

M. G. P. Tchouto<sup>1\*</sup>,  
J. J. F. E. de Wilde<sup>2</sup>,  
W. F. de Boer<sup>3</sup>,  
L. J. G. van der Maesen<sup>2</sup> &  
A. M. Cleef<sup>4</sup>

<sup>1</sup>Ecole Nationale des Eaux et  
Forêts, BP 69 Mbalmayo,  
Cameroon

<sup>2</sup>Biosystematics Group,  
Wageningen University,  
Generaal Foulkesweg 37, 6703  
BL, Wageningen,  
the Netherlands

<sup>3</sup>Resource Ecology Group,  
Wageningen University,  
Droevendaalsesteeg 3a,  
6708PB Wageningen,  
the Netherlands

<sup>4</sup>Institute for Biodiversity and  
Ecosystem Dynamics,  
Palynology and  
Palaeo/Actuo-ecology,  
University of Amsterdam,  
Kruislaan 318, 1090 GB  
Amsterdam, the Netherlands

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## Bio-indicator species and Central African rain forest refuges in the Campo-Ma'an area, Cameroon

**Abstract** This study aims to examine the geographical position of late Pleistocene forest refuges in the tropical lowland rain forest in southern Cameroon by analysing the distribution of 178 selected bio-indicator species. We studied the distribution patterns of these species, such as strict and narrow endemics, as well as a number of well-known slow dispersal species, to test whether the entire Campo-Ma'an rain forest was part of a late Pleistocene rain forest refuge. Special attention was given to taxa with slow dispersal abilities such as those within *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia*, *Rinorea* spp., Caesalpinioideae and Rubiaceae. Species that occur in other rain forest refuges and that reach their northern limit of distribution in the Campo-Ma'an area were also included in the analysis. The distribution patterns of the 178 bio-indicator species were displayed in several maps. There was a high concentration of bio-indicator species in the lowland evergreen forest rich in Caesalpinioideae, and in the submontane forests in the National Park and in the Kribi-Campo-Mvini area, and a relatively low concentration of these species in the Ma'an area. Similar patterns were observed for the distribution of strict and narrow endemic species, *Begonia*, Caesalpinioideae and Rubiaceae. Most of these species were particularly frequent on higher altitudes in the lowland rain forests, especially along the upper slopes of hills near the top, or along riverbanks. There was a relatively even distribution of bio-indicator species from the Rubiaceae family within the Campo-Ma'an area. The distribution of *Begonia* showed that some species were frequent in mountainous areas, along slopes near hilltops in the lowland forest and others were located along small streams in the lowland forest. As for the Caesalps, their distribution showed a high concentration of species in the evergreen forest rich in Caesalpinioideae with a decrease in number in the coastal forest and the mixed evergreen and semi-deciduous forest. As for the *Rinorea*, many indicator species were mostly confined to the lowland forest, particularly in the evergreen forest rich in Caesalpinioideae. These species distribution patterns corroborate the view of many authors who argue that during glacial times forests were restricted to the upper slopes of hills, upper altitudinal zones in the lowland forests, or along riverbanks. Our findings, therefore, suggest that the Campo-Ma'an area falls within a series of postulated rain forest refuges in Central Africa as proposed by previous authors.

**Key words** Biodiversity, Campo-Ma'an, conservation, dispersal, endemic species, plant diversity, Pleistocene, species distribution, tropical rain forest

\*Corresponding author. Email: peguy2000@yahoo.com

## Introduction

Although there is much debate about the Pleistocene forest refuge theory in South America (van der Hammen & Hooghiemstra, 2000; Colinvaux *et al.*, 2001; Haffer & Prance, 2001), investigators generally agree that during the glacial periods limited and isolated patches of tropical rain forest (tropical rain forest refuges) persisted and survived the unfavourable climatic conditions in Africa. In Central Africa, a number of these so-called Pleistocene forest refuges are found in Gabon and Cameroon, amongst them the Campo-Ma'an area (Aubréville, 1962; White, 1979, 1983; Hamilton, 1982; Maley, 1987; Sosef, 1994). However, there is a disagreement about the exact location of these refuges within these areas (Robbrecht, 1996; Sosef, 1996; Leal, 2001). This is probably because tropical rain forest refuges are often studied on a large scale (Maley, 1987, 1989). Understanding the present-day location of tropical rain forest refuges requires the use of direct evidence or 'palaeo-evidence' such as palynological or palaeobotanical data, or indirect evidence, such as the distribution patterns of endemic and slow dispersal species, or genetic studies (Hardy *et al.*, 2003). More often, endemism and patterns in the distribution of slow dispersal taxa have been used to identify the location and extent of regional forest refuges (Rietkerk *et al.*, 1996; Robbrecht, 1996; Sosef, 1996; Achoundong, 2000). These studies interpreted locations with a high degree of endemism and plant diversity to coincide with former forest refuge areas.

Bio-indicator species are usually defined as species whose status and ecology provide information on the overall condition of the ecosystem (Heywood & Watson, 1995). Therefore, refuge indicators should be ecologically discriminating with limited dispersal and colonisation abilities. Sosef (1994) argued that when such species are strictly limited to rain forest vegetation their present day distributions will coincide with the late Pleistocene refuges. In this study, the distribution patterns of strict and narrow endemic rain forest species (respectively endemic to the Campo-Ma'an, or south-western Cameroon), together with well-known slow dispersal taxa and species that reach their northern limit of distribution in the Campo-Ma'an area, were used to examine the geographical position of a postulated Pleistocene rain forest refuge in south-western Cameroon. Special attention was given to taxa with slow dispersal abilities such as those within *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia*, *Rinorea* spp., *Caesalpinioideae* and *Rubiaceae*.

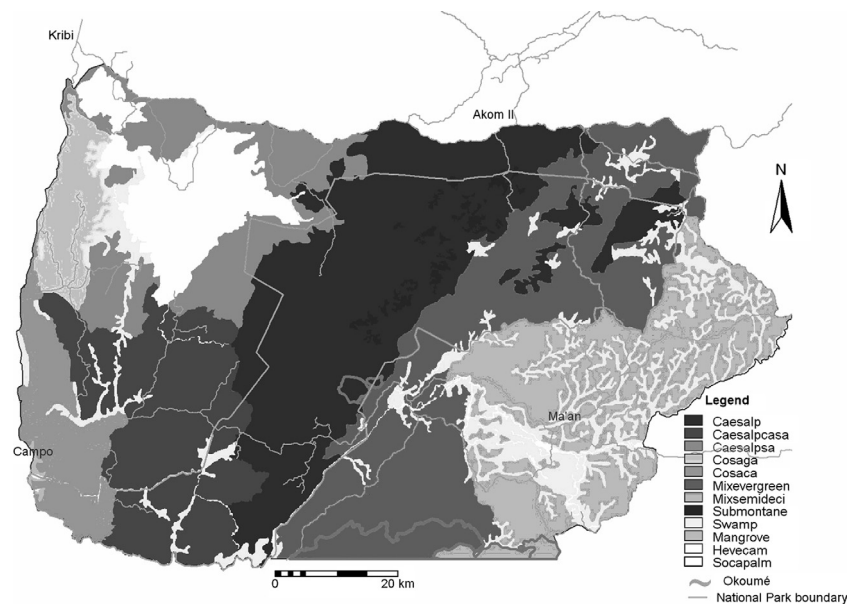
## Late Quaternary vegetation changes in Central Africa

Maley (1993) has identified four main climatic phases of the late Quaternary in Central Africa. The Maluekian (70 000–40 000 BP) corresponded to a relatively dry period marked by extensive forest retreat. The Njilian, lasting from 40 000–30 000 BP, was relatively wet, and was marked by a forest expansion. The Leopoldian (30 000–12 000 BP) was relatively dry and marked by a new expansion of open savannah environments. The Kibangian (12 000 BP to present) was rel-

atively wet until 3500 BP (Kibangian A), and was marked by a new phase of forest expansion. Later came another drier period from 3500 BP to present (Kibangian B) corresponding to the beginning of another savannah expansion in some parts of Central Africa. According to the refugium theory, Central African rain forest underwent a series of climatic fluctuations in the Pleistocene during which a considerable portion of the tropical lowland rain forest was repeatedly reduced to relatively small isolated patches, called forest refuges, due to unfavourable climatic conditions (Hamilton, 1982; White, 1993; Maley, 1989, 1990, 1996a, b, c). During the dry-out phases, some forest species were captured in these refuges, and at least some surviving species were not or hardly capable of migrating out of these again, due to their extremely low dispersal abilities (White, 1993).

Geological and palynological research of lake sediments from several sites has shown that 2500 BP the Central African forest experienced a catastrophic destruction that led to a major extension of the savannah (Maley & Brenac, 1998; Maley, 2002). Detailed pollen records from Lake Barombi Mbo in western Cameroon, lake Ossa in south Cameroon, Lake Kitinia in western Congo, Lakes Mboandong and Njupi in south Congo reveal the presence of pseudo-periods of about 2000–2500 BP for several tree taxa typical of mature undisturbed forest (Elenga *et al.*, 1994, 1996; Reynaud-Ferrera *et al.*, 1996). During this phase, the rainfall suddenly became more seasonal, reducing the moisture available for the vegetation, and therefore leading to a mass disappearance of mature forest tree species in several parts of Central Africa (Reynaud & Maley, 1994; Maley & Brenac, 1998; Maley, 1987, 2001). Reynaud and Maley (1994) argued that punctual climatic perturbations may have taken place in the 13th century followed by a phase with favourable climatic conditions from the 18th century onward that may have favoured the natural reforestation process that is being observed today. This was well illustrated in Cameroon and Gabon with the colonisation of savannah by the forest (Letouzey, 1968; White *et al.*, 2000).

Several climatological studies showed that in recent times the southern part of Cameroon has suffered from a series of climatic crises, marked by a severe decrease in rainfall that occurred repeatedly every 10–15 years, such as in 1973 and 1983 (Reynaud & Maley, 1994). In this region, the contrast of excess and deficit of rainfall is particularly pronounced in the Atlantic littoral zone (Letouzey 1968, 1985), where the coastal forest with *Lophira alata* and *Sacoglottis gabonensis* is found, more so than inland where the lowland evergreen rain forest rich in *Caesalpinioideae* is located. These past climatic changes must have had serious impacts on the vegetation patterns found in the area, since lowland *Caesalpinioideae* forests normally develop where the dry seasons do not exceed about 2 months, while semi-deciduous forests prevail when the dry season varies between 2–3 months (Reynaud & Maley, 1994). Therefore, closed evergreen rain forests are mainly found in areas with high precipitation ( $>2000 \text{ mm year}^{-1}$ ). Between 1500–2000 mm, the number of deciduous and semi-deciduous elements increase and below 1500 mm there is a relatively dry deciduous forest. The vegetation in the Campo-Ma'an area therefore varies from the lowland evergreen rain forest



**Figure 1** Vegetation map of the Campo-Ma'an area (Tchouto, 2004). Where Caesalp: Lowland evergreen forest rich in Caesalpinoideae; Caesalpcsa: Lowland evergreen forest rich in Caesalpinoideae with *Calpocalyx heitzii* and *Sacoglottis gabonensis*; Caesalpsa: Lowland evergreen forest rich in Caesalpinoideae and *Sacoglottis gabonensis*; Cosaga: Coastal forest with *Sacoglottis gabonensis*; Cosaca: Coastal forest with *Sacoglottis gabonensis* and *Calpocalyx heitzii*; Mixevergreen: Mixed evergreen and semi-deciduous forest with elements of evergreen forest predominant; Mixemideci: Mixed evergreen and semi-deciduous forest with semi-deciduous elements predominant; Submontane: Submontane forest on hill tops; Okoumé: small patches of Okoumé populations; Hevecam & Socapalm: agro-industrial plantations.

rich in Caesalpinoideae in the wetter Campo area to a mixed evergreen and semi-deciduous forest in the drier Ma'an area (Tchouto, 2004).

The past climatic oscillations presumably also resulted in fluctuations of the sea level along the Campo-Ma'an coastline. Oslisly (2001) argued that between 35 000–40 000 BP the coastline was at 40 m above the present sea level and the sea was warmer than at present. From 30 000 BP onward, a new arid period began with a further regression of the coastline that reached its lowest level at –120 m below the present sea level. During this period Bioko Island (Equatorial Guinea) was still attached to the continent. It is only between 10 000–11 000 BP that the sea level started to rise, reaching its present level towards 5000 BP.

There is an ongoing debate on refuges and speciation. A small minority of investigators more or less refute the idea that speciation is linked to fragmentation and isolation of forest biomes, while other investigators suggest that these isolations are at the origin of a great number of taxa (Maley, 2001). Although many scientists have discussed these issues, it is difficult to come to any conclusions given the problems of dating the appearance of different taxa. However, several investigators pointed out that speciation in ecologically isolated environments (niches) and speciation in geographically isolated environments (vicariance), particularly under the effect of arid periods, are not incompatible, and can complement each other (Maley, 2001). For this reason and due to the lack of information related to the dating of endemic species, we did not classify the endemic species recorded during our study into neo- or palaeoendemic categories.

## Material and methods

### Study area

The study was conducted in the Campo-Ma'an rain forest in south Cameroon. The site covers about 7700 km<sup>2</sup> and is located between latitudes 2°10'–2°52' N and longitudes 9°50'–10°54' E (Fig. 1). The Campo-Ma'an area comprises a National Park, five forest management units, two agro-industrial plantations, and a multi-uses zone. The site falls under the Guineo–Congolian Regional Centre of Endemism that is reported to be species-rich with high levels of endemism (White, 1983; Davis *et al.*, 1994). It lies in the middle of the Atlantic Biafran forest zone that extends from southeast Nigeria to Gabon and the Mayombe area in Congo. This forest belt, which is extremely important in terms of conservation priorities, has a high concentration of endemic species and rich forest species diversity.

Following the FAO classification system, soils in the Campo-Ma'an area are generally classified as Ferralsols and Acrisols (Franqueville, 1973; Muller, 1979; van Gemerden & Hazeu, 1999). They are strongly weathered, deep to very deep, and clayey in texture (except at the seashores and in river valleys where they are mainly sandy). The soils are acid and low in nutrients with pH (H<sub>2</sub>O) values generally around 4. The topography ranges from undulating to rolling in the lowland area, to steeply dissect in the more mountainous areas. In the Campo area, altitudes are mostly low, ranging from sea level to about 500 m. In the quite mountainous eastern part the altitude varies between 400–1100 m.

The area has a typical equatorial climate with two distinct dry seasons (November to March and July to mid-August) and two wet seasons (April to June and mid-August to October). The average annual rainfall generally decreases with an increasing distance from the coast, ranging from 2950 mm year<sup>-1</sup> in Kribi, and 2800 mm in Campo, to 1670 mm in Nyabissan in the Ma'an area. The average annual temperature is about 25 °C, with little variation between years. The hydrography of the area shows a dense pattern with many rivers, small river basins, fast-flowing creeks and rivers in rocky beds containing rapids and waterfalls. Generally, the area has a low population density of about 10 inhabitants per km<sup>2</sup> and is sparsely populated (c. 61 000 inhabitants), with most people living around Kribi, along the coast, and in agro-industrial and logging camps (ERE Développement, 2002; de Kam *et al.*, 2002).

### Sampling method

In order to cover most of the area, we used a random stratified sampling method during which representative vegetation types were selected on the basis of human and physical factors such as rainfall, altitude, slopes, soils and land use. Sampling was carried out in small plots of 0.1 ha (50 m × 20 m) in these representative and homogeneous vegetation types. In total 145 plots covering 14.5 ha were established in undisturbed and matured secondary forests in the Campo-Ma'an area. In each 0.1 ha plot, all vascular plants with dbh (≥ 1 cm (diameter at breast height, about 1.3 m above ground) were measured, recorded and identified. For unknown species, we collected a voucher specimen. Furthermore, 136 subplots of 5 m × 5 m each were established in some of the 0.1 ha plots. In each of these small subplots all vascular plants below 1 cm dbh were recorded. The study also involved the collection of fertile specimens encountered in plots, vegetation types and specific habitats. The geographic co-ordinates of each plot and specimen were recorded using a Global Positioning System (GPS). The various distribution maps obtained were mainly based on botanical specimens collected in the Campo-Ma'an area during the present study, or by previous scientists. It is worth mentioning that this field work was largely conducted between 1998 and 2003 as part of Tchouto's (2004) PhD project.

### Criteria for taxa selection

The distribution patterns of species that are strictly endemic to the Campo-Ma'an area and those of narrow endemic species that also occur in south-western Cameroon (area that extends from Campo-Ma'an to Bipindi and Lolodorf) were used to verify the geographic position of late Pleistocene forest refuges. Other bio-indicator species comprise taxa with specialised ecological and biological features. They are lowland rain forest species with restricted seed dispersal abilities, ecologically selective and intolerant to changing environmental conditions. Furthermore, species that occur in other proposed rain forest refuges and that reach their northern limit of distribution in the Campo-Ma'an area were also taken into consideration, as long as floras, monographs or taxonomic expertise giving sound identification and providing sufficient reliable distribution data were available.

## Groups of selected bio-indicator species used

### Endemic species

Strict and narrow endemic species are suitable to serve as bio-indicators because they generally have lower overall reproductive capacity and poorer dispersal abilities than widespread species. They are often susceptible to environmental changes and disturbance. Therefore, patterns of congruence of narrow endemism are important for the identification of forest refuges since areas with unusually high numbers of endemics are likely to coincide with areas where forests persisted during glacial periods (Williams, 1993). Note that the selected list of strict and narrow endemic species (Appendix 1, which is available as "Supplementary data" on Cambridge Journals Online: [http://www.journals.cup.org/abstract\\_S1477200008002892](http://www.journals.cup.org/abstract_S1477200008002892)) also includes endemic *Begonia*, *Rinorea*, *Caesalpinioideae* and *Rubiaceae* species.

### *Begonia*

In his work on *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia*, Sosef (1994) used these *Begonia* species to study the location of Pleistocene refuges in West and Central Africa. In our study we will only focus on those *Begonia* species that are endemic to the Lower-Guinea region as defined by White (1979). *Begonias* from these groups are rhizomatous terrestrial or rock-dwelling herbs, which are found in mature and old secondary forests. They have indehiscent fruits that remain some months on the mother plant. Fruits of species in sect. *Scutobegonia* bend towards the substrate before disintegration (Sosef, 1994). While rotting away, they release their seeds slowly at the base of the parent plant. Sosef (1994) argued that in addition to the fact that many of these species have a self-incompatibility system of reproduction, dispersal over a long distance will probably not occur since the seeds are so slowly dispersed. However, some seeds might also be transported by animals (with mud on the legs of passing animals), or by water because a number of species also occur near small streams (de Lange & Bouman, 1992; Sosef, 1994).

### *Caesalpinioideae*

Several studies on the distribution patterns of *Caesalpinioideae* suggested that they are suitable bio-indicators for locating late Pleistocene tropical rain forest refuges in Central Africa (Rietkerk *et al.*, 1996; Wieringa, 1999; Leal, 2001). *Caesalps* belong to the dominant canopy tree species in the Atlantic Biafran forest (Letouzey, 1968, 1985). They are often found in undisturbed mature and in old secondary rain forests, and contain many species that occur gregariously. The explanation for the gregarious nature of these species might stem partly from the fact that they have ballistic seed dispersal abilities that limit dispersal distance, ectomycorrhizal relationships and large cotyledons with copious nutrients that enable their seedlings to realise initial growth under dark conditions (van der Burgt, 1994; Newbery & Gartlan, 1996; Wieringa, 1999; Leal, 2001). Most *Caesalps* show seeds that disperse through the explosion of the pods, a process in which the seeds are ejected to a maximum of 60 m from the mother tree (van der Burgt, 1994).

Area	Strict and narrow endemic	<i>Begonia</i>	<i>Caesalps</i>	<i>Rinorea</i>	<i>Rubiaceae</i>	Northern limit of distribution	Total number of selected bio-indicator species	Total %
Campo-Ma'an National Park	39	10	26	11	51	16	153	77
Kribi-Campo-Mvini area	33	7	25	10	46	11	132	66
Nyabissan-Ma'an-Mekok area	9	4	18	9	29	23	92	46
Campo-Ma'an area	58	13	32	13	59	24	199*	

**Table 1** Occurrence of the selected bio-indicator species in the different geographical areas in Campo-Ma'an.

\*Note that the total number of selected bio-indicator species in this Table (199) is higher than the total number of species listed in Appendix S1 (178) because some species occur in more than one group which is available as "Supplementary data" on Cambridge Journals Online: [http://www.journals.cup.org/abstract\\_S1477200008002892](http://www.journals.cup.org/abstract_S1477200008002892).

### *Rinorea*

Achoundong (1996, 2000) found that *Rinorea* species are sensible bio-indicators for forest typification. *Rinorea* species are understorey shrubs or small trees that are usually found in the lowland rain forest and sometimes in the submontane forest. They are characterised by slow seed dispersal ability. The capsule of most species dehisces with 3 valves. Each valve contains 1–4 seeds that are released in the vicinity of the parent plant, a reason why they are often locally frequent. Hekking (1988) argued that ants might also disperse part of the seeds, because there is a caruncle at the base of the seed. He went further to mention that nearly all species are restricted to their special habitats, implying that their history of distribution and speciation is strictly connected with that of the tropical rain forest in which they occur.

### *Rubiaceae*

All species used in our study are small trees, shrubs and herbs that are confined to the understorey of the lowland evergreen rain forest, since weedy species of *Rubiaceae* with fast dispersal mechanisms were not taken into consideration in this study. Robbrecht (1996) argued that although most *Rubiaceae* species have fleshy fruits (drupes or berry-like) that allow for long-distance dispersal by birds, they possess some advanced morphological syndromes by which cross-pollination becomes obligatory. As a consequence, their breeding system probably renders isolated cases of long-distance dispersal of single diaspores ineffective, because a self-incompatibility system is present in the majority of the species (Robbrecht, 1988, 1996). Therefore, one may expect that relict *Rubiaceae* populations will need a long time to recolonise the expanding spread of forest when favourable climatic conditions return after a period of forest reduction during a glacial period (Robbrecht, 1996).

### Data analysis

After a taxonomic search in existing floras, monographs and herbaria, taxa were selected using the criteria discussed above. A list of selected taxa was given to specialists for further checking and the resulting species distribution maps of each group

mentioned above were analysed in a search for species showing discrete patterns. We compared the distribution patterns of each group in order to identify areas of frequent occurrence of these bio-indicator species. The distribution patterns found were used to identify the position of late Pleistocene rain forest refuges in south-western Cameroon.

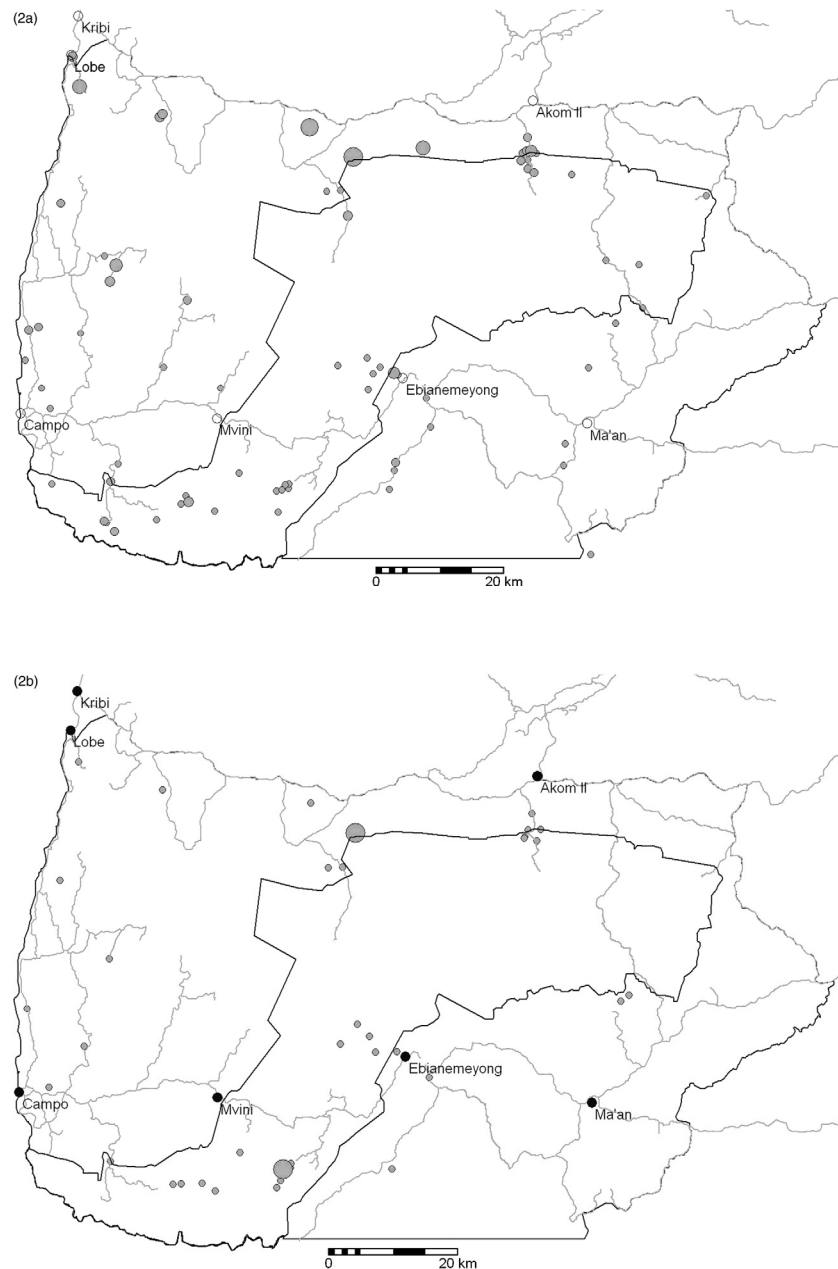
## Results

### Distribution patterns of bio-indicator species

In total 178 bio-indicator species (Appendix 1, available online) were selected on the basis of their biology (life strategy) and/or distribution (endemic). The list includes 58 strict and narrow endemics, 59 species of *Rubiaceae*, 32 species of *Caesalpinioideae*, 13 species of *Begonia*, 13 species of *Rinorea*, and 24 species that reach their northern limit of distribution in the Campo-Ma'an area. As shown in Table 1, 77% of the total number of selected bio-indicator species was recorded in the National Park, 66% in the Kribi-Campo-Mvini area, and 46% in the Nyabissan-Ma'an-Mekok area. Several maps were produced to display the distribution patterns of bio-indicator species within their respective groups (Figures 2 and 3). Overall, there was a high concentration of bio-indicator species in the Park and in the Kribi-Campo-Mvini area, and a relatively low concentration of these species in the Nyabissan-Ma'an-Mekok area (Table 1 and Figure 3), which can not be fully explained by a difference in sampling effort (Tchouto 2004).

The lowland evergreen forest rich in *Caesalpinioideae* and the submontane forest located in the National Park and in the western part of the Campo-Ma'an area were rich in bio-indicator species, while the mixed evergreen and semi-deciduous forest was characterised by a low concentration of these species (Figs 1 and 3).

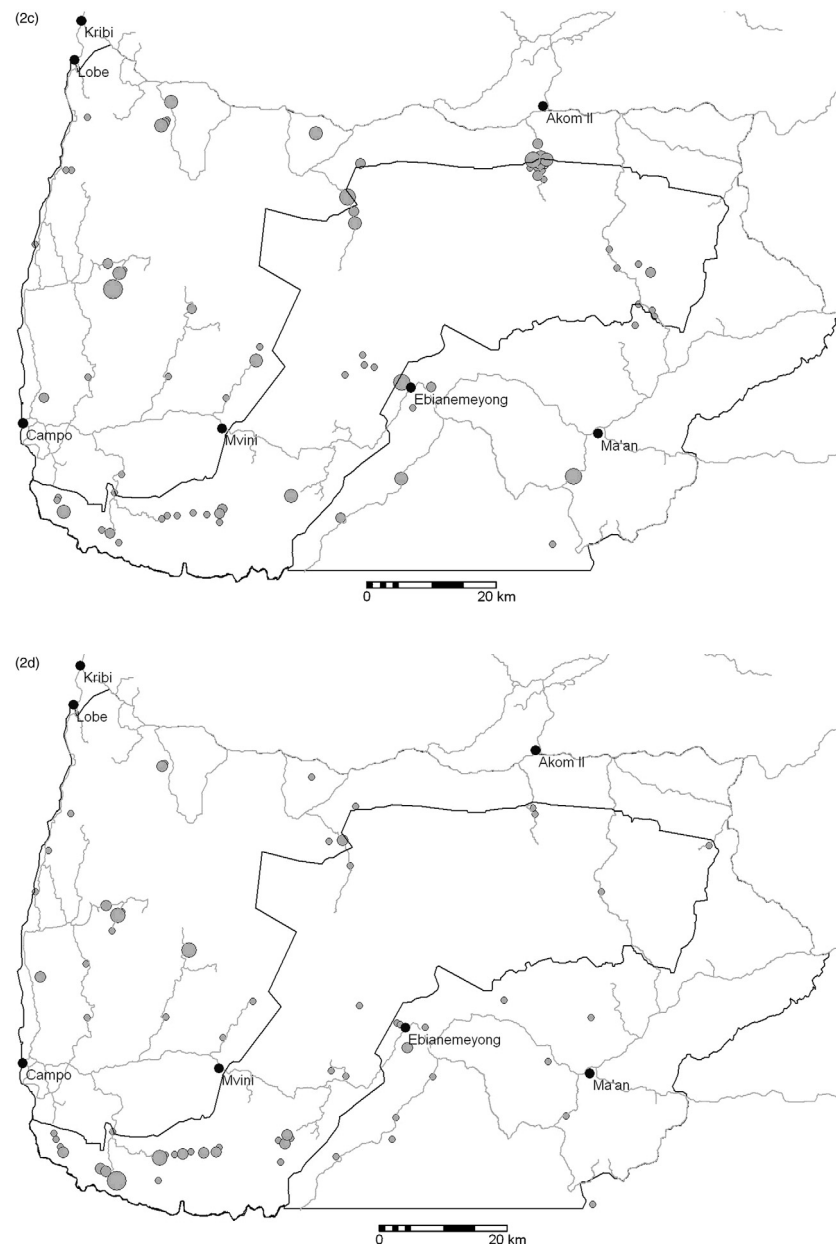
The distribution of the strict and narrow endemics was mainly limited to the Park and the Kribi-Campo-Mvini area, with a larger number of species in the northern part



**Figure 2** Distribution maps of 58 strict and narrow endemic plant species that only occur in the Campo-Ma'an area, and south-western Cameroon (2a); 13 species of the *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia* that are strictly endemic to the Campo-Ma'an and south-western Cameroon, endemic to Cameroon and Lower Guinea region, or that reach their northern limit of distribution in Campo-Ma'an (2b); 32 species of Caesalpinoideae that are strictly endemic to the Campo-Ma'an and south-western Cameroon, endemic to Cameroon and Lower Guinea region, or that reach their northern limit of distribution in Campo-Ma'an.

of the study area (Figure 2a). The distribution of *Begonia* (Figure 2b) showed that some species were often found in mountainous areas between Ebianemeyong and Akom II, or along slopes near hilltops in the lowland forest, and others were located along small streams in the lowland forest. Surprisingly, many of these *Begonias* were not recorded in the mixed evergreen and semi-deciduous forest in the Ma'an area. As for the Caesalps, their distribution showed a high concentration of species in the park and in the Kribi-Campo-Mvini area (Figure 2c). There was also a decrease in the number of Caesalps in the coastal forest rich in *Sacoglottis gabonensis* (Campo area) and in the mixed evergreen and semi-

deciduous forest with a predominance of semi-deciduous elements (Ma'an area). In *Rinorea*, many indicator species were mostly confined to the lowland forest, particularly in the evergreen forest rich in Caesalpinoideae (Figure 2d). There was a decrease in the number of these species with increasing altitude, and some of them were most frequent in the coastal forest. There was a relatively even distribution of bio-indicator species from the Rubiaceae family within the Campo-Ma'an area, although the Ma'an area showed a relatively low concentration of these species (Figure 2e). As for species that reach the northern limit of their distribution in the Campo-Ma'an area, there was a decrease in numbers from the



**Figure 2** (2c); 13 species of *Rinorea* that are strictly endemic to the Campo-Ma'an and south-western Cameroon, endemic to Cameroon and Lower Guinea region, or that reach their northern limit of distribution in Campo-Ma'an (2d); 59 species of Rubiaceae that are strictly endemic to the Campo-Ma'an and south-western Cameroon, endemic to Cameroon and Lower Guinea region, or that reach their northern limit of distribution in Campo-Ma'an.

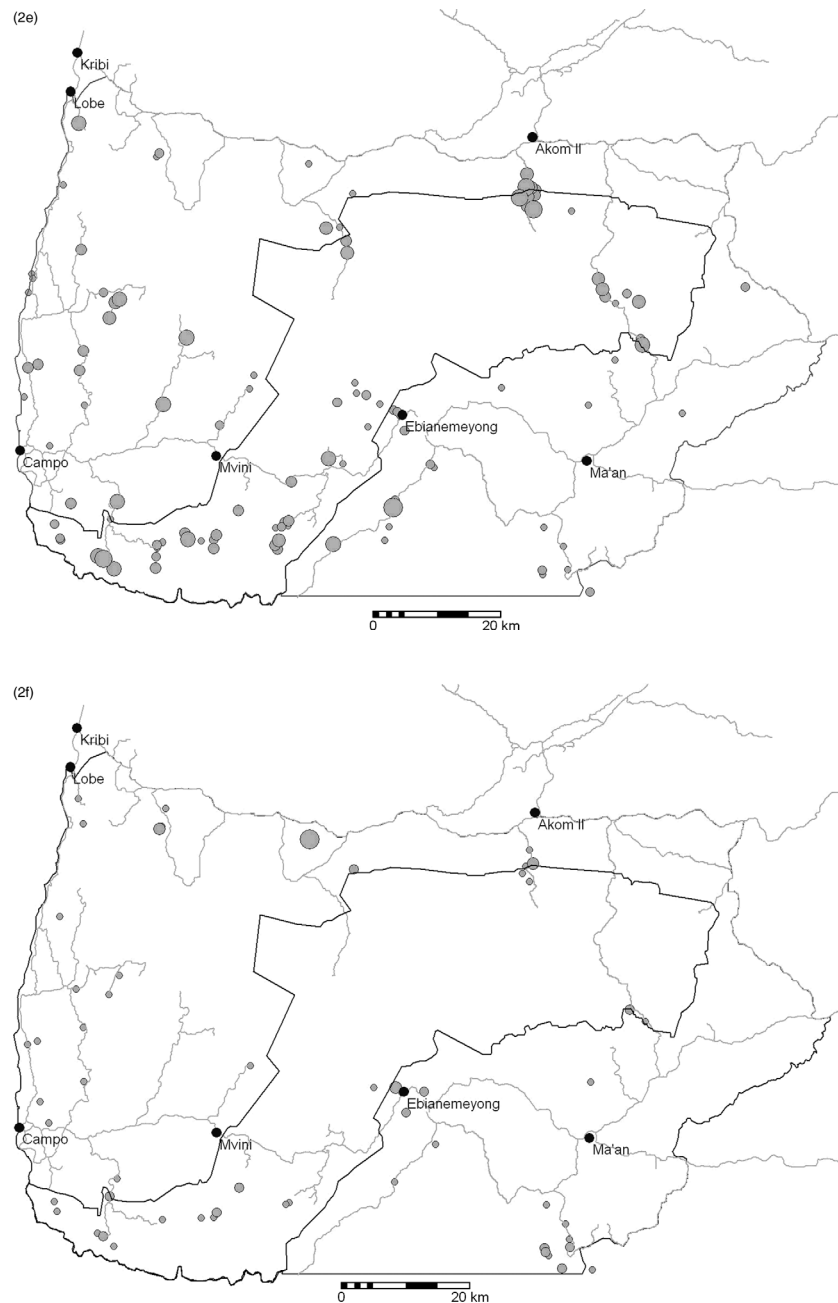
border with Equatorial Guinea to the Kribi-Akom II area further north (Figure 2f). Some species such as *Aucoumea klaineana*, *Dacryodes buettneri*, *Deinbollia pycnophylla* and *Tes-tulea gabonensis* were limited to the southern part of Campo-Ma'an in the Ma'an area, to Dipikar Island, and recorded from around Ebianemeyong and Mvini.

## Discussion

### Evidence for a late Pleistocene refuge in the Campo-Ma'an rain forest

The Campo-Ma'an rain forest is characterised by a rich and diverse flora with more than 2297 species of vascular plants,

ferns and fern allies belonging to 851 genera and 155 families. It has about 114 strict and narrow endemic species, 29 of which are only known from the area, another 29 only occur in southwestern Cameroon, and 56 are near endemics that also occur in other parts of Cameroon (Tchouto, 2004). The distribution of 178 bio-indicator taxa selected on the basis of their biology, endemism and growth forms, more or less fitted the glacial forest refuge as proposed or discussed by several authors (Hamilton, 1982; Maley, 1987, 1989, 1990, 1993, 1996a, b, c; Rietkerk *et al.*, 1996; Robbrecht, 1996; Sosef, 1994, 1996; Achoundong, 2000). Overall, there was a high concentration of bio-indicator species in the lowland evergreen forest rich in Caesalpinioidae and in the submontane forests in the National Park and Kribi-Campo-Mvini area, and a relatively low



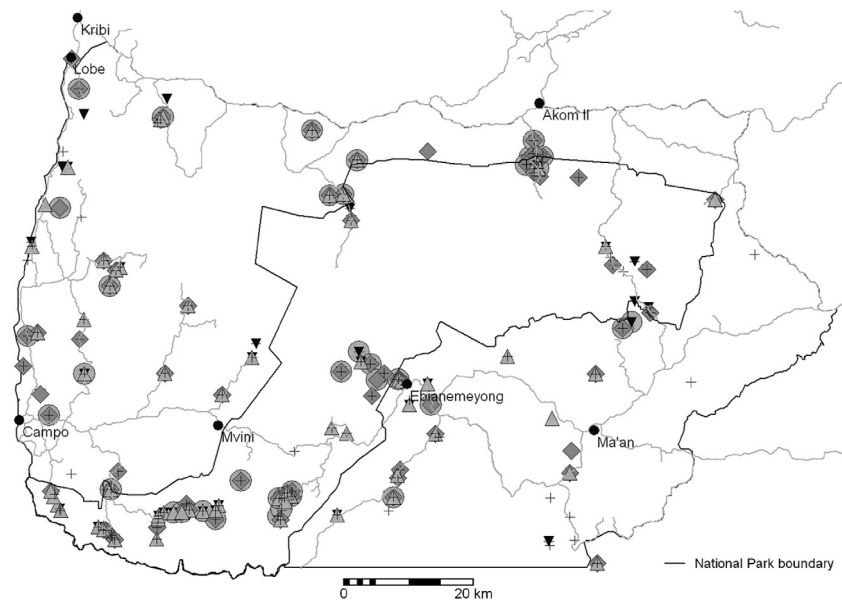
**Figure 2** (2e); 24 species that reach their northern limit of distribution in the Campo-Ma'an area (2f). Note that the size of the circle is proportional to the number of different species that occur at a certain location.

concentration of these species in the Ma'an area (Figure 3). Similar patterns were observed for the distribution of strict and narrow endemic species, *Begonia*, Caesalpinoideae and Rubiaceae (Figure 2). Achoundong (1996, 2000) mentioned that in terms of distribution, two groups of *Rinorea* species could be distinguished in Cameroon: a group that is limited to the coastal plain and another group which is mainly found inland. In the Campo-Ma'an area, the distribution of *Rinorea* species showed that *Rinorea microglossa* and *Rinorea* sp. nov.1. were restricted to the coastal area between Kribi and Campo, while other species were mostly found in the lowland evergreen forest rich in Caesalpinoideae.

The Atlantic Biafran forest rich in Caesalpinoideae is often considered to represent the real climax forest vegetation,

while the Atlantic littoral forest type is regarded as the result of its degradation (Letouzey, 1983). In the Campo-Ma'an area, the distributions of Caesalps show a high concentration of bio-indicator species in the lowland evergreen forest rich in Caesalpinoideae, and in the submontane forest. There is a decrease in the number of species in the coastal forest rich in *Sacoglottis gabonensis*, and particularly in the mixed evergreen and semi-deciduous forest where semi-deciduous and secondary forest species become increasingly important. Furthermore, there was a high concentration of bio-indicator species in the park and in the Kribi-Campo-Mvini area in the submontane forest, on higher altitudinal zones in the lowland forests, and along riverbanks. This pattern supports the view that during glacial times, patches of forest were restricted to





**Figure 3** Distribution patterns of 178 selected bio-indicator taxa in the Campo-Ma'an area. Where: □ (grey) = Strict and narrow endemics; ○ (grey) = *Begonia*; ▼ (grey) = *Caesalpinioideae*; △ (grey) = *Rinorea* and + = *Rubiaceae* species.

higher elevations in the lowland forests, especially along the upper slopes of hills near the top (F.J. Breteler *pers. comm.*), or along riverbanks where the humidity was high enough for their survival. We can therefore hypothesise that past glacial forest expansion started in the Campo-Ma'an area from isolated patches of mid and higher elevation evergreen rain forest rich in *Caesalpinioideae*, located within the mountainous range that extends from Ebiamemeyong to the Akom II. Moreover, the Campo-Ma'an area has a dense hydrographical pattern with many rivers and streams that may have played an important role during the dry-out periods, as they supplied humid conditions that may have allowed the survival of some forest types. This is illustrated today with the occurrence of indicator species such as *Aphanocalyx ledermannii*, *Begonia anisosepala*, *B. zenkeriana*, and *Gilbertiodendron demonstrans*, which are often found in marshlands and along stream and river banks in the coastal forest, and on Dipikar Island. At the same time it may be hypothesised that the persistence of *Caesalpinioideae* forests in this western part of the south Cameroon forest refuge prevented *Aucoumea klaineana* from extending its distribution further northwards.

The Campo-Ma'an rain forest, with its high concentration of endemic species and rich forest species diversity, is probably part of a late Pleistocene refuge as postulated in south-western Cameroon by several authors (Aubreville, 1962; White, 1979, 1983; Maley, 1987, 1989; Sosef, 1994, 1996). We assume that this refuge may probably extend further north-east along the mountainous range that goes up to the Bipindi area, because many narrow endemic species were also known to occur in the Akom II-Bipindi-Lolodorf areas. Overall, the distribution maps of the various bio-indicator species showed a low concentration of these species in the mixed evergreen and semi-deciduous forest located in the drier Nyabissan-Ma'an-Mekok area. A similar pattern was also observed from the distribution of strict and narrow endemic species. As shown

in Table 1, only 15% of the total number of strict and narrow endemics and 46% of the selected bio-indicator species were recorded in this area. Furthermore, the drier Ma'an area is characterised by a semi-deciduous forest type with a discontinuous canopy and the presence of many fully grown secondary forest species. This suggests that the Ma'an area might have suffered from past human disturbance, or that it has been colonised by an open vegetation type during the dry-out periods. Therefore, it is probably undergoing a phase of forest recolonisation under the present climatic conditions. Taking into consideration the fact that the Ma'an vegetation shows a strong secondary character in terms of its species composition with many semi-deciduous elements, we can hypothesise that it was not part of the postulated forest refuge in south-western Cameroon.

It should be noted that these patterns in species richness are also the result of past and present biotic and abiotic structuring processes (Tchouto, 2004). Taking into consideration the fact that palaeo-evidence provides more information regarding the identification of the location and extent of these refuges, the distribution patterns of bio-indicator species are often used to check the position of these forest refuges. In the absence of palaeo-evidence, it is almost impossible to unravel the role of the postulated rain forest refuges in the framework of other environmental processes that operated in the past without creating circular arguments. Furthermore, past and present climatic changes, biological interaction, ecosystem dynamics, and regional and evolutionary processes often acted simultaneously, and should be taken into account when explaining the high level of endemism and diversity recorded in the area. It is therefore suggested that further research to date the origin of endemic and slow dispersal species using recent modern molecular and phylogenetic (cladistic) techniques as well as detailed phylogeographic analyses of several candidate species should be encouraged for a better understanding of

the evolutionary processes of tropical rain forest taxa and the history of the Central African rain forest.

## Conclusions

This study added some evidence in support to the view that the Campo-Ma'an area forms part of a series of postulated tropical rain forest refuges in Central Africa. The distributions of 178 bio-indicator taxa selected on the basis of their life strategy, endemism and/or growth forms showed a pattern that roughly coincides with a glacial forest refuge in south-western Cameroon, as proposed by several authors. Overall, there was a high concentration of narrow endemic and bio-indicator species in the National Park and in the Kribi-Campo-Mvini areas, and a relatively low concentration of these species in the Ma'an area. These bio-indicator species were particularly frequent in the submontane forest, in the lowland evergreen forest rich in Caesalpinioidae (especially at higher altitudes along the upper slopes of hills near the top) or along riverbanks.

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