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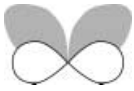
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The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity

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Abstract

Aim Tropical rain forests are often regarded as pristine and undisturbed by humans. In Central Africa, community-wide disturbances by natural causes are rare and therefore current theory predicts that natural gap phase dynamics structure tree species composition and diversity. However, the dominant tree species in many African forests recruit poorly, despite the presence of gaps. To explain this, we studied the disturbance history of a species-rich and structurally complex rain forest.

Location Lowland rain forest in Southern Cameroon.

Methods We identified the recruitment conditions of trees in different diameter classes in 16 ha of species-rich and structurally complex ‘old growth’ rain forest. For the identification of recruitment preference we used independent data on the species composition along a disturbance gradient, ranging from shifting cultivation fields (representing large-scale disturbance), to canopy gaps and old growth forest.

Results In nine of sixteen 1-ha forest plots the older trees preferred shifting cultivation fields for recruitment while younger trees preferred gaps and closed forest conditions. This indicates that these nine sites once experienced large-scale disturbances. Three lines of evidence suggest that historical agricultural use is the most likely disturbance factor: (1) size of disturbed and undisturbed patches, (2) distribution of charcoal and (3) historical accounts of human population densities.

Main conclusions Present-day tree species composition of a structurally complex and species-rich Central African rain forest still echoes historical disturbances, most probably caused by human land use between three to four centuries ago. Human impact on African rain forest is therefore, contrary to common belief, an issue not of the last decades only. Insights in historical use will help to get a more balanced view of the ‘pristine rain forest’, acknowledging that the dualism between ‘old growth’ and ‘secondary’ forest may be less clear than previously thought.

Keywords

Tropical rain forest, biodiversity, shifting cultivation, historical land use, Africa, Cameroon.

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INTRODUCTION

Tropical rain forests are among the most complex and species-rich ecosystems of the world (Wilson, 1995). However, the processes that structure this high diversity remain yet unclear. A common element in current theories on the maintenance of tree diversity is the role of disturbances, which create opportunities for species to claim previously utilized space and resources (Huston, 1994; Hubbell, 2001). Therefore, insight in the history, magnitude and impact of disturbances is critical in understanding rain forest tree diversity.

In large parts of the African rain forest biome, large disturbances such as hurricanes, river dynamics and volcanic activity are rare (Olivry, 1986; Jans *et al.*, 1993). Small-scale gap phase dynamics are therefore considered to be the main disturbance regime to provide colonization sites for especially the light-demanding tree species. Intriguingly, many of the large tree species that currently dominate these forests are found to recruit poorly within the forest despite the presence of canopy gaps (Aubréville, 1938; Richards, 1952; Letouzey, 1968; Newberry & Gartlan, 1996; Poorter *et al.*, 1996). Thus, the conditions needed for recruitment of the canopy species seem not to correspond with those occurring in natural gap phase dynamics. A number of rain forest studies have therefore questioned the view that only small-scale gap phase dynamics determine the present-day forest composition (Denevan, 1992; Hart *et al.*, 1996; Brown & Jennings, 1998; Whitmore & Burslem, 1998). Instead, the current species composition of African rain forests may still reflect large-scale historical disturbances, such as human impact (Jones, 1955, 1956; Letouzey, 1968, 1985; White & Oates, 1999), or periods of sudden, extensive droughts (Reynaud & Maley, 1994; Newberry *et al.*, 1998).

The human use of African rain forest areas during the last millennia may have been more widespread than previously thought. Evidence of human activities up to 3000 years ago was found as charcoal, pottery and banana phytoliths in forest soils in Nigeria, Zaire and Cameroon (Hart *et al.*, 1996; White & Oates, 1999; Mindzie *et al.*, 2001; Oslisly *et al.*, in press). These past human activities may have had a large impact on what we presently appreciate as 'pristine' and undisturbed rain forests. However, most biodiversity conservation strategies are implicitly based on the assumption that humans have never disturbed old growth rain forests. As a result, biogeographical setting and recent land use history are considered as the main determinants of conservation value in rain forest areas (Myers *et al.*, 2000). At present, the long-term impact of past human activities on current forest characteristics important to conservation, e.g. species composition and levels of biodiversity, is poorly understood.

The role of past human activities in shaping current community composition in African rain forests has generally been analysed on the basis of charcoal, pollen and distribution patterns of a limited number of well-known species (Letouzey, 1968, 1985; Reynaud & Maley, 1994; Hart *et al.*, 1996). These studies give insight into historical land

use patterns but fail to assess the full effects of past human disturbances on current community composition. An alternative method to assess both disturbance history and quantify its effects on species composition and diversity may be the interpretation of current tree species composition in terms of life history strategies. Most rain forest trees species have considerable life spans and therefore current tree species composition will, to a large extent, reflect historical disturbance regimes.

To test whether old growth forest in southern Cameroon still reflects historical large-scale disturbance, we developed a new approach that allows characterization of the disturbance history that shaped the forest's species composition and diversity. We characterized the species in different diameter classes in 16 ha of old growth forest with respect to their preferred recruitment conditions. For the identification of recruitment preference we used independent data on the species composition along a disturbance gradient, ranging from shifting cultivation fields (representing large-scale disturbance), to canopy gaps and old growth forest. We expect that canopy trees belong to species that recruit in canopy gaps or closed forest if gap phase dynamics were important in structuring the present-day species assemblage. If historical large-scale disturbances were important, we expect that recruits of canopy trees will be found mainly in large forest clearings, comparable in size with shifting cultivation fields. If a forest stand was subject to a large disturbance event a long time ago and has not been disturbed since, this means that older trees established under conditions similar to shifting cultivation, while younger trees established in closed forest (or its gaps). Therefore, an increase in preference for large-scale disturbance with diameter was interpreted as evidence that historical large-scale disturbances structured present community composition, while a decrease supports the hypothesis of small-scale gap phase dynamics.

MATERIAL AND METHODS

Study site

The study was conducted in the Bibindi – Akom II – Lolodorf region, south Cameroon (3° N, 10° E). The climate is humid tropical with two distinct wet seasons (March–May, August–November) and two relative drier periods. The average annual rainfall is 2000 mm (Waterloo *et al.*, 2000). Average monthly temperatures vary between 22.9 and 27.5 °C (Olivry, 1986). The parent material consists of Precambrian metamorphic rocks and old volcanic intrusions (Franqueville, 1973). Topography varies from flat erosional plains to rolling uplands with isolated hills, and mountains. Altitude varies from 50 to 1000 m above sea level. Soils range from moderately acid sandy clay loam to highly clayey and strongly acid and classify as Haplic Acrisols, and Plinthic and Xanthic Ferrasols (van Gernerden & Hazeu, 1999). Evergreen forests of the Atlantic Biafrian type largely cover the area (Letouzey, 1968, 1985). These forests are characteristically rich in Leguminosae–Caesalpinioideae and have a closed canopy at 30–40 m with emergents often

surpassing 55 m. The area is rich in plant species. At present a total of 1264 species have been recorded, including 261 species that are endemic to the lower Guinea forest region (Nigeria–Gabon) of which fifty-one species are restricted to the rain forests of Cameroon (B.S. van Gernerden, unpublished data).

During the last centuries, human populations in the Central African rain forest region were highly mobile as group semi-nomadism was the principal way of life (Diaw, 1997). Between the sixteenth and nineteenth century, drought and slave trade evoked mass migration from savannah to forest regions on several occasions. Rivalry between immigrants and already settled populations resulted in further shifts in population composition and pressure (Laburthe-Tolra, 1981). The last exponent of these mass migrations is the arrival in the research area of the Bulu around 1870 who now form the majority of the population. More recently, the German colonial rulers forced the population to abandon the villages that were scattered in the forests to settle along the main roads (van den Berg & Biesbrouck, 2000). As a result of these mass migrations, population pressure and related land use patterns varied strongly during the last centuries.

The area is at present sparsely populated by humans (8.6 persons km⁻²) and population increase is marginal (Lescuyer *et al.*, 1999). Most people practice shifting cultivation, a form of agriculture in which forest patches of 0.5–1.5 ha are cleared, burned and interplanted with a variety of crops. A few large or valuable trees are often maintained in field preparation. Depending on soil productivity, the tending and harvesting gradually stop after 2–3 years and the land is left fallow for at least 7–15 years (Nounamo & Yemefack, 2002). Shifting cultivation is confined to the direct surroundings of villages and along the main access roads (van Gernerden & Hazeu, 1999). In addition, hunting and gathering of non-timber forest products widespread and relatively intense throughout the area (van Dijk, 1999).

The main current economic activity in the area is timber exploitation. International companies have selectively logged most of the area, and some parts twice. The logging involves the use of heavy machinery for road construction and log extraction. Present logging activities focus on *Lophira alata* (Azobe, 60% of the extracted volume), *Erythrophleum ivorense* (Tali), and *Pterocarpus soyauxii* (Padouk). The logging intensity is low (10 m³ ha⁻¹ or 0.7 tree ha⁻¹). The felling and extraction of logs causes physical damage to 5% of the area but locally much higher

(25%) disturbance rates have been observed (Jonkers & van Leersum, 2000). Individual crown fall gaps caused by commercial logging are between 300 and 900 m² (Parren & Bongers, 2001) but simultaneous felling of clumps of commercially interesting trees often creates much larger gaps (B.S. van Gernerden, unpublished data).

Vegetation sampling

We used two independent data sets to analyse the disturbance history of old growth forest in south Cameroon. Species' recruitment preference was based on a survey of sixty-five plots of 625 m² (25 × 25 m), hereafter referred to as the *recruitment plots*. Present-day tree species composition of old growth forest was based on a survey of sixteen 1-ha plots (100 × 100 m), hereafter referred to as the *forest plots*.

In the sixty-five recruitment plots, we enumerated all woody plants with height ≥50 cm and diameter at breast height (d.b.h.) <10 cm. The majority of individuals in this size range have recruited relatively recently and therefore the present conditions were assumed to reflect the conditions in which they recruited. Plots were located in sites with different disturbance histories. The three disturbance histories studied were old growth forest (no signs of disturbance), logging gaps, and shifting cultivation fields (Table 1). Successional age since disturbance ranged in logging sites from 5–14 years and in shifting cultivation sites from 10–40 years. Land use history was determined with the help of local informants, often the proprietors of the sites. Information on logging activities in the area was also provided by the state forestry service ONADEF (Hazeu *et al.*, 2000). Recruitment plots in old growth forest were distributed over five sample areas that represent the most important variation in vegetation, soil, landform and altitude in the Bibindi–Akom II–Lolodorf region (van Gernerden & Hazeu, 1999). Recruitment plots in logged forest and shifting cultivation fields were located respectively in four and one of these sample areas. In general, secondary vegetation and especially regrowth in old agricultural fields was found to be very similar throughout the region (van Gernerden & Hazeu, 1999). Plots in logging gaps were positioned in the estimated centre of the tree crown fall. Plots in fallow vegetation were positioned well away from sudden changes in vegetation structure or other anomalies. Within plot variation in topography, vegetation and drainage characteristics were minimal. Alongside the recruitment survey, we inspected soil profiles of 104 sites for charcoal.

Table 1 Distribution of recruitment plots (individuals with height ≥50 cm and d.b.h. <10 cm) and soil charcoal observations (auguring to maximally 120 cm) over disturbance types

| Vegetation age (years) | Disturbance type | | | Total |
|--|-------------------|-------------------|-----------------------------------|-------|
| | Old growth forest | Logging gaps 5–14 | Shifting cultivation fields 10–40 | |
| No. of recruitment plots (625 m ²) | 36 | 17 | 12 | 65 |
| Survey area (ha) | 2.25 | 1.06 | 0.75 | 4.06 |
| No. of charcoal observations | 39 | 43 | 22 | 104 |

Soil observations were distributed over old growth forest, logging gaps and shifting cultivation fields (Table 1). Soils in each of the inspected sites were augered up to a maximum depth of 120 cm. In general, three samples were taken in the approximate centre of each plot while minimum distance to the nearest tree (d.b.h. >10 cm), and between samples, was at least 1 m. The depth of observable charcoal fragments in the deepest profile was used for the analyses of charcoal distribution.

In the sixteen forest plots, species identity and d.b.h. of all trees with d.b.h. ≥ 10 cm were determined. Plots were located in the Minwo catchment (3°05' N, 10°45' E) in the central part of the Bipindi–Akom II–Lolodorf region. Forest plots were clustered in an area of 300 ha. Altitude varied little between plots (520 \pm 40 m) and soils were remarkably uniform throughout the area. Floristically, the vegetation was homogeneous with *Greenwayodendron suaveolens* (Annonaceae), *Podococcus barteri* (Palmae) and *Crotonogyne preussii* (Euphorbiaceae) as characteristic species (van Gernerden & Hazeu, 1999). The area had never been logged at the time of our survey and no signs were found of recent shifting cultivation activities. Plots were positioned in fully developed old growth forest and plots did not include aberrant sites, e.g. steep slopes, boulders, large gaps and imperfectly drained soils.

In both surveys, the most common and readily identifiable species were directly named in the field and plant material was collected of all other species. Voucher material was processed at the Kribi Herbarium (Tropenbos-Cameroon Herbarium) and sent to the National Herbarium of Cameroon (IRAD Yaoundé) and the National Herbarium of the Netherlands – Wageningen University branch for identification by specialists. Material that could not be identified to species level was categorized as morphospecies. Nomenclature follows Lebrun *et al.* (1991–1997).

We classified species according to maximum stature in two classes, large trees (>15 m tall) and understory trees (3–15 m tall) on the basis of taxonomic literature, mainly Cable & Cheek (1998), Aubréville & Leroy (1963–2001, 1961–1992) and Keay & Hepper (1954–1972), and own field observations. In literature, information about the general ecology of African rain forest tree species is scarce. However, Hawthorne (1996) and Cable & Cheek (1998) classified a subset of the species occurring in the forest plots into three categories on the basis of shade tolerance. The inferred ecological guilds are: *shade-bearers* (both young and older plants frequent in shaded environments), *non-pioneer light demanders* (young plants frequent in shade but need higher light levels to fully develop), and *pioneers* (both young and older plants in high light levels). Of species not occurring in these references we attributed an ecological guild only if information in available taxonomic literature was sufficiently detailed.

Data analysis

We identified species' recruitment preference on the basis of the distribution of species along the disturbance gradient

from low disturbance (old growth forest) via intermediate disturbance (logging gaps) to high disturbance (shifting cultivation fields). Three methods were used: occurrence preference, abundance preference and weighted average index (WAI). Occurrence preference was calculated on the basis of species presence/absence data per recruitment plot. Significance of preference was tested with a chi-square. Species with a significant ($P < 0.05$) preference were attributed to the disturbance type with the highest percentage of occurrence. Abundance preference was calculated on the basis of the number of individuals per recruitment plot. Number of individuals was log transformed to homogenize variance among groups. Analysis of variance was used to test significance of preference. Species with a significant ($P < 0.05$) preference were attributed to the disturbance type with the highest abundance. As many species were likely to have intermediate preferences, we calculated the optimal conditions for recruitment of each species along a disturbance gradient. For this, we used species composition data from recruitment plots in old growth forest (disturbance index = 1), logging gaps in old growth forest (index = 2) and shifting cultivation fields (index = 3). Next, we calculated for each species the mean value of the disturbance index, weighing for the mean log abundance (number of individuals) in each stage. This WAI was then used as a species trait, indicating the relative recruitment preference of a species ranging from undisturbed forest (WAI = 1) to recent large-scale disturbance (WAI = 3).

Basal areas were based on measured d.b.h. For all other analyses, the trees were assigned to diameter classes (10–20, 20–30, ≥ 100 cm). Species diversity was expressed as Shannon diversity (see Magurran 1988). For all species together and for large tree species separately, we regressed average WAI per tree on diameter class and tested significance of regression using an *F*-test ($P < 0.05$). In the regression, the largest diameter class (d.b.h. ≥ 100) was excluded because this class had a much larger range of diameters than the other classes. Furthermore, as large trees are often left standing in field preparation in current shifting cultivation practices, individuals in this diameter class may have recruited under a different disturbance history than smaller trees.

RESULTS

Tree species composition

We recorded a total of 8349 trees (d.b.h. ≥ 10 cm) in the sixteen 1-ha forest plots in the Minwo catchment. More than 96% of the individuals were identified to species level and the rest was categorized as morphospecies. A total of 400 species from 53 families and 230 genera were recorded. Predominant families were the Euphorbiaceae (47 species), Leguminosae–Caesalpinioideae (31), Rubiaceae (28), Annonaceae (26) and Sterculiaceae (21). Only 28 species represented more than half of the individuals and the ten most abundant species accounted for 31% of the individuals. Maximum stature was identified for 241 species. Species with the potential to reach the forest canopy (large tree

species) accounted for 64% of the individuals recorded. Number of tree species per hectare ranged from 105 to 149 (average 127). Shannon diversity index ranged from 3.97 to 4.42 (average 4.22) and basal area ranged from 29.7 to 42.6 m² ha⁻¹ (average 35.6 m² ha⁻¹). The ten most dominant species represented 38% of the basal area. Diameter distribution was typically skewed towards the smaller size classes, with on average 523 trees ≥10 cm, 105 ≥30 cm and 38 ≥50 cm ha⁻¹. Average d.b.h. of the five largest trees per plot ranged from 103 to 143 cm (average 122 cm).

Recruitment preference

We identified recruitment preference for the 142 tree species that occurred in both the recruitment and in the forest plots. These species represent 36% of the species, 67% of the individuals and 76% of the basal area recorded in the forest plots. Abundance preference was significant for 49 species while occurrence preference was significant for forty-four species. Preference for shifting cultivation fields was high among the species with a significant preference (Table 2). The remaining species did not show a significant preference for old growth, logging gaps or shifting cultivation fields. WAI was calculated for all 142 species (see Appendix S1 in Supplementary Material). Species were normally distributed over WAI with most species having intermediate values. WAI values did not differ significantly between large and small tree species ($F_{1,137} = 2.67$, $P = 0.105$). Ecological guild was identified for seventy-three species. In general, the ecological

Table 2 Identified recruitment preference of 142 tree species based on occurrence (presence/absence) and abundance (log transformed number of individuals) in old growth forest, logging gaps and shifting cultivation fields

| Recruitment preference for | Occurrence preference no. of species (% species) | Abundance preference no. of species (% species) |
|-----------------------------|--|---|
| Old growth forest | 12 (8.6) | 13 (9.2) |
| Logging gaps | 13 (9.2) | 13 (9.2) |
| Shifting cultivation fields | 19 (13.4) | 23 (16.2) |
| No preference | 98 (69.0) | 93 (65.5) |

guild classification corroborated well with preference based on WAI. Average WAI increased from shade-bearers to non-pioneer light-demanders and pioneers ($F_{2,70} = 10.28$, $P < 0.001$). Tukey tests ($P < 0.05$) indicated that shade-bearers and light demanding non-pioneers had significantly lower average WAI compared with pioneers.

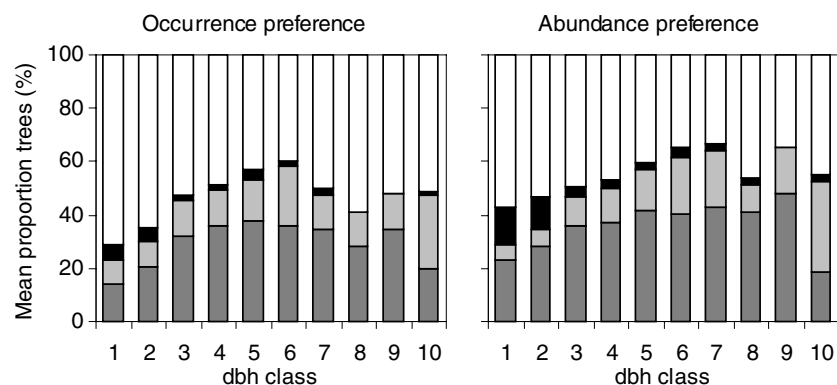
The proportion of trees in the forest plots for which the recruitment pattern was identified varied with diameter class ($F_{9,144} = 3.50$, $P = 0.001$). Tukey tests ($P < 0.05$) indicated that only diameter classes 1 and 2 differed significantly from diameter classes 9 and 10. The rest of the classes were intermediate. Average proportion of trees with identified recruitment preference was 69% in classes 1 and 2, and 88% in classes 9 and 10. As large trees are less abundant, we do not expect that these small differences will influence the general outcome of the analyses.

Patterns of recruitment preference

Recruitment preference composition of forest plots changed with diameter. Both occurrence preference and abundance preference showed a general trend of decreasing old growth preference and increasing field and gap preference (Fig. 1). Of the trees with a significant preference for one of the disturbance types, the majority belonged to species that prefer shifting cultivation fields for recruitment. Trees with d.b.h. ≥100 were dominated by species that recruit in gaps. The relation between average WAI per tree and diameter class varied between plots (Fig. 2). WAI increased significantly with diameter in nine plots and showed no increase in seven plots. When all plots were included, regression of average WAI on diameter class was still significant ($r^2 = 0.251$, $P < 0.001$). Analysis based on only the large tree species gave similar results. Plots with and without a significant increase in WAI with diameter were evenly distributed over the area.

Plots with and without increase in average WAI with diameter did not differ significantly in species richness, Shannon diversity and basal area. However, the species–area curves (Fig. 3) showed that the set of plots without a significant increase in WAI accumulate species much more rapidly (ANCOVA, log-area × trend type interaction, $F_{1,15} = 21.24$, $P = 0.001$).

Figure 1 Recruitment preference of trees in different diameter classes in 16 ha of lowland rain forest in southern Cameroon. Recruitment preference is based on species presence (occurrence preference) and log-transformed number of individuals (abundance preference) along a disturbance gradient (individuals height ≥ 50 cm and d.b.h. <10 cm). Preference classes are shifting cultivation fields (dark grey), logging gaps (light grey), old growth forest (black) and no preference (white).



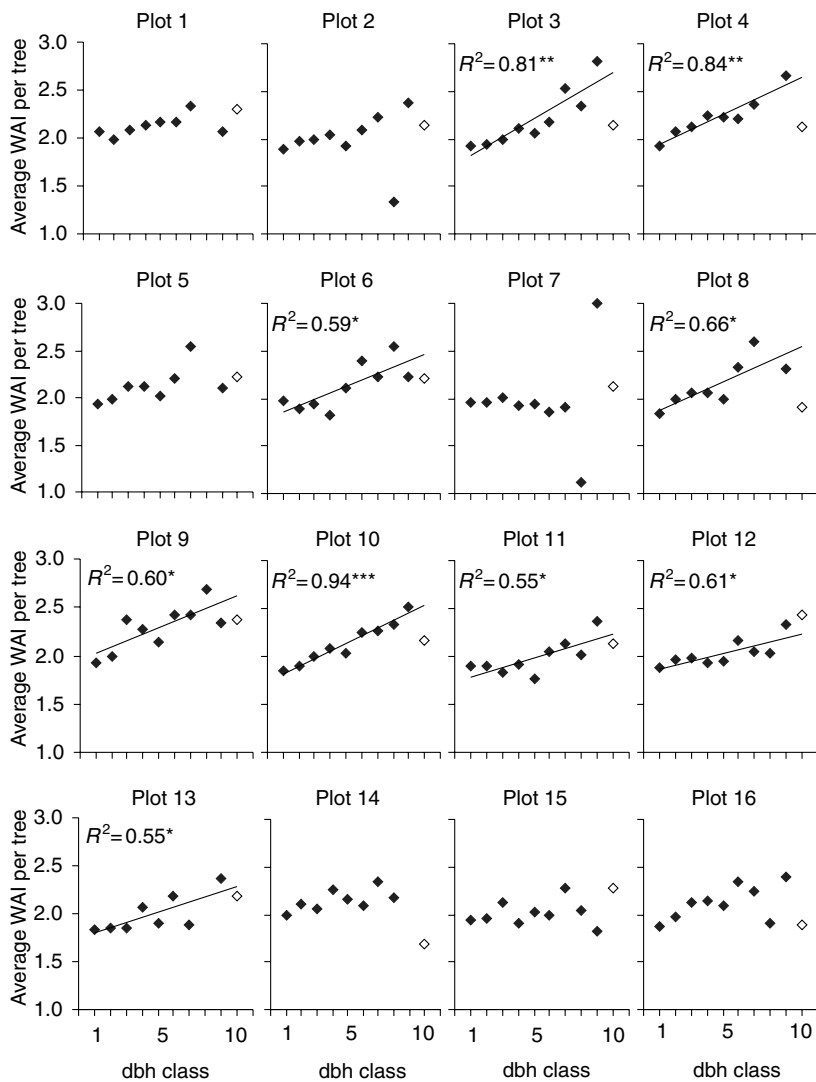


Figure 2 Average weighted average index (WAI) of trees in relation to diameter class in sixteen 1-ha plots of lowland rain forest in southern Cameroon. WAI indicates the relative recruitment preference of species and ranges from undisturbed forest (WAI = 1) to shifting cultivation fields (WAI = 3). Significant ($P < 0.05$) regressions of average WAI on diameter class are indicated.

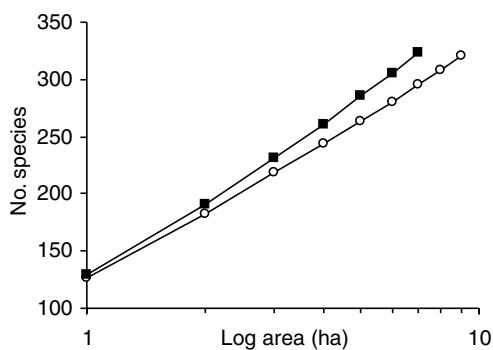


Figure 3 Cumulative species–area curves for forest plots with (open circles) and without (solid squares) significant increase of average weighted average index (WAI) with diameter. Significant increase of average WAI with diameter indicates historical large-scale disturbance. Data shown are mean values after fifty random permutations of plot order.

Charcoal

Charcoal was present in 29% of the sample points of the soil survey ($n = 104$). Charcoal depth varied from 4 to 120 cm. Of the sample points with charcoal, 20% had charcoal between 0 and 30 cm, 47% between 30 and 60 cm, 33% between 60 and 90 cm, and 23% deeper than 90 cm. Total charcoal frequency did not differ significantly between disturbance types (Kruskal–Wallis test: $\chi^2_2 = 3.77$, $P = 0.152$). Charcoal frequency per soil depth was also not significantly different between disturbance types (Fig. 4; 0–30 cm: $\chi^2_2 = 0.42$, $P = 0.81$; 30–60 cm: $\chi^2_2 = 2.62$, $P = 0.27$; 60–90 cm: $\chi^2_2 = 5.55$, $P = 0.06$; and >90 cm: $\chi^2_2 = 4.61$, $P = 0.10$).

DISCUSSION

In this study, we found that the larger (older) trees in nine of sixteen old growth forest plots preferred shifting cultivation

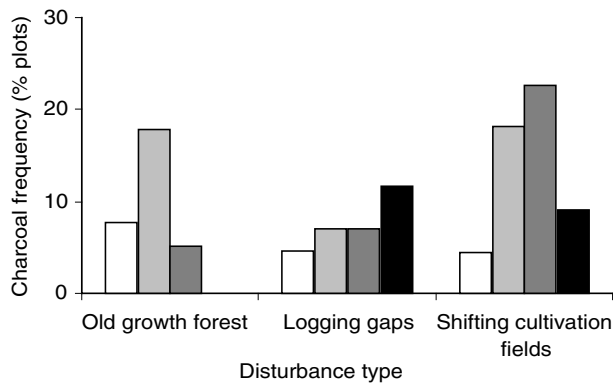


Figure 4 Soil charcoal frequency in sites differing in recent disturbance history. Charcoal frequency is expressed as percentage of the sample points with charcoal (old growth forest: $n = 39$, logging gaps: $n = 43$, and shifting cultivation fields: $n = 22$). Soil depth classes are 0–30 cm (white), 30–60 cm (light grey), 60–90 cm (dark grey) and 90–120 cm (black). Charcoal frequency per soil depth class did not differ significantly between disturbance types (Kruskal–Wallis test, $P < 0.05$).

fields for recruitment. In contrast, the forest understorey of these plots was largely made up of species that prefer smaller-scale disturbances like logging gaps. This shift in recruitment preference with diameter indicates that these nine sites once experienced a large-scale disturbance after which the forest was left to recover. The remaining seven plots did not show a significant shift in recruitment preference between size cohorts, suggesting that present community composition of these plots was mainly influenced by smaller gap-phase dynamics. Plots affected by large-scale events were evenly distributed spatially indicating the patchy nature of the large-scale historical disturbances.

The likely date of these suggested large-scale historical disturbances may be inferred from the diameter distribution of the trees. In the majority of the disturbed plots, the diameter class 90–100 cm has the highest average WAI (Fig. 2) and is likely to contain the trees that have recruited directly after the disturbance. Worbes & Junk (1999) found a strong general relationship between d.b.h. and age of Central American rain forest species. Application of their formula ($d.b.h. = 0.33 \times \text{age}$) suggests that the trees of 90–100 cm in our survey, recruited between 273 and 303 years ago. Jones (1956) suggested that the average annual diameter increment of Nigerian forest trees is 0.25 cm and therefore trees of 90–100 cm are estimated to be 360–400 years old. However, it should be noted that these are only crude estimates, because of the potentially large variability in the general size and age relationships.

Three lines of evidence suggest that shifting cultivation is the most likely historical disturbance factor: (1) the size of disturbed and undisturbed patches, (2) distribution of charcoal, and (3) historical accounts of human population densities. The variation between plots in history of disturbance (Fig. 2) suggests that historical shifting cultivation has created a mosaic of more and less disturbed forest patches at the

scale of our plots (1 ha). The current size of fields in shifting cultivation varies between 0.5 and 1.5 ha (Nounamo & Yemefack, 2002), and is likely to have been in this range during the last centuries as the solar energy need of cultivated crops cannot be assured in smaller fields (M. Yemefack, pers. comm.). About 56% (nine of sixteen) of the plots appear to have been disturbed in the past. This corresponds to current land use in shifting cultivation areas, where between 40% and 60% of the area consists of young secondary forests, actual and recently abandoned fields (van Gemerden & Hazeu, 1999). Furthermore, the widespread and frequent occurrence of charcoal supports the hypothesis of historical shifting cultivation. High charcoal occurrence in the soil is generally associated with human activities as naturally occurring forest fires are rare in the African rain forest region (Schwartz, 1993; Hart *et al.*, 1996). We found that 29% of the studied soil profiles in this area contained charcoal fragments, which is much higher than the 6% reported by Newberry *et al.* (1998) for a likely undisturbed site in Korup in west Cameroon. The soils in the study area are not subject to sedimentation or erosion, and therefore charcoal in especially the topsoil was expected to reflect recent land use. In the present survey no clear relation was found between recent land use, charcoal frequency and depth. Possibly fire also carbonizes root material, which may at least partly explain the apparent random distribution of charcoal in the soil. Finally, Letouzey (1968, 1985) provides anthropological evidence that during the eighteenth century, population densities were high in the littoral forests of Cameroon. Large areas appear to have been cultivated and may explain the predominance of the pioneer species *Lophira alata* in the canopy but the virtual lack of regeneration in the forest understorey. Letouzey (1968, 1985) also found charcoal and artefacts in many places, which indicate the high population density in these regions a few hundred years ago. As also suggested by other studies (White & Oates, 1999; Oslisly *et al.*, in press), these different lines of evidence suggest that large-scale, community-wide disturbances in this rain forest area are probably caused by widespread historical human impact.

Alternatively, historical widespread droughts may be responsible for the 'signature' of large-scale disturbance in the current forest composition. Especially relevant for the present study are the droughts that occurred in the 1765–1799 El Niño Southern Oscillations epoch (Quinn, 1992; Newberry *et al.*, 1998). Reynaud & Maley (1994) and Newberry *et al.* (1998) speculate that a drought or a series of droughts strongly increased mortality of the most drought-sensitive species, which lead to more and larger canopy gaps in which species with a competitive advantage regenerated massively. However, the assumption that many large trees will die as a result of a relatively short dry period may not be valid. The dry season in the African rain forest region is generally overcast and misty, and therefore the water stress plants are exposed to is not as severe as for example in Amazonia (Maley & Brenac, 1998; Charles-Dominique *et al.*, 2001). Moreover, mortality because of short dry periods is likely to be a largely non-

specific random process (Hubbell, 2001). Therefore, a sudden drought in this region is likely to affect forest dynamics and the regional species pool only to a limited extent and does not explain the current dominance of species that prefer large disturbances for recruitment. A non-selective perturbation, like forest clearing for agriculture, followed by a long period of recovery appears to be a much more robust explanation for this pattern. However, droughts may have enabled escaped human fires to spread short distances into the marginally inflammable forest, increasing the size of the disturbed site (Hart *et al.*, 1996). We thus think that historical droughts are unlikely to be a separate, alternative explanation to historical human impact for the current forest composition. However, they may have contributed to the extent of the disturbances.

It has been argued that the absence of large-scale disturbances in tropical rain forests may lead to low tree diversity (Hart *et al.*, 1989; Huston, 1994) as species adapted to low disturbance will ultimately competitively displace species adapted to higher levels of disturbance. Contrary to the patterns of tree diversity in Guyana, where the least species-rich sites were those that are believed to have been the least used by pre-Colombian Amerindians (ter Steege & Hammond, 2000), we found that areas without historical human impact accumulated species more quickly (Fig. 3). Our results suggest that historical large-scale disturbances have a significant negative effect on tree species diversity at larger scales and do not support the idea that large-scale disturbances promote diversity. Moreover, these findings question the validity of the common assumption of many current biodiversity conservation strategies that all old growth forests are equally important. Expanding the analysis to include sites from other Central African rain forests is likely to provide more insights in to the long-term effects of human disturbance on conservation values.

Our descriptive approach to analyse old growth forest in south Cameroon in terms of the recruitment preference of its species, enables the identification of the disturbance history that shaped species composition and diversity of this forest. The described method enables to distinguish between areas with and without historical human impact and is therefore potentially interesting for conservation planning, especially if existing survey data can be used. Ideally all tree species occurring in old growth forest are included in the analysis of disturbance history. However, the ecology of many rain forest species is poorly studied and systematic characterization of their preferred recruitment conditions are scarce (e.g. Hawthorne, 1996; Cable & Cheek, 1998). In the present study, the ecological guild of only 18% of the old growth forest species was found in literature. Therefore, time-consuming and generally little cost-efficient recruitment surveys are still required to maximize the number of species included in the analyses. Quality and speed of the analyses would improve if patterns of recruitment in different disturbance regimes, preferably in different parts of a species biogeographical distribution range, were well documented. Including important functional traits such as fruit type, seed size, dispersal mode and wood density can further refine the

classification of recruitment preference (Gitay *et al.*, 1999; Weiher *et al.*, 1999).

We conclude that present-day tree species composition of a structurally complex and species-rich Central African rain forest still echoes historical large-scale disturbances, most probably caused by human land use. Human impact on African rain forests is, contrary to common belief, an issue not of the last decades only, which is relevant for biodiversity conservation planning. Most likely, gaining more insights into historical use will help to get a more balanced view of the 'pristine rain forest', acknowledging that the dualism between 'old growth' and 'secondary' forest may be less clear than previously thought.

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SUPPLEMENTARY MATERIAL

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Appendix S1

Annotated list of 142 species included in the analysis of disturbance history of 16 ha of lowland rain forest in southern Cameroon.

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