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A reconstruction of Atlantic Central African biomes and forest succession stages derived from modern pollen data and plant functional types

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Abstract

New detailed vegetation reconstructions are proposed in Atlantic Central Africa from a modern pollen data set derived from 199 sites (Cameroon, Gabon and Congo) including 131 new sites. In this study, the concept of plant functional classification is improved with new and more detailed plant functional types (PFTs) and new aggregations of pollen taxa. Using the biomisation method, we reconstructed (1) modern potential biomes and (2) potential succession stages of forest regeneration, a new approach in Atlantic Central African vegetation dynamics and ecosystem functioning reconstruction. When compared to local vegetation, potential biomes are correctly reconstructed (97.5% of the sites) and tropical evergreen to semi-evergreen forest (TRFO biome) is well identified from semi-deciduous forest (TSFO biome). When the potential biomes are superimposed on the White's vegetation map, only 76.4% of the sites are correctly reconstructed. But using botanical data, correspondence and cluster analyses, the 43 sites from Congo (Mayombe) evidence more affinities with those of central Gabon and so they can also be considered as correctly reconstructed as TRFO biome and White's map must be revised. In terms of potential succession stages of forest regeneration, the mature forest (TMFO) is well differentiated from the secondary forest (TSFE), but inside this latter group, the young and the pioneer stages are not clearly identified due probably to their low sampling representation. Moreover, linked to their progressive and mosaic character, the boundaries between two forest biomes or two forest stages are not clearly detected and need also a more intensive sampling in such transitions.

1 Introduction

Plant functional classifications were first proposed by a core project of IGBP, "Global Change and Terrestrial Ecosystems", in the early-mid 1990's as a tool to model vegetation dynamics and ecosystem functioning in response to climate and CO_2. Such classifications appeared as an ecological alternative to traditional taxonomic entities

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for the simplification of floristic complexity in global vegetation models (e.g. Prentice et al., 1992; Woodward and Cramer, 1996; Haxeltine and Prentice, 1996; Cramer, 1997; Leemans, 1997; Smith et al., 1997) and for mapping vegetation patterns at key periods in the past (Prentice and Webb, 1998; Prentice et al., 2000). Since then, extensive research has been carried out to identify plant functional types (PFTs) which are sets of plant species exhibiting similar responses to environmental conditions and grouped on the basis of structural and functional characters (e.g. Noble and Gitay, 1996; Diaz and Cabido, 1997; Diaz Barradas et al., 1999). These PFTs are characterised by a set of common biological attributes correlated with their behaviour (Gitay and Noble, 1997; Lavorel et al., 1997; Lavorel and Garnier, 2002; Lavorel et al., 2007).

In Africa, the notion of plant functional types by the means of pollen data was developed for the first time by Jolly et al. (1998a, b), then by Elenga et al. (2000a), Peyron et al. (2000, 2006), Ngomanda (2005) and Vincens et al. (2006) to reconstruct biomes and climate at key periods (Present, 6000 BP and 18 000 BP) or along quaternary pollen sequences. Skarpe (1996), Jolly and Haxeltine (1997) and Hély et al. (2006) have also used such a classification to test the sensitivity of African biomes to changes in climatic parameters (e.g. the precipitation regime or in CO_2 concentration). According to the high species diversity of the African flora, plant functional classifications have proved to be a good tool for understanding the present, past and future functioning of the African ecosystems.

The aim of this paper is to apply this concept of classification on a large modern pollen data set (199 pollen assemblages, 272 taxa) from Atlantic Central Africa. In this region the main ecosystems, particularly the forest ones, were not always previously accurately identified due to their low sampling representation. Plant functional classifications, associated with the biomisation method (Prentice et al., 1996), were used following two ways: (1) the reconstruction of modern potential biomes and (2) the reconstruction of potential succession stages of forest regeneration, a new approach in Atlantic Central African vegetation dynamics and ecosystem functioning reconstruction. New PFTs and aggregations of pollen taxa in these plant functional types are proposed.

2 Botanical environmental setting

The study area, covering the southern Cameroon, the Gabon and the southern Congo, is located between latitude 5° N and 5° S and between longitude 10° and 15° E (Fig. 1; Table 1). It is mainly occupied by lowlands, with an average altitude of 400 m.

This area is floristically located in the Guineo-Congolian centre of endemism (White, 1983). In this region three main types of vegetation occurring on well-drained soils are differentiated by this author.

2.1 The wetter types of Guineo-Congolian rain forest

These types of forest includes: (i) The coastal evergreen rain forest characterized by the presence of *Sacoglottis gabonensis* and *Lophira alata* in Cameroon (Letouzey, 1957; Tchouto Mbatchou, 2004), this latter tree being replaced by *Okoumea klaineana* in Gabon (De Saint Aubin, 1963; Caballé, 1978) and Congo (Hecketsweiler and Mokoko Ikonga, 1991; Doumenge, 1992). This forest type is called "Atlantic littoral forest" by Letouzey (1968, 1985). Inland, on the small hills and low mountains, this evergreen rain forest is replaced by an evergreen rain forest very rich in Caesalpiniaceae ("Biafran forest", Letouzey, 1968, 1985). (ii) The mixed moist semi-evergreen rain forest ("Congolian forest", Letouzey, 1968, 1985), well developed in south-eastern Cameroon (Letouzey, 1968, 1985) and the eastern half Gabon (Nicolas, 1977) is characterized by a mixture of evergreen and some semi-deciduous species becoming more important in the canopy. The Guineo-Congolian wet rain forest represents the climax ecosystem of the central part of the study area. The upper stratum of this formation is generally 35–45 m high and is well-distributed in diameter classes. The high canopy density precludes the development of an herbaceous strata and favours epiphytes. The thermal gradient in the canopy is very marked, while the atmospheric moisture is permanently

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high. This type of forest does not show any noticeable seasonal behaviour (Mayaux et al., 1997, 1999).

2.2 The drier types of Guineo-Congolian rain forest ("semi-deciduous rain forest", Letouzey, 1968, 1985)

These forests, also called dry peripheral semi-evergreen rain forest by White (1983), are located at the border of the wet rain forest and are floristically richer than the previous ones. More individuals of the common largest tree species are deciduous (up to 70% in the upper stratum) and lose their leaves during the dry season allowing the development of a continuous shrub stratum. The diameter classes' distribution of the upper layer is irregular. The thermal gradient is less marked than in the previous type, while the seasonality is more marked in mesological conditions (Mayaux et al., 1997, 1999).

Secondary forest, occurring on past cultivated areas, is widespread in the region, and corresponds to various stages of forest regrowth in which light-demanding species and pioneers are abundant (e.g. Kahn, 1982; Catinot et al., 1983; White, 1983; Mayaux et al., 1997, 1999). The upper layer of the secondary formations is continuous and homogenous and often characterised by a monospecific composition in its earliest stages, with heliophytic and fast height growth pioneer species.

2.3 The mosaic of rain forest and secondary grassland

Much of the rain forest at the northern and southern limits of the Guineo-Congolian region has been destroyed by cultivation and fire and replaced by secondary grassland which often occurs in mosaic with small, usually severely degraded, patches of the original forest.

Inside the Guineo-Congolian domain appear vast savannas, either as large patches surrounding the forest massif, or as small islands enclosed within the forest. The trees and shrubs of these savannas are sparse while grasses form a continuous and high stratum. Where they occur, the climax formation is a forest one. They find their origin in soil conditions (poorly developed, sandy or lateritic soils), in past and present human activity (settlements, fire) or in past climatic changes (e.g. Robyns, 1936; Richards, 1952; Schwartz et al., 2000).

3 The modern pollen data set

A total of 199 modern pollen spectra were compiled in a data set. They all have been exclusively extracted from surface soil (in savanna) or litter (in forest) samples collected following the Wright method (1967) widely used in African modern pollen studies (e.g. Jolly et al., 1996; Lézine and Edorh, 1991; Bonnefille et al., 1993; Vincens et al., 1997, 2000; Elenga et al., 2000b). The location of the study modern pollen samples is given in Fig. 1 and Table 1. Seventy three samples were collected in southern Cameroon (Vincens et al., 2000 and unpublished data; Lebamba et al., 2009), eighty three in Gabon (Jolly et al., 1996; Lebamba et al., 2009; Ngomanda, unpublished data) and forty three in southern Congo (Elenga et al., 2000b). All samples come from vegetation formations occurring on well-drained soils excluding riparian and swampy formations since these formations are not directly linked to climate but rather to local hydrological conditions. They cover the three main White's vegetation types described above. Local vegetation at each site, extracted from field observations or detailed inventories, is given in Table 1.

The pollen data set comprises a total of 272 pollen taxa which nomenclature was standardized following the list of taxa available in Vincens et al. (2007) and on the African Pollen Data base web site (2008). This list refers to the botanical nomenclature proposed by Lebrun and Stork (1991–1997).

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4 The biomisation method and its application to the modern pollen data set

The biomisation method classifies the plant taxa represented in the pollen assemblages into a number of plant functional types (PFTs) which are broad classes of plants defined by life form (e.g. tree/shrub/lianas/herbs), leaf form (e.g. broad-leaved/needle-leaved), phenology (e.g. evergreen/deciduous) and bioclimatic factors. Pollen taxa are assigned to one or more PFTs, then affinity scores are calculated for each biome in turn based on its list of characteristic PFTs. The pollen sample is assigned to the biome to which it has the highest affinity. This method, initially developed for Europe and now used worldwide, was described in detail by Prentice et al. (1996).

In this paper the biomisation procedure has been applied on our modern pollen data set from Atlantic Central Africa, following two ways: (1) the reconstruction of modern potential biomes and (2) the reconstruction of potential succession stages of forest regeneration. Comparisons with local or more regional botanical data were performed in the aim to test the level of confidence of our reconstructions, and particularly of our taxa-PFT assignments.

4.1 Potential biome reconstructions

The taxon versus site matrix used for these reconstructions include 245 pollen taxa among the 272 identified in the 199 spectra, corresponding to native and non-edaphic pollen taxa. We removed marshy or aquatic herbs and shrubs (Cyperaceae, *Burnatia*, *Sesbania*, *Typha*, Eriocaulaceae, *Mimosa pigra*, *Utricularia*, *Hydrocotyle*), typical swamp trees such (*Symphonia globulifera*, *Phoenix reclinata*, *Raphia*, *Pandanus*, *Rhizophora*, *Morelia senegalensis*, *Clappertonia*), anthropogenic taxa (*Cassia didymobotrya*, *Ricinus communis*, *Capsicum*, *Zea mais*, *Eucalyptus*, *Plantago* and *Elaeis guineensis*), all the Pteridophyta which generally were not identified at a high level of determination (genus or species), but also pioneer taxa which distribution is not primarily related to climate (*Musanga*, *Anthocleista*, *Vismia guineensis* and *Polyscias fulva*).

Compared to previous works undertaken in Africa, we propose in this paper the creation of new PFTs taking into account: (1) a more precise definition of the life form of plants which produce the pollen taxa (trees or shrubs, lianas and herbs) and (2) the place these plants occupy in the different central African ecosystems (e.g. tropical wet rain forest, tropical dry rain forest forest...), mainly linked to bioclimatic factors (e.g. rainfall, temperature, cloud cover, atmospheric humidity...). We have differentiated the trees and shrubs from the lianas and herbs. In the PFTs Te1 (wet tropical evergreen), Te2 (dry tropical evergreen), Tr1 (wet tropical raingreen), Tr2 (dry tropical raingreen) and Tr3 (driest tropical raingreen) as defined by Jolly et al. (1998b) or Vincens et al. (2006) we have only included the tropical tree and shrub taxa. We have created four new PTFs, corresponding to tropical wet lianas (TLw), tropical dry lianas (TLd), tropical herbs from humid forest environments (THw) and from dry open environments (THd). As Peyron et al. (2000) and Vincens et al. (2006), grasses (Poaceae) represent a particular PFT (g). Thus, a total of 10 PFTs is used in this work (Table 2).

The 245 pollen taxa have been allocated to one or more of these PFTs (Table 3). When a taxa is assigned to more than one PFT, this is generally due to its low level of identification (family or genus). Thus, it can include several species with different biology (e.g. Rubiaceae, *Danieilla*, *Parinari*....) or it can comprise species that can adopt different habits in different environments (e.g. *Acacia* a tree in savanna and a liana in forest...). The taxa-PFT allocation has been adapted to the study area and so shows many differences compared to the works of Jolly et al. (1998b), Peyron et al. (2000) or Vincens et al. (2006). The corresponding plant life form and habitat of pollen taxa have been determined using West and Central African botanical literature (e.g. Flore du Congo Belge et du Ruanda-Urundi, 1948–1963; Flore du Congo, du Rwanda et du Burundi, 1967–1971; Flore d'Afrique Centrale (Zaïre, Rwanda, Burundi), 1972–2004; Hutchinson and Dalziel, 1954–1972; Flore du Gabon, 1961–2004; Flore du Cameroun, 1963–2001; Letouzey, 1968, 1985; Lebrun and Stork, 2003, 2006; Tchouto Mbatchou, 2004). Then, a final matrix involving the allocation of plant functional types to the 4 main biomes (TRFO (tropical rain forest), TSFO (tropical seasonal forest), TDFO (tropical dry forest) and SAVA (savanna)) occurring in Atlantic Central Africa has been created (Table 4).

4.2 Potential succession stage reconstructions

The same numerical procedure than the one used for potential biome reconstructions has been applied for the reconstruction of the succession stages of forest regeneration. The pollen data set comprises 250 taxa, including here *Elaeis guineensis*, *Musanga*, *Anthocleista*, *Vismia guineensis* and *Polyscias fulva*, pioneer taxa which play an important role in the regeneration of the forest in its youngest stages.

The matrix taxa-PFTs comprises 14 PFTs including 13 new ones whose definition is based: (1) on the life form of the plants as for biome reconstructions and (2) on the place they occupy in the forest succession in function of their behaviour and growth strategies (savanna, regrowth, young secondary, old secondary and mature stages) (Richards, 1952; Descoings, 1969; Letouzey, 1968, 1985; Schell, 1976; Kahn, 1982; Catinot et al., 1983; White, 1983; White and Abernethy, 1996; Achoundong, 2000; Moutsamboté et al., 2000; Lebrun and Stork, 2003, 2006; Tchouto Mbatchou, 2004; de Namur, unpublished) (Table 5). Such succession status classification was already successfully applied for the aggregation of tropical tree species of the Sabah's lowland rain forests in Indonesia by Köhler et al. (2000) to suit for applications with process-based rain forest growth models. As above, the 250 pollen taxa have been allocated to one or more of these PFTs (Table 6).

Instead of "biomes" we have created dynamic "stages" of succession of forest reconstruction which are from the youngest to the oldest one:

- SAVA: corresponding to the grass herbaceous to semi-woody stage;

- TRFE: corresponding to the forest regrowth stage. In this stage the dominant shrubs and small trees, mainly heliophilous, such as *Albizia*, *Anthocleista*, *Harungana*, *Tetrorchidium*, *Trema* and *Vernonia conferta* are mixed with many coarse herbs (e.g. Zingiberaceae), softly woody shrubs and small climbers (e.g. *Dioscorea*).

– TYSF: characteristically this young secondary stage is dominated by the fast growing heliophilous *Musanga cecropioides* which is the most abundant and characteristic secondary forest tree in tropical Africa, associated with *Myrianthus*, *Macaranga* or *Albizia* for the most abundant trees. The herbaceous and shrubby layer is dense and lianas are abundant (e.g. Apocynaceae).

– TOSF: this old secondary stage is dominated by semi-heliophilous species of moderately rapid growth. Characteristic species occurring in the canopy are: *Alstonia boonei*, *Canarium*, *Ceiba pentandra*, *Zanthoxylum macrophylllum*, *Pycnanthus angolensis*, *Terminalia superba, Triplochiton scleroxylon*. . . .

– TMFO: This is the ultimate stage, or climacic mature stage, of forest regeneration. The floristic composition of this forest stage, the presence of shrub and herbaceous strata depends on the status of the forest: semi-deciduous or mixed semi-evergreen.

The final matrix involving the allocation of plant functional types to the 5 main succession stages is shown in Table 7.

5 The results

5.1 Reconstruction of the Atlantic Central Africa biomes

5.1.1 Comparison between reconstructed biomes and vegetation at each sampled site

The results of the comparison (Table 8 and for detailed results refer to Table 1) show that among the 199 pollen sites considered in this study, 87 are correctly reconstructed as a potential biome Tropical Rain Forest (TRFO). They correspond to 74 sites of rain forest from Gabon and to 13 sites from the Cameroon littoral rain forest (8) and from the Dja forest area at the wet/dry rain forest transition (5). For the 43 other sites, all originating in the Mayombe forest massif in southern Congo, a potential TRFO biome is reconstructed. This result arises the problem of the nature and status of this forest in Atlantic Central Africa mapped by White (1983) as Guineo-Congolian dry rain forest (Fig. 1), i.e. such as the Letouzey's semi-deciduous forest of southern Cameroon (see specific discussion below, in Sect. 6.1).

A potential biome Tropical Seasonal Forest (TSFO) is reconstructed at 49 sites. Among them, 45 sites from Cameroon, located in dry rain forest and 3 in the Dja forest area at the wet/dry rain forest transition are correctly reconstructed. Three other sites inside the wet rain forest of Gabon (2) and Cameroon (1) are clearly incorrectly reconstructed as potential TSFO biome such as one savanna in Cameroon.

All the 20 remaining sites are reconstructed as a potential biome Savanna (SAVA). Among them, 19 are really savanna, and one is from a forest regrowth, but largely disturbed by Man for cultivation, leading to high frequencies of Poaceae in the pollen spectra.

5.1.2 Comparison between reconstructed biomes and White's Central Atlantic vegetation types

The results of the comparison are given in Fig. 1a and Table 9. Among the 199 sites, 65 sites from the wetter types of rain forest (i.e. Cameroon coastal evergreen forest and the Gabon mixed moist semi-evergreen rain forest) (vegetation type 1a, White, 1983) are correctly reconstructed as potential TRFO biome.

In the Dja area in southern Cameroon, where occurs the transition between the mixed moist semi-evergreen forest (type 1a) and the dry rain forest (type 2) (indicated in Table 9 as 1a/2 transition) the 9 sites can be considered as correctly reconstructed with 5 sites as potential TRFO biome and 4 sites as potential TSFO biome.

Inside the White's dry rain forest (type 2), only 8 Cameroon sites are correctly reconstructed as potential TSFO biome. One site is reconstructed as a SAVA but, corresponding locally to an enclosed savanna inside the forest, this reconstruction can be considered as correct. The 43 remaining sites are all the forest sites from the Congolese Mayombe massif which are reconstructed as potential TRFO biome and not as potential TSFO biome as it could be expected according to White's vegetation map.

The last White's vegetation type occurring in Central Africa (of drier type in southern Cameroon, and wetter type in central and southern Gabon) – mainly developed at the border of the forest massif – is the mosaic of rain forest and secondary grassland (type 11a). Inside this vegetation type, 17 Gabon sites are reconstructed as TRFO biome (Lopé area), 34 Cameroon sites as TSFO biome (Kandara area) and 19 Gabon and Cameroon sites as SAVA biome (Lopé area and southern Gabon, Kandara area) indicating well the mosaic character of the vegetation. For each site (total of 70), when the potential biome proposed is compared to the local vegetation as defined in the field (Table 1), it appears that all sites are well reconstructed. This shows the importance to have a minimum of botanical information at each sampling site.

5.2 Reconstruction in terms of forest dynamics

In a first step, we have considered all the succession stages which can be observed in a dynamics of reconstruction of the forest, from the younger herbaceous stage (SAVA) to the Tropical Mature FOrest stage (TMFO), including successively the Tropical Forest REgrowth (TFRE), the Tropical Young Secondary Forest (TYSF) then the Tropical Old Secondary Forest (TOSF). The results of the comparison between potential reconstructed stages and local vegetation show that only 3 stages can be considered as correctly reconstructed, with a number of correct assignments exceeding the number of incorrect ones (Table 10a and for details at each site refer to Table 1). These are the TMFO (148 sites), TOSF (6 sites) and SAVA (19 sites) stages. The youngest stages of arboreal recolonisation are poorly (TYSF) or totally uncorrected (TFRE) reconstructed.

According to these results we have re-arranged these stages into only 3 main stages: TMFO, TSFE (Tropical Secondary Forest) grouping all secondary succession stages, and SAVA (Table 10b and Fig. 1b). In this way, the potential stages correctly reconstructed are of 97.4% (148 sites), 66.6% (18 sites) and 95% (21) of confidence, respectively.

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6 Discussion

Our reconstructions in terms of biomes or succession stages of forest regeneration arise some questions concerning (1) the status of the Congolese Mayombe forest inside the Guineo-Congolian forest massif and (2) the boundary features between two biomes or two succession stages.

6.1 The status of the Congolese Mayombe forest

The potential biomes reconstructed at all the sites from the Congolese Mayombe forest show discrepancies compared with the White's Central Atlantic vegetation type locations. Indeed, all these sites are located in the dry rain forest (type 2) and are reconstructed as Tropical Rain Forest biome (TRFO) such as the Gabon forested sites and not as Tropical seasonal Forest biome (TSFO) as it could be expected (Table 1).

As in this work, White's vegetation map, based on a combination of physiognomic and floristic factors, is classically used by African palynologists to localise modern samples or fossil pollen sedimentary sequences (e.g. Lézine and Edorh, 1991; Vincens et al., 2005; Lézine et al., submitted). Sometimes it has been locally modified and complemented according to regional botanical and ecological data such as by Maley (1990), Maley and Elenga (1993) or more recently in Giresse et al. (2008) for Central Africa. But these authors have always conserved the status of semi-deciduous forest or dry rain forest as defined by White (1983) for the Mayombe forest in spite of detailed contradictory botanical field works in this area (e.g. Dowsett-Lemaire, 1991; Hecketsweiler and Mokoko Ikonga, 1991; Doumenge, 1992; de Namur, unpublished). As observed by Dowsett-Lemaire (1991) the striking feature of the Mayombe forest is the importance of the Caesalpiniaceae, locally dominant in the canopy. Among the dominant and most widespread emergent are found two families: the Irvingiaceae, and the Myristicaceae. Other very large and frequent trees belong to the Burseraceae, Combretaceae, Mimosaceae and Sapotaceae. The canopy in the Mayombe is also characterized by a significant proportion of briefly deciduous species; several species, however, are found essentially in secondary situations along roads and in abandoned farmlands and their importance must have increased with the spread of human disturbances. The epiphytic flora is especially rich in the central Mayombe between 400 and 500 m altitude. According to its floristic composition, Dowsett-Lemaire (1991) considers that the Mayombe forest is a rather complex assemblage of two main types of forest: the Atlantic coastal evergreen rain forest and the mixed moist semi-evergreen rain forest, and so, it must be classified as Guineo-Congolian wet rain forest. Such a conclusion seems to be confirmed by Doumenge (1992) who considers that the Mayombe forest has many affinities with the Biafran forest rich in Caesalpiniaceae described by Letouzey (1985) in Cameroon, extending southward in Central Gabon as evergreen forest (Nicolas, 1977; Caballé, 1978). Doumenge (1992) estimates that the Mayombe forest on well-drained soils is of dense wet semi-evergreen type. Before these works, Descoings (1969) mapped the Mayombe forest as equatorial rain forest, of the same type than those that occur in northern Congo on well-drained soils and Sita (1989) classified it as dense mixed wet semi-evergreen forest. Moreover, on the Central African vegetation map produced by de Namur (1990) the Mayombe massif appears as of transitional type between an evergreen type to a semi-deciduous one, as are mapped also forests from the northern Gabon (including the Makokou area) and from the southern Cameroon (including the Dja area).

In the light of these botanical information, we have analysed part of our pollen data set – i.e. considering only forest sites (176 and 272 taxa) – using hierarchical cluster analysis (Ward, 1963) and correspondence analysis (CA) (Benzécri, 1973) to identify the possible affinities between pollen assemblages from Congo and those from Gabon and Cameroon.

The dendrogram of the cluster analysis (Fig. 2) shows, at a first level of division (1), a clear differentiation between the Cameroon pollen spectra of Kandara and Mayos located in the northern dry peripheral rain forest (or semi-deciduous forest) and all the others. The next division (2) separates the spectra from Makokou and Belinga in Gabon and from Mayombe (Congo) from the others. At the third level of division (3a) spectra from Makokou and Belinga are well differentiated from those from the Mayombe and (3b) spectra from the Lopé (Gabon) are well separated from the other Cameroon and Gabon spectra. The correspondence analysis (Fig. 3) displays the same features than the cluster analysis showing along the first axis a clear separation of pollen spectra from the dry peripheral rain forest of Cameroon (Kandara and Mayos) from the others, and along the axis 2 better affinities between the Congolese Mayombe spectra and the Makokou and Belinga ones than with all the others.

These results show that the Mayombe forest at the sampling sites is not a semi-deciduous type such as those of southern Cameroon (Kandara and Mayos areas) but rather exhibits more affinities with the central Gabon forest as previously proposed by Doumenge (1992) and mapped by de Namur (1990).

6.2 The boundaries between biomes or succession stages

If the boundary between grassland and rain forest is clearly identified in the field and on aerial or satellite photographs, by their floristic composition, structure and physiognomy, as well as in pollen assemblages by the abundance of the Poaceae versus arboreal taxa, inside the forest massif the limit between the wet and the dry rain forest, and between the old secondary and the mature forest, is often difficult to establish.

The difference between the wet and the dry forest types is chiefly floristic and this floristic difference does not produce a fundamentally different physiognomy. The transition from one community to the other is usually gradual; one passing into the other imperceptibly except where a concomitant change of soil and climate occurs, it may then be more abrupt (Aubreville, 1938; Richard, 1952). The gradual character of this transition, but also its mosaic character (Tchouto Mbatchou, 2004) is well evidenced in our biome reconstructions in sites of southern Cameroon in the Dja forest area (Nkoul and Cyrie sites) where some sites are reconstructed as TRFO potential biome and others as TSFO potential biome, so they have all been considered as correctly reconstructed (Tables 1 and 8).

The same problem is observed at the boundary of old secondary forest and mature forest. Richards (1952) estimates that it is almost impossible to differentiate these two types of forest formation. In tropical central American forest Budowski (1970) used 3 criteria to differentiate the old secondary forest: (1) a high concentration of deciduous species in the evergreen domain, (2) abundance of lianas of low diameter and (3) the paucity in epiphytes, which are also the most characteristic criteria of the west and central old African secondary forest (Kahn, 1982). Other authors base the boundary of these two forest types in central Africa on the presence of markers such as *Elaeis guineensis* only in the old secondary forest (Kahn, 1982) or species of *Rinorea* only in the mature one (Achoundong, 1996, 2000) or in dynamic term, on the acquisition of the mechanism of regeneration by windfall that get forest species in position to regenerate in mature forest (Kahn, 1982).

But, all these criteria used by botanists in the field are very difficult to consider in our palynological work due to the lack of detailed botanical inventories at each pollen site and to the level of identification of our pollen taxa, more generally at the genus or family levels. Only the site of Kandara can illustrate this transition between old secondary forest and mature forest, pollen samples being collected along 2 continuous transects (Vincens et al., 2000 and unpublished data). Along these transects the boundary between the two formations has been placed following botanical inventories and mainly the presence of *Rinorea* species only in the mature forest (Achoundong, 2000). Unfortunately, pollen grains of *Rinorea* have not been identified in our samples due probably to the entomophilous character of the pollination of this plant. This boundary is not clearly identified by our pollen assemblages since some samples from the old secondary forest are reconstructed as a TMFO potential stage and some samples from the mature forest as a TOSF potential stage (Table 1). But often the calculated scores for these two stages in a same sample are very close. There is probably not a well defined boundary between these two types of forest such as between dry and wet forest; instead we suggest a transitional zone with a mosaic character. Moreover, our work being based on pollen analysis, part of pollen grains produced by the plants growing on a plot (mainly great pollen producers with well dispersed pollen grains) can be transported in a contiguous plot and so affect the local pollen rain. This could also explain why the regrowth (TRFE) and the young secondary forest (TYSF) stages are not well reconstructed by pollen assemblages, probably associated also with a high anthropogenic impact in the northern Kandara transect.

7 Conclusion

The application of biomisation to Atlantic Central African pollen data using a larger data set, a new and more precise classification of plant functional types and new allocations of pollen taxa to these PFTs adapted to the study area than in previous works, demonstrates that this objective and quantitative method is able to accurately predict the potential vegetation in a tropical forest region with high taxonomic diversity. In the majority of the cases, the results are comparable to site-specific descriptions of the vegetation. Savannas (SAVA potential biome), tropical rain forests (TRFO potential biome) and tropical seasonal forests (TSFO potential biome) are correctly reconstructed at 97.5% of the sites, such as the main succession stages of forest regeneration (93% of the sites): savanna (SAVA potential stage), tropical secondary forest (TSFE potential stage) and tropical mature forest (TMFO potential stage). But inside the secondary forest the young and the pioneer stages are not clearly identified due probably to their low sampling representation. Some reconstructions can remain questionable mainly at sites located at the boundary of two forest biomes (wet rain forest and dry rain forest) or two forest stages (old secondary forest and mature forest) due to the lack of precise botanical inventories on these sites and to the fact that it does not occur a clear boundary between these forest types but a gradual and transitional zone, with also a probable mosaic character.

A comparison between reconstructed potential biomes and White's Central Atlantic vegetation types has raised the problem of the status of the Congolese Mayombe forest inside the Central Atlantic forest massif. Our reconstructions (all sites in TRFO biome) associated with numerical analyses (correspondence and cluster analysis) and local detailed botanical inventories show that this forest, though under lower mean annual rainfall (1400 mm/year) and with a longer dry season of 4 months, has more floristic affinities with the wet inland evergreen semi-evergreen rain forest occurring in Gabon (mean of 1600 mm/year, a dry season of 3 months) than with the dry Cameroon semi-deciduous rain forest (1600 mm/year, a dry season of 3 months) as mapped by White (1983). This would confirm the hypothesis expressed by Lebamba et al. (2008) suggesting the importance of the role played by the cloud cover and the relative atmospheric humidity during the dry season in the floristic composition of forests north and south of the meteorological equator, rather than the annual rainfall amount and/or the length of the dry season. High values of these two climatic parameters, linked to monsoon influences from the Gulf of Guinea in Congo and Gabon, are measured during June, July and August versus low values in Cameroon linked to influences of continental trade winds (Harmattan) during December, January and February (Nicholson, 2000; FAO Web LocClim, 2008).

This work evidences the ability of modern pollen data to predict accurately the present potential vegetation in tropical African forest ecosystems in terms of biomes but also for the first time in Africa in terms of vegetation dynamics. These positive results open the possibility to use with confidence fossil pollen data to reconstruct more precisely potential vegetation and its dynamics in Atlantic Central Africa during the Late Quaternary from lacustrine pollen sequences.

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Table 1. Location of modern pollen samples in Atlantic Central Africa, derived vegetation and reconstructed biomes and succession stages (column A, authors of the data: **(a)** Vincens, unpublished; **(b)** Lebamba et al., 2009; **(c)** Vincens et al., 2000; (d) Jolly et al., 1996; (e) Ngomanda, unpublished; (f) Elenga et al., 2000b); (Reconstructed biomes: TRFO (Tropical Rain Forest), TSFO (Tropical Seasonal Forest) and SAVA (savanna); Reconstructed stages: TMFO (Tropical Mature Forest), TOSF (Tropical Old Secondary Forest), TYSF (Tropical young Secondary Forest) and SAVA (Savanna)). (in bold italics, not correctly reconstructed potential biomes and stages compared to local vegetation).

Samples	Location	Country	Lat.	Long.	Alt (m)	Local observed vegetation	Reconstructed biomes	Reconstructed stages
C83 **(b)**	Ndokoua	Cameroon	4.38	11.72	516	savanna	SAV	SAVA
ka1620 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	***TOSF***
ka1600 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	TMFO
ka1580 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	TMFO
ka1560 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	***TOSF***
ka1540 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	old secondary semi-deciduous forest	TSFO	***TMFO***
ka1520 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	old secondary semi-deciduous forest	TSFO	TOSF
ka1500 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	old secondary semi-deciduous forest	TSFO	TOSF
ka1480 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	old secondary semi-deciduous forest	TSFO	TOSF
ka1460 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	old secondary semi-deciduous forest	TSFO	TOSF
ka1440 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TMFO***
ka1420 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka1400 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka1380 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka1360 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka1300 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	savanna	***TSFO***	***TOSF***
ka1280 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka1260 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka1240 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	forest regrowth	TSFO	***TMFO***
ka1220 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	forest regrowth	***SAV***	***SAVA***
ka1200 **(a)**	Kandara Nord	Cameroon	4.33	13.72	640	forest regrowth	TSFO	***SAVA***
ka735 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka705 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka675 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka645 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka615 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka585 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka555 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka525 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	savanna	SAV	SAVA
ka502 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	forest regrowth	TSFO	***TYSF***
ka480 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	forest regrowth	TSFO	***TOSF***
ka450 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka420 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka390 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka360 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka330 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	young secondary semi-deciduous forest	TSFO	***TOSF***
ka300 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	old secondary semi-deciduous forest	TSFO	TOSF
ka270 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	old secondary semi-deciduous forest	TSFO	***TMFO***
ka240 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	old secondary semi-deciduous forest	TSFO	TOSF
ka210 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	***TOSF***

Table 1. Continued.

Samples	Location	Country	Lat.	Long.	Alt (m)	Local observed vegetation	Reconstructed biomes	Reconstructed stages
ka180 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	***TOSF***
ka150 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	TMFO
ka120 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	TMFO
ka90 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	TMFO
ka60 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	TMFO
ka40 **(c)**	Kandara Sud	Cameroon	4.33	13.72	640	mature semi-deciduous forest	TSFO	TMFO
may1 **(a)**	Mayos	Cameroon	4.32	13.57	600	old secondary semi-deciduous forest	TSFO	***TMFO***
may2 **(a)**	Mayos	Cameroon	4.32	13.57	600	old secondary semi-deciduous forest	TSFO	***TMFO***
may3 **(a)**	Mayos	Cameroon	4.32	13.57	600	mature semi-deciduous forest	TSFO	TMFO
C58 **(b)**	Nebodo	Cameroon	4.01	12.64	662	mature semi-deciduous forest	TSFO	TMFO
C84 **(b)**	Nyek	Cameroon	4.00	12.22	693	savanna	SAV	SAVA
C60 **(b)**	Biba	Cameroon	3.88	12.24	667	mature semi-deciduous forest	TSFO	TMFO
C61 **(b)**	Biba	Cameroon	3.86	12.24	671	mature semi-deciduous forest	TSFO	TMFO
C62 **(b)**	Biba	Cameroon	3.85	12.24	643	mature semi-deciduous forest	TSFO	TMFO
C63 **(b)**	Biba	Cameroon	3.85	12.24	687	mature semi-deciduous forest	TSFO	TMFO
C75 **(b)**	Cyrie (Dja)	Cameroon	3.82	13.31	668	mature rain forest/semi-deciduous forest transition	TRFO	TMFO
C76 **(b)**	Cyrie (Dja)	Cameroon	3.82	13.31	678	mature rain forest/semi-deciduous forest transition	TRFO	TMFO
C77 **(b)**	Cyrie (Dja)	Cameroon	3.82	13.31	684	mature rain forest/semi-deciduous forest transition	TRFO	TMFO
C78 **(b)**	Cyrie (Dja)	Cameroon	3.82	13.31	681	mature rain forest/semi-deciduous forest transition	TSFO	TMFO
C66 **(b)**	Tissongo	Cameroon	3.58	11.00	26	mature rain forest	TRFO	TMFO
C67 **(b)**	Tissongo	Cameroon	3.58	11.00	14	mature rain forest	TRFO	TMFO
C68 **(b)**	Tissongo	Cameroon	3.58	11.00	11	mature rain forest	TRFO	TMFO
C69 **(b)**	Nsah	Cameroon	3.56	11.00	17	mature rain forest	TRFO	TMFO
C70 **(b)**	Nsah	Cameroon	3.54	11.00	19	mature rain forest	TRFO	TMFO
C72 **(b)**	Nsah	Cameroon	3.54	11.00	15	mature rain forest	TRFO	TMFO
C71 **(b)**	Nsah	Cameroon	3.54	11.00	19	mature rain forest	***TSFO***	TMFO
C82 **(b)**	Nkoul (Nja)	Cameroon	3.36	13.52	697	mature rain forest/semi-deciduous forest transition	TRFO	TMFO
C80 **(b)**	Nkoul (Nja)	Cameroon	3.36	13.52	697	mature rain forest/semi-deciduous forest transition	TSFO	TMFO
C81 **(b)**	Nkoul (Nja)	Cameroon	3.36	13.52	699	young secondary rain forest/semi-deciduous forest transition	TSFO	***TMFO***
C73 **(b)**	Nkoul (Nja)	Cameroon	3.35	13.53	710	mature rain forest/semi-deciduous forest transition	TRFO	TMFO
C74 **(b)**	Nkoul (Nja)	Cameroon	3.35	13.53	716	mature rain forest/semi-deciduous forest transition	TSFO	TMFO
eb1 **(a)**	Eboundja	Cameroon	2.82	9.90	10	mature rain forest	TRFO	TMFO
eb2 **(a)**	Boussibelika	Cameroon	2.73	9.87	20	mature rain forest	TRFO	TMFO
GA2B **(d)**	Belinga	Gabon	1.12	13.12	925	mature rain forest	TRFO	TMFO
GA1M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
GA2M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
GA9M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G10M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G12M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G13M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G14M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G16M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G17M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G18M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G19M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G20M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G21M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G25M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G26M **(d)**	Makokou	Gabon	0.65	12.71	470	mature rain forest	TRFO	TMFO
G50 **(b)**	Ntsiete	Gabon	0.48	13.08	501	mature rain forest	TRFO	TMFO
G20 **(b)**	Ntsiete	Gabon	0.40	13.04	528	mature rain forest	TRFO	TMFO
G22 **(b)**	Makokou	Gabon	0.37	12.21	442	mature rain forest	TRFO	TMFO
G51**(b)**	Ntsiete	Gabon	0.37	13.12	534	mature rain forest	***TSFO***	TMFO
G23 **(b)**	Ovan	Gabon	0.33	12.07	413	mature rain forest	TRFO	TMFO
G52 **(b)**	Ntsiete	Gabon	0.33	13.18	554	mature rain forest	TRFO	TMFO
G16 **(b)**	Ivindo (camp)	Gabon	0.18	12.54	327	mature rain forest	TRFO	TMFO
G48 **(b)**	Djidji	Gabon	0.02	12.40	420	mature rain forest	TRFO	TMFO
G47 **(b)**	Djidji	Gabon	0.01	12.44	500	mature rain forest	TRFO	TMFO
G19 **(b)**	Djjidji	Gabon	0.01	12.44	540	mature rain forest	TRFO	TMFO

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Table 1. Continued.

Samples	Location	Country	Lat.	Long.	Alt (m)	Local observed vegetation	Reconstructed biomes	Reconstructed stages
G46 **(b)**	Djidji	Gabon	0.01	12.44	540	mature rain forest	***TSFO***	TMFO
G49 **(b)**	Djidji	Gabon	−0.02	12.35	424	mature rain forest	TRFO	TMFO
G45 **(b)**	Ivindo National Park	Gabon	−0.16	12.51	547	mature rain forest	TRFO	TMFO
G12 **(b)**	Ivindo National Park	Gabon	−0.17	12.25	324	mature rain forest	TRFO	TMFO
G13 **(b)**	Ivindo National Park	Gabon	−0.17	12.25	325	mature rain forest	TRFO	TMFO
G14 **(b)**	Ivindo National Park	Gabon	−0.17	12.25	326	mature rain forest	TRFO	TMFO
G15 **(b)**	Ivindo National Park	Gabon	−0.17	12.25	327	mature rain forest	TRFO	TMFO
G17 **(b)**	Langoué bai	Gabon	−0.17	12.57	360	mature rain forest	TRFO	TMFO
G18 **(b)**	Langoué bai	Gabon	−0.17	12.55	360	mature rain forest	TRFO	TMFO
G31 **(b)**	Langoué bai	Gabon	−0.17	12.54	495	mature rain forest	TRFO	TMFO
G37 **(b)**	Langoué forest	Gabon	−0.17	12.53	500	mature rain forest	TRFO	TMFO
G44 **(b)**	Ivindo National Park	Gabon	−0.17	12.53	500	mature rain forest	TRFO	TMFO
G36 **(b)**	Langoué forest	Gabon	−0.17	12.54	515	mature rain forest	TRFO	TMFO
G41 **(b)**	Langoué forest	Gabon	−0.18	12.54	459	mature rain forest	TRFO	TMFO
G35 **(b)**	Langoué forest	Gabon	−0.18	12.54	468	mature rain forest	TRFO	TMFO
G38 **(b)**	Langoué forest	Gabon	−0.18	12.54	495	mature rain forest	TRFO	TMFO
G42 **(b)**	Langoué forest	Gabon	−0.18	12.54	463	mature rain forest	TRFO	TMFO
G13L **(e)**	Lopé National Park	Gabon	−0.18	11.59	250	savanna	SAV	SAVA
G33 **(b)**	Langoué bai	Gabon	−0.18	12.54	460	mature rain forest	TRFO	TMFO
G39 **(b)**	Langoué forest	Gabon	−0.18	12.54	455	mature rain forest	TRFO	TMFO
G11L **(e)**	Lopé National Park	Gabon	−0.18	11.67	250	mature rain forest	TRFO	TMFO
G25 **(b)**	Ivindo (camp)	Gabon	−0.18	12.54	460	mature rain forest	TRFO	TMFO
G40 **(b)**	Langoué forest	Gabon	−0.18	12.54	460	mature rain forest	TRFO	TMFO
G29 **(b)**	Langoué bai	Gabon	−0.18	12.50	350	mature rain forest	TRFO	TMFO
G28 **(b)**	Langoué bai	Gabon	−0.19	12.50	342	mature rain forest	TRFO	TMFO
G32 **(b)**	Langoué bai	Gabon	−0.19	12.54	450	mature rain forest	TRFO	TMFO
G30 **(b)**	Langoué bai	Gabon	−0.19	12.50	360	mature rain forest	TRFO	TMFO
G34 **(b)**	Langoué bai	Gabon	−0.19	12.54	380	mature rain forest	TRFO	TMFO
G43 **(b)**	Langoué forest	Gabon	−0.19	12.54	461	mature rain forest	TRFO	TMFO
G27 **(b)**	Langoué bai	Gabon	−0.19	12.55	370	mature rain forest	TRFO	TMFO
G10L **(e)**	Lopé National Park	Gabon	−0.19	11.59	250	mature rain forest	TRFO	TMFO
G17L **(e)**	Lopé National Park	Gabon	−0.19	11.57	350	mature rain forest	TRFO	TMFO
G18L **(e)**	Lopé National Park	Gabon	−0.19	11.58	300	mature rain forest	TRFO	TMFO
GA9L **(e)**	Lopé National Park	Gabon	−0.20	11.58	250	mature rain forest	TRFO	TMFO
G12L **(e)**	Lopé National Park	Gabon	−0.20	11.68	250	mature rain forest	TRFO	TMFO
G15L **(e)**	Lopé National Park	Gabon	−0.20	11.56	450	mature rain forest	TRFO	TMFO
G16L **(e)**	Lopé National Park	Gabon	−0.20	11.58	400	mature rain forest	TRFO	TMFO
G14L **(e)**	Lopé National Park	Gabon	−0.20	11.55	500	mature rain forest	TRFO	TMFO
G24 **(b)**	Lake Nguene	Gabon	−0.21	10.50	28	mature rain forest	TRFO	TMFO
GA8L **(e)**	Lopé National Park	Gabon	−0.21	11.59	250	mature rain forest	TRFO	TMFO
GA6L **(e)**	Lopé National Park	Gabon	−0.22	11.59	250	mature rain forest	TRFO	TMFO
GA7L **(e)**	Lopé National Park	Gabon	−0.23	11.59	300	mature rain forest	TRFO	TMFO
GA1L **(e)**	Lopé National Park	Gabon	−0.68	11.75	350	mature rain forest	TRFO	TMFO
GA2L **(e)**	Lopé National Park	Gabon	−0.68	11.79	330	mature rain forest	TRFO	TMFO
GA3L **(e)**	Lopé National Park	Gabon	−0.68	11.73	320	mature rain forest	TRFO	TMFO
GA4L **(e)**	Lopé National Park	Gabon	−0.68	11.78	350	mature rain forest	TRFO	TMFO
GA5L **(e)**	Lopé National Park	Gabon	−0.69	11.79	350	mature rain forest	TRFO	TMFO
G1 **(b)**	Lambaréné-Fougamou	Gabon	−0.94	10.47	148	mature rain forest	TRFO	TMFO
G2 **(b)**	Lambaréné-Fougamou	Gabon	−0.94	10.47	148	mature rain forest	TRFO	TMFO

Table 1. Continued.

Samples	Location	Country	Lat.	Long.	Alt (m)	Local observed vegetation	Reconstructed biomes	Reconstructed stages
G3 **(b)**	Lambaréné-Fougamou	Gabon	−0.94	10.47	148	mature rain forest	TRFO	TMFO
G4 **(b)**	Doubou	Gabon	−1.75	10.87	89	savanna	SAV	SAVA
G5 **(b)**	Doubou	Gabon	−1.75	10.87	89	savanna	SAV	SAVA
G6 **(b)**	Doubou	Gabon	−1.75	10.87	89	savanna	SAV	SAVA
G11 **(b)**	Bengui	Gabon	−2.02	11.11	92	young secondary rain forest	TRFO	TYSF
G8 **(b)**	Biendi	Gabon	−2.06	11.07	139	savanna	SAV	SAVA
G10 **(b)**	Lake Massou	Gabon	−2.19	11.20	134	savanna	SAV	SAVA
G9 **(b)**	Sogadel	Gabon	−2.44	11.42	153	savanna	SAV	SAVA
CO29 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO30 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO31 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO32 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO33 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO34 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO35 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO36 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO37 **(f)**	Mandzi	Congo	−4.08	12.15	200	mature rain forest	TRFO	TMFO
CO1 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO2 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO3 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO4 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO5 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO6 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO7 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO8 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO9 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO10 **(f)**	La Tour	Congo	−4.17	12.38	360	mature rain forest	TRFO	TMFO
CO41 **(f)**	Mpassi Mpassi	Congo	−4.17	12.5	350	mature rain forest	TRFO	TMFO
CO11 **(f)**	Dimonika	Congo	−4.22	12.43	380	mature rain forest	TRFO	TMFO
CO12 **(f)**	Dimonika	Congo	−4.22	12.43	380	mature rain forest	TRFO	TMFO
CO13 **(f)**	Dimonika	Congo	−4.22	12.43	380	mature rain forest	TRFO	TMFO
CO14 **(f)**	Dimonika	Congo	−4.22	12.43	380	mature rain forest	TRFO	TMFO
CO15 **(f)**	Dimonika	Congo	−4.22	12.43	380	mature rain forest	TRFO	TMFO
CO16 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO17 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO18 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO19 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO20 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO21 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO22 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO23 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO24 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO25 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO26 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO27 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO28 **(f)**	Mindou	Congo	−4.28	12.07	90	mature rain forest	TRFO	TMFO
CO42 **(f)**	Les Bandas	Congo	−4.28	12.58	350	mature rain forest	TRFO	TMFO
CO43 **(f)**	Les Bandas	Congo	−4.28	12.58	350	mature rain forest	TRFO	TMFO
CO39 **(f)**	Kitina	Congo	−4.32	12.2	115	mature rain forest	TRFO	TMFO
CO40 **(f)**	Kitina	Congo	−4.32	12.2	115	mature rain forest	TRFO	TMFO
CO38 **(f)**	Les Saras	Congo	−4.35	12.32	390	mature rain forest	TRFO	TMFO

Table 2. Plant functional types proposed for the Atlantic Central African areas under investigations for biome reconstructions and corresponding tropical ecosystems.

Codes	Plant functional types
Te1	wet tropical evergreen trees and shrubs
Te2	dry tropical evergreen trees and shrubs
Tr1	wet tropical raingreen trees and shrubs
Tr2	dry tropical raingreen trees and shrubs
Tr3	driest tropical raingreen trees and shrubs
TLw	wet tropical lianas
TLd	dry tropical lianas
THw	wet tropical herbs
THd	dry tropical herbs
g	grasses

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Table 3. Allocation of the pollen taxa derived from all sites listed in Table 1 to the plant functional types used for the biomes reconstructions.

Family	Taxa	Te1	Te2	Tr1	Tr2	Tr3	TLw	TLd	THw	THd	g
ACANTHACEAE	Acanthaceae undiff.	x	x	x	x	x	x		x	x	
ACANTHACEAE	Anisotes			x							
ACANTHACEAE	Asystasia gangetica-type								x		
ACANTHACEAE	Mendoncia						x				
ACANTHACEAE	Thomandersia	x	x	x							
AMARANTHACEAE	Achyranthes-type aspera									x	
AMARANTHACEAE	Cyathula-type								x	x	
AMARANTHACEAE	Sericostachys-type scandens						x				
AMARANTHACEAE/CHENOPODIACEAE	Amaranthaceae/Chenopodiaceae undiff.						x		x	x	
ANACARDIACEAE	Anacardiaceae undiff.	x	x	x	x	x	x				
ANACARDIACEAE	Antrocaryon-type	x	x	x							
ANACARDIACEAE	Antrocaryon-type klaineanum			x							
ANACARDIACEAE	Fegimanra				x						
ANACARDIACEAE	Lannea-type		x	x	x	x					
ANACARDIACEAE	Pseudospondias-type	x	x								
ANACARDIACEAE	Sorindeia-type	x	x	x							
ANACARDIACEAE	Trichoscypha-type	x	x	x			x				
ANISOPHYLLEACEAE	Anisophyllea	x									
ANISOPHYLLEACEAE	Anopyxis klaineana	x	x								
ANNONACEAE	Annonaceae undiff.	x	x	x	x	x	x				
APIACEAE	Apiaceae undiff.									x	
APOCYNACEAE	Alstonia-type	x	x								
APOCYNACEAE	Alstonia-type boonei	x	x								
APOCYNACEAE	Apocynaceae undiff.	x	x	x	x	x	x	x			
APOCYNACEAE	Funtumia-type		x	x							
APOCYNACEAE	Landolphia-type						x	x			
APOCYNACEAE	Oncinotis-type						x				
APOCYNACEAE	Picralima-type nitida	x	x	x							
APOCYNACEAE	Pleiocarpa			x							
APOCYNACEAE	Rauvolfia	x	x	x							
APOCYNACEAE	Tabernaemontana			x							
ASTERACEAE	Asteraceae undiff.				x	x				x	
ASTERACEAE	Vernonieae undiff.				x	x				x	
BALANITACEAE	Balanites	x	x	x							
BEGONIACEAE	Begonia								x		
BOMBACACEAE	Bombacaceae undiff.		x	x							
BOMBACACEAE	Ceiba pentandra		x	x							
BORAGINACEAE	Boraginaceae undiff.			x	x	x				x	
BORAGINACEAE	Cordia platythyrsa-type			x							
BORAGINACEAE	Ehretia			x	x	x					
BORAGINACEAE	Heliotropium indicum-type									x	
BORAGINACEAE	Heliotropium steudneri-type									x	
BURSERACEAE	Aucoumea klaineana	x									
BURSERACEAE	Burseraceae undiff.	x	x	x		x					
BURSERACEAE	Canarium-type	x	x	x							

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Table 3. Continued.

Family	Taxa	Te1	Te2	Tr1	Tr2	Tr3	TLw	TLd	THw	THd	g
BURSERACEAE	Commiphora edulis-type					x					
BURSERACEAE	Dacryodes-type	x	x								
BURSERACEAE	Santiria-type	x	x								
CAESALPINIACEAE	Anthonotha-type	x	x	x							
CAESALPINIACEAE	Berlinia-type	x	x	x							
CAESALPINIACEAE	Caesalpiniaceae undiff.	x	x				x				
CAESALPINIACEAE	Copaifera-type	x	x								
CAESALPINIACEAE	Crudia-type gabonensis	x									
CAESALPINIACEAE	Daniellia	x			x	x					
CAESALPINIACEAE	Detarium	x	x	x	x						
CAESALPINIACEAE	Dialium	x	x	x		x					
CAESALPINIACEAE	Dialium pachyphyllum-type	x									
CAESALPINIACEAE	Distemonanthus benthamianus-type	x	x	x							
CAESALPINIACEAE	Duparquetia orchidacea					x					
CAESALPINIACEAE	Gilbertiodendron-type	x									
CAESALPINIACEAE	Guibourtia	x									
CAESALPINIACEAE	Guibourtia demeusei-type	x									
CAESALPINIACEAE	Hylodendron gabunense	x	x	x							
CAESALPINIACEAE	Hymenostegia-type pellegrinii	x									
CAESALPINIACEAE	Tessmannia	x									
CAPPARIDACEAE	Capparidaceae undiff.	x	x	x	x	x				x	
CELASTRACEAE/HIPPOCRATEACEAE	Celastraceae/Hippocrateaceae undiff.	x	x	x	x	x	x	x			
CHRYSOBALANACEAE	Chrysobalanus-type icaco	x									
CHRYSOBALANACEAE	Maranthes-type	x	x	x							
CHRYSOBALANACEAE	Parinari-type	x	x	x	x	x					
CLUSIACEAE	Allanblackia	x									
CLUSIACEAE	Garcinia epunctata-type	x	x	x							
CLUSIACEAE	Mammea africana-type	x	x	x							
COMBRETACEAE	Combretaceae undiff.	x	x	x	x	x	x				
COMBRETACEAE	Terminalia-type	x	x	x	x	x					
COMBRETACEAE/MELASTOMATACEAE	Combretaceae/Melastomataceae undiff.	x	x	x	x	x	x		x	x	
CONNARACEAE	Cnestis	x	x	x			x				
CONVOLVULACEAE	Convolvulaceae undiff.						x		x	x	
CONVOLVULACEAE	Evolvulus-type									x	
CONVOLVULACEAE	Ipomoea-type								x	x	
CUCURBITACEAE	Coccinia									x	
CUCURBITACEAE	Cucurbitaceae undiff.								x	x	
CUCURBITACEAE	Luffa-type									x	
DILLENIACEAE	Tetracera	x	x	x			x				
DIOSCOREACEAE	Dioscorea								x	x	
DRACAENACEAE	Dracaena	x	x	x	x	x					
EBENACEAE	Diospyros	x	x								
EUPHORBIACEAE	Acalypha			x	x	x				x	
EUPHORBIACEAE	Alchornea	x	x	x							
EUPHORBIACEAE	Anthostema-type	x									
EUPHORBIACEAE	Antidesma-type	x	x	x	x	x					
EUPHORBIACEAE	Bridelia ferruginea-type			x	x	x					

Table 3. Continued.

Family	Taxa	Te1	Te2	Tr1	Tr2	Tr3	TLw	TLd	THw	THd	g
EUPHORBIACEAE	Bridelia micrantha-type	x	x	x	x	x					
EUPHORBIACEAE	Centroplacus glaucinus	x	x	x							
EUPHORBIACEAE	Cleistanthus-type polystachyus	x	x								
EUPHORBIACEAE	Croton-type			x							
EUPHORBIACEAE	Cyathogyne	x							x		
EUPHORBIACEAE	Cyttaranthus congolensis	x	x	x							
EUPHORBIACEAE	Discoglypremna caloneura	x	x	x							
EUPHORBIACEAE	Drypetes-type	x	x	x							
EUPHORBIACEAE	Elaeophorbia-type			x							
EUPHORBIACEAE	Euphorbia-type									x	
EUPHORBIACEAE	Euphorbiaceae undiff.	x	x	x	x	x	x		x	x	
EUPHORBIACEAE	Klaineanthus gaboniae	x									
EUPHORBIACEAE	Macaranga-type	x	x	x							
EUPHORBIACEAE	Mallotus-type oppositifolius	x	x	x							
EUPHORBIACEAE	Margaritaria discoidea	x	x	x							
EUPHORBIACEAE	Martretia quadricornis	x									
EUPHORBIACEAE	Phyllanthus-type	x	x	x	x	x			x	x	
EUPHORBIACEAE	Plagiostyles-type africana	x									
EUPHORBIACEAE	Tetrorchidium	x	x	x							
EUPHORBIACEAE	Uapaca	x	x	x							
EUPHORBIACEAE	Uapaca guineensis-type	x	x	x							
EUPHORBIACEAE	Uapaca heudelotii-type	x	x	x							
FABACEAE	Baphia-type	x	x	x							
FABACEAE	Aeschynomene baumii-type				x	x					
FABACEAE	Fabaceae undiff.	x	x	x	x	x	x	x	x	x	
FABACEAE	Indigofera									x	
FABACEAE	Pterocarpus-type	x	x	x	x	x					
FLACOURTIACEAE	Caloncoba-type	x	x	x	x	x					
FLACOURTIACEAE	Camptostylus	x	x	x							
FLACOURTIACEAE	Casearia	x	x	x	x						
FLACOURTIACEAE	Flacourtiaceae undiff.	x	x	x	x	x					
FLACOURTIACEAE	Homalium	x	x	x							
FLACOURTIACEAE	Scottelia klaineana-type	x	x								
FLAGELLARIACEAE	Flagellaria							x			
HYMENOCARDIACEAE	Hymenocardia			x	x	x					
HYMENOCARDIACEAE	Hymenocardia ulmoides-type			x	x						
HYPERICACEAE	Harungana madagascariensis-type				x	x					
ICACINACEAE	Icacinaceae undiff.	x	x	x			x				
ICACINACEAE	Raphiostylis	x					x				
IRVINGIACEAE	Irvingia-type gabonensis	x	x	x							

Table 3. Continued.

Family	Taxa	Te1	Te2	Tr1	Tr2	Tr3	TLw	TLd	THw	THd	g
LAMIACEAE	Hoslundia-type opposita				x	x					
LAMIACEAE	Lamiaceae undiff.				x	x				x	
LECYTHIDACEAE	Petersianthus-type macrocarpus	x	x								
LEGUMINOSAE	Leguminosae undiff.	x	x	x	x	x	x	x	x	x	
LOGANIACEAE	Strychnos	x	x	x	x	x	x				
LORANTHACEAE	Loranthaceae undiff.	x	x	x	x	x					
MALPIGHIACEAE	Acridocarpus			x	x	x	x	x			
MELASTOMATACEAE	Melastomataceae undiff.	x	x	x	x	x			x	x	
MELIACEAE	Carapa-type procera	x	x	x							
MELIACEAE	Entandrophragma-type	x	x	x							
MELIACEAE	Khaya-type	x	x	x							
MELIACEAE	Meliaceae undiff.	x	x	x							
MELIACEAE	Trichilia-type	x	x	x							
MENISPERMACEAE	Menispermaceae undiff.						x	x			
MENISPERMACEAE	Tiliacora-type funifera						x				
MIMOSACEAE	Acacia					x	x				
MIMOSACEAE	Albizia-type			x	x	x					
MIMOSACEAE	Calpocalyx-type	x									
MIMOSACEAE	Calpocalyx-type letestui	x									
MIMOSACEAE	Cylicodiscus-type gabunensis	x									
MIMOSACEAE	Entada-type				x	x	x	x			
MIMOSACEAE	Mimosaceae undiff.	x	x	x	x	x	x	x			
MIMOSACEAE	Parkia			x	x	x					
MIMOSACEAE	Pentaclethra macrophylla	x	x	x							
MIMOSACEAE	Pentaclethra-type eetveldeana	x	x	x							
MIMOSACEAE	Piptadeniastrum-type africanum	x	x	x							
MIMOSACEAE	Tetrapleura tetraptera-type	x	x	x							
MONOCOTYLEDONEAE	Monocotyledoneae undiff.								x	x	
MORACEAE	Antiaris-type toxicaria	x	x	x							
MORACEAE	Dorstenia-type								x		
MORACEAE	Ficus	x	x	x	x	x	x				
MORACEAE	Milicia-type excelsa	x	x	x							
MORACEAE	Moraceae undiff.	x	x	x	x	x	x				
MORACEAE	Myrianthus-type arboreus		x	x							
MORACEAE	Treculia	x	x	x							
MORACEAE	Trilepisium-type madagascariensis			x							
MYRISTICACEAE	Coelocaryon	x									
MYRISTICACEAE	Pycnanthus angolensis-type	x	x	x							
MYRISTICACEAE	Scyphocephalium	x									
MYRISTICACEAE	Staudtia kamerunensis	x	x	x							

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Table 3. Continued.

Family	Taxa	Te1	Te2	Tr1	Tr2	Tr3	TLw	TLd	THw	THd	g
MYRTACEAE	Syzygium-type	x	x	x	x	x					
OCHNACEAE	Campylospermum	x	x	x							
OCHNACEAE	Lophira alata-type	x									
OLACACEAE	Coula edulis	x									
OLACACEAE	Heisteria	x	x	x							
OLACACEAE	Olax	x	x	x							
OLACACEAE	Strombosia	x	x								
OLACACEAE	Strombosia scheffleri-type	x	x								
OLACACEAE	Strombosiopsis tetrandra	x									
PALMAE	Borassus-type aethiopum					x					
PALMAE	Podococcus barteri	x									
PALMAE	Sclerosperma	x									
PANDACEAE	Microdesmis	x	x	x							
POACEAE	Poaceae undiff.										x
RANUNCULACEAE	Clematis-type						x	x			
RHAMNACEAE	Rhamnaceae undiff.	x	x	x	x	x	x				
RUBIACEAE	Aidia-type	x									
RUBIACEAE	Aidia-type micrantha	x									
RUBIACEAE	Crossopteryx febrifuga				x	x					
RUBIACEAE	Hallea-type	x									
RUBIACEAE	Hallea-type rubrostipulata	x									
RUBIACEAE	Hymenodictyon-type floribundum				x	x					
RUBIACEAE	Keetia-type gueinzii			x	x	x	x	x			
RUBIACEAE	Macrosphyra-type					x		x			
RUBIACEAE	Morinda			x	x	x					
RUBIACEAE	Nauclea-type	x	x	x	x	x					
RUBIACEAE	Oldenlandia-type									x	
RUBIACEAE	Oligocodon-type cuniliffeae						x				
RUBIACEAE	Pausinystalia-type macroceras	x	x								
RUBIACEAE	Psychotria	x	x	x							
RUBIACEAE	Psydrax-type schimperiana	x									
RUBIACEAE	Psydrax-type subcordata	x									
RUBIACEAE	Rubiaceae undiff.	x	x	x	x	x	x	x	x	x	
RUBIACEAE	Sherbournia bignoniiflora-type						x				
RUBIACEAE	Spermacoce-type									x	
RUBIACEAE	Uncaria-type africana						x				
RUTACEAE	Rutaceae undiff.	x	x	x			x				

Table 3. Continued.

Family	Taxa	Te1	Te2	Tr1	Tr2	Tr3	TLw	TLd	THw	THd	g
RUTACEAE	Vepris-type	x	x	x							
RUTACEAE	Zanthoxylum-type		x	x			x				
SAPINDACEAE	Allophylus	x	x	x	x	x	x				
SAPINDACEAE	Aphania-type senegalensis	x	x	x							
SAPINDACEAE	Blighia	x	x	x	x	x					
SAPINDACEAE	Cardiospermum						x	x			
SAPINDACEAE	Chytranthus-type	x									
SAPINDACEAE	Dodonaea				x						
SAPINDACEAE	Eriocoelum	x									
SAPINDACEAE	Ganophyllum-type giganteum		x	x							
SAPINDACEAE	Laccodiscus	x									
SAPINDACEAE	Lecaniodiscus-type			x							
SAPINDACEAE	Pancovia-type	x									
SAPINDACEAE	Placodiscus	x					x				
SAPINDACEAE	Sapindaceae undiff.	x	x	x	x	x	x	x			
SAPOTACEAE	Sapotaceae undiff.	x	x	x							
SOLANACEAE	Solanum-type									x	
STERCULIACEAE	Cola cordifolia-type		x	x							
STERCULIACEAE	Mansonia altissima-type			x							
STERCULIACEAE	Nesogordonia			x							
STERCULIACEAE	Sterculiaceae undiff.		x	x	x	x					
STERCULIACEAE	Sterculia-type		x	x	x	x					
STERCULIACEAE	Triplochiton scleroxylon-type			x							
THYMELAEACEAE	Thymelaeaceae undiff.	x	x	x	x		x				
TILIACEAE	Grewia-type	x	x	x	x	x	x				
TILIACEAE	Tiliaceae undiff.	x	x	x	x	x	x			x	
TILIACEAE	Triumfetta-type									x	
ULMACEAE	Celtis		x	x							
ULMACEAE	Chaetacme aristata			x							
ULMACEAE	Holoptelea grandis			x							
ULMACEAE	Trema-type orientalis	x	x	x	x	x					
ULMACEAE	Ulmaceae undiff.	x	x	x	x	x					
URTICACEAE	Urticaceae undiff.						x		x		
VERBENACEAE	Vitex-type			x	x	x					
VITACEAE	Cissus quadrangularis-type									x	
VITACEAE	Vitaceae undiff.						x	x	x	x	

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Table 4. Atlantic Central African Biomes and their characteristic plant functional types (abbreviations for PFTs as in Table 2).

Codes	Biomes	Plant functional types
TRFO	tropical rain forest	Te1, Te2, TLw, THw
TSFO	tropical seasonal forest	Te2, Tr1, TLw, THw
TDFO	tropical dry forest	Tr2, TLd, THd, g
SAV	savanna	Tr3, TLd, THd, g

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Table 5. Plant functional types proposed for the Atlantic Central African areas under investigation for dynamic reconstructions.

Codes	Plant functional types
Tma	tropical mature forest trees and shrubs
Lma	tropical mature forest lianas
Hma	tropical mature forest herbs
Tosf	tropical old secondary forest trees and shrubs
Tysf	tropical young secondary forest trees and shrubs
Lsf	tropical secondary forest lianas
Hsf	tropical secondary forest herbs
Tpi	tropical forest pioneer trees and shrubs (regrowth)
Lpi	tropical forest pioneer lianas (regrowth)
Hpi	tropical forest pioneer herbs (regrowth)
Tr3	tropical savanna trees and shrubs
Lr3	tropical savanna lianas
Hr3	tropical savanna herbs
g	grasses

Table 6. Allocation of the pollen taxa derived from all sites listed in Table 1 to the plant functional types used in dynamics reconstructions.

Family	Taxon	Tma	Lma	Hma	Tosf	Tysf	Lsf	Hsf	Tpi	Lpi	Hpi	Tr3	Lr3	Hr3	g
ACANTHACEAE	Acanthaceae undiff.	x	x	x	x	x	x	x	x	x	x			x	
ACANTHACEAE	Anisotes	x													
ACANTHACEAE	Asystasia gangetica-type			x							x				
ACANTHACEAE	Mendoncia		x												
ACANTHACEAE	Thomandersia	x													
AMARANTHACEAE	Achyranthes-type aspera										x			x	
AMARANTHACEAE	Cyathula-type			x				x			x			x	
AMARANTHACEAE	Sericostachys-type scandens		x				x			x					
AMARANTHACEAE/CHENOPODIACEAE	Amaranthaceae/Chenopodiaceae undiff.		x	x			x	x		x	x			x	
ANACARDIACEAE	Anacardiaceae undiff.	x	x		x	x			x			x			
ANACARDIACEAE	Antrocaryon-type	x			x										
ANACARDIACEAE	Antrocaryon-type klaineanum	x			x										
ANACARDIACEAE	Fegimanra								x			x			
ANACARDIACEAE	Lannea-type	x			x	x			x			x			
ANACARDIACEAE	Pseudospondias-type	x													
ANACARDIACEAE	Sorindeia-type	x													
ANACARDIACEAE	Trichoscypha-type	x	x												
ANISOPHYLLEACEAE	Anisophyllea	x			x	x			x						
ANISOPHYLLEACEAE	Anopyxis klaineana	x			x										
ANNONACEAE	Annonaceae undiff.	x	x		x	x	x		x						
APIACEAE	Apiaceae undiff.										x			x	
APOCYNACEAE	Alstonia-type	x			x										
APOCYNACEAE	Alstonia-type boonei	x			x										
APOCYNACEAE	Apocynaceae undiff.	x	x		x	x	x		x	x		x	x		
APOCYNACEAE	Funtumia-type	x			x	x									
APOCYNACEAE	Landolphia-type		x				x			x			x		
APOCYNACEAE	Oncinotis-type		x				x			x					
APOCYNACEAE	Picralima-type nitida	x													
APOCYNACEAE	Pleiocarpa	x													
APOCYNACEAE	Rauvolfia	x			x	x									
APOCYNACEAE	Tabernaemontana	x			x	x			x						
ARALIACEAE	Polyscias fulva-type				x	x			x						
ASTERACEAE	Asteraceae undiff.											x		x	
ASTERACEAE	Vernonieae undiff.				x	x			x		x	x		x	
BALANITACEAE	Balanites	x													
BEGONIACEAE	Begonia			x											
BOMBACACEAE	Bombacaceae undiff.	x			x										
BOMBACACEAE	Ceiba pentandra	x			x										
BORAGINACEAE	Boraginaceae undiff.	x			x	x			x		x	x		x	
BORAGINACEAE	Cordia platythyrsa-type	x			x	x			x						
BORAGINACEAE	Ehretia	x			x	x						x			
BORAGINACEAE	Heliotropium indicum-type										x			x	
BORAGINACEAE	Heliotropium steudneri-type													x	
BURSERACEAE	Aucoumea klaineana	x			x	x			x						
BURSERACEAE	Burseraceae undiff.	x			x							x			
BURSERACEAE	Canarium-type	x			x										
BURSERACEAE	Commiphora edulis-type											x			
BURSERACEAE	Dacryodes-type	x													
BURSERACEAE	Santiria-type	x													
CAESALPINIACEAE	Anthonotha-type	x													
CAESALPINIACEAE	Berlinia-type	x													
CAESALPINIACEAE	Caesalpiniaceae undiff.	x	x		x	x			x		x	x		x	
CAESALPINIACEAE	Copaifera-type	x													
CAESALPINIACEAE	Crudia-type gabonensis	x													

Table 6. Continued.

Family	Taxon	Tma	Lma	Hma	Tosf	Tysf	Lsf	Hsf	Tpi	Lpi	Hpi	Tr3	Lr3	Hr3	g
CAESALPINIACEAE	Daniellia	x			x	x						x			
CAESALPINIACEAE	Detarium	x										x			
CAESALPINIACEAE	Dialium	x										x			
CAESALPINIACEAE	Dialium pachyphyllum-type	x													
CAESALPINIACEAE	Distemonanthus benthamianus-type	x			x										
CAESALPINIACEAE	Duparquetia orchidacea								x			x			
CAESALPINIACEAE	Gilbertiodendron-type	x													
CAESALPINIACEAE	Guibourtia	x													
CAESALPINIACEAE	Guibourtia demeusei-type	x													
CAESALPINIACEAE	Hylodendron gabunense	x			x										
CAESALPINIACEAE	Hymenostegia-type pellegrinii	x													
CAESALPINIACEAE	Tessmannia	x													
CAPPARIDACEAE	Capparidaceae undiff.	x	x		x	x	x	x			x	x	x	x	
CELASTRACEAE/HIPPOCRATEACEAE	Celastraceae/Hippocrateaceae undiff.	x	x		x	x	x		x	x		x	x		
CHRYSOBALANACEAE	Chrysobalanus-type icaco	x													
CHRYSOBALANACEAE	Maranthes-type	x													
CHRYSOBALANACEAE	Parinari-type	x										x			
CLUSIACEAE	Allanblackia	x													
CLUSIACEAE	Garcinia epunctata-type	x													
CLUSIACEAE	Mammea africana-type	x													
COMBRETACEAE	Combretaceae undiff.	x	x		x	x	x		x	x		x			
COMBRETACEAE	Terminalia-type	x			x							x			
COMBRETACEAE/MELASTOMATACEAE	Combretaceae/Melastomataceae undiff.	x	x	x	x	x	x	x	x	x	x	x		x	
CONNARACEAE	Cnestis	x	x			x	x			x					
CONVOLVULACEAE	Convolvulaceae undiff.		x	x				x			x			x	
CONVOLVULACEAE	Evolvulus-type													x	
CONVOLVULACEAE	Ipomoea-type			x				x			x			x	
CUCURBITACEAE	Coccinia							x			x			x	
CUCURBITACEAE	Cucurbitaceae undiff.			x				x			x			x	
CUCURBITACEAE	Luffa-type										x			x	
DILLENIACEAE	Tetracera	x	x		x	x	x		x	x					
DIOSCOREACEAE	Dioscorea			x				x			x			x	
DRACAENACEAE	Dracaena	x			x	x			x			x			
EBENACEAE	Diospyros	x													
EUPHORBIACEAE	Acalypha	x			x	x			x		x	x		x	
EUPHORBIACEAE	Alchornea	x			x	x			x						
EUPHORBIACEAE	Anthostema-type	x													
EUPHORBIACEAE	Antidesma-type	x			x	x			x			x			
EUPHORBIACEAE	Bridelia ferruginea-type	x			x	x			x			x			
EUPHORBIACEAE	Bridelia micrantha-type	x			x	x			x			x			
EUPHORBIACEAE	Centroplacus glaucinus	x			x										
EUPHORBIACEAE	Cleistanthus-type polystachyus	x													
EUPHORBIACEAE	Croton-type	x			x	x			x						
EUPHORBIACEAE	Cyathogyne	x		x											
EUPHORBIACEAE	Cyttaranthus congolensis	x													
EUPHORBIACEAE	Discoglypremna caloneura	x			x										
EUPHORBIACEAE	Drypetes-type	x													
EUPHORBIACEAE	Elaeophorbia-type	x			x	x			x						
EUPHORBIACEAE	Euphorbia-type										x			x	
EUPHORBIACEAE	Euphorbiaceae undiff.	x	x	x	x	x		x	x		x	x		x	
EUPHORBIACEAE	Klaineanthus gaboniae	x													
EUPHORBIACEAE	Macaranga-type	x			x	x			x						
EUPHORBIACEAE	Mallotus-type oppositifolius	x			x	x			x						
EUPHORBIACEAE	Margaritaria discoidea	x			x	x			x						
EUPHORBIACEAE	Martretia quadricornis	x													

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Table 6. Continued.

Family	Taxon	Tma	Lma	Hma	Tosf	Tysf	Lsf	Hsf	Tpi	Lpi	Hpi	Tr3	Lr3	Hr3	g
EUPHORBIACEAE	Phyllanthus-type	x		x	x	x		x	x		x	x		x	
EUPHORBIACEAE	Plagiostyles-type africana	x			x	x									
EUPHORBIACEAE	Tetrorchidium	x			x	x			x						
EUPHORBIACEAE	Uapaca	x			x										
EUPHORBIACEAE	Uapaca guineensis-type	x			x										
EUPHORBIACEAE	Uapaca heudelotii-type	x													
FABACEAE	Aeschynomene baumii-type											x			
FABACEAE	Baphia-type	x			x	x			x						
FABACEAE	Fabaceae undiff.	x	x		x	x	x	x	x	x	x	x	x	x	
FABACEAE	Indigofera										x			x	
FABACEAE	Pterocarpus-type	x										x			
FLACOURTIACEAE	Caloncoba-type	x			x	x			x			x			
FLACOURTIACEAE	Camptostylus	x													
FLACOURTIACEAE	Casearia	x			x	x						x			
FLACOURTIACEAE	Flacourtiaceae undiff.	x			x	x			x			x			
FLACOURTIACEAE	Homalium	x			x	x			x						
FLACOURTIACEAE	Scottelia klaineana-type	x			x										
FLAGELLARIACEAE	Flagellaria									x			x		
HYMENOCARDIACEAE	Hymenocardia	x							x			x			
HYMENOCARDIACEAE	Hymenocardia ulmoides-type	x							x			x			
HYPERICACEAE	Harungana madagascariensis-type					x			x			x			
HYPERICACEAE	Vismia guineensis					x			x						
ICACINACEAE	Icacinaceae undiff.	x	x		x	x	x		x	x					
ICACINACEAE	Raphiostylis	x	x												
IRVINGIACEAE	Irvingia-type gabonensis	x			x										
LAMIACEAE	Hoslundia-type opposita								x			x			
LAMIACEAE	Lamiaceae undiff.								x		x	x		x	
LECYTHIDACEAE	Petersianthus-type macrocarpus	x			x										
LEGUMINOSAE	Leguminosae undiff.	x	x		x	x	x	x	x	x	x	x	x	x	
LOGANIACEAE	Anthocleista					x			x			x			
LOGANIACEAE	Strychnos	x	x		x	x	x		x			x			
LORANTHACEAE	Loranthaceae undiff.	x				x			x			x			
MALPIGHIACEAE	Acridocarpus	x	x		x	x	x		x			x	x		
MELASTOMATACEAE	Melastomataceae undiff.	x		x	x	x		x	x		x	x		x	
MELIACEAE	Carapa-type procera	x			x										
MELIACEAE	Entandrophragma-type	x			x										
MELIACEAE	Khaya-type	x			x										
MELIACEAE	Meliaceae undiff.	x			x	x			x						
MELIACEAE	Trichilia-type	x			x										
MENISPERMACEAE	Menispermaceae undiff.		x				x			x			x		
MENISPERMACEAE	Tiliacora-type funifera		x				x			x					
MIMOSACEAE	Acacia		x				x			x		x			
MIMOSACEAE	Albizia-type				x	x			x			x			
MIMOSACEAE	Calpocalyx-type	x													
MIMOSACEAE	Calpocalyx-type letestui	x													
MIMOSACEAE	Cylicodiscus-type gabunensis	x													
MIMOSACEAE	Entada-type		x				x		x	x		x	x		
MIMOSACEAE	Mimosaceae undiff.	x	x		x	x	x		x	x		x	x		

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Table 6. Continued.

Family	Taxon	Tma	Lma	Hma	Tosf	Tysf	Lsf	Hsf	Tpi	Lpi	Hpi	Tr3	Lr3	Hr3	g
MIMOSACEAE	Parkia	x										x			
MIMOSACEAE	Pentaclethra macrophylla	x			x	x									
MIMOSACEAE	Pentaclethra-type eetveldeana	x			x	x									
MIMOSACEAE	Piptadeniastrum-type africanum	x			x										
MIMOSACEAE	Tetrapleura tetraptera-type	x			x	x			x						
MONOCOTYLEDONEAE	Monocotyledoneae undiff.			x				x			x			x	
MORACEAE	Antiaris-type toxicaria	x													
MORACEAE	Dorstenia-type			x				x							
MORACEAE	Ficus	x	x		x	x	x		x			x			
MORACEAE	Milicia-type excelsa	x			x										
MORACEAE	Moraceae undif.	x	x		x	x			x			x			
MORACEAE	Musanga-type					x			x						
MORACEAE	Myrianthus-type arboreus	x			x	x			x						
MORACEAE	Treculia	x													
MORACEAE	Trilepisium-type madagascariensis	x			x										
MYRISTICACEAE	Coelocaryon	x													
MYRISTICACEAE	Pycnanthus angolensis-type	x			x										
MYRISTICACEAE	Scyphocephalium	x													
MYRISTICACEAE	Staudtia kamerunensis	x													
MYRTACEAE	Syzygium-type	x			x	x			x			x			
OCHNACEAE	Campylospermum	x			x	x			x						
OCHNACEAE	Lophira alata-type	x			x	x			x						
OLACACEAE	Coula edulis	x													
OLACACEAE	Heisteria	x													
OLACACEAE	Olax	x													
OLACACEAE	Strombosia	x													
OLACACEAE	Strombosia scheffleri-type	x													
OLACACEAE	Strombosiopsis tetrandra	x													
PALMAE	Borassus-type aethiopum											x			
PALMAE	Elaeis guineensis				x	x			x						
PALMAE	Podococcus barteri	x													
PALMAE	Sclerosperma	x													
PANDACEAE	Microdesmis	x			x	x			x						
POACEAE	Poaceae undiff.														x
RANUNCULACEAE	Clematis-type									x			x		
RHAMNACEAE	Rhamnaceae undiff.	x	x		x	x	x		x	x		x			
RUBIACEAE	Aidia-type	x													
RUBIACEAE	Aidia-type micrantha	x													
RUBIACEAE	Crossopteryx febrifuga								x			x			
RUBIACEAE	Hallea-type	x													
RUBIACEAE	Hallea-type rubrostipulata	x													
RUBIACEAE	Hymenodictyon-type floribundum											x			
RUBIACEAE	Keetia-type gueinzii	x	x									x	x		
RUBIACEAE	Macrosphyra-type											x	x		
RUBIACEAE	Morinda	x										x			
RUBIACEAE	Nauclea-type	x			x	x			x			x			
RUBIACEAE	Oldenlandia-type										x			x	
RUBIACEAE	Oligocodon-type cuniliffeae		x												

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Table 6. Continued.

Family	Taxon	Tma	Lma	Hma	Tosf	Tysf	Lsf	Hsf	Tpi	Lpi	Hpi	Tr3	Lr3	Hr3	g
RUBIACEAE	Pausinystalia-type macroceras	x													
RUBIACEAE	Psychotria	x			x	x			x						
RUBIACEAE	Psydrax-type schimperiana	x													
RUBIACEAE	Psydrax-type subcordata	x													
RUBIACEAE	Rubiaceae undiff.	x	x	x	x	x	x	x	x	x	x	x	x	x	
RUBIACEAE	Sherbournia bignoniiflora-type		x												
RUBIACEAE	Spermacoce-type													x	
RUBIACEAE	Uncaria-type africana		x												
RUTACEAE	Rutaceae undiff.	x	x		x	x	x		x						
RUTACEAE	Vepris-type	x													
RUTACEAE	Zanthoxylum-type	x	x		x	x	x		x						
SAPINDACEAE	Allophylus	x	x		x	x	x		x			x			
SAPINDACEAE	Aphania-type senegalensis	x													
SAPINDACEAE	Blighia	x										x			
SAPINDACEAE	Cardiospermum		x				x			x			x		
SAPINDACEAE	Chytranthus-type	x													
SAPINDACEAE	Dodonaea								x			x			
SAPINDACEAE	Eriocoelum	x													
SAPINDACEAE	Ganophyllum-type giganteum	x													
SAPINDACEAE	Laccodiscus	x													
SAPINDACEAE	Lecaniodiscus-type	x													
SAPINDACEAE	Pancovia-type	x													
SAPINDACEAE	Placodiscus	x	x			x									
SAPINDACEAE	Sapindaceae undiff.	x	x		x	x	x		x	x		x	x		
SAPOTACEAE	Sapotaceae undiff.	x													
SOLANACEAE	Solanum-type													x	
STERCULIACEAE	Cola cordifolia-type	x													
STERCULIACEAE	Mansonia altissima-type	x													
STERCULIACEAE	Nesogordonia	x													
STERCULIACEAE	Sterculiaceae undiff.	x			x	x			x			x			
STERCULIACEAE	Sterculia-type	x			x	x			x			x			
STERCULIACEAE	Triplochiton scleroxylon-type	x			x										
THYMELAEACEAE	Thymelaeaceae undiff.	x	x		x	x			x	x		x			
TILIACEAE	Grewia-type	x	x		x	x			x			x			
TILIACEAE	Tiliaceae undiff.	x	x		x	x	x		x			x		x	
TILIACEAE	Triumfetta-type										x			x	
ULMACEAE	Celtis	x			x	x									
ULMACEAE	Chaetacme aristata	x			x	x			x						
ULMACEAE	Holoptelea grandis	x			x										
ULMACEAE	Trema-type orientalis	x			x	x			x			x			
ULMACEAE	Ulmaceae undiff.	x			x	x			x			x			
URTICACEAE	Urticaceae undiff.		x	x			x	x		x	x				
VERBENACEAE	Vitex-type	x			x	x			x			x			
VITACEAE	Cissus quadrangularis-type										x			x	
VITACEAE	Vitaceae undiff.		x				x	x		x	x		x	x	

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Atlantic Central African biomes and forest succession stages

J. Lebamba et al.

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Table 7. Atlantic Central African succession stages and their characteristic plant functional types (abbreviations for PFTs as in Table 4).

Codes	Stages	Plant functional types
TMFO	tropical mature forest	Tma, Lma, Hma
TOSF	tropical old secondary forest	Tosf, Lsf, Hsf
TYSF	tropical young secondary forest	Tysf, Lsf, Hsf
TFRE	tropical forest regrowth	Tpi, Lpi, Hpi
SAVA	savanna	Tr3,Lr3, Hr3, g

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Table 8. Numerical comparison between pollen-derived (p) and observed (o) biomes at each sampled site.

	TRFO (p)	TSFO (p)	TDFO (p)	SAVA (p)	Potential biomes correctly reconstructed (%)
TRFO (o)	*87+43*	3	0	0	97.7
TSFO (o)	0	*45*	0	1	97.8
TDFO (o)	0	0	0	0	
SAVA (o)	0	1	0	*19*	95

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Table 9. Numerical comparison between pollen-derived biomes (p) and the main Atlantic Central African vegetation types defined by White (1983) (White's vegetation types: 1a – wetter types of Guineo-Congolian rain forest; 2 – drier types of Guineo-Congolian rain forest; 11a – mosaic of rain forest and secondary grassland).

	TRFO (p)	TSFO (p)	SAVA (p)
1a	*65*	3	0
1a/2 transition	*5*	*4*	0
2	43 (Congo)	*8*	*1*
11a	*17*	*34*	*19*

Table 10. Numerical comparison between pollen-derived (p) and observed (o) succession stages at each sampled site.

(a)	TMFO (p)	TOSF (p)	TYSF (p)	TFRE (p)	SAVA (p)	Potential stages correctly reconstructed (%)
TMFO (o)	*148*	4	0	0	0	97.4
TOSF (o)	3	*6*	0	0	0	66.6
TYSF (o)	3	9	*1*	0	0	7.6
TFRE (o)	1	1	1	*0*	2	0
SAVA (o)	0	1	0	0	*19*	95

(b)	TMFO (p)	TSFE (p)	SAVA (p)	Potential stages correctly reconstructed (%)
TMFO (o)	*148*	4	0	97.4
TSFE (o) (TOSF+TYSF+TFRE)	7	*18*	2	66.6
SAVA (o)	0	1	*19*	95

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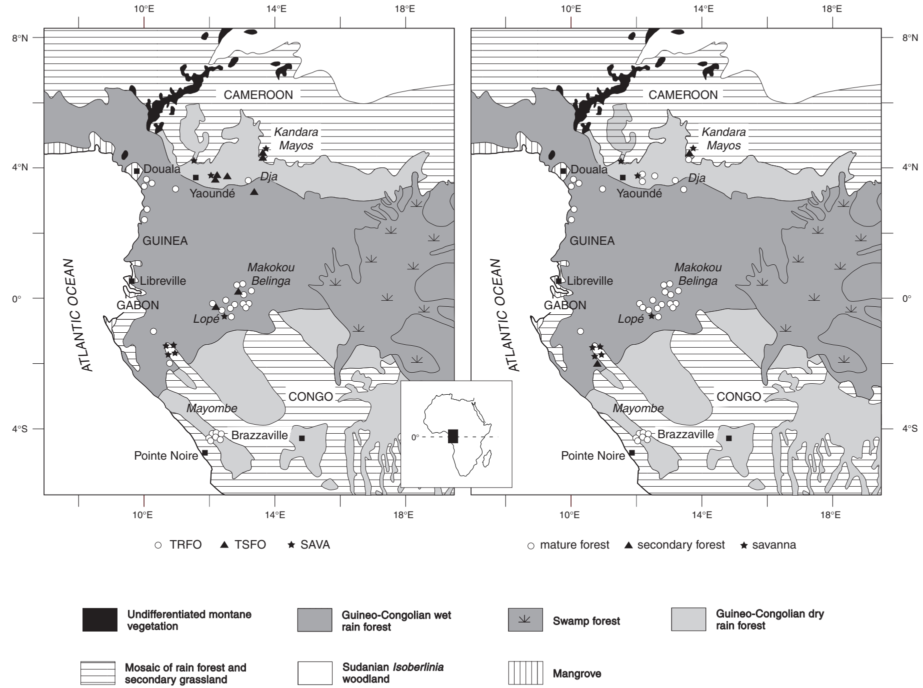

Fig. 1. Location of modern pollen samples in Central Africa according to White's vegetation map. **(a)** Reconstructed potential biomes (TRFO: Tropical rain forest; TSFO: Tropical seasonal forest; SAVA: Savanna), **(b)** Reconstructed succession stages of forest regeneration.

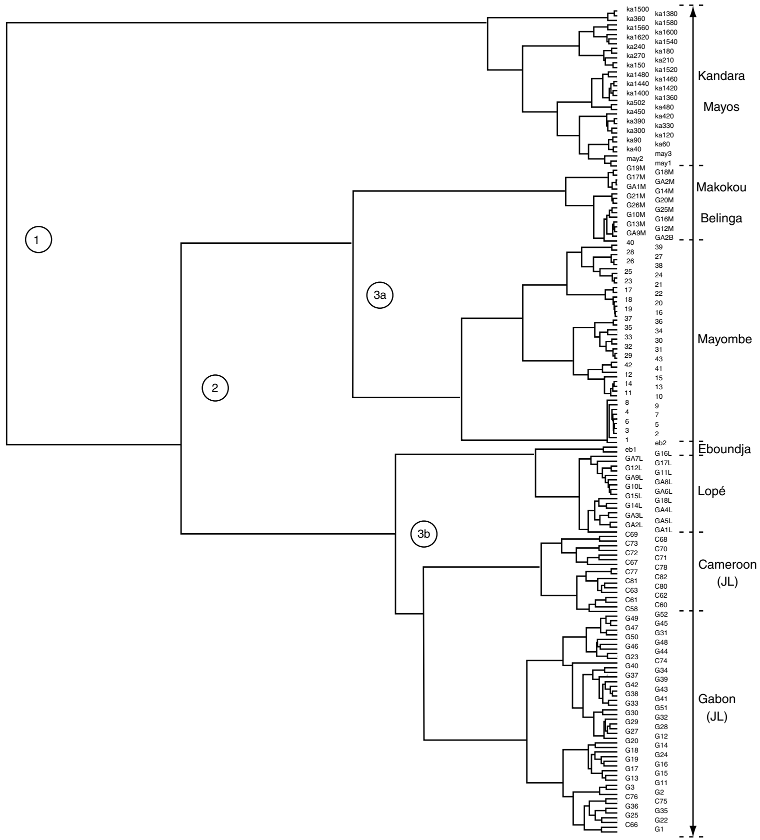

Fig. 2. Cluster analysis of the 176 modern pollen spectra from Atlantic Central African forest (JL: Lebamba et al., 2009).

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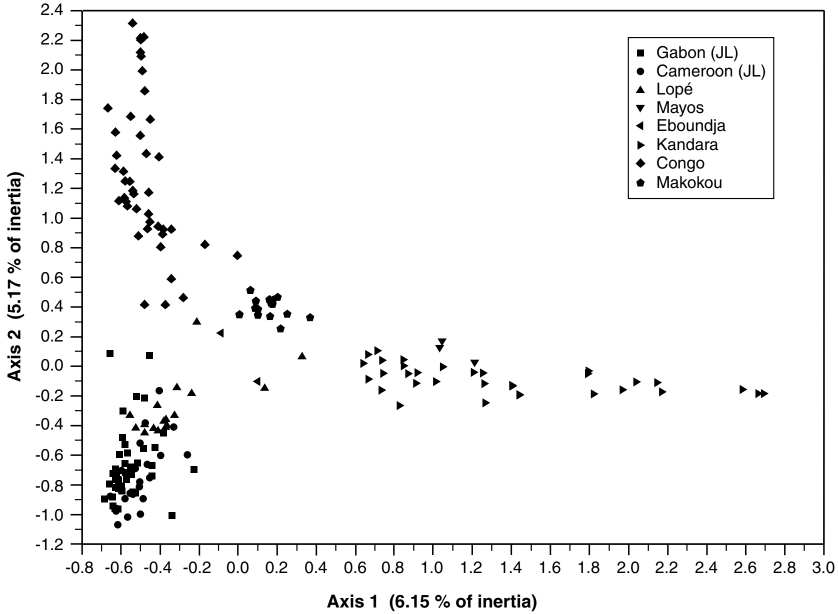

Fig. 3. Correspondence analysis with respect to CA axes 1 and 2 of the 176 modern pollen spectra from Atlantic Central African forest (JL: Lebamba et al., 2009).