VEGETATION GROUPS FROM LIFE-HISTORY TRAITS FOR THE MANAGEMENT OF A SAVANNAH–FOREST MOSAIC

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PALLA F, GACHET S, PICARD N & RIERA B. 2013. Vegetation groups from life-history traits for the management of a savannah–forest mosaic. This study defined ecological groups of tree species based on species life-history traits within the savannah–forest mosaic of the Lopé National Park, Gabon in order to understand the connection between different types of forest within this study area. Three life-history traits were the most efficient at discriminating species groups within the floristic assemblage, namely, functional guild, dispersal type and phytogeographic type. The combination of dispersal potential and functional guild enabled us to rank the 169 studied species on gradient of forest types. A species classification into functional groups based on similar biological traits was proposed for the purpose of conservation management and development of new conservation areas. This first classification distinguished between canopy species and understorey species, thus suggesting the existence of two separate dynamics for tree species and three functional groups. These results are useful to set conservation priorities to achieve management plans.

Keywords: Functional groups, guild, dispersal potential, multivariate analysis

PALLA F, GACHET S, PICARD N & RIERA B. 2013. Kumpulan vegetasi daripada ciri-ciri sejarah hidup untuk pengurusan mozaik hutan savana. Kajian ini menentukan kumpulan ekologi spesies tumbuhan berdasarkan ciri-ciri sejarah hidup di dalam mozaik hutan savana di Taman Negara Lopé, Gabon. Tujuannya adalah untuk memahami hubungan antara jenis hutan yang berbeza di dalam kawasan kajian. Tiga ciri sejarah hidup dapati membezakan kumpulan spesies dengan tepat dalam himpunan flora iaitu kumpulan fungsi, jenis sebaran dan jenis fitogeografi. Gabungan potensi sebaran serta kumpulan fungsi membolehkan kami menilai 169 spesies yang dikaji berdasarkan gradien jenis hutan. Pengelasan spesies mengikut kumpulan fungsi disyorkan berdasarkan ciri-ciri biologi yang serupa bagi tujuan pengurusan pemuliharaan serta pembangunan kawasan pemuliharaan yang baharu. Kelasifikasi yang pertama membezakan antara spesies kanopi dengan spesies tingkat bawah. Ini mencadangkan wujudnya dua dinamik berbeza untuk spesies pokok dan tiga kumpulan fungsi. Keputusan ini bermanfaat untuk menetapkan keutamaan pemuliharaan agar rancangan pengurusan tercapai.

INTRODUCTION

The savannah is a vegetation type; its dynamics and occupation range is strongly linked to climatic change in Central Africa. Depending on temperature and precipitation, the distribution of savannah versus tropical forest can be broadly predicted. In the absence of human intervention (e.g. logging or fire), a transformation from savannah to forest is to be expected (Baeza et al. 2007). Therefore, the origin of savannah–forest mosaic transitory ecotone which has long been controversial remains. Thus, the characterisation by traits of the different vegetation groups in this ecosystem is an important and timely research topic. Most studies on the savannah–forest mosaic focused on relationship between trees and grasses (Youtta 1998, Favier et al. 2004) without any particular emphasis on the role of the species initiating colonisation and/or allowing the persistence of the savannah–forest ecosystem. The forest composition is always dynamic and forms different eco-units composed of characteristic species which determine the functioning of the ecosystem. However, structural parameters alone are not enough to characterise the developmental stage of the forest (Favrichon 1994).

For a few years, trait-based analyses comparing plant communities have become increasingly common (Lavorel & Garnier 2002), constituting

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an efficient method to achieve a general understanding of plant community structure and function (Keddy 1992). Moreover, the study of the species traits of the floristic assemblage is required in order to find specific physiological links to behaviours that explain the current processes (Lavorel et al. 1997, Kahmen & Poschold 2008). The classification of tropical tree species into functional groups (i.e. groups of species playing the same role in the dynamics) has been an important focus for studies for the past 30 years. Although other studies placed emphasis on isotopic and geochemical evidences of influence of the forest on the savannah (Schwartz et al. 2000), it is also possible to discriminate between the two on the basis of species traits.

Our study was carried out at the Lopé National Park, Gabon (0° 4' S, 11° 44' E), which is a typical example of a climatic savannah in a dynamic state (Palla et al. 2011). Following White (1983), our study focused on the Guineo–Congolian centre of endemism. This region is recognised as being occupied by different types of rainforests that coexist with other formations, including periforest and intraforest savannahs (Schwartz et al. 2000). Plant traits approach of the savannah–forest mosaic in the park can be used to describe the dynamics observed for the past 1000 years (Delègue et al. 2001). The present study was aimed at (1) defining trait-based functional groups which explained what the dynamic processes currently underway in the fores–savannah mosaic were and why was forest colonising savannahs within the savannah–forest mosaic of the Lopé National Park, and (2) identifying those traits that were specifically linked to the canopy and understorey strata. This trait-based approach is quite novel for management of protected areas and should provide interpretation tools to monitor past and current dynamical changes.

MATERIAL AND METHODS

Species traits

A dataset of six traits for 169 tree species was compiled from the literature (Senterre 2005, Kouob 2009, Soussou 2009) and adapted to vegetation groups of the Congo Basin. We distinguished two main groups of traits:
(1) structural and functional traits, with four categorical traits: (a) biological type with six levels (see Table 1 for the definition of these levels), (b) dimensions of the leaves (or foliage type) with six levels (Table 2), (c) functional types with seven levels (Table 3) and (d) functional guild with three levels (Table 3)
(2) chorological traits, with two categorical traits: (a) distribution of the phytogeographic types with 13 levels (Table 4) and (b) types of dispersal with six levels (Table 5).

In total, our dataset comprised six traits with 41 levels. For biological type, we focused on shrub and tree strata to see the progression of forest over savannah and ignored the herbaceous stratum that would require a specific treatment (particularly Marantaceae and Zingiberaceae). There were some missing data. All traits were known for 146 of the 169 species. However, 16 species had fewer than three missing traits and 7 species had more than four missing traits. Two methods were considered in dealing with missing data, namely, either taking into account only complete cases or estimating missing data.

Table 1   Definition of the biological types (Senterre 2005)

Stratum	Biological type	
	Description	Level
Upper strata (height > 20 m)	Emergent tree	E
	Dominant tree	Ass
	Codominant tree	Aco
Medium strata (6–20 m)	Dominated tree	Ad
Lower strata (height < 6 m)	Shrub	arb
	Woody liana	Lli

Table 2   Definition of the foliage types (Senterre 2005, Kouob 2009)

Foliage type	Level	Indicative dimension (cm²)
Microphyllous	Mi	2–20
Mesophyllous	Mé	40–200
Notophyllous	No	20–40
Macrophyllous	Ma	2–20
Nanophyllous	Na	0.2–2
Leptophyllous	Le	< 0.2 cm²

Table 3   Definition of the functional guilds and functional types with the correspondence between these two types as adapted from Senterre (2005) and Kouob (2009)

Behaviour	Functional guild		Functional type	
	Description	Level	Description	Level
Short-lived colonising specie	Pioneer	Pi	Pioneer species with high dispersal capacities	PiD
Colonising species that contribute to the vertical reconstitution	Short-lived cicatricial	Ci	Cicatricial with high dispersal capacities	CiD
			Cicatricial with low dispersal capacities	CiS
Long-lived species that contribute to the canopy closing	Long-lived cicatricial	Ci	Cicatricial with high dispersal capacities	CiD
			Cicatricial with low dispersal capacities	CiS
Long-lived species that form the climax stage	Sedentary	Se	Sedentary species with high dispersal capacities	SeD
			Sedentary species with low dispersal capacities	SeS
Understorey species			Large seeds with high dispersal capacities	GD
			Large seeds with low dispersal capacities	GS

Table 4   Definition of the phytogeographic types (Senterre 2005)

Phytogeographic type	Level
African multi-regional	PRA
Peripheral Guineo–Congolese (semi-evergreen forest)	GCp
Omni or subomni Guineo–Congolese	GC
Congolese	C
Afro–American	AA
Lower-Guinean	BG
Afro–Madagascan	AM
Atlantic lower Guinean	BGA
Littoral Atlantic lower Guinean	BGALit
Oriental Atlantic lower Guinean	BGAOr
Central-Guinean (C + BG)	CG
Guinean (HG + BG)	G
Littoral Guinean (littoral HG + BGALit)	GLit

Table 5   Definition of the dispersal types (Senterre 2005)

Fruit	Level	Dispersal type
Not fleshy	Bal	Ballochorous
Not fleshy	Bar	Barochorous
Not fleshy	Pté	Pterochorous
Not fleshy	Pog	Pogochorous
Fleshy	Sar	Sarcochorous
Not fleshy	Scl	Sclerochorous

Study site

The species studied were those found at the Lopé National Park. The study site included 300 km² of savannah and savannah–forest mosaic along the northern and eastern limits of the park (Figure 1). Lopé has the lowest rainfall in Gabon (MEN 1983). Mean annual rainfall recorded at the Gorillas and Chimpanzees Research Station located at the centre of the study site between 1984 and 2004 was 1474 ± 44.8 (SE) mm. There is a marked seasonality with a long dry season between mid-June and mid-September, and the severity and duration of this dry season vary between years. A shorter and more variable dry season also occurs around January and February. The comparatively low rainfall at Lopé results from a rain-shadow effect from the Chaillu Mountains, south-west of Lopé National Park and a low band of rainfall associated with the Ogooué River (White 2007). Temperature varies little throughout the year, although it is slightly cooler in the long dry season due to almost constant cloud cover. A temperature logger placed in the open savannah at the research station recorded an overall mean daily temperature of 25.9 °C (SE ± 0.06) from January 2003 till December 2004, with temperatures ranging from 17.5–38.8 °C. The topography is dominated by the hills of the Okanda chain (450–850 m in height) in the south. The northern part was a former lake basin that was opened when the Ogooué River eroded through the Okanda chain. There is significant erosion on the slopes.

Vegetation in Lopé is a complex mosaic of associated plants. Three main forest types can be found at Lopé, namely, gallery forests and copses within the savannah–forest mosaic, young forests and mature forests. A classification of tree species into floristic groups on the basis of their abundance in different plots was defined at Lopé by Palla et al. (2011). These floristic groups were compared with the trait-based functional groups.

Statistical analyses

The 169 × 6 matrix giving the six traits for each species was analysed using a multiple correspondence analysis to identify potential associations between species and specific traits (Härdle & Simar 2003). Missing data were dealt with in two ways: firstly, the data set was restricted to those 146 species for which all traits were known, and the resulting 146 × 6 matrix was analysed using a standard multiple correspondence analysis. Secondly, missing data were replaced by average values computed in the following way: let Y be the complete disjunctive table constructed from a factor table X. Analysing X with a multiple correspondence analysis was equivalent to analysing Y with a correspondence analysis. Any missing trait in Y was replaced by the mean of the column to which it belonged (the mean value being computed from the known values). This was equivalent to replacing a missing trait for a given species by the distribution of the levels of this trait computed from the species for which this trait was known.

For instance, there were 156 species for which functional guild trait was known and 13 species for which this trait was missing. Levels of the functional guild trait for these 156 species were 22% for cicatricial species, 1% for pioneer species and 76% for sedentary species. For the 13 species without functional guild, Y was calculated using
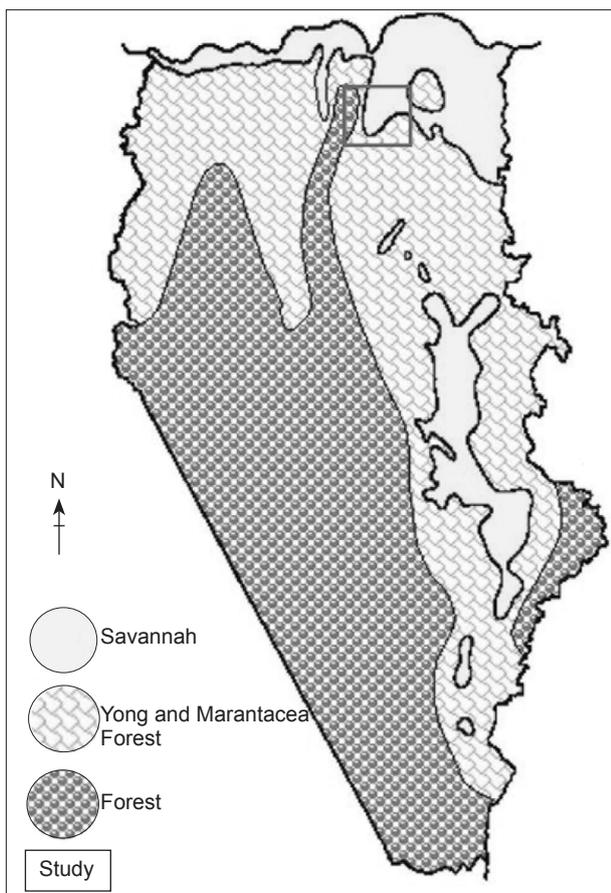
Figure 1   Savannah-forest mosaic at Lopé, Gabon illustrating the vegetation of the national park of Lopé simplified based on images of 1992 Intera Radar; source: White 1983

the values 0.224, 0.013 and 0.763 for cicatricial, pioneer and sedentary species respectively. Table Y was therefore completed but still had properties of a complete disjunctive matrix: its row summed equal the number of traits and its column mean gave the proportion of each modality in the population. The complemented matrix Y was finally analysed using a correspondence analysis.

As mean values did not contribute to the definition of axes in multivariate analyses, replacing missing data by mean values did not alter the contribution of variables to the axes. The second strategy to deal with missing data had the advantage that a species was not withdrawn if a single trait was missing. Thus, all available data were used unlike in the first strategy where some data might be discarded. We compared these two strategies to deal with missing data and they produced similar results. Therefore, we reported only results of the second strategy.

The multiple correspondence analysis was completed by a hierarchical cluster analysis that was used to partition the 169 species into groups (Härdle & Simar 2003). This cluster analysis uses the Euclidean metric and the species scores on the two first axes of the multiple correspondence analysis to measure differences between species. Ward's method was used to cluster groups (Ward 1963). The number of groups was determined by visual inspection of the cluster dendrogram. Statistical analyses were performed using R software version 2.10.0 (2005) and the ade4 package (2004) for multivariate analyses. In order to test for the association between traits and the resulting groups of species, chi-squared (χ^2) tests were performed. For each trait, a χ^2 test, which cross-tabulated species according to the levels of this trait and to the species groups, was applied to the contingency table.

Relationship between traits and abundance

Palla et al. (2011) classified 265 sampled species at Lopé into six floristic groups on the basis of their abundance in 258 sampling plots (Figure 2). If the traits were known for all the 265 species sampled at Lopé, then the matrix of species abundance and the matrix of traits could have been jointly analysed using a two-table analysis (Dray et al. 2003) such as co-inertia analysis or the analysis of trait profiles (Garnier et al. 2004). However, in the present case, the 169 species for which traits were collected and the

265 species found in the forest inventory at Lopé shared 168 species. Restricting the matrix of species abundance to these 168 species to analyse traits can flaw the analysis (Pakeman & Quested 2007). So, we preferred a more robust but less informative analysis based on species groupings. The relationship between floristic groups and groups of species based on their traits was tested using one-sided Monte Carlo test based on the Rand index (Meilă 2007). The Rand index (Rand 1971) was developed to compare two classifications. It was based on counting the pairs of species on which the two classifications agreed/disagreed. Rand index is defined as $(N_1 + N_0)/[S(S − 1)/2]$, where N_1 = number of species pairs that are in the same group under both classifications, N_0 = number of species pairs in different groups under both classifications, $S = 168$, which is the number of species and $S(S − 1)/2$ = number of pairs of species. Rand index varies between 0 (no agreement between the two classifications) and 1 (perfect agreement between the two classifications). In addition to the test based on the Rand index, for each trait, a χ^2 test on the contingency table determined the association between this trait and floristic groups.

RESULTS

Species groups on the basis of their traits

We examined the interrelations between traits in order to use these patterns as a key to interpretation of the current processes in the organisation of forest mosaic. Multiple correspondence analysis of the traits for the 169 species defined six groups of species (Figure 3). Figure 4 shows the projection of the species on the two first axes with the six groups of species. The projection of the levels of traits on the two first axes is shown in Figure 5, together with the six groups of species.

The discrimination for these six groups was mainly based on their functional types and functional guild. Group 1 included 47% of the species and was a default core group without any characteristic trait. Group 2 included 10% of the species and was characterised by the levels of cicatricial species (such as groups 4 and 6) of the functional guild, cicatricial with high dispersal capacities (group 4) of the functional type and African multi-regional of the phytogeographic type. Group 3 included 28% of the species and
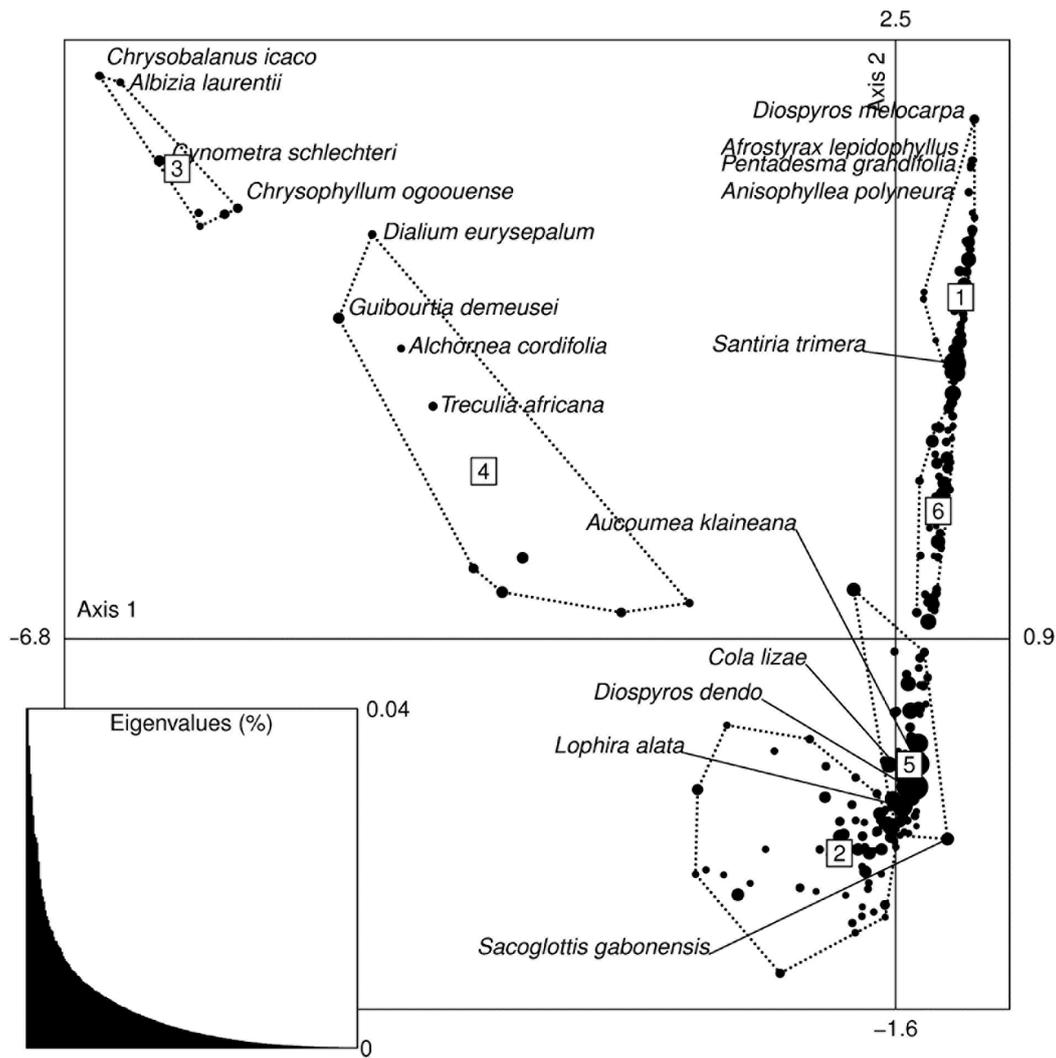
Figure 2   Projection of the 265 species on the two first axes of the correspondence analysis of their abundances in 258 sampling plots at Lopé National Park, Gabon; dotted polygons indicate the six floristic groups, size of dots is proportional to the square root of species abundances; this figure is adapted from Figure 3 in Palla et al. (2011), such that polygons in the current figure show the groups of species, while ellipses in the Figure 3 by Palla et al. (2011) show the groups of sampling plots

was characterised by emergent trees (group 4) of the biological type, not fleshy fruits of the dissemination type and by lower-Guinean level of the phytogeographic type.

Group 4 included 7% of the species and was characterised by six traits as follows: the emergent trees (group 3), cicatricial functional guild (groups 2 and 6), functional type identified by cicatricial species with high dispersal capacities (group 2), a leptophyllous foliage type, two dissemination types (pogochorous and ptérochorous), and peripheral Guineo–Congolese of the phytogeographic type. Group 5 included 3% of the species and was characterised by three traits and five associated levels as follows:

shrub biological type, pioneer functional guild of trait functional guild and large seeds with strong or low dispersal capacities of the functional type. Group 6 included 2% of the species and had in common with groups 2 and 4 the level cicatricial species of the functional guild. Moreover, it was characterised by cicatricial with low dispersal capacities of the functional type, a nanophylleous foliage type and not fleshy fruit of the dissemination type.

The ordination of the species based on their traits showed that there was a continuum which ran from level pioneer species to level cicatricial species of the functional guild trait, corresponding to a light requirement species gradient. The
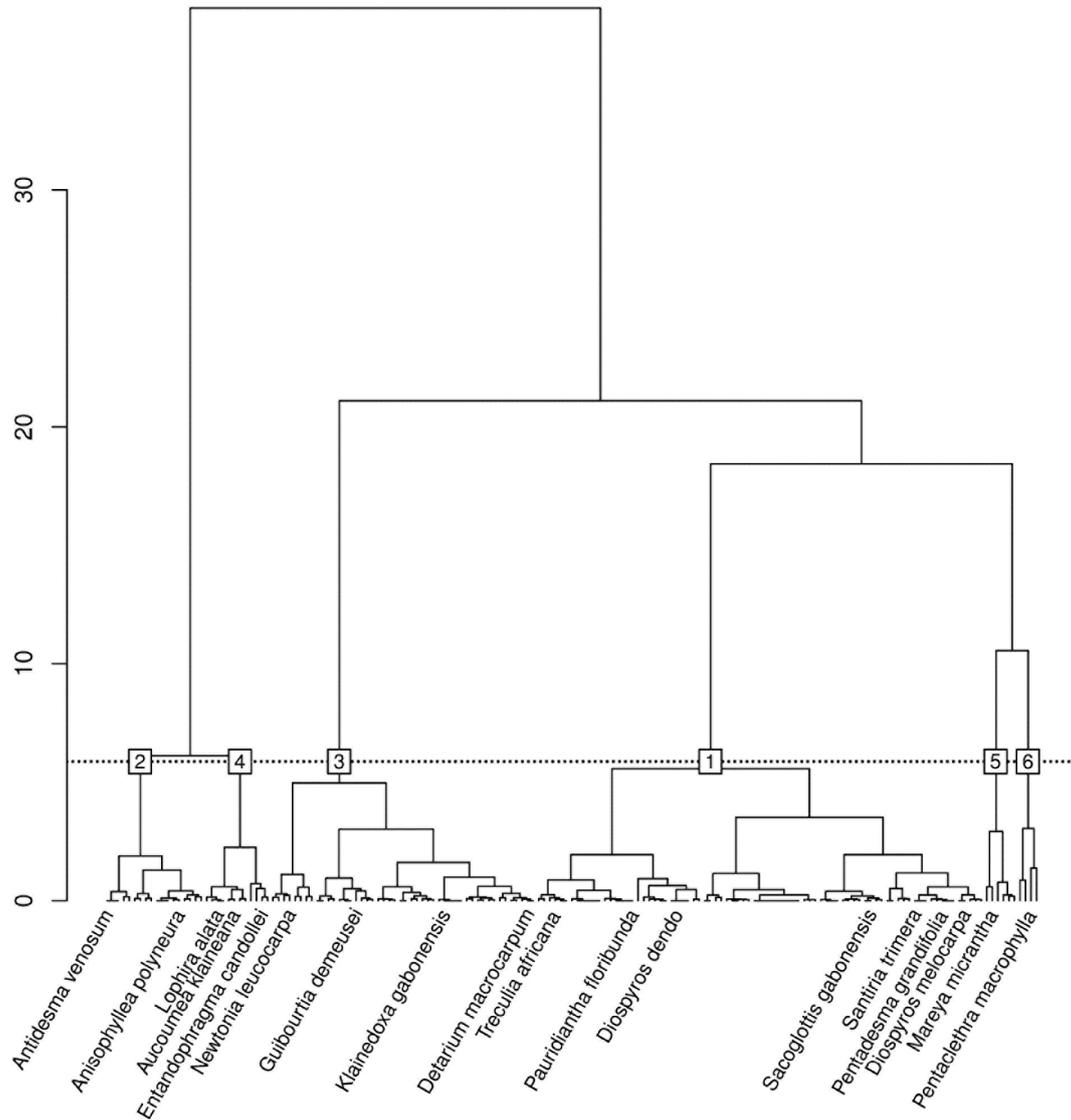
Figure 3   Dendrogram of the hierarchical cluster analysis that defines six species groups based on their traits; hierarchy shows that the six species groups can be clustered at a higher level into three functional groups (groups 1, 5, 6, group 3, and groups 2, 4) with some indicators species for each of them; dotted line shows where the dendrogram was cut to define the species groups

ordination also showed a continuum which ran from pioneer species of strong dispersal potential towards species of weak dispersal potential (pionneer species with high dispersal capacities as well as cicatricial with high and low dispersal capacities). Shrub species stood in between. Furthermore, although the sarcochorous type was the most common dispersal type (67.5% of the species), groups 3, 4 and 6 cumulated 37% of species with dissemination type barachorous, pogochorous/ptérochorous and ballochorous respectively. They corresponded to seed types that were distinguishingly not fleshy.

Groups 1 and 3 were at the centre of the ordination gradient and seemed to be discriminated by the phytogeographic types. Group 1 with 81 species (47%) and group 3 with 48 species (28%) included the major part of the species in this study. Group 4 contained species such as *Aucoumea klaineana*, *Hylodendron gabunense* and *Lophira alata* which were species structuring the canopy at our study site.

The gradient evidenced by the ordination of the species based on their traits could also be interpreted as a continuum which ran from savannah to forest (with emergent species in
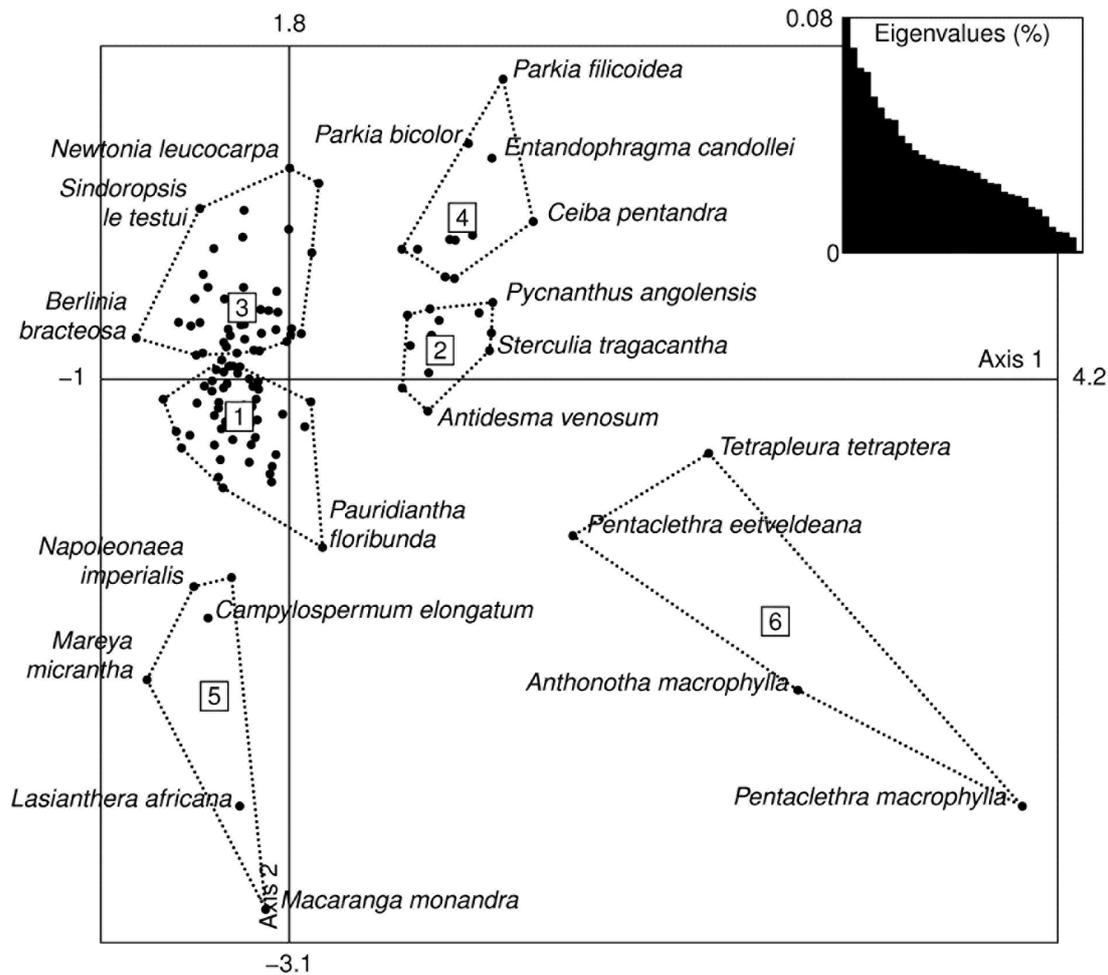
Figure 4　Projection of the 169 species on the two first axes of the multiple correspondence analysis of their traits; dotted polygons indicate the six groups of species based on their traits

groups 1, 3 and 4, and shrub species in groups 5 and 6), showing coexistence of two biomes. This gradient also corresponded to an opposition between species with small (canopy) and large (understory strata) foliages.

The χ^2 tests showed that all traits except phytogeographic types were significantly related to the six trait-based groups of species at 5% level: biological type ($\chi^2 = 191.5$, p < 0.001), functional guild ($\chi^2 = 200.6$, p < 0.001), functional types ($\chi^2 = 387.6$, p < 0.001), foliage type ($\chi^2 = 133.2$, p < 0.001) and types of dispersal ($\chi^2 = 195.2$, p = 0.004).

Relationship between traits and floristic groups

There was significant relationship between the six floristic groups and the six groups of species based on their traits (Rand index = 0.60,

p = 0.049), although the p was very close to the level of 5%. This relationship mainly resulted from an association between floristic group 2 and trait-based groups 4 and 6 on the one hand, and from an association between floristic group 5 and trait-based group 2 on the other hand (Table 6). Due to restriction from 258 to 168 species, floristic group 3 was not represented in the contingency table that cross-tabulated floristic groups and the groups of species based on their traits. This group 3, at the far left of the floristic gradient shown in Figure 2 (see Palla et al. (2011) for interpretation of this gradient) had *Cynometra schlechteri*, *Albizia laurentii* and *Chrysobalanus icaco* as characteristic species.

Moreover, some of the traits were significantly related to the floristic groups. The traits functional guild ($\chi^2 = 26.8$, p = 0.030) and phytogeographic type ($\chi^2 = 117.8$, p = 0.002) were significantly related to the floristic groups: level cicatricial of trait

Figure 5   Projection of the levels of the traits on the first two axes of the multiple correspondence analysis of species traits; polygons indicate the six groups of species based on their traits

functional guild was associated with floristic groups 2 (with *Sacoglottis gabonensis* as a characteristic species) and 5 (*Cola lizae, Aucoumea klaineana, L. alata, Diospyros polystemon* and *Xylopia hypolampra* as characteristic species), and levels AfroMadagascan and Congolese of trait phytogeographic types were associated with floristic group 4 (*Guibourtia demeusei, Alchornea cordifolia* and *Treculia africana* as characteristic species). The trait functional types showed near-significant association with the floristic groups ($\chi^2 = 39.9$, $p = 0.056$) whereas traits biological type ($\chi^2 = 16.8$, $p = 0.64$), foliage type ($\chi^2 = 9.8$, $p = 0.97$) and types of dispersal ($\chi^2 = 14.3$, $p = 0.76$) were not significantly related to the floristic groups.

Floristic group 1 (*Santiria trimera, Centroplacus glaucinus, Strombosiopsis tetrandra, Dacryodes klaineana* and *Coula edulis* as characteristic species) and floristic group 6 (*Desbordesia glaucescens, Dialium guineense, Carapa procera, Grewia coriacea* and *Scyphocephalium mannii* as

characteristic species) were not significantly related to any specific trait and they were consistently not associated with any trait-based group (Table 6). These two groups formed the right hand-side of the floristic gradient in Figure 2.

DISCUSSION

Traits linked to the ongoing processes

Biological type and functional guild

Four levels of these traits contributed to discriminate trait-based groups. We distinguished the pioneer and cicatricial species. This distinction subdivided species of the lower vegetation stratum from the higher ones. We then looked at two separate possible dynamics, integrating lianas and shrubs as part of groups 1

Table 6 Contribution matrix for the Monte Carlo test of association based the Rand index between floristic groups and groups of species based on their traits

Floristic group	Trait-based group					
	1	2	3	4	5	6
1	0.58	-1	0.26	-1	-1	-1
2	-0.25	1.60	-0.76	3.03	-1	3.43
4	0.44	-1	-1	-1	-1	-1
5	-0.19	1.93	-0.39	0.13	-1	1.07
6	-0.26	-0.87	1.12	-0.70	1	-1

and 5 that contained several taxa that could be encountered in the savannah such as *S. gabonensis* (the only representative of Humiriaceae).

Functional type

We distinguished species with higher (pioneer species with high dispersal capacities, cicatricial with high dispersal capacities, large seeds with low dispersal capacities) and lower (cicatricial with low dispersal capacities, large seeds with low dispersal capacities) dispersion capacities. The combination between behaviour and dispersal potential is recommended for the study of vegetation groups in tropical forests because functional groups follow behavioural types (Senterre 2005). This approach allowed us to compensate for lack of data about the species dispersal and allowed an integrative definition that included spatial distribution generated by dispersal potential. The behaviour makes reference to a vertical microclimate gradient (Oldeman 1974) and to the importance of light for species development in the forest mosaic. Access to light was the factor that made it possible to distinguish the strategy of the species in the processes of forest recolonisation (nanophyllous for shrub species in group 6, and leptophyllous for emergent species in group 4). There is substantial variation between sun leaf traits of trees and lianas compared with shade leaves of understorey species (Santiago & Wright 2007).

Phytogeographic type

Among the 13 levels of this trait, we noted that African multi-regional, lower-Guinean and peripheral Guineo–Congolese strongly characterised trait-based groups 2, 3 and 4

respectively. Microclimatic vertical variations are much more important in tropical forests than macroclimatic horizontal variations (Oldeman 1974). Hence, the lower strata such as understorey may respond to local environmental variations differently from the upper strata. Foliage type was correlated with growth, as the species with the largest leaves also had the highest growth rates (Leroy-Deval 1973). This trait was preferred compared with summer greenness as it could vary within a species (Senterre 2005). The functional type was similar to the function guild but additionally specified the potential for dispersal of the species. These two traits clarified the successional status of the species. Dispersal type was related to the geographical range of the species. The part of the tree that performed dispersal function was not restricted to seeds since it could be performed by fruit. Type of diaspore was correlated with dispersal distance. The more open a type of vegetation or a stratum (e.g. upper canopy), the greater the proportion of species with a high dispersal capacity.

Relationship between floristic groups and group traits

The six floristic groups defined by Palla et al. (2011) corresponded to a gradient of forest types (along the first axis in Figure 2), from young to old forests depending on the stage of recovery of the forest over the savannah. These forest types were also associated with altitude, hydrography or their status as forest colonisers of savannahs (Palla et al. 2011). From Table 6, we could link between these forest types and the trait-based groups of species, and define a complementary gradient that explained the ongoing process of forest recovery over savannah.

Floristic group 2 (that corresponded to trait-based group 6), representing the colonising forests, comprised short-lived cicatricial species and was followed by cicatricial canopy-structuring species of trait-based groups 2 and 4 such as *A. klaineana* (corresponding to floristic group 5). The trait-based group 3 representing floristic group 4 had species such as *G. demeusei* as characteristic species. The understorey shrubby stratum (lianas and shrubs) corresponded to trait-based group 5 with functional types large seeds with high dispersal capacities, large seeds with low dispersal capacities and pioneer species.

The dendrogram (Figure 3) showed that the six trait-based groups could be clustered at a higher level of the hierarchy into three functional groups that confirmed that the observed gradient from pioneer species to cicatricial species was materialised by short-lived and long-lived species. These species achieved different functions depending on whether they colonised or contributed to the canopy and to the vertical stratum structure. These results suggested that there were three possible ongoing dynamics relating to the reconquest forest: one for the understorey species, one for liana and shrubs and one for arboreal species. Given that the savannah–forest mosaic is a transition ecotone, this means that species groups with a high dispersal potential should be more specifically monitored and controlled to maintain the mosaic. On the basis of the definition of Oldeman and Van Dijk (1991) and our results, we can state that there is a gradient of functional guilds that follows the gradient of the forest types. For many authors (Smith et al. 1998, Hooper et al. 2002, Blondel 2003, Hoehn 2008), functional guild is sufficient to distinguish the groups of species.

The canopy opening caused proliferation of shrubs and vines that could smother young trees that would normally obliterate windfalls created. The occurrence of liana might be a solution to slow down the advance of the forest over the savannah, after the abandonment of forest exploitation (Rollet 1983).

Implications for the maintenance of the savannah–forest mosaic

Taking account of forest types is useful to manage the patterns of change of vegetation groups in the savannah–forest mosaic of the Lopé National Park, using simple keys, i.e. traits and structural as well as floristic variables. As part of the floristic assemblages considered here (continuous forest, copse and gallery forest), regular fire control to prevent spontaneous reafforestation may also be a way to maintain the savannah. Nevertheless, the disappearance of savannah tree species in favour of forest tree species can accelerate the process of reconquest by the forest and, thus, undermines efforts to achieve the development goals of the Lopé National Park. There are 13 parks in Gabon, of which six contain savannahs with the specificity that only the Lopé National Park has implemented a fire plan. One of the missions of the park is to conserve habitats, with emphasis on the savannah and forest–savannah mosaic. Earlier studies advocated the conservation of the groves of trees and the gallery forest which were related to the existence of a strong dispersal potential, namely, the seeds of the new vegetative species (Ukizintambara et al. 2007). However, this did not take into account other disturbances and development perspectives of the savannah–forest mosaic in the context of global changes. A typology of savannahs in relation with their burning schedule will provide a basis for judging the patterns of progression of the forest while taking account other factors such as the hydrography or the relief.

The Lopé National Park can be seen as an educational case study (Descoing 1974) and isotopic chemical studies (Schwartz et al. 2000) have already made it possible to distinguish the C_3 or C_4 plants. However, these results do not yet explain the coexistence and maintenance of the two co-occurring types of vegetation formations. The use of life-history traits offers a method to orientate the management process and combine key characteristics of species which characterise the vegetation groups of Lopé National Park. If the main threat is the loss of the savannah area, we must invest in maintaining the existing area. It is necessary to have simple indicators for each monitoring system and to support decision at Lopé National Park. It could, therefore, limit the number of indicators to the number of features of the study in order to establish functional groups. For the manager of a protected area, it is the act of placing a spatial scale of reference in the protected area (that of the forest–savannah mosaic) that will make him aware of the impact of certain adjustments on objectives. In general, it is assumed that plant traits can be used to

determine which species can be monitored to maintain the savannah as a complementary tool to fire.

It appears from our results that the implementation of conservation management at Lopé National Park to maintain the savannah–forest mosaic has limitations both in terms of methodology, resources used and unit tracking of savannahs. The use of both tools will achieve the objectives of the management and fire plans implemented in this park in 2006 and 1995. However in practice, size and accessibility of the park make impossible interventions in all savannahs. The identification of a group of species and specific traits allows the implementation of adaptive management, defined as continuous improvement of policies and management practices based on the knowledge of the environment (Petit-Berghem 2004). This sometimes involves testing practices emerging from the 'standard' to determine how the indicators in our study will react to a variety of conditions. In the context of practical conservation, it would probably be more relevant to use all available species data rather than restricting the selection to a subset of the available species (Larsen et al. 2007). Thus, the implementation of our approach will necessitate the preparation of species data of suitable quality and possibly the allocation of additional resources for the acquisition of new data for species that are either of special conservation concern or believed to be good indicators.

CONCLUSIONS

The relationship between the functional ecological groups and the floristic groups provides a basis for characterising the vegetation of the savannah–forest mosaic of the Lopé National Park, and for managing specific areas depending on their species characteristics in order to achieve the maintenance of the savannah. We observed a progressive change in species which also meant a change in the composition and/or all other characteristics which facilitated the understanding of the processes.

Our results confirm the work of Senterre (2005) on the typologies of tropical forest in determining the adaptive characteristics of species. These characteristics can be divided into categories defined as functional types or groups that behave as functional types. These traits express the regeneration dynamics and the long-term reaction to climate disturbances. They facilitate the expression of these processes.

In terms of ecosystem management, this may serve as an important key to interpretation for managers of protected areas in Central Africa with the aim of maintaining the ecosystems after disturbance. Whether for the upper or for the understorey strata, two determining elements were observed, i.e. behaviour with respect to limiting factors (light, short- and medium-term disturbances) and dispersal strategy (long-term disturbances). Our results gave an indication of the existing groups of species that should be considered to set up priorities. Our results showed that careful selection of indicator species could improve the effectiveness of indicator groups, particularly for species of special conservation concern. We conclude that in the absence of forest exploitation, strictly light-demanding species with high dispersal potential will colonise the open environment and form monodominant forests dominated by a single species of *A. klaineana* or *L. alata*.

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