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# Diversity and community composition of herbaceous plants in different habitat types in south-east Cameroon

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## Abstract

The composition of herbaceous vegetation was evaluated with the aim of characterizing forests at various ages of stand development. Herb stems were sampled in 250 4-m<sup>2</sup> square plots distributed within six habitat types. A total of 36 herb species belonging to 15 families were recorded. Species richness did not significantly differ between habitat types. Most herb species occurred in all habitat types and were therefore generalists. However, a few indicator herb species were detected, and the results roughly suggested that herb species of the families Poaceae and Araceae were indicative of late successional forests; Zingiberaceae are indicative of early successional forests; and Commelinaceae, Costaceae, Cyperaceae and Marantaceae are indicators of flooded habitats. Species diversity and stem density of herbaceous plants did not change with forest succession as a decrease in abundance and frequency of occurrence of pioneer species in late successional forests was counterbalanced by the presence of generalist and late successional species. However, increasing proportions of dwarf stems in late successional forests translated to changes in the vertical structure of herbaceous plant communities. Herbivory pressure by gorillas did not have a notable effect on herbaceous plant community development. This study contributes to the definition of herbaceous ecological indicators of forest succession in different settings.

**Résumé:** La composition de la végétation herbeuse a été évaluée afin de caractériser les différents stades de développement des forêts. Nous avons collecté les pousses d'herbes dans 250 parcelles de 4 m<sup>2</sup> réparties dans six types d'habitats. Nous avons enregistré un total de 36 espèces d'herbes appartenant à 15 familles. La richesse en espèces ne différait pas significativement selon les types d'habitats. La plupart des espèces d'herbes se trouvaient dans tous les types d'habitats et étaient donc généralistes, mais nous avons détecté quelques espèces indicatrices, et nos résultats suggèrent, en gros, que les herbes des familles des *Poaceae* et des *Araceae* indiquent des forêts en fin de cycle de succession, que les *Zingiberaceae* indiquent des forêts en début de cycle, et que les *Comelinaceae*, *Costaceae*, *Cyperaceae* et *Marantaceae* sont le signe d'habitats inondés. La diversité d'espèces et la densité de pousses de plantes herbacées ne changeaient pas avec la succession des stades forestiers parce que la diminution de l'abondance et de la fréquence d'occurrence des espèces pionnières dans les forêts plus anciennes était compensée par la présence d'espèces généralistes et/ou caractéristiques de stades postérieurs. Cependant, de plus fortes proportions de

pousses plus courtes dans les forêts de stade plus avancé se traduisaient par des changements de la structure verticale des communautés de plantes herbacées. La pression exercée par les gorilles n'avait pas d'effet notable sur le développement des communautés de plantes herbacées. Cette étude contribue à définir des indicateurs écologiques herbacés du stade d'évolution de la forêt dans différents milieux.

#### KEYWORDS

Dja Biosphere Reserve, forest succession, herb community composition, indicator species, species richness, tropical understorey herbs

## 1 | INTRODUCTION

African landscapes display considerable variability from deserts to rainforests (White, 1986). White (1986) grouped rainforests into two main types: semi-evergreen and evergreen forests; these broad categories represent forests that grow under different ecological conditions and display contrasting features (see also Dupuy, 1998 and references therein). As reviewed by Dupuy (1998), basal area and stem density of trees >10 cm diameter at breast height (DBH) considerably vary in African forests, and can reach up to 40 m<sup>2</sup>/ha and 680 stems/ha, respectively. Dominant canopy height is usually >30 m, and dominant trees belong to many families, including, but not limited to, Leguminosae, Meliaceae, Sapotaceae, Irvingiaceae and Ulmaceae (Dupuy, 1998; White, 1986). The physiognomy and phytomass of rain forests are determined to a large extent by trees, and woody species are by far higher in number compared to herbaceous species (White, 1986).

Data on tree growth, mortality, regeneration and shade tolerance have been used to infer forest successional patterns (Holm, Shugarta, van Bloemb, & Larocque, 2012; Lienard, Florescu, & Strigul, 2015; Lienard, Gravel, & Strigul, 2015). It has been suggested that habitats or vegetation formations can be identified based on structural features such as physiognomy (Kollmann, 2000). For example, vegetation has been classified based on physiognomy and tree heights, without necessarily having precise knowledge of the species composition (Tutin & Fernandez, 1984). This approach can be misleading as it does not accurately assess the stand age and the vegetation stage. For example, as various tree species differ in height when they attain maturity, forest classification based on tree heights or other structural features may be misleading, causing unnecessary differentiation of truly similar eco-units and pooling together vegetation units that are largely different (White, 1986). Moreover, information obtained only from trees can inaccurately describe trends in forest biodiversity (Tchouto, De Boer, De Wilde, & Van Der Maesen, 2006). Additional investigations into plant community composition and indicator species can therefore complement the classification based on structural features and provide qualitative information for more accurate descriptions of vegetation stages (Loya & Jules, 2008; Moffatt & McLachlan, 2004). Comprehensive information on forest understorey vegetation is particularly relevant because forest inventories seldom include these data (Lienard, Gravel, et al., 2015). It has

been shown that forest structure and tree species composition are modified as forest succession progresses from early to late successional stages (Lienard, Florescu, et al., 2015; Martinez-Ramos, Alvarez-Buylla, & Sarukhan, 1989; White & Edwards, 2000). However, further investigation is required to determine whether the herbaceous plant community follows the same trend.

Herbaceous plants represent a significant proportion of the forest biodiversity, but they remain largely understudied despite their ecological relevance: they contribute to ecological processes, serve as ecological indicators of habitat quality and provide food and shelter for numerous wildlife species (reviewed in Ruben, Bolger, Peart, & Ayres, 1999; Wyatt & Silman, 2010; Jones, Cicuzza, van Straaten, Veldkamp, & Kessler, 2014; Willie, Tagg, Petre, Pereboom, & Lens, 2014). Studies on herbaceous plant abundance, distribution, diversity and composition in forest stands at different successional stages can inform biodiversity conservation policy and forest management practices (Allen, Platt, & Coker, 1995; Duffy & Meier, 1992; Fraser, Jentsch, & Sternberg, 2014; Willie, 2014; Wyatt & Silman, 2010).

Herbaceous plant species diversity and composition are affected by forest structure, tree species composition and topographic and environmental variables (Akhtar & Bergmeier, 2015; Berger & Puettmann, 2000; Ellum, Ashton, & Siccama, 2010; Jones et al., 2014; McKenzie, Halpern, & Nelson, 2000). In habitats such as light gaps, herbaceous plant species richness or density can be high due to a conducive environment (Qin et al., 2010; Willie, Petre, Tagg, & Lens, 2013). Several herbaceous plant species may initially be present at early stages of succession but later display different successional dynamics due to idiosyncratic differences among species and habitat characteristics (Ohtsuka, Sakura, & Ohsawa, 1993). Abiotic factors and forest stand structure can have different effects on the herbaceous plant community development during various phases of the succession trajectory (Gilliam & Turrill, 1993), and some forest understorey herb species seem to be more sensitive to variations in ecological conditions than others (Jones et al., 2014; Qin et al., 2010). The species diversity and composition of herbaceous plant communities can therefore vary depending on habitat settings.

Animal activity may also account for the modification of the structure of plant communities. Animals can positively or negatively shape a plant community (Andresen & Levey, 2004; Poveda, Steffan-Dewentera, Scheub, & Tschamtkke, 2005; Smallwood, 2001; Tilman, 1983; Tutin, Williamson, Rogers, & Fernandez, 1991). Tilman (1983)

demonstrated that herbivore activity within a plant community can modify species composition and counteract competitive exclusion, resulting in the hypothesis that these animals may influence succession patterns and species diversity within a plant community. Here, we test this hypothesis by investigating how the biotic pressure by major herbivores, especially gorilla foraging and nest building using preferred plant species in specific habitat types, influences the herbaceous plant community structure. On the basis of limited competitive exclusion in locations where herbivores are more active (Tilman, 1983), one would predict a high level of herbaceous plant species coexistence. We therefore verify whether localized, intense and selective herbaceous plant use by gorillas in early successional habitats, such as light gaps and young secondary forests (Willie, Petre et al., 2013, 2014), can result in a high abundance and diversity of herbaceous plants in such habitats, as opposed to rarely used late successional habitats.

Terrestrial herbaceous species richness culminates in tropical rain forests (Gentry & Dodson, 1987); hence, the herbaceous plant community represents a model group for investigating the effects of ecological drivers on plant community dynamics in forest ecosystems and testing related hypotheses. Herbs can be classified as generalists which occur in all habitat types; early successional species which occur in light gaps and young secondary forest; or late successional species which occur in old secondary and near primary forest. In addition to testing the hypothesis outlined above, this study aims to assess understory herb community structure and identify possible herb indicators of forest development for different successional stages. Here, the diversity, composition and vertical structure (inferred using the heights to which plants grow) of herbaceous plants in terra firma forests and tree fall gaps are compared to assess how these features vary with forest succession. To supplement this information and provide a general description of habitats in the study area, the same features are compared among flooded and riparian habitats. The study will also contribute to the classification of herbs into groups and will help to verify whether herbs in various habitat types form distinct communities.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and species

Research was carried out in the northern periphery of the Dja Biosphere Reserve (DBR, 5,260 km<sup>2</sup>), specifically in "La Belgique" research site (40 km<sup>2</sup>) located between 013°07'–013°11' E and 03°23'–03°27' N. This area is located in the transition zone between the semi-deciduous (semi-evergreen) forests of Equatorial Guinea and the evergreen forests of the Congo basin (Letouzey, 1985). The climate is equatorial and humid. Average rainfall during a two-year period (April 2009–March 2011) was  $1,637.9 \pm SD\ 105.1$  mm, with mean minimum and maximum daily temperatures ranging between  $19.5 \pm SD\ 1.3$  and  $26.3 \pm SD\ 2.4^\circ\text{C}$  (Willie et al., 2014). The Dja forest is situated on the Precambrian plateau; its altitude varies from 400 to 800 m, and relief is characterized by shallow valleys (Fomete & Tchanou, 1998; McGinley, 2008). The research site is officially

unprotected and situated within the forest management unit 10,047, one of the numerous forest management units surrounding the DBR. The research site comprises a dense network of watercourses and seasonal swamps. Results from an earlier study indicate that swamps and *terra firma* represent about 20% and 75% of the site, respectively (Willie, Petre, et al., 2013). Logging activities occurred in the 1970s. However, some villagers trace the movements of their direct ancestors by indicating forest sites that are abandoned nowadays. Hence, nomadic people in the area (including Baka pygmies) have previously resided in several settlements, and it is therefore likely that the mosaic of forest types (at different levels of stand development) that characterize the area is the result of historical human movements and more recent vegetation disturbance through selective logging operations. For the purpose of this study, we targeted all herbaceous species of the understory layer. Abundant herb families in the study site include Marantaceae and Zingiberaceae. They occur in swamps and *terra firma* forests where they can form clumps reaching more than two metres in height. Some Marantaceae are climbing species; for example, *Haumania* can attach to and climb up neighbouring plants and reach up to 5 m in height (Dhetchuvi, 1993). Some species comprise several varieties (Dhetchuvi & Diafouka, 1993). For a detailed description of these species, see Koechlin (1965).

### 2.2 | Habitat types

We adapted previous vegetation classifications in the area (Djoufack, 2003; Dupain, Guislain, Nguenang, de Vleeschouwer, & van Elsacker, 2004; Nguenang & Dupain, unpubl.) and distinguished six habitat types: (i) near primary forest (NPF) dominated by large tree species of height >30 m (e.g. *Omphalocarpum procerum*, *Uapaca* spp., *Greenwayodendron suaveolens* and *Piptadeniastrum africanum*), with little undergrowth and a closed canopy; (ii) old secondary forest (OSF) with trees of height 25–30 m (e.g. *Terminalia superba*, *Piptadeniastrum africanum* and *Petersianthus macrocarpus*), more pronounced undergrowth than NPF and a discontinuous canopy layer; (iii) young secondary forest (YSF), dominated by early successional trees of <25 m (e.g. *Tabernaemontana crassa*, *Myrianthus arboreus*), and a relatively dense undergrowth; (iv) light gaps (LG) which are open-canopied environments resulting from tree and branch fall or elephant activity; (v) swamps (SW) principally characterized by high densities of *Raphia* spp., few (<5%) *raphia*-free open areas (clearings), and a hydromorphic soil, and which seasonally dry out; and (vi) riparian forest (RF), located in the transition zone between SW and other forest types, with a mixture of species from all forest types. NPF, OSF, YSF and LG are referred to collectively as *terra firma* habitats. SW and RF are (periodically) flooded habitats. NPF, OSF and YSF represent different stages of forest succession. But for the purposes of this study, they have been considered as distinct habitat units, in the same way as LG, RIP and SW.

### 2.3 | Sampling design

Stems of all herb species were sampled in 250 4-m<sup>2</sup> square plots placed along 10 6-km transects, at a bearing of 45°. In each transect,

25 plots were set 250 m apart. All plots were set along the right edge of transects, at a perpendicular distance of 5 m. For each plot, the habitat type was noted. This design enabled the distribution of samples over a larger area (and thus across the entire research site), thus obtaining a more spatially representative set of herbaceous vegetation plots for each habitat type. Local guides involved in data collection consistently used local names to identify plants. In some cases, the same local name is traditionally used to refer to several species from the same genus: for example, most *Aframomum* spp. are referred to as Étihlé. Local nomenclature in such cases is misleading and can incur biases in the dataset. To avoid such biases, name extensions were added to traditional local names whenever necessary and were consistently used during field surveys (e.g. Étihlé sp1, Étihlé sp2). In addition, a botanist from the National Herbarium of Yaoundé Cameroon (Fulbert Tadjouteu) worked alongside local assistants in the study site to assign scientific names to plant species. In the field, the botanist was able to determine scientific names for a handful of species; in addition, he collected many vouchers for identification at the herbarium. These efforts resulted in a checklist of species and their corresponding local names (see Appendix S1).

To compare species richness across habitat types, the sampling process was monitored using rarefaction (individual-based) and first-order Jackknife (Jack1) curves, as recommended by Willie, Petre, Tagg, and Lens (2012). For detailed descriptions of these estimators, see Colwell and Coddington (1994), Chazdon, Colwell, Denslow, and Guariguata (1998) and Gotelli and Colwell (2001). In addition, curves for Chao1, a nonparametric richness estimator, were plotted, as predictions of asymptotic species richness using the multinomial model were based on this estimator.

## 2.4 | Average species richness and evenness

Species richness (total number of species found) and species evenness (relative distribution of species among individuals) were used as diversity indices. Habitats with high indices were considered the most diversity-rich. However, if two habitats had the same number of species (species richness), but differed significantly in evenness, the habitat with high species evenness was considered as having the highest diversity. We used the Diversity module of Ecosim 7.0 software package (<http://garyentsminger.com/>), which is a statistical sampling model, to compute average species richness and evenness and associated 95% confidence intervals (CIs). Statistical differences ( $p < .05$ ) between two habitat types occurred only when CIs did not overlap. The probability of interspecific encounters by Hurlbert (Hurlbert's PIE) was used as an index of evenness (Hurlbert, 1971). This index gives the probability that two randomly sampled individuals from a given habitat type represent two different species. Ecosim 7.0 estimates diversity curves by randomly drawing a specified number of individuals from the data matrix. For each simulation, species diversity indices are determined and the process is repeated several times, thus generating a mean, variance and 95% CIs. We used the Ecosim 7.0 default settings of 1,000 iterations and the independent sampling algorithm.

## 2.5 | Prediction of asymptotic species richness using the multinomial model

Prediction of species richness beyond the reference sample size (number of individuals inventoried) is carried out using the multinomial model (Colwell et al., 2012). This model extrapolates the rarefaction curve (observed species richness) to estimate the expected number of species that can be found in a habitat type for additional levels of sampling effort. After an initial survey,  $n$  is the total number of individuals inventoried,  $S_{\text{obs}}$  is the observed species richness (total number of species found),  $f_1$  is the number of species represented by one individual (Singletons), and  $f_2$  is the number of species represented by two individuals (Doubletons). For  $m$  additional individuals sampled, the multinomial model predicts species richness  $S(n + m)$  as

$$S(n + m) = S_{\text{obs}} + \hat{f}_0 \left[ 1 - \exp \left( -\frac{m f_1}{n \hat{f}_0} \right) \right] \quad (1)$$

where  $\hat{f}_0$  is the Chao1 estimate of the number of species present in the habitat, but not detected in the initial survey, calculated as follows:

$$\hat{f}_0 = \frac{f_1^2}{2f_2} \text{ for } f_2 > 0 \text{ or } \hat{f}_0 = \frac{f_1(f_1 - 1)}{2(f_2 + 1)} \text{ for } f_2 = 0$$

To reach asymptotic species richness estimates, the extra number of individuals to sample  $m$  is calculated as  $m = nx$ , where  $x$  is the solution to the equation

$$2f_1(1 + x) = \exp \left[ x \left( \frac{2f_2}{f_1} \right) \right]$$

solved using the Newton method (Chao, Colwell, Lin, & Gotelli, 2009).

Values of  $m$  were then used in Equation 1 to estimate the asymptotic species richness for each habitat type. Data were analysed in SPADE (<http://chao.stat.nthu.edu.tw/>).

## 2.6 | Herb community composition across habitats types

We used a multiple response permutation procedure (MRPP) as a nonparametric method for comparing herb community composition between habitat types (Mielke & Berry, 2001). Data were analysed in PC-ORD (version 4.01; MjM software, Gleneden Beach, OR, U.S.A.) with the Bray–Curtis distance measure. The species matrix measured 250 plots  $\times$  36 species. A nonmetric multidimensional scaling ordination (NMDS) was performed to corroborate the results of MRPP analyses.

## 2.7 | Indicator species analysis

To supplement the MRPP analyses, we used indicator species analysis (ISA) which describes the extent to which each herb species separates among habitat types (Dufrene & Legendre, 1997). This method generates indicator values (I.V.s) for each species in each habitat type by combining information on the species' abundance and frequency in a particular habitat type. The overall I.V. for a given herb species was the highest I.V. of that species across habitat types.

**TABLE 1** Herb community features in different habitat types

Parameter	NPF	OSF	YSF	LG	RF	SW
Number of plots	36	93	55	21	9	36
Average stem density (stems/m <sup>2</sup> )	5.99	5.74	6.09	5.57	5.11	6.88
Coefficient of dispersion of stems <sup>a</sup>	8.28	6.33	5.64	9.21	2.75	7.46
Average species richness	19.92	21.79	22.48	20.40	20.00	19.33
95% CI lower bound	17.00	19.00	20.00	18.00	20.00	16.00
95% CI upper bound	23.00	25.00	25.00	23.00	20.00	23.00
Average species evenness	0.88	0.91	0.91	0.90	0.91	0.85
Patchiness <sup>b</sup>	12	9	9	10	9	15
95% CI lower bound	0.86	0.90	0.90	0.88	0.91	0.82
95% CI upper bound	0.90	0.92	0.93	0.91	0.91	0.87
% Dwarf stems <sup>c</sup> (all herbs)	43.35	43.69	46.91	31.78	69.44	48.46
% Dwarf stems <sup>c</sup> (Marantaceae & Zingiberaceae only)	49.67	47.37	41.45	26.40	84.62	50.17

Species diversity indices are estimated for 184 individuals, the smallest number of individuals among all habitat types. Significant differences ( $p < .05$ ) occur when confidence intervals do not overlap.

NPF, Near primary forest; OSF, old secondary forest; YSF, young secondary forest; LG, light gaps; RF, riparian forest; SW, swamps.

<sup>a</sup>Calculated as the variance-to-mean ratio.

<sup>b</sup>Calculated as  $(1 - \text{average species evenness}) \times 100$ .

<sup>c</sup>Results obtained in the study site by measuring the heights of herb stems in 250 plots distributed across all habitat types (see Willie, de la Peña, et al., 2013).

I.V.s were tested for statistical significance using a Monte Carlo simulation of 1,000 runs with a critical value of .05. All analyses were performed in PC-ORD.

### 3 | RESULTS

#### 3.1 | Herb density and diversity

We recorded 36 herb species, belonging to 15 families. Average herb density was 5.98 stems/m<sup>2</sup>, and stem density did not significantly vary across habitat types (Median test:  $\chi^2 = 4.76$ ;  $df = 4$ ;  $p = .315$ ). Similar patterns emerged while comparing species richness (Table 1).

However, relatively low values of species evenness were found in near primary forest and swamps where species distributions were patchier (Table 1). Species richness estimator curves for most habitat types were still increasing (Figure 1). However, the probability of discovering new species in a further survey was low in all habitat types, usually below .005, therefore implying that no additional sampling effort was needed in most cases (Table 2). Predictions using the multinomial model revealed no statistical difference in asymptotic species richness across habitat types (Table 2). Estimated and observed values of richness were similar for all habitat types.

#### 3.2 | Herb community composition

The global MRPP test indicated significant differences in herb composition between all habitat types, but this result reflected strong differences between swamps and *terra firma* habitats (Table 3). This trend would remain unchanged even after adjusting  $p$ -values using a Bonferroni correction (original  $p$ -value  $\times$  number of tests).

Significant differences in herb community composition were also detected between light gaps and late successional forests (old secondary and near primary forest), although the magnitude of the difference was not high despite statistical significance. Other pairwise comparisons were statistically nonsignificant.

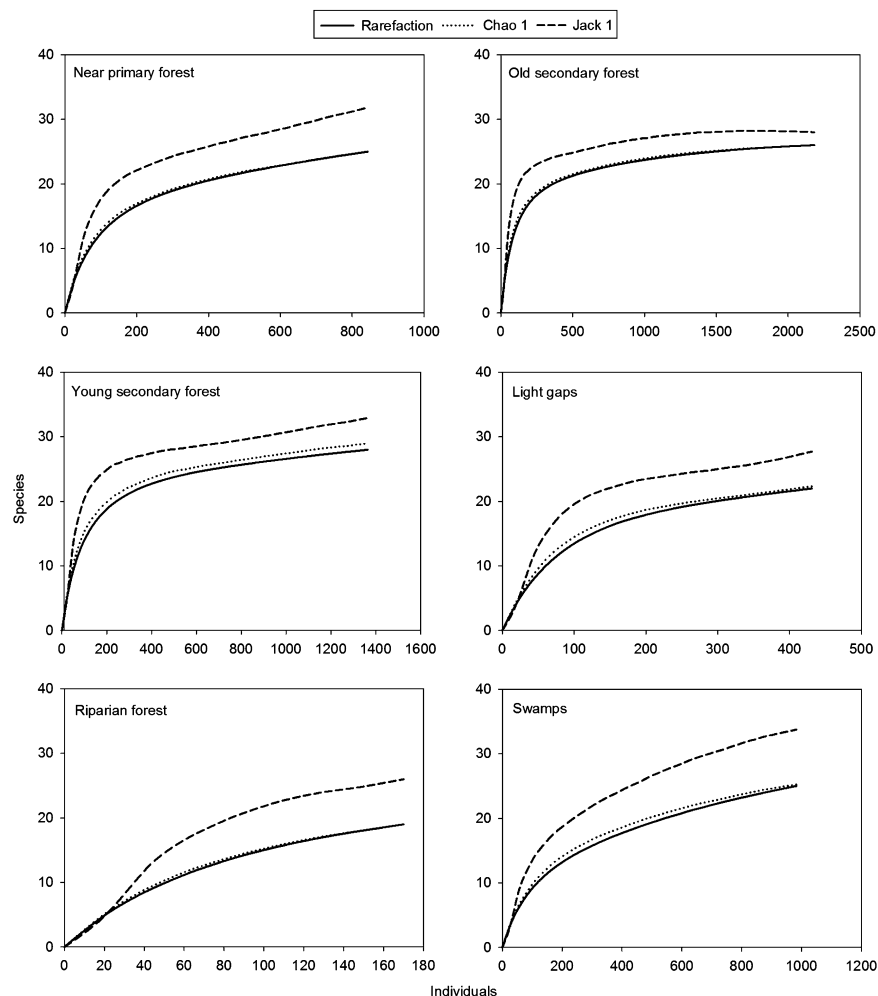
The nonmetric multidimensional scaling ordination performed in R using the Euclidian distance on log transformed abundances resulted in a two-dimensional solution, and the final stress was 0.24 (Figure 2). Although plots from all habitat types considerably overlapped, plots in swamps and light gaps tended to form distinct groups, a trend supporting the results of MRPP. Among *terra firma* plots, young secondary, old secondary and near primary forest plots formed a large cluster, in contrast to plots in light gaps. However, there were considerable differences among young secondary forest plots, and they featured at the edge of this cluster. Riparian forest plots also formed a group next to this large cluster, and they showed a great degree of similarity with both swamp and *terra firma* plots.

#### 3.3 | Indicator species

Of the 36 herb species inventoried, only nine were significant indicators (Table 4). For the other species, highest indicator values did not greatly exceed the mean value, implying that they did not have any clear pattern of occurrence in the study site.

### 4 | DISCUSSION

The comparison of herbaceous communities in relation to habitats (flooded and *terra firma*) and in relation to succession (*terra firma*



**FIGURE 1** Rarefaction and species richness estimator curves for each habitat (—) Rarefaction, (.....) Chao1, (---) Jack1

forests only) both allow for the definition of ecological indicators, but the latter comparison also helps to test hypotheses regarding plant community dynamics in tropical forest settings. This study compares the structural features of herbaceous plant communities in all habitat types found in a tropical forest site of south-east Cameroon. These habitats were roughly grouped into two main categories: flooded habitats (riparian forest and swamps) and *terra firma* habitats (light gaps, young secondary forest, old secondary forest and near primary forest).

In this study, only understory herbs were surveyed, but a sampling of both herbs and undergrowth woody species (e.g. seedlings of all tree species) would have resulted in a higher number of stems and species. The survey helped to detect most species with some certainty. The sampling curves did not stabilize in most cases (Figure 1), suggesting that sampling effort was insufficient, and that other species could be detected in further surveys (Colwell & Coddington, 1994; Gotelli & Colwell, 2001; Williams, Witkowski, & Balkwill, 2007). However, extrapolations at larger sample size using the multinomial model did not indicate important differences between observed and predicted values of species richness (Table 2). For example, in light gaps, predictions showed that 493 additional individuals (more than 100% of the initial sampling effort) would need

to be inventoried in order to detect one additional species (Table 2). In a previous study conducted in the research site, it was observed that despite the substantial number of additional plots in light gaps and old secondary forest (about 100%–200% of the initial number), no species new to the survey was discovered in these habitats (Willie et al., 2012). In most cases, species richness estimators did not stabilize at initial sampling effort due to the patchy nature of species distributions (Chazdon et al., 1998; Palmer, 1995). Thus, the observed values of herb species richness for the various habitat types can be considered as “accurate” estimates, closely matching the predicted values, given that the probability of finding new species was very low in all cases. Moreover, comparison of species richness across habitat types based on observed values did not reveal any significant differences (Table 1), and predicted values displayed a similar pattern (Table 2). Our results therefore suggest that all habitat types had similar levels of herb species richness.

There was a great overlap in herb community composition across habitat types despite the presence of some indicator species. The test statistic *T* was consistently highly negative in all pairwise comparisons of swamps with all other habitat types (Table 3), thus emphasizing the peculiarity of herb community composition in this habitat. As a transition zone between permanently flooded swamps



**TABLE 2** Estimated herb species richness in different habitat types

Habitat	<i>n</i>	<i>f</i> <sub>1</sub>	<i>f</i> <sub>2</sub>	<i>S</i> <sub>obs</sub>	<i>q</i> <sub>0</sub>	<i>S</i> <sub>est</sub>	<i>m</i>	<i>S</i> <sub>est</sub> 95% CI low	<i>S</i> <sub>est</sub> 95% CI upp
Near primary forest	863	1	2	25	0.0012	25.3	0	25.0	29.7
Old secondary forest	2,134	0	1	26	0.0000	26.0	0	26.0	26.0
Young secondary forest	1,339	1	0	27	0.0007	27.0	0	27.0	27.0
Light gaps	468	2	2	23	0.0043	24.0	493	23.1	34.1
Riparian forest	184	2	3	20	0.0109	20.7	115	20.1	27.8
Swamps	990	1	2	26	0.0010	26.3	0	26.0	30.7

*N*, total number of individuals inventoried; *f*<sub>1</sub>, number of singletons (species represented by one individual); *f*<sub>2</sub>, number of doubletons (species represented by two individuals); *S*<sub>obs</sub>, observed species richness; *q*<sub>0</sub>, probability that the next individual inventoried represents a new species ( $q_0 = f_1/n$ ); *S*<sub>est</sub>, estimated asymptotic species richness (Chao1 estimator); *M*, number of additional individuals required to detect 100% of *S*<sub>est</sub>; *S*<sub>est</sub> 95%CI low, 95% confidence interval lower bound of *S*<sub>est</sub>; *S*<sub>est</sub> 95%CI upp, 95% confidence interval upper bound of *S*<sub>est</sub>. Significant differences ( $p < .05$ ) occur when confidence intervals do not overlap.

and *terra firma* forests, riparian forest is periodically flooded and presents more heterogeneous features than do other habitats. This heterogeneity may partly account for the considerable overlap in herb species composition between this habitat and all other habitat types, as habitat heterogeneity partly determines species diversity (Spies, Hemstrom, Youngblood, & Hummel, 2006). Many more herb species were indicative of swamps than other habitats (Table 4), and this resulted in strong differences in herb community composition, as shown by the MRPP results. Generalists (e.g. species of fern: *Asplenium* sp., *Cyclosorus afer* and *Pityrogramma calomelanos*) occurred everywhere, but indicators such as Marantaceae and Zingiberaceae species were more localized. Other generalists and indicators of late successional forests (species of Araceae and Poaceae) were small-sized herb species compared to indicators of early successional forest stages and flooded habitats which had relatively

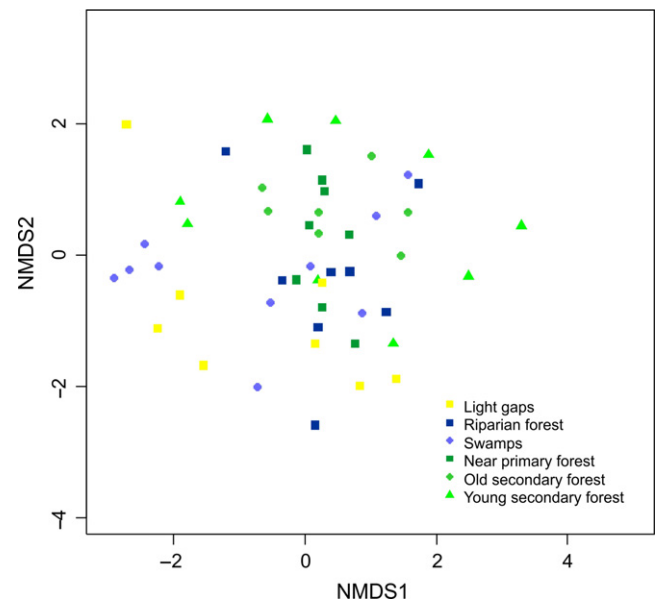
large stems, sometimes reaching more than two metres in height. As also observed by Fay (1997), proportions of dwarf stems increase in late successional forests (Table 1). These results suggest that the vertical structure of the herbaceous plant community changed across habitat types, although stem density seemed to be similar. This is consistent with the fact that horizontal visibility increases from light gaps to near primary forest (Willie, Petre, et al., 2013).

Given that most tropical herb species thrive in light gaps compared to late successional forests where shade conditions predominate (Wright, 1992), one would expect the highest stem density and/or species diversity in light gaps, as observed by Fay (1997). However, our results do not support this hypothesis. This is probably due to the fact that generalist species, including ferns, can also persist in shade conditions through coping mechanisms that enable them to thrive despite the limited amount of light (Crawley, 1997).

**TABLE 3** Results of multiple response permutation procedure showing all pairwise comparisons in herb species composition

Comparison	<i>T</i>	<i>p</i> -Value
All habitat types	−16.04	.00001*
Near primary vs. Old secondary	−1.74	.0554
Near primary vs. Young secondary	−1.58	.0690
Near primary vs. Light gaps	−2.14	.0302*
Near primary vs. Riparian	−1.71	.0593
Near primary vs. Swamps	−19.39	.00001*
Old secondary vs. Young secondary	−0.60	.2524
Old secondary vs. Light gaps	−3.04	.0062*
Old secondary vs. Riparian	−2.02	.0373
Old secondary vs. Swamps	−23.75	.00001*
Young secondary vs. Light gaps	−1.12	.1335
Young secondary vs. Riparian	−0.98	.1590
Young secondary vs. Swamps	−19.71	.00001*
Light gaps vs. Riparian	−0.27	.3575
Light gaps vs. Swamps	−11.45	.00001*
Riparian vs. Swamps	−4.58	.0007*

The separation between habitats is measured by the test statistic *T*. The more negative is *T*, the stronger the separation. Original *p*-values are presented. Asterisks indicate significant differences ( $p < .05$ ).

**FIGURE 2** Nonmetric multidimensional scaling ordination showing overlap in herbaceous plant community composition across six habitat types. Plots that are close to each other are more similar in species composition



**TABLE 4** Indicator herb species for each habitat type

Habitat	Scientific name	Family	I.V.	Mean	p-Value
Near primary forest	<i>Puelia schumanniana</i> Pilg.	Poaceae	21.8	13.5	.039*
	<i>Cercestis dinklagei</i> Engl.	Araceae	12.6	8.8	.116
	<i>Nephtytis poissonii</i> (Engl.) N.E.Br.	Araceae	6.8	6.4	.310
	<i>Marantochloa filipes</i> (Benth. & Hook.f.) Hutchinson	Marantaceae	1.0	3.0	.979
Old secondary forest	<i>Geophila flaviflora</i> Aké Assi	Rubiaceae	15.0	8.1	.039*
	<i>Aframomum arundinaceum</i> K.Schum.	Zingiberaceae	7.3	7.3	.357
Young secondary forest	<i>Haumania danckelmaniana</i> (J.Braun & K.Schum.) Milne-Redhead	Marantaceae	13.3	13.3	.374
	<i>Pityrogramma calomelanos</i> (L.) Link	Pteridaceae	10.8	10.0	.303
	<i>Polia condensata</i> C.B.Clarke	Commelinaceae	8.2	6.7	.215
	<i>Streptogyna crinita</i> P.Beauv.	Poaceae	7.5	4.5	.101
	<i>Hypselodelphys scandens</i> Louis & Mullend.	Marantaceae	5.9	4.2	.153
	<i>Palisota barteri</i> Hook.	Commelinaceae	5.7	7.6	.733
	<i>Aframomum</i> sp.	Zingiberaceae	3.4	4.7	.590
	<i>Olyra latifolia</i> L.	Poaceae	2.0	3.7	.793
	<i>Thonningia sanguinea</i> Vahl	Balanophoraceae	1.8	2.3	.609
Light gaps	<i>Aframomum sulcatum</i> (Oliv. & D.Hanb. ex Baker) K.Schum	Zingiberaceae	17.1	5.5	.011*
	<i>Selaginella</i> sp.	Selaginellaceae	4.8	2.4	.119
	<i>Marantochloa leucantha</i> (K.Schum.) Milne-Redhead	Marantaceae	4.7	6.2	.639
	<i>Renealmia cincinnata</i> Baker	Zingiberaceae	2.8	3.0	.376
Riparian forest	<i>Palisota ambigua</i> (P.Beauv.) C.B.Clarke	Commelinaceae	32.0	11.1	.002*
	<i>Megaphrynium macrostachyum</i> (Benth.) Milne-Redhead	Marantaceae	12.5	8.1	.105
	<i>Trachypodium braunianum</i> Baker	Marantaceae	11.1	2.4	.039*
	<i>Asplenium</i> sp.	Aspleniaceae	8.2	9.9	.662
	<i>Tristemma</i> sp.	Melastomataceae	6.9	3.3	.073
	<i>Geophila repens</i> (L.) I.M.Johnst.	Rubiaceae	6.8	6.4	.323
	<i>Renealmia africana</i> Benth.	Zingiberaceae	6.0	4.1	.142
Swamps	<i>Marantochloa purpurea</i> (Ridley) Milne-Redhead	Marantaceae	52.2	5.5	.001*
	<i>Halopegia azurea</i> K.Schum.	Marantaceae	33.3	4.6	.001*
	<i>Costus afer</i> Ker Gawl.	Costaceae	30.6	5.1	.001*
	<i>Scleria verrucosa</i> Willd.	Cyperaceae	9.6	4.1	.038*
	<i>Megaphrynium velutinum</i> (Baker) Koechl.	Marantaceae	8.8	9.5	.459
	<i>Sarcophrynium brachystachyum</i> K.Schum.	Marantaceae	8.4	11.3	.863
	<i>Cyclosorus afer</i> Ching	Thelypteridaceae	5.4	9.8	.982
	<i>Pilea</i> sp.	Urticaceae	2.8	2.4	.419
	<i>Sarcophrynium prionogonium</i> K.Schum.	Marantaceae	2.8	2.4	.410
	<i>Ataenidia conferta</i> (Benth.) Milne-Redh	Marantaceae	2.8	2.5	.429

I.V. is the highest indicator value for a given herb species across all habitat types. Observed I.V.s were tested for statistical significance using a Monte Carlo simulation of 1,000 runs. The mean of randomized indicator values is presented in each case.

\*Significant indicators ( $p < .05$ ).

Nevertheless, pioneer herbs such as Zingiberaceae species attain their highest densities in light gaps and then decline as succession progresses (Willie, de la Peña, Tagg, & Lens, 2013; Willie et al., 2012), in conformity with the “intermediate disturbance” hypothesis (Sheil, 1999). Decreases in abundance and frequency of occurrence of pioneer herb species lead to differences in species composition between light gaps and old successional forests.

Despite the gradual decline of pioneer herb species, all stages of forest succession displayed similar levels of herbaceous plant species coexistence: stem density and species diversity did not change as succession progressed from early to late stages (Table 1). In the study site, herbivory pressure by gorillas is high in light gaps and young secondary forests where large herb stems predominate (Willie, Petre, et al., 2013; Willie, et al., 2014). According to Tilman (1983),

herbivore activity in specific locations may create microhabitats where change in the magnitude of abiotic factors promotes the establishment of less competitive plant species, thus minimizing competitive exclusion. In the study site, however, competitive exclusion also appears to be lower in late successional forest patches where herbivory by gorillas is rare and strong interspecific competition is more likely to occur due to the limited amount of light. Gorilla “absence” in late successional forests did not alter the herbaceous plant community diversity and density, a pattern already observed by Royo and Carson (2005) in the neotropics. In the study site, gorilla activity in early successional forests may therefore be counterbalanced by other herbivores in late successional forests. Another possibility is that niche plasticity within the herbaceous plant community may promote species coexistence in forest patches where resources are more limited (Ashton, Miller, Bowman, & Suding, 2010). This is consistent with the phenotypic plasticity exhibited by some herb species in the site (which occur in all forest types, but develop dwarf stems where light is limited; Willie, de la Peña, et al., 2013). However, further research that includes all components of the understory vegetation strata is needed to draw firm conclusions.

Our study has provided insights on the structural features of tropical forest understory herbs. The horizontal structure did not vary as herb species richness and stem density did not appear to change across habitats or with forest succession. However, among *terra firma* habitats, dwarf stems predominated in near primary forest, thus indicating changes to the vertical structure. Some distinctions in herbaceous plant community composition between swamps and other habitat types were noted, but the separation was much less pronounced among other habitats. Although pioneer species of the family Zingiberaceae featured highly in light gaps and young secondary forest, while other species of Araceae and Poaceae were more common in old secondary and near primary forest, most herb species occurred everywhere, and were therefore generalists. Despite the higher frequency and intensity of gorilla–herbaceous plant interactions in early successional habitats in the study site, all stages of forest succession displayed similar levels of herbaceous plant stem abundance and species diversity, and largely overlapped in terms of species composition. The herbaceous plant community development therefore seemed to be independent of gorilla activity. The description criteria emerging from this work complement traditional forest stage descriptors based on trees (e.g. Lienard, Florescu, et al., 2015) and improve knowledge of understory herb community structure and indicators of forest development in African rain forests.

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