimated as species accumulation curves did not plateau. This could be attributed to the short duration of the germination experiment. Indeed, stopping germination experiment few weeks after the last germination observed probably did not allow for dormant seeds to germinate. Ter Heerdt et al. (1996)

suggested to let the soil dry, crumble it, and start watering again during another period to stimulate further germination.

4.2 | Tree taxa found in the seed bank

Seed bank studies carried in tropical forests have highlighted a dominance of pioneer species and a heterogeneity of life-forms, regeneration guilds, and dispersal syndromes (Daïnou et al., 2011; Hall & Swaine, 1980; Sanou et al., 2019). In this study, 46% of seeds in the seed bank belonged to tree species, and their proportion was significantly influenced by depth and degradation. This proportion is higher than the 30.2% previously reported by Daïnou et al. (2011) in Cameroon and the 34.9% by Douh et al. (2018) in the northern Republic of Congo. This could be explained by our sampling locations, which included community forests and recently logged forests. In these environments, short-lived pioneer tree species (*Musanga cecropioides*, *Trema orientalis*, and *Macaranga* spp.) are much more abundant in the canopy. The majority of the tree species found in the seed bank produce large quantities of small and dormant seeds (Bekker et al., 1998). Such seeds may have lignified integuments that enable them to resist predation (Chen et al., 2019).

The seed density of woody species, such as *Musanga cecropioides*, was inversely related to soil depth (indirectly displayed in Figure 2a), suggesting a lower persistence in soils (see also Douh et al., 2018). Pioneer species were more abundant in the seed bank than the other regeneration guilds. Hopkins and Graham (1987) also observed high densities of pioneer species able to survive between 2 and 30 years in forest soils. The proportion of shade-bearer species (from 0% to 11% in the different soil depths) was not comparable with the 12% to 21% of shade-bearer trees observed by Liew (1973) and Swaine and Hall (1988), respectively.

As observed by Daïnou et al. (2011), Douh et al. (2018), and Hall and Swaine (1980), seeds of timber species are present in the seed bank, notably *Erythrophleum suaveolens* (Tali), *Milicia excelsa* (Iroko), *Nauclea diderrichii* (Bilinga), and *Terminalia superba* (Fraké). These tree species play an important role in the timber trade internationally, although forest inventory data have shown population structure with few trees in the smaller diameter classes indicative of a regeneration deficit (Morin-Rivat et al., 2017).

4.3 | Low similarity between the seed bank and the standing vegetation

Despite the low similarity between the composition of the seed bank and the standing vegetation, all tree genera found in the seed bank were present in the standing vegetation. The litter seed bank is richer than all the other sampling depths as it contains newly deposited persistent and transient seeds (Drake, 1998; Lambers et al., 2005) awaiting burial or eventual predation. The similarity between the litter seed bank and the soil seed bank with different components of the standing vegetation (seedling and sapling bank then small and larger trees) was higher than that observed by Daïnou et al. (2011) and Hall and Swaine (1980). This may arise because previous authors did not separate the litter from the soil samples. In addition, our comparison was at the genus level in contrast to earlier studies at the species level (But see Figure S3 and Table S5 for the same comparison at the species level). Comparisons at the genus level may be more appropriate when botanical identification of emerging seedlings is uncertain.

The litter seed bank is expected to be more similar to the standing vegetation than soil seed bank, especially for seedlings, as has been reported in Argentina (Lipoma et al., 2019). In fact, the seedling bank mainly comes from the germination of seeds in the litter seed bank. Regarding forest resilience, our results showed that in our study area land use has little influence on seed bank density and diversity. However, the species traits present may differ, with more woody species in the most disturbed areas. These results are quite encouraging and show that forest cover recovery is possible once the disturbance is stopped. However, these results cannot be extrapolated to other areas where human population densities would be higher than those observed in our study area (seven habitants/km²).

Despite the presence of woody species, the seed bank plays only a limited role in the regeneration of commercial species in terms of the number of taxa represented. Among the woody species observed, only a few provide valuable timber: bilinga (*Nauclea diderrichii*), iroko (*Milicia excelsa*), limba (*Terminalia superba*), tali (*Erythrophleum suaveolens*), and secondarily olon (*Zanthoxylum heitzii*) and onzabili (*Antrocaryon klaineanum*). These species are the only commercial value species in the region with dormant seeds (Daïnou et al., 2011). All are pioneer species. Densities of bilinga and to a lesser extent iroko are nevertheless high, indicating that environmental disturbance (including logging) would be necessary for their regeneration. The observation of a few other species of interest such as sapelli (*Entrandrophragma cylindricum*) or longhi (*Chrysophyllum lacourtianum*) can be explained by recent seeds present in the litter.

In summary, we have reported in this study conducted in south-eastern Cameroon that timber logging intensity did not have a significant influence on the density of the soil seed bank and little influence on diversity and species traits (life-form, regeneration guild, and dispersal syndrome). We found viable seeds down to 20 cm depth in soils, but seed density and diversity were higher in the upper 10 cm soil layers. The litter layer showed an intermediate seed bank diversity and was characterized by the abundance of pioneer species. Different life-forms were present in the seed banks but were dominated by tree species, including some commercial timber species, sarchocore, and light-demanding species. We also found that tree species composition in the seed bank shows little relationship with the overstory vegetation, including the seedling bank.

AUTHOR CONTRIBUTIONS

DZ conceived and designed the study with the help of KD, JD, and AF. DZ performed the field work with the help of BS, JD, KD, ML, and VD. DZ analyzed the data with the help of AF and ML. JD and BS provided funding for the project. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.gtht76hng (Zebaze et al., 2021).

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