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Research Article

Involvement of the Soil Seed Bank in the Natural Regeneration of Forest Ecosystems in the Northern Sector of the Léfini Reserve (Republic of Congo)

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The study on the involvement of the soil seed bank in the natural regeneration of forests was carried out in the northern sector of the Léfini reserve. The aim was to assess the resilience of these woody formations. Data were collected in 8 isolated plots of 1 ha, in which woody trees of dbh ≥ 10 cm were inventoried and counted, and soil samples were taken at 5 points. At a rate of 40 samples per level, the horizons involved were: 0–5 and 5–10 cm. The floristic inventory reveals 2903 trees for 113 species, 38 families and 92 genera. The main taxa were *Tetraberlinia bifoliolata*, *Petersianthus macrocarpus*, *Duvigneaudia inopinata*, *Pentaclethra eetveldeana* and *Diospyros dendo*. Germination tests on soil samples revealed 1763 individuals belonging to 50 species in 32 families. The dominant species were *Polia condensata*, *Musanga cecropioides*, *Trema orientalis* and *Harungana madagascariensis*. The specific composition of the soil seed bank reveals low diversity and heterogeneity associated with forest facies and soil horizons, as underpinned by biodiversity indices. Although the soil seed bank is dominated by native herbaceous plants and pioneer woody plants, mature forest species are almost exclusively confined to the first horizon. Renewal of the flora depends mainly on animals and, to a lesser extent, on anemochory. The standing flora is not very similar to that of the soil seed bank. The low degree of similarity between the floristic composition and the soil seed bank, which is dominated by pioneer taxa, suggests that the front may be characterised by disturbance. In order to ensure the long-term survival of the forests that are essential to people's well-being, assisted natural regeneration is recommended, particularly for the most prized taxa.

Keywords: Congo; Léfini reserve; natural regeneration; plant ecology; soil seed bank

1. Introduction

The role of dense tropical rainforests in climate regulation and biodiversity conservation is well established [1]. The forests of the Congo Basin, which account for 70% of the woody formations on the African continent, are biodiversity hotspots [2]. Because of the low rate of deforestation in the region, these ecosystems are in a better overall state of

conservation than many other tropical forest formations [3]. Despite this asset, these ecosystems are subject to increasing human pressure, sometimes leading to severe degradation. The combined effects of these factors are likely to lead to the impoverishment of many populations, who are intimately dependent on spontaneous natural resources [2].

In Central Africa in general, and the Congo in particular, the high level of biodiversity, particularly plant diversity, is

being stretched to the point where the harvesting of forest products is becoming abusive [4–7]. As a result, there has been a steady decline in forest area, resulting in a reduction in floristic resources and an erosion of taxa and genes [5, 8]. Subsistence farming, largely dominated by slash-and-burn systems, the mining sector, logging, the construction of physical communication infrastructures and uncontrolled urbanisation are other significant factors in the loss of biodiversity and the degradation or even regression of forest areas [3, 9]. All these factors contributing to the decline in biodiversity affect the natural regeneration potential of these ecosystems, both in terms of soil and vegetation [7, 10, 11]. As a result, natural regeneration and the renewal of forest stands are compromised. This suggests the need for sustainable development policies, of which protected areas would be one [12].

The soil seed bank is all the seeds and fruits present on or in (i) soil, (ii) litter and (iii) humus [13]. Edaphic seminal potential contributes to the diversification and dynamics of plant communities and, in certain ecosystems, is crucial for species maintenance or ecological restoration [13–15]. The soil seed bank is therefore of considerable importance for the ecological resilience of forest ecosystems, via the natural regeneration of plant stands or the spontaneous reappearance of certain species that have apparently disappeared for varying lengths of time [16].

Work on soil seed banks is not common throughout the dense rainforests of Central Africa. Despite Cameroon [17, 18], in Congo the existing data are mostly limited to the forest massifs of the Haute and Basse-Sangha that are subject to sustained industrial timber production [19–22]. With the exception of the study by Missamba-Lola et al. [23] in the Tchimpounga sanctuary, these studies are systematically oriented toward the natural regeneration of plots that have undergone industrial timber exploitation [19, 21, 22].

Since forest cover has several facies, in terms of floristic composition, structure and status [12, 24, 25], no studies have been carried out in the mesophilic and tropophilic forests of the Congo. As well as being destined for biodiversity conservation, the Léfini Wildlife Reserve is home to important human communities and abounds in highly prized nontimber forest products such as *Grewia coriacea*, *Laccosperma secundiflorum* and *Chrysophyllum lacourtianum* [25, 26].

Studies on forest stand renewal should take into account more than one aspect of forest dynamics [27]. Thus, in a context of sustainable management and forest resilience, the present study focuses on aspects inherent in edaphic seminal potential in its relationship with the standing stand. The general objective of this study is to study the resilience of forest facies in the northern sector of the Léfini reserve. Specifically, the study aims to (i) describe the standing woody flora, (ii) characterise the soil seed bank and (iii) assess the potential for natural regeneration of the standing woody stand using the soil seed bank.

2. Materials and Methods

2.1. Study Site. The Léfini Faunal Reserve is located in south-eastern Congo. This reserve was created by decree no. 3671 of 26 November 1951 over an area of 400,000 ha and then

extended to 6,300,000 ha by decree no. 0046/MAEEFGR-CH-CN of 7 January 1963 [28]. According to Hecksweiler [25] and to the law n°24-2024 of 8 October 2024, this reserve straddles the Djoué-Léfini and Plateaux prefectures, particularly the sub-prefectures of Odziba (Southern sector) and Ngo (Northern sector) (Figure 1). Northern sector lies between South latitudes 02°21'12.348"–3°04'10.776" and East longitudes 15°06'03.600"–15°46'16.824".

The study area is subject to an equatorial climate of the Guinean forest type, corresponding to Aw4 according to Köppen's classification [29–33]. Precipitation is fairly constant, fluctuating between 1600 and 1800 mm/year. The average annual temperature is 25.5°C. The seasonal pattern is marked by a 3-month dry season and a 9-month rainy season (Figure 2). The dry season, from June to August, is characterised by low rainfall and mild (cool) temperatures. The rainy season, from September to May, is characterised by heavy rainfall and high temperatures.

The geological bedrock is represented by sedimentary formations of Cenozoic (Tertiary) age, of a sandstone nature where they form the polymorphous sandstone series or Batékés sandstone series [34–36]. Depending on the author, this bedrock is either Upper Kalahari or the result of alteration of the schisto sandstone system in situ. The Batékés sandstone series consists of a layer of sandy silt over a layer of soft, fine-grained, regular sandstone with no marked stratification.

The soils in the Léfini reserve are of 3 types: impoverished yellow ferrallitic on clayey-sandy material on the high plateaux; impoverished yellow ferrallitic on sandy material on the lower plateaux and slopes; and hydromorphic with gley at the level of the watercourses [25]. On these soils, the vegetation cover is marked by savannah dotted with forest patches (gallery forests and forest islands on the slopes and edges of plateaux).

Most of the Léfini Faunal Reserve is located on the Nsah-Ngo Téké plateau, at altitudes of between 600 and 750m. To a lesser extent, the reserve is on the Mbé plateau, at an altitude of between 600 and 760 m. The plateaux are bordered by imposing polymorphous sandstone cliffs [30].

The Léfini Faunal Reserve is watered by the watershed of the Léfini river, which flows to the south [29, 30, 34]. The main tributaries of the Léfini that originate in the reserve are the Nambouli, which forms the western boundary of the reserve, and the Djouélé [37]. The Nambouli has tributaries in the Nkanou, Ligélé and Ngonfon rivers. In addition to the Nambouli and Djouélé rivers, the Louna (a tributary of the Léfini) forms a boundary with the Lesio-Louna Gorilla Nature Reserve.

2.2. Materials. The soil material consists of soil samples taken from forest ecosystems in the Léfini reserve. The biological material consists of trees with dbh $\geq$ 10 cm and seedlings from the soil seed bank. During the inventory, species were identified in situ for the most common species. A reference herbarium was set up for unidentified specimens to facilitate their *ex situ* identification at the National Herbarium (IEC) located at IRSEN in Brazzaville. The

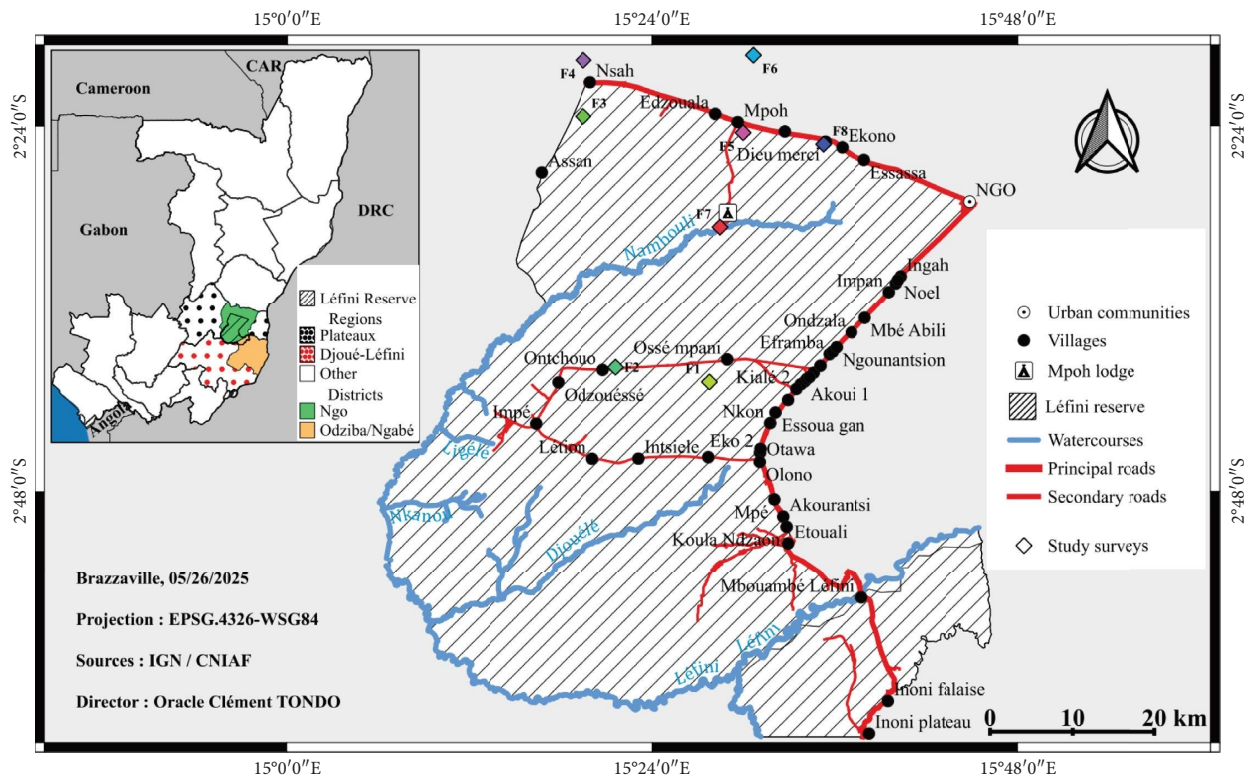


FIGURE 1: Map showing the location of the Léfini reserve.

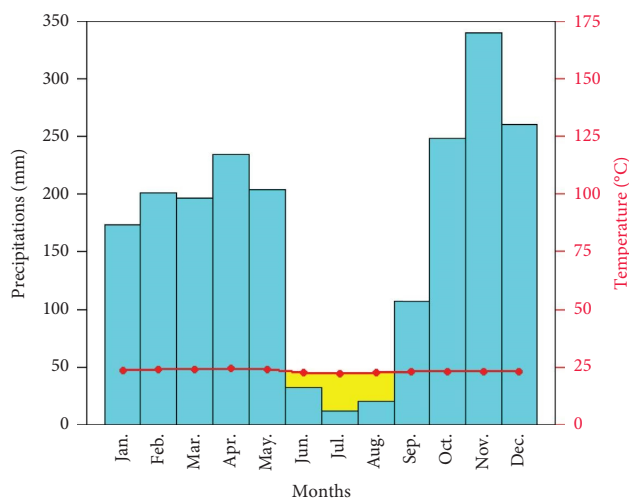


FIGURE 2: Umbrothermal diagram for Djambala.

classification adopted is based on APG IV [38] and the taxonomic nomenclature is in accordance with Lebrun and Stork [39]. The species surveyed were classified according to functional traits: diaspore type (DT), for standing woody flora, and morphological and DT for the soil seed bank.

Morphological types (MT) indicate the ultimate stage of development of individuals. Four types were selected for this study: trees (T), shrubs (sh), herbs (H) and lianas (L) [6, 40].

The DT adopted are those defined by Dansereau, Lems and Lebrun [41, 42], namely: ballochores (Ballo): diaspores expelled by the plant itself; barochores (Baro): dry or fleshy,

heavy diaspores; pogonochores (Pogono): diaspores with feathery or silky appendages, aigrettes hairs; pterochores (Ptero): diaspores with aliform appendages; sarcochores (Sarco): totally or partially fleshy diaspores; sclerochores (Sclero): relatively light, nonfleshy diaspores.

2.3. Sampling and Data Collection. Eight plots, each with a surface area of 1 ha (100 × 100 m), were installed (Figure 3). Each plot was subdivided into 16 plots of 625 m² (25 × 25 m) in which all woody individuals of dbh ≥ 10 cm were counted [43].

Soil samples were collected from 19 to 29 July 2022. For each plot, 5 collection points were set up, including 4 in the angular plots and one in the centre (Figure 3). Each collection point corresponded to a 1 m equilateral triangle. At each of these points, three samples were taken at the apexes of the triangle using an auger measuring 10 cm × 10 cm on each side and 5-cm deep (Figure 3) [17, 20, 21, 44]. Each sample was subdivided into two horizons: 0–5 cm and 5–10 cm. For each horizon, a composite sample was made up, with samples taken at each summit, in order to take better account of the heterogeneity of the seed bank. Ten composite samples were obtained per plot, i.e. 80 for the eight plots. The soil samples were packed in plastic bags for storage and transfer to the germination site.

Each composite soil sample was labelled with a code giving information on: the plot (F ranging from 1 to 8), the sample (E ranging from 1 to 5) and the depth (H1 = 0–5 cm and H2 = 5–10 cm).

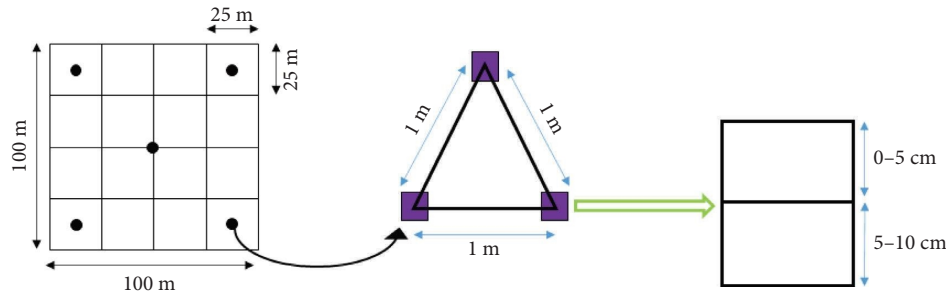


FIGURE 3: Floristic inventory and soil sample collection system.

Each collection point has a surface area of 300 cm², i.e. 1500 cm² for each plot and 12,000 cm² or 1.2 m² for the eight plots. In terms of volume, each composite sample was 1500 cm³, i.e. 3000 cm³ per collection point, 15,000 cm³ per plot and 120,000 cm³ or 0.12 m³ for the eight plots.

2.4. Estimation of Seed Viability. Once at the germination site (IRF nursery), the number of viable seeds in the soil was estimated using the germination method [45]. The soil samples were cleaned of vegetative plant parts and coarse mineral elements. The soil was heat sterilised to destroy plant pathogens and any seeds that might bias the results. Once the potting soil had been sterilised, the germination tests were carried out in circular, flat, wide plastic tubs under glass.

The soil samples were placed on top of a layer of sterilised potting soil, so that the depth of the soil spread was around 2 cm. The contents of the trays were kept moist until the end of the experiment by regular watering. Four bins containing only sterilised potting soil were used as controls to check for possible contamination by exogenous seeds.

Germination was monitored every 2–3 days for 16 weeks (from 5 August to 24 November 2022). When the stage of development allowed (3 to 6 leaves and from 7 cm), the plants were carefully removed and transplanted individually into plastic pots filled with a mixture of 75% sterilised potting soil and 25% sawdust. This mixture helps to maintain humidity in the pots, prevent settling and allow good aeration of the potting soil. The advantage of transplanting was that it facilitated identification and comparison with the flora identified during the floristic inventories.

2.5. Expressing Results

- Jaccard's similarity coefficient [46, 47]:

$$S(\%) = \frac{C}{A + B - C} \times 100, \quad (1)$$

where A = number of species in the first group, B = number of species in the second group, C = number of species common to both groups.

- Hierarchical ascending classification (HAC) based on Jaccard's dissimilarity was carried out using R software (vegan 2.6-4 package) for plots and horizons in order to identify similarities in their floristic composition.

- Shannon's biological diversity index (H'), which corresponds to the diversity achieved by a community [46, 47]:

$$H' = - \sum_{i=1}^S p_i \ln p_i, \quad (2)$$

where $p_i = n_i/n$; n_i = number of individuals in the species and/or family and n = total number of individuals.

- The maximum diversity index ($H'_{\max}$), which corresponds to the maximum diversity that a community can achieve [46, 47]:

$$H'_{\max} = \ln S, \quad (3)$$

where S = the total number of species.

- The Pielou equitability index [46, 47]:

$$J = \frac{H'}{H'_{\max}}. \quad (4)$$

- Indicator species

To identify the indicator species from the soil seed bank, the indicator value index (IndVal) was calculated using R software (package labdsv 2.0-1) at the significance threshold $\alpha = 0.05$. This index, described by Dufrène and Legendre [48]:

$$\text{IndVal} = A_{kj} B_{kj}, \quad (5)$$

where $A_{kj} = N_{\text{individuals}kj} / N_{\text{individuals} + k}$ and $B_{kj} = N_{\text{sites}kj} / N_{\text{sites} + k}$.

In the A_{kj} formula, $N_{\text{individuals}kj}$ is the average abundance of species j in sites in group k , while $N_{\text{individuals} + k}$ is the sum of the average abundances of species j in the various groups. In the formula B_{kj} , $N_{\text{sites}kj}$ is the number of sites in group k where species j is present and $N_{\text{sites} + k}$ is the total number of sites in the group. B_{kj} is maximum when species j is present in all the sites in group k . A_{kj} is a measure of specificity based on abundance values, while B_{kj} is a measure of fidelity calculated from presence data. The groups are formed by the different plots (F1 to F8) and the sites by the samples (1–5). Indeterminate species were not taken into account in the ordering.

- Raw and weighted spectra of MT and diaspores [49];

$$SB(\%) = \frac{\text{Number of species by category}}{\text{Total number of species}} \times 100, \quad (6)$$

$$SP(\%) = \frac{\text{Number of plants or sprouted seeds per category}}{\text{total number of plants or germinated seeds}} \times 100. \quad (7)$$

- The basal area (BA), for woody plants, which corresponds to the projection of the sections of trunks assumed to be circular at ground level:

$$BA = \frac{\sum \pi d_i^2}{4}, \quad (8)$$

with $\pi = 3.14$ and d_i corresponds to the diameter of an individual.

- Density (D) which is the number of germinated seeds (N) per unit area (S):

$$D = \frac{N}{S}. \quad (9)$$

- Relative density (RD), which is the percentage ratio of the density of one taxon (D_i) to the total density of all taxa (D_t):

$$RD = \frac{D_i}{D_t} \times 100. \quad (10)$$

- Frequency (F) is the ratio of the number of sampling points (P_i) where a taxon is encountered to the total number of sampling points (P_t):

$$F = \frac{P_i}{P_t}. \quad (11)$$

- Relative frequency (RF) is the percentage ratio of the frequency of a taxon (F_i) to the total frequency of all taxa (F_t):

$$RF = \frac{F_i}{F_t} \times 100. \quad (12)$$

- Species Importance Value Index (IVI). described by Douh et al. [20] provides information on the number of individuals and their distribution.

$$IVI = RD + RF. \quad (13)$$

- Nonmetric Multidimensional Scaling (NMDS). To compare the floristic composition of the soil seed bank between the eight sites of the soil seed bank with that of the woody flora as well as of the woody flora between the eight sites, an NMDS based on abundance data (per soil sample, plots or plots) was performed. This method makes no assumptions about the data and is considered among the appropriate methods for graphical representation of floristic ordination [50–52]. NMDS has been applied in the R environment, with the vegan package (v. 2.6-4) [18]. Indeterminate species were not considered in the ordination.

- Assessment of Natural Regeneration Potential The potential for natural regeneration was assessed by establishing a list of species common to the soil seed bank and the woody flora, with the exception of undetermined species, and then calculating Jaccard's similarity coefficient between the woody flora and the woody species in the soil seed bank using the formula in equation (1).

2.6. Statistical Processing. The data were processed statistically using R (v. 4.1.2.) with its RStudio interface (v. 0.99.903.), Past (v. 4.03.) and Excel (v. 2016). The Excel spreadsheet was used to create the database for this study. Means were expressed with the standard error (SE).

The results were subjected to the one-factor ANOVA test or Student's t test to assess the significance of the data for the abundance and biodiversity parameters using R software at the $\alpha = 0.05$ probability threshold. These tests were only performed when the data followed a normal distribution after the Shapiro–Wilk normality test. If the data did not follow a normal distribution, they were transformed and their normality rechecked. For significant differences, Tukey's post hoc multiple comparison test was applied to determine significance. The chi-square test of homogeneity was performed to verify the homogeneity of the floristic composition of the different plots. The conformity test was used to check the match between the overall distribution of ecological types and that at plot level.

3. Results

3.1. Standing Woody Flora

3.1.1. Floristic Composition. The standing woody flora comprises 2903 individuals representing 113 species from 38 families and 92 genera. The taxa (3.54%) with more than 100 individuals represent 20.32% of the stand and are *Duvigneaudia inopinata*, *Petersianthus macrocarpus*, *Diospyros dendo* and *Pentaclethra eetveldeana*. Those with between 60 and 100 individuals represent 30.42% of the population. This cohort, which accounts for 10.62% of species, is made up of *Staudtia kamerunensis*, *Pycnanthus angolensis*, *Macaranga spinosa*, *Sorindeia* sp., *Musanga cecropioides*, *Tetraberlinia bifoliolata*, *Millettia laurentii*, *Grewia coriacea*, *Pancovia laurentii*, *Strychnos* sp., *Dialium pachyphyllum* and *Heisteria parvifolia*. Species (21.24%) with a minimum of 20 individuals represent 29.66% of the total. This group includes *Barteria fistulosa*, *Trichilia monadelpha*, *Macaranga* sp., *Blighia welwitschii*, *Parinari excelsa*, *Trichilia prieuriana*, *Pterygota bequaertii*, *Maranthes glabra*, *Oncoba welwitschii*, *Treculia africana*, *Myrianthus arboreus*, *Xylopia wilwerthii*, *Markhamia tomentosa*, *Piptadeniastrum africanum*, *Strombosia grandifolia*, *Grossera macrantha*, *Beilschmiedia insularum*, *Antidesma laciniatum*, *Pentaclethra macrophylla*, *Coltoecema dewevrei*, *Funtumia africana*, *Kigelia africana*, *Macaranga monandra* and *Albizia zygia*. All the other species (64.60%), with fewer than 20 individuals each, represent 11.61% of the stand.

In terms of plots, the number of families, genera and species ranged from 14 to 26, 17 to 46 and 18 to 51, respectively (Table 1). The absolute density of the plots ranges from 297 to 410 plants/ha and the distribution of this density by species ranges from 1 to 107 plants/ha/species. Table 1 also lists the main species supporting the density in each plot.

Among the dominant species, the upper strata are less well represented in the different plots. Moreover, these species vary from one plot to another, highlighting the heterogeneity of the floristic composition. This floristic variation is evidence of the existence of different forest facies. The NMDS (Figure 4) shows that F3, F4 and F7 stand out from the rest of the plots. As for the other plots, F1 seems to deviate from the group, while F2, F5, F6 and F8 are broadly similar.

3.1.2. BA. The average BA of the various plots was $30.3 \pm 3.79 \text{ m}^2/\text{ha}$. At plot level, BA varied from 20.35 to $52.87 \text{ m}^2/\text{ha}$. These values are, on the whole, lower than the data for the dense humid forests of Central Africa, but in line with the data for mesophilic and tropophilic forests.

3.1.3. Spectrum of Diasporas. Figure 5 shows the spectra of diaspores. At the scale of the study, sarcochorous species (76.99%) outnumber pterochores (10.62%) by seven and ballochores (7.96%) by ten. The weighted spectrum reveals a clear dominance of sarcochores (72.37%) ahead of ballochores (12.78%) and pterochores (11.99%) throughout the area. Although the three dominant types (ballochores, pterochores and sarcochores) are also dominant at plot level, the weighted spectra between plots show differences in the distribution of all types (chi-square p value ≤ 0.001). However, the distribution was less influenced by the survey at the specific level (chi-square p value = 0.790). The dominance of sarcochores indicates that most plants depend on animals for their spread. This dominance also highlights the maturity and stability of the plant communities studied.

3.2. Characteristics of the Soil Seed Bank

3.2.1. Taxonomic Data and Abundance. Table 2 summarises the taxonomic and abundance data from the soil seed bank. The study counted 1763 seeds belonging to 50 species and 32 families. Of the 50 species, 70% have been completely identified, 22% have only been identified at family level and 8% are in the process of being identified. The number of species is significantly higher in the first horizon than in the second (p value = 0.022) but does not vary significantly between surveys (p value = 0.057). The number of individuals did not vary significantly between horizons (p value = 0.291). However, this number did vary significantly between surveys (p value ≤ 0.001).

3.2.2. Floristic Composition and Characteristics of the Soil Seed Bank. With more than 100 seeds, *Polia condensata*, *Musanga cecropioides* and *Trema orientalis* represent around 70.05% of the population. However, with at least 10 seeds,

Harungana madagascariensis, Indeterminate 13, *Palisota ambigua*, Indeterminate 1, Indeterminate 12, *Centotheca lappacea*, *Parinari excelsa*, Indeterminate 2, *Mikania cordata*, *Tristemma hirtum*, Indeterminate 6, *Oncoba welwitschii* and *Macaranga spinosa* represent 23.09% of the seeds (Supporting Information 1). The remaining 34 species, each with fewer than 10 seeds, account for 6.86% of the total. The seeds density of the study area was $1469.17 \text{ seeds/m}^2$. The chi-square homogeneity test shows that the floristic composition is significantly different between the soil horizons surveyed (p value ≤ 0.001) and not between the surveys.

At plot level, the absolute density varied from 566.67 to 2400 seeds/ m^2 and the contribution of the species to this density ranged from 6.67 to 1620 seeds/ $\text{m}^2/\text{species}$ (Table 3). Table 3 also highlights the main species that support the density of each plot.

Apart from *Parinari excelsa*, the key species in the soil seed bank on the different facies studied are pioneers, both woody and herbaceous. Furthermore, the woody flora and the flora in the soil seed bank do not have the same dominance. The soil seed bank does not sufficiently reflect the surrounding flora. These differences can be attributed to the types of diaspore and dissemination.

The IVIs for the different plots show that the most important species are *Musanga cecropioides* with 63.22% and 53.89%, respectively, in plots F1 and F5, *Polia condensata* with 42.14%, 78.38% and 96.77%, respectively, in plots F2, F3 and F6, *Trema orientalis* with 44.78% in plot F4, Indeterminate 1 with 30.21% in plot F7 and *Harungana madagascariensis* with 37.74% in plot F8. With the exception of *Polia condensata*, which is an open grass, the most important species are all pioneer woody plants.

The seed bank indicator species are: *Palisota ambigua* (IndVal = 0.780 and p value = 0.001) in F2, *Trema orientalis* (IndVal = 0.349 and p value = 0.046) in F3, *Tristemma hirtum* (IndVal = 0.431 and p value = 0.010) in F4, *Musanga cecropioides* (IndVal = 0.341 and p value = 0.004) in F5, *Tristemma mauritianum* (IndVal = 0.600 and p value = 0.010) in F6, *Cyperus mapanioides* (IndVal = 0.600 and p value = 0.007) and *Geophila afzelii* (IndVal = 0.584 and p value = 0.014) in F7 and *Parinari excelsa* (IndVal = 0.475 and p value = 0.018) in F8. The indicator species of the soil seed banks of the forests of the Léfini reserve are bioindicators of forest disturbance. Only *Parinari excelsa*, in plot F8, is a mature forest species.

3.2.3. Biodiversity Parameters. The biodiversity indices for the plots are shown in Table 4. The Shannon diversity index varies from 0.83 to 2.27 (i.e. 1.72 ± 0.17 on average), and the maximum diversity varies from 2.56 to 3.04 (i.e. 2.83 ± 0.06 on average). However, equitability varies from 0.32 to 0.78 (i.e. 0.61 ± 0.06 on average). Biodiversity is low and species distribution tends to be gregarious in F3, F5, F6 and throughout the study area. The Shannon (p value = 0.006) and Pielou (p value = 0.027) indices show significant differences between the surveys, while the maximum diversity index does not show significant differences (p value = 0.058).

Overall, the biological diversity indices do not show any differences between the horizons surveyed, with the

TABLE 1: Summary of taxonomic and floristic data for standing woody plants by plot.

Plots	Family number	Genus number	Species number	Density (plants/ha)	Species density (plants/ha/ species)	Principal species
F1	23	39	41	381	1 to 73	<i>Duvigneaudia inopinata</i> , <i>Tetraberlinia bifoliolata</i> , <i>Staudtia kamerunensis</i> , <i>Diospyros dendo</i> , <i>Colletocema dewevrei</i> , <i>Trichilia prieuriana</i> , <i>Pycnanthus</i> <i>angolensis</i> and <i>Trichilia monadelpha</i>
F2	26	41	45	367	1 to 107	<i>Duvigneaudia inopinata</i> , <i>Petersianthus macrocarpus</i> , <i>Pentaclethra eetveldeana</i> , <i>Heisteria parvifolia</i> , <i>Diospyros dendo</i> , <i>Maranthes glabra</i> , <i>Dialium pachyphyllum</i> and <i>Pycnanthus angolensis</i>
F3	20	35	41	364	1 to 28	<i>Antidesma laciniatum</i> , <i>Pycnanthus angolensis</i> , <i>Petersianthus macrocarpus</i> , <i>Myrianthus arboreus</i> , <i>Funtumia africana</i> , <i>Oncoba welwitschii</i> , <i>Kigelia africana</i> and <i>Pterygota bequaertii</i>
F4	19	41	43	327	1 to 72	<i>Macaranga spinosa</i> , <i>Musanga cecropioides</i> , <i>Pentaclethra eetveldeana</i> , <i>Petersianthus</i> <i>macrocarpus</i> , <i>Treculia africana</i> , <i>Blighia welwitschii</i> and <i>Oncoba welwitschii</i>
F5	23	41	49	297	1 to 34	<i>Pancovia laurentii</i> , <i>Petersianthus macrocarpus</i> , <i>Strombosia grandifolia</i> , <i>Macaranga</i> <i>monandra</i> , <i>Pentaclethra macrophylla</i> , <i>Pentaclethra eetveldeana</i> , <i>Treculia africana</i> , <i>Dialium pachyphyllum</i> , <i>Musanga cecropioides</i> and <i>Staudtia kamerunensis</i>
F6	26	46	51	410	1 to 97	<i>Petersianthus macrocarpus</i> , <i>Pentaclethra eetveldeana</i> , <i>Grewia coriacea</i> , <i>Duvigneaudia inopinata</i> , <i>Parinari excelsa</i> , <i>Pancovia laurentii</i> , <i>Staudtia</i> <i>kamerunensis</i> , <i>Dialium pachyphyllum</i> , <i>Trichilia monadelpha</i> and <i>Pycnanthus</i> <i>angolensis</i>
F7	14	17	18	353	1 to 106	<i>Diospyros dendo</i> , <i>Strychnos</i> sp., <i>Milletia laurentii</i> , <i>Xylopia wilwerthii</i> , <i>Grossera</i> <i>macrantha</i> , <i>Anisophyllea purpurascens</i> , <i>Markhamia tomentosa</i> and <i>Pterygota</i> <i>bequaertii</i>
F8	25	41	46	404	1 to 78	<i>Sorindeia</i> sp., <i>Pentaclethra eetveldeana</i> , <i>Macaranga</i> sp., <i>Heisteria parvifolia</i> , <i>Diospyros dendo</i> , <i>Parinari excelsa</i> , <i>Duvigneaudia inopinata</i> , <i>Beilschmiedia</i> <i>insularum</i> , <i>Maranthes glabra</i> , <i>Pycnanthus angolensis</i> , <i>Barteria fistulosa</i> and <i>Dialium pachyphyllum</i>

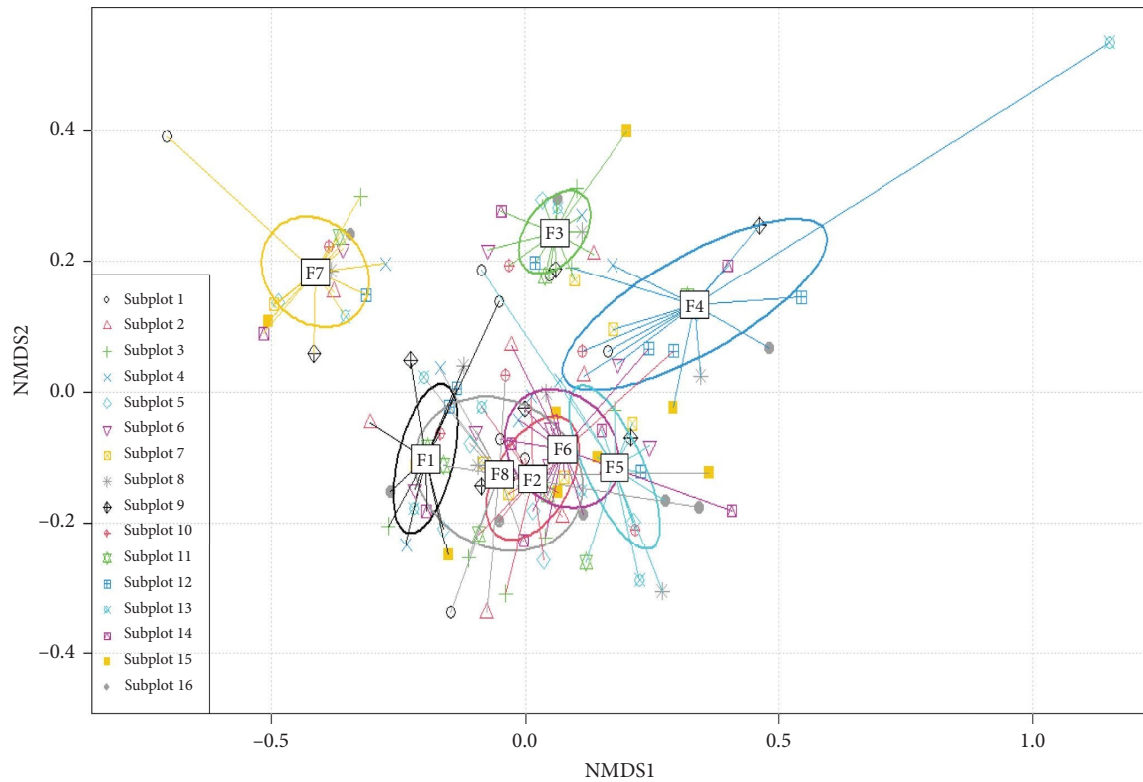


FIGURE 4: Nonmetric multidimensional scaling (NMDS) of woody flora.

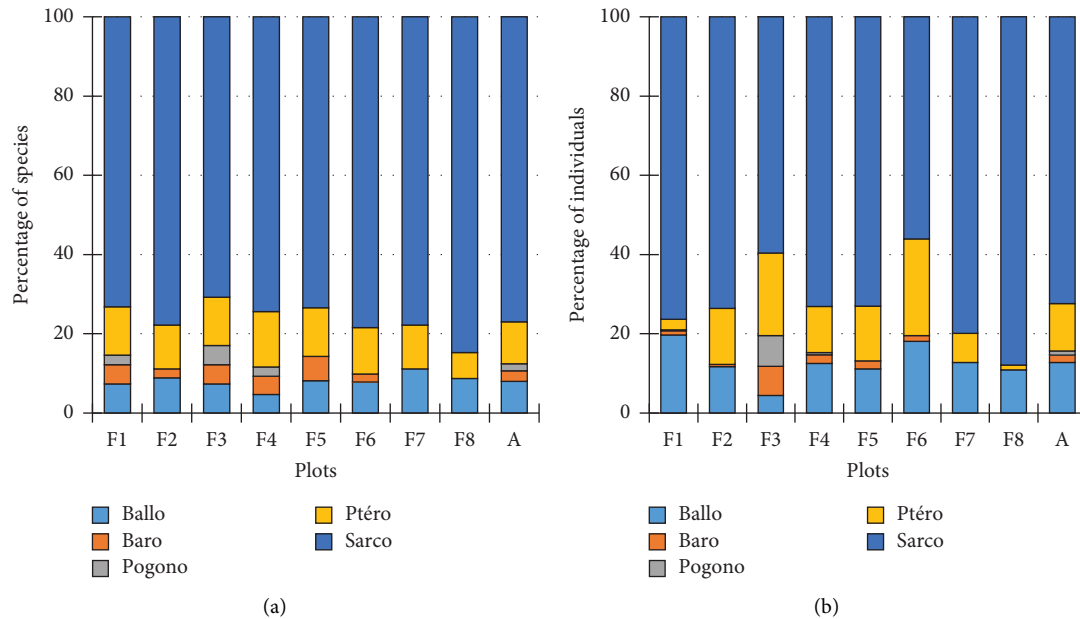


FIGURE 5: Spectra of the diaspora. Raw spectrum (a); weighted spectrum (b).

exception of F6, where Student's t test on the Shannon diversity index data shows a significant difference (Figure 6).

The Jaccard similarity coefficient values range from 13.89% to 57.69%. At the 50% threshold, Figure 7 shows the existence of seven groups: F8, F1, F2, F3-F4, F5, F6 and F7. The soil seed bank of F7, which is more than 70% dissimilar to the other plots, is fundamentally different

from a floristic point of view. The flora of the soil seed bank of the forest facies in the northern sector of the Léfini reserve is therefore very heterogeneous. This leads us to consider several different forest facies within the study area.

Jaccard's similarity coefficient for the horizons of the different plots varies from 4.55% to 60.87%. At the 50%

TABLE 2: Overview of taxonomic and abundance data.

Plot	Families	Species	N	N _{H1}	N _{H2}
F1	13	14 ^{a*}	85 ^a	45	40
F2	12	18 ^a	209 ^{abc}	135	74
F3	17	21 ^a	360 ^b	165	195
F4	17	20 ^a	181 ^{abc}	108	73
F5	13	16 ^a	333 ^{bc}	240	93
F6	12	13 ^a	320 ^{bc}	143	177
F7	13	20 ^a	171 ^{abc}	96	75
F8	13	15 ^a	104 ^{ac}	50	54
Average ± SE	13.75 ± 0.73	17.13 ± 1.08	220.38 ± 37.34	122.75 ± 22.51	97.63 ± 20.14
Study area	32	50	1763	982	781

*The means of values not followed by the same letter in the same column are significantly different at the $\alpha = 0.05$ threshold according to the Tukey test.

threshold, Figure 8 shows 12 groups: F7H1, F7H2, F6H2, F3H2, F6H1, F1H2, F3H1- F4H1-F4H2, F2H1-F2H2, F8H1, F8H2, F5H2-F5H1 and F1H1. The horizons of plot F7 are fundamentally different from those of the other plots. Most of the strongest floristic similarities were found between horizons of the same facies. The soil seed bank therefore has a floristic composition that varies less at the intra-ecosystem level than at the inter-ecosystem level. Without taking indeterminate species into account, the NMDS (Figure 9) shows that F7 and F8 are broadly similar to and different from F1, F2, F3, F4 and F5. However, F6 is only slightly similar to all the other plots.

3.2.4. Ecological Spectra. The raw spectrum shows the dominance of herbaceous species and lianescents at the scale of the area (Figure 10(a)). The chi-square compliance test (p value = 0.006) highlights differences in proportions between the overall study area and the plots. In plots F1 and F2, shrub species are more prominent than other MT. In plots F3 and F4, lianas dominate the plant life compared with the other MT. Plots F5 and F8 show a co-dominance of shrubby and herbaceous taxa. Herbaceous species predominate in plots F6 and F7. The weighted spectrum shows a dominance of herbaceous individuals in the study area (Figure 10(b)). This overall distribution is not the same at plot level (chi-square p value ≤ 0.001). Trees predominate in plots F1 and F8. The weighted spectrum highlights grasses in plots F2, F3, F5, F6 and F7. Shrubs are highlighted in plot F4. These results highlight the existence of openings in the canopy favourable to the establishment of grasses.

The raw (Figure 11(a)) and weighted (Figure 11(b)) spectra show a clear dominance of sarcochorous taxa across all plots. The overall distribution of diaspores differed significantly between surveys in terms of the number of individuals (chi-square p value ≤ 0.001), but not in terms of species richness (chi-square p value = 0.307). Most of the species depend on animals for their spread, so the facies are relatively evolved. The weighted spectrum for plot F7 favours sclerochore diaspores ahead of sarcochores, highlighting anemochory as the main mode of dissemination and the relatively young state of the facies in question.

3.3. Assessment of Natural Regeneration Potential

3.3.1. Common Species. There are 10 woody species in common between the soil seed bank and the woody flora (i.e. 8.85% of the woody flora). These include *Macaranga monandra*, *Macaranga* sp., *Macaranga spinosa*, *Musanga cecropioides*, *Oncoba welwitschii*, *Parinari excelsa*, *Riciodendron heudelotii*, *Tetrorchidium didymostemon*, *Xylopia hypolampra*, *Xylopia staudtii* and *Zanthoxylum* sp. The mature forest woody species counted are *Parinari excelsa*, *Riciodendron heudelotii*, *Xylopia hypolampra*, *Xylopia staudtii* and *Zanthoxylum* sp.

3.3.2. Floristic Similarity. The NMDS (Figure 12) shows that the floristic composition is broadly similar between the soil horizons but fundamentally different between the soil horizons and the woody flora. Furthermore, Jaccard's similarity coefficient between the soil seed bank and the surrounding woody flora is 08.20%. The similarity is 0 in plots F1 and F7, 03.77% in plot F2, 06.67 in plot F3, 08.89 in plot F4, 03.70% in plot F5, 07.69% in plot F6 and 05.88% in plot F8. The floristic composition of the two compartments studied was therefore highly dissimilar. The soil seed bank reflects very little of the woody flora compartment of the forest facies studied in the Léfini reserve.

4. Discussion

4.1. Diversity and Structure of the Woody Stand. The tropical rainforests of Central Africa, although less rich than the tropical formations of the Amazonian and Borneo-Mekong basins, constitute a significant biodiversity hotspot at global level [1, 8, 53]. Based on structural and biodiversity data, the forest facies of Léfini are paucispersic compared with the dense rainforests of Central Africa [53–57]. The low number of stems per hectare and the low value of the projection of trunk sections on the ground highlight the pauciflorous nature of the ecosystems studied [1, 8, 58–61]. The paucispecific and pauciflorous characteristics of the Léfini forests bring them into line with the mesophilous and tropophilous facies of the Plateau des Cataractes and the Niari Valley [40, 62–64]. However, two facies (Ossémpa

TABLE 3: Summary of floristic and abundance data from the soil seed bank.

Plots	Density (seeds/m ²)	Species density (seeds/m ² /species)	Principal species
F1	566.67	6.67 to 253.33	<i>Musanga cecropioides</i> , Indeterminate 13, <i>Harungana madagascariensis</i> and <i>Trema orientalis</i>
F2	1393.33	6.67 to 480	<i>Pollia condensata</i> , <i>Musanga cecropioides</i> , <i>Palisota ambigua</i> and <i>Harungana madagascariensis</i>
F3	2400	6.67 to 1573.33	<i>Pollia condensata</i> , <i>Trema orientalis</i> , <i>Musanga cecropioides</i> and <i>Harungana madagascariensis</i>
F4	1207.67	6.67 to 413.33	<i>Trema orientalis</i> , <i>Musanga cecropioides</i> , indeterminate 3, <i>Pollia condensata</i> and <i>Mikania cordata</i>
F5	2220	6.67 to 893.33	<i>Pollia condensata</i> , <i>Musanga cecropioides</i> , <i>Trema orientalis</i> and <i>Harungana madagascariensis</i>
F6	2133.33	6.67 to 1620	<i>Pollia condensata</i> , <i>Musanga cecropioides</i> and indeterminate 3
F7	1140	6.67 to 246.67	Indeterminate 1, <i>Centotheca lappacea</i> , indeterminate 12 and <i>Harungana madagascariensis</i>
F8	693.33	6.67 to 153.33	<i>Harungana madagascariensis</i> , indeterminate 13, <i>Parinari excelsa</i> and <i>Musanga cecropioides</i>

TABLE 4: Variation in soil seed bank biological diversity indices.

Indices	F1	F2	F3	F4	F5	F6	F7	F8	Average $\pm$ SE	A
H'	1.79 ^{ab*}	1.95 ^a	1.28 ^{ab}	2.08 ^a	1.48 ^{ab}	0.83 ^b	2.27 ^{ab}	2.10 ^{ab}	1.72 $\pm$ 0.17	2.19
H max	2.64 ^a	2.89 ^a	3.04 ^a	3.00 ^a	2.77 ^a	2.56 ^a	3.00 ^a	2.71 ^a	2.83 $\pm$ 0.06	3.91
J	0.68 ^a	0.68 ^a	0.42 ^{ab}	0.70 ^a	0.53 ^{ab}	0.32 ^b	0.76 ^a	0.78 ^a	0.61 $\pm$ 0.06	0.56

*The means of values not followed by the same letter in the same line are significantly different at the $\alpha=0.05$ threshold according to the Tukey test.

and Ontsouo) stand out with data similar to the dense rainforests of the region. Moreover, in terms of their floristic composition, these synusia are close to the climax of the Batéké Plateau forests defined by Makany [24], indicating an apparent progressive evolution.

The most advanced stages of the sylvigenetic cycle in the forest ecosystems of the Batéké plateaux in general and the northern sector of the Léfini reserve in particular are characterised by *Parinari excelsa* [24, 65, 66]. These forests go through intermediate, relatively stable stages with *Pentaclethra eetveldeana*, *Millettia laurentii* and *Dialium corbisieri* before reaching this climax [24]. The dominance of *Parinari excelsa* and, more generally, the dense rainforest species *Tetraberlinia bifoliolata* and *Petersianthus macrocarpus*, testifies to the level of maturity reached by the forest ecosystems of the Léfini reserve.

4.2. Diversity of the Soil Seed Bank. The soil seed bank is not very diverse overall. However, a comparison of the different facies shows that biodiversity is relatively higher in the forest at the Mpoh site, at Dieu Merci and in the nonconserved forest at Nsah. This forest facies compartment tends to be gregarious in the conserved plot at Nsah and the two plots at Mpoh, which are dominated by *Pollia condensata*. The dominance of this herbaceous species would be synonymous with a high degree of canopy openness favourable to the spread and establishment of pioneer taxa.

The specific composition and richness of the soil seed bank differ according to horizon and forest patch. The vertical gradient could be due to the substrate of the different facies. The burial and longevity of seeds depend on the type of soil [18, 20, 67, 68]. Moreover, nonpioneer or sub-pioneer species are almost exclusively found in the 0–5-cm horizon, while nonpreferential behaviour is noted for pioneer species. This can be explained by the fact that the soil seed bank is formed by the gradual accumulation of seeds in the soil over time [18, 67, 68]. The deepest seeds are the first to have been deposited on the soil and the shallowest are from a more recent deposit. Thus, nonpioneer species, which germinate almost exclusively in the shallowest horizon, are generally less long-lived than pioneer species that germinate in both horizons. This distribution of species categories, which also makes it possible to retrace the history of the forest facies in the Léfini reserve, shows that the latter are in a progressive, nonregressive dynamic in the absence of any disturbance.

The horizontal gradient expressed could be due not only to the divergent floristic composition observed in the woody flora of the different facies, but also to the fauna and the degree of openness of the canopy and undergrowth [10, 11, 17, 69, 70]. In the Léfini reserve, the soil seed bank has a lower species richness than in other forest ecosystems

studied in the Republic of Congo [20–23]. Although not significant, species richness is significantly higher on facies at Nsah and the Mpoh deposit, which are thought to be secondarised and/or disturbed, than on other facies, which are thought to be fairly mature. These differences confirm the fact that the species richness of the soil seed bank is higher in disturbed ecosystems than in mature ecosystems [18, 20, 21, 23, 67]. This indicates a system that is evolving towards maturity and stability.

4.3. Abundance and Spatial Distribution of the Soil Seed Bank.

Seed density incorporates the values predicted for forests in tropical regions [71]. This seed density is higher in the Léfini reserve than in other studies [17, 20]. However, the density is close to the values obtained by Zebaze et al. and Zamebe-Ndong [18, 21]. In Léfini, seed density varies from one forest facies to another and shows a variable vertical gradient. The vertical gradient decreases in the reserve at Ossémpana, Ontsouo, Mpoh and the Mpoh deposit, and outside the reserve at Nsah. However, the gradient increases in the other three plots. Studies carried out in the Republic of Congo and Cameroon have shown a gradient that decreases with depth for the same horizons [18, 20–22]. On the other hand, in a *Celtis* forest, an increasing density with depth was observed for the same horizons [20].

These differences in gradients could be linked to the composition and spatial distribution of the woody flora of the different facies [13]. The intrinsic characteristics of species, such as reproductive phenology, senescence and seed dormancy, can influence the expression of edaphic seminal potential [72]. Seed germination under favourable microclimatic conditions can also contribute to the reduction of this potential [73, 74]. Other factors explaining the observed heterogeneity are extrinsic in nature. These extrinsic factors are the intensity of predation and the nature and activity of disseminators, which can vary in space and time [10, 11, 74, 75]. But there are also human activities and their pressures, which sometimes radically modify ecosystems and disrupt more than one interaction [9, 76].

4.4. Contribution of the Soil Seed Bank to Forest Regeneration.

As in other studies conducted in tropical forests, the soil seed bank here only very partially reflects the surrounding woody flora [13, 17, 18, 20, 23, 67, 77]. This dissimilarity is due to the fact that in soil seed bank studies, floristic inventories are often spatially limited. This type of inventory could therefore minimise the capacity for long-distance dissemination by zoochory, which most tropical forest species exhibit, and by anemochory in gaps and young phytocenoses [5, 10, 11, 53, 56, 57, 64].

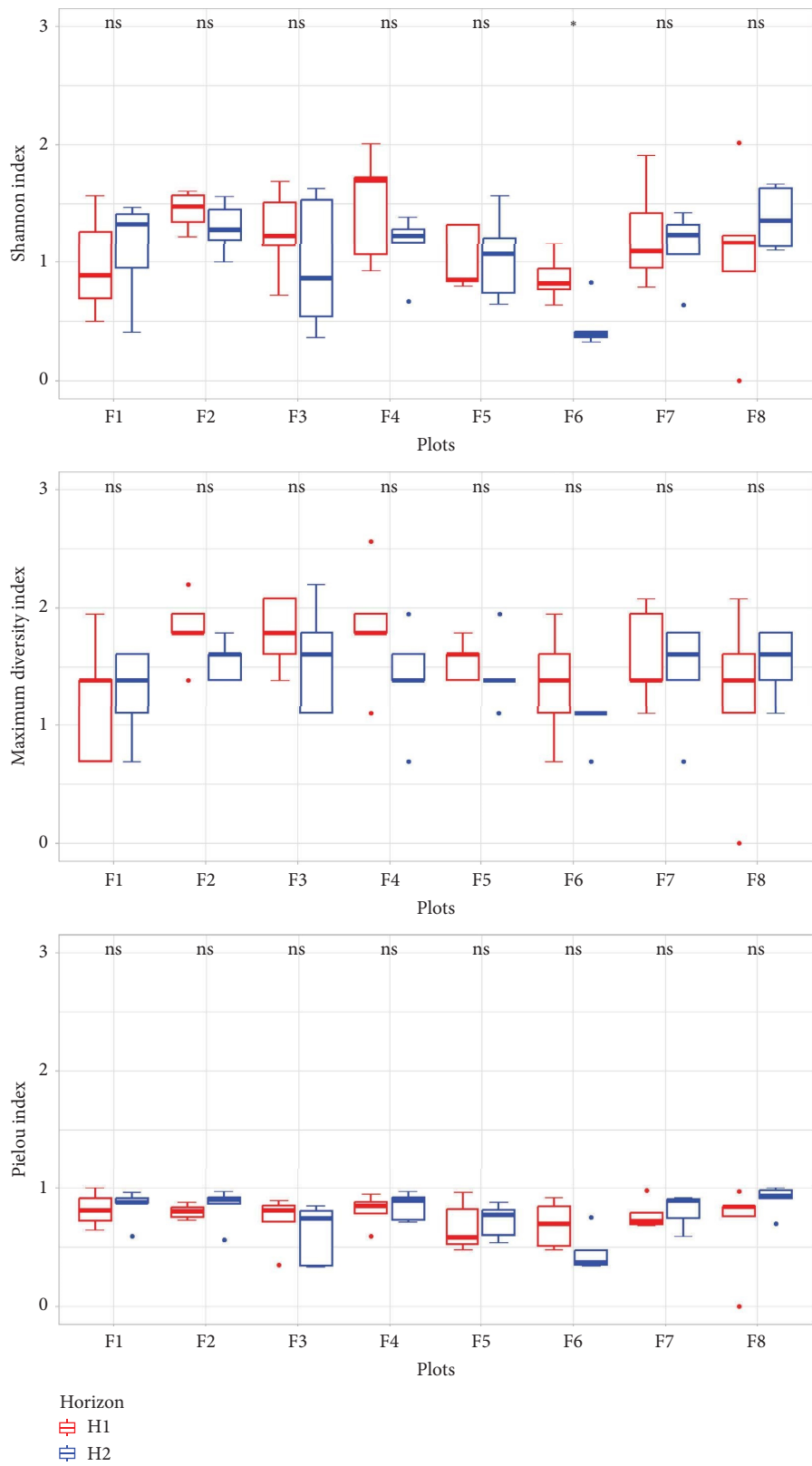


FIGURE 6: Variation in diversity indices according to soil horizons.

The woody species common to both compartments are pioneers, most of them *Macaranga monandra*, *Macaranga spinosa*, *Macaranga* sp., *Musanga cecropioides*, *Tetrorchidium*

didymostemon, *Oncoba welwitschii* and *Ricinodendron heudelotii*. Only *Parinari excelsa*, *Xylopia hypolampra*, *Xylopia staudtii* and *Zanthoxylum* sp. are mature forest species shared

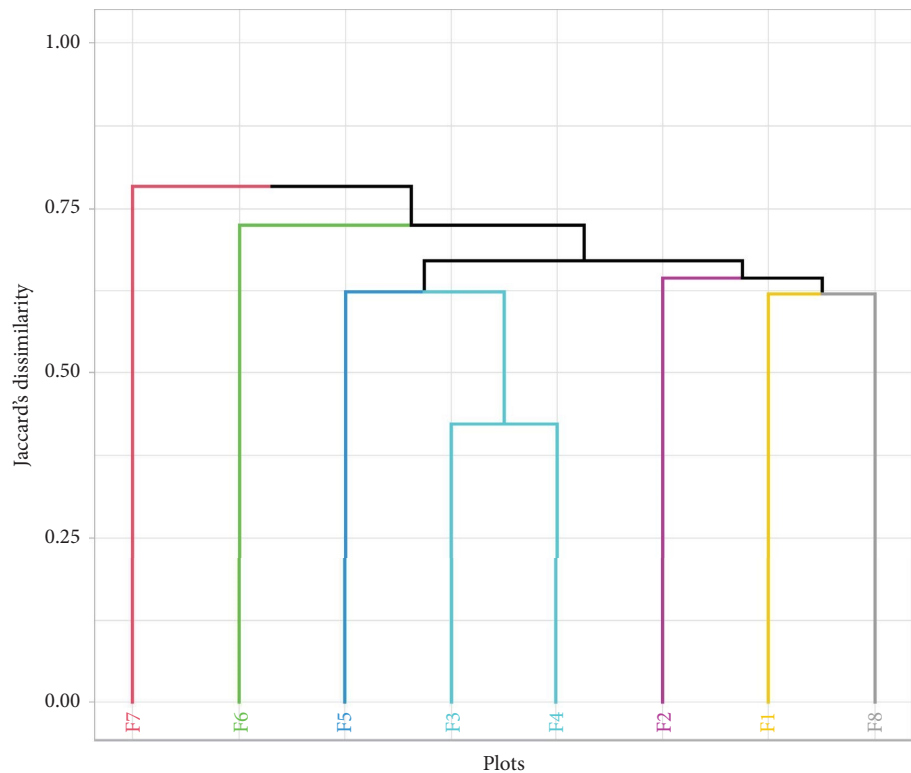
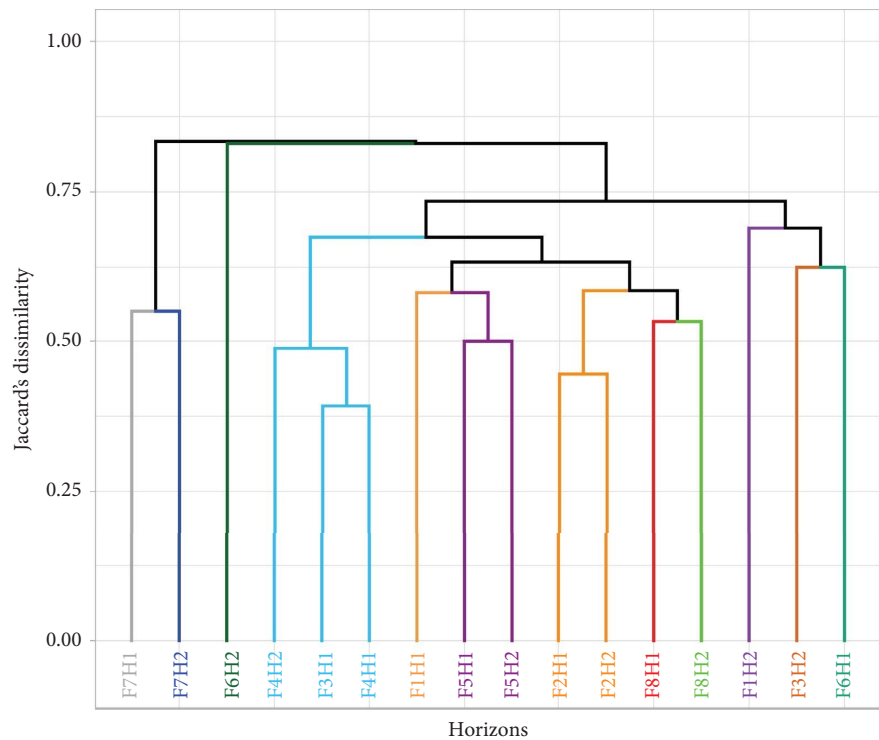


FIGURE 7: HAC (hierarchical ascending classification) of SSB (soil seed bank facies) according to Jaccard's similarity coefficient.



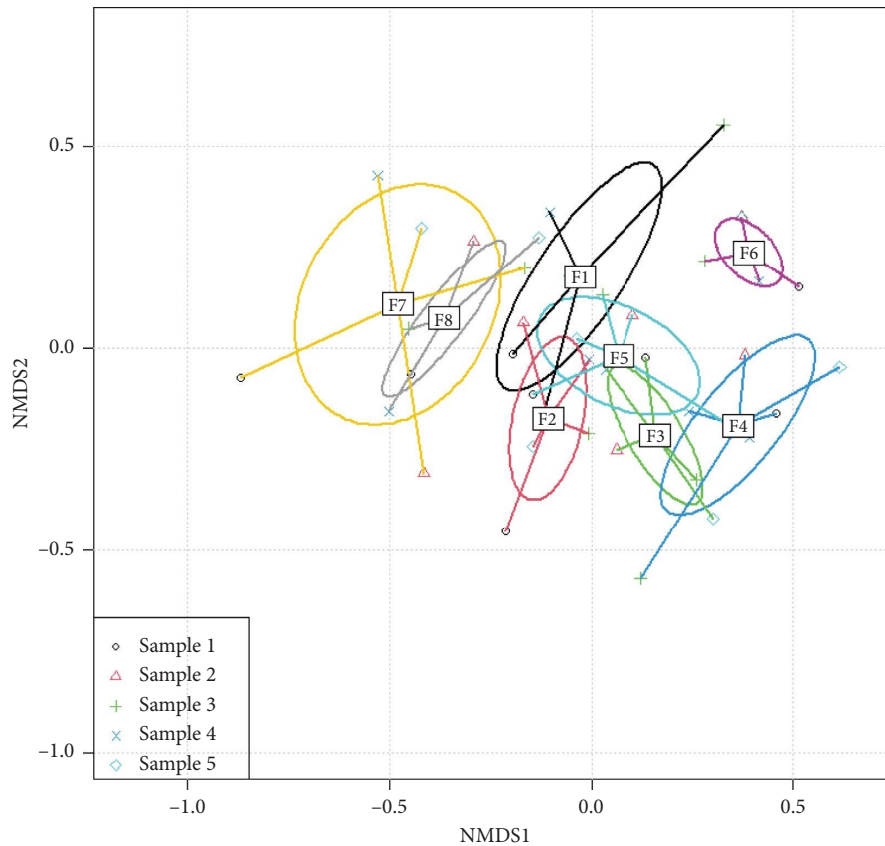


FIGURE 9: Nonmetric multidimensional scaling (NMDS) of the soil seed bank.

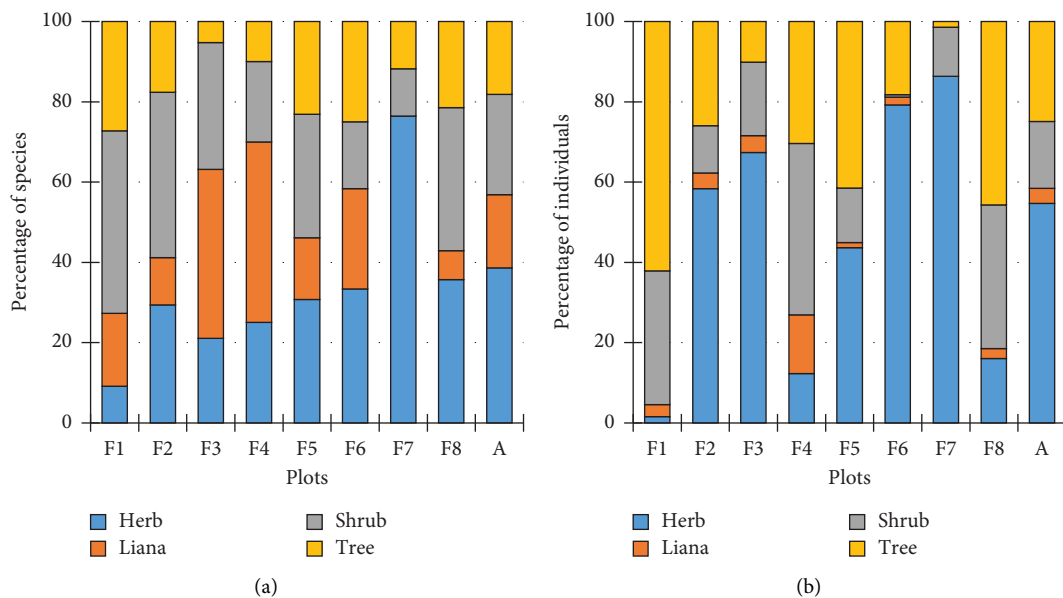


FIGURE 10: Morphological spectra. Raw spectrum (a); weighted spectrum (b).

Others, however, which are not pioneers, such as *Microdesmis puberula* and *Ficus cf. exasperata*, do not contribute to the formation of the emergent stratum [79]. The dominance of pioneers in the seed bank may be due to the relative longevity of their seeds [10, 11, 68, 80, 81]. Taxa

exclusive to the soil seed bank are the result of seed rain (advective seminal potential of exogenous contribution) resulting from long-distance dissemination from seed sources absent from the study plots [10, 11, 17, 20, 80]. This long-distance dissemination is the result of zoochory,

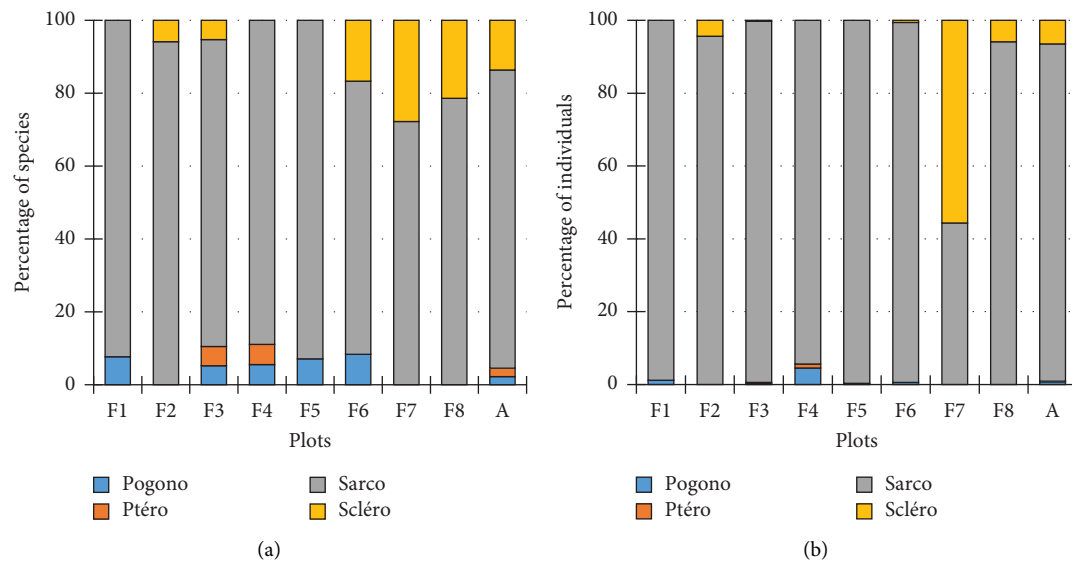


FIGURE 11: Spectra of the diaspora. Raw spectrum (a); weighted spectrum (b).

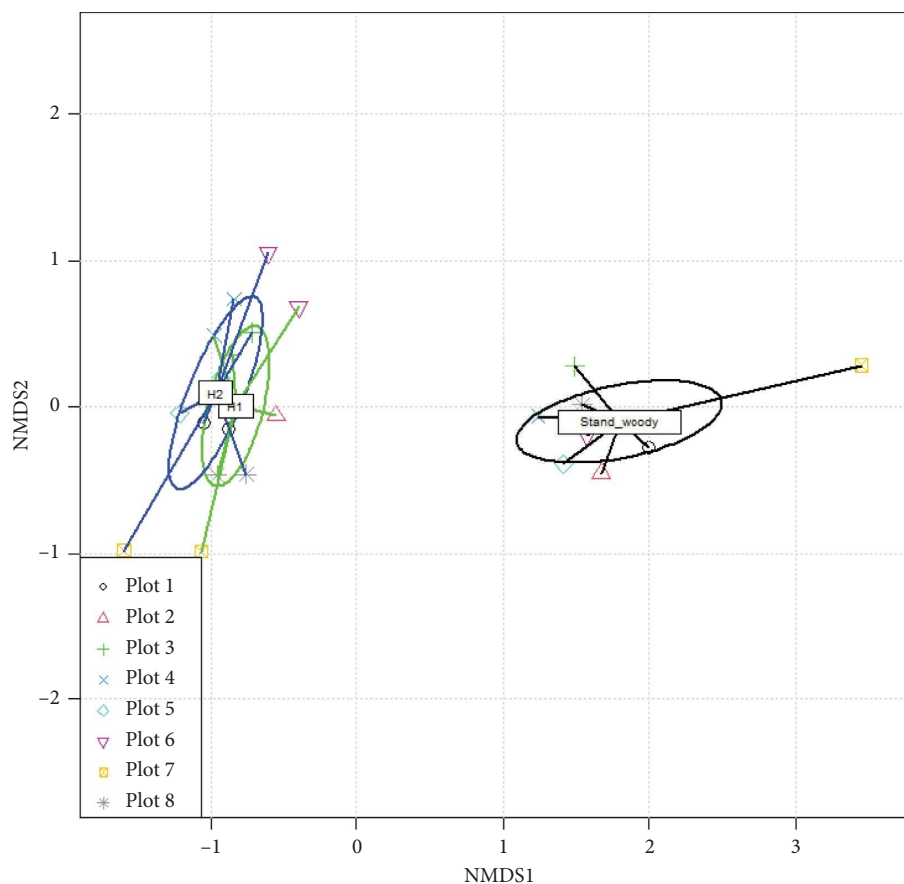


FIGURE 12: Nonmetric multidimensional scaling (NMDS) of soil seed bank horizons and woody flora.

particularly endozoochory, as demonstrated by the predominance of sarcochores in both the woody flora and the soil seed bank [8, 11]. The main agents of dissemination are the avian and mammalian fauna of these forests [6, 8, 57, 69, 70, 80, 82].

In the forest at the Mpoh site, there is no similarity between the two compartments and the soil seed bank contains no mature forest woody species. Sclerochores, which make up the majority of the soil seed bank, are represented solely by herbaceous plants native to the forest

understory. The woody plants in the seed bank, all of which spread zoochoreally as on the other facies in the reserve, are less represented in terms of numbers of individuals. In this forest on sandy soil, the majority of recolonisation will therefore be carried out by the herbaceous species of the forest undergrowth (Commelinaceae, Amaranthaceae, Melastomataceae, Poaceae). This plant succession may be the result of the numerous passages of *Loxodonta africana cyclotis*, whose presence in the Nambouli baïs is attested by Inkamba-Nkulu and Tsoumou [37]. These pachyderms contribute to the sparse state of the undergrowth, which is favourable to anemochory: the dissemination of sclerochore diaspores. In addition, by trampling, these animals compact the soil, reducing aeration and seed viability.

The low similarity between the two compartments suggests that the current flora will be replaced by a native pioneer flora, both woody and herbaceous, in the event of disturbance. This succession shows that the forest facies studied are sufficiently resilient. The predominance of herbaceous and woody pioneers can be explained by the fact that (i) these plants produce a large quantity of small seeds capable of escaping predation by granivorous animals [80, 83], (ii) the seeds gradually accumulate in large quantities and live for several decades in the soil [84–86], (iii) seeds can be disseminated over long distances and (iv) these plants can rapidly colonise the environment. Notwithstanding these elements, this post-disturbance flora resulting from edaphic seminal potential may contain mature forest species in small proportions. Only the Dieu Merci facies, where *Parinari excelsa* is dominant and characteristic, and the Ossémpana facies, characterised by *Xylopia hypolampra*, could have a high proportion of mature forest individuals in the early phases of the succession. Given the dissimilarities between the soil seed bank and the woody stand, the former cannot guarantee the renewal of the latter. Assisted natural regeneration would be of great help in the process of renewing the woody stand in the forest ecosystems of the northern sector of the Léfini reserve.

5. Conclusion

The aim of this study, carried out in the Léfini reserve, was to assess the resilience of the reserve's forest ecosystems by taking into account the woody flora and the soil seed bank. The woody flora is paucispecific and pauciflorous compared with the dense semi-deciduous forests of Central Africa. The renewal of the flora depends mainly on the avian and mammalian fauna of the sites. Structural data coupled with phytodiversity data reflect the mesophilic and tropophilic nature of the forests studied.

The soil seed bank is not very diverse. Species richness and floristic composition vary significantly from one facies to another and between soil horizons. Mature forest species are better represented on the 0–5-cm horizon, while pioneer species are not preferred. The ecological spectra highlight the zoochorous and anemochorous origins of the taxa, as well as the dominance of herbaceous and lianascent taxa. These functional traits are signs of the degradation and/or secondarisation of the facies studied.

There is very little similarity between the standing woody flora and the soil seed bank. On the one hand, woody taxa from the edaphic seed potential are mostly pioneers and absent from the standing woody flora. On the other hand, grasses and lianas predominate in the soil seed bank. In the event of disturbance, the existing vegetation would be replaced by a pioneer facies, the starting point of a new sylvigenetic cycle. The seed bank is therefore not sufficient to maintain the woody stand in equilibrium. In order to ensure the long-term survival of the forests that are essential to people's well-being, assisted natural regeneration is recommended, particularly for the most prized taxa.

Data Availability Statement

Data will be available from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare no conflicts of interest.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. (*Supporting Information*)

The floristic composition and the functional and abundance characteristics of the soil seed bank are given in the attached table.

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