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Forest perturbations and biodiversity during the last ten thousand years in French Guiana

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Abstract – Tropical forests can be described as a mosaic of juxtaposed eco-units corresponding to different stages of regeneration after treefals. However, these small-scale regeneration mechanisms alone cannot account for the different patterns of species distribution, plant communities and population structures found in this habitat. The presence of charcoal layers in the soil and the study of sediments along streams suggest that large-scale forest fires deeply affected the tropical forest vegetation, even in high rainfall areas such as French Guiana. Many atypical plant distribution and population structure patterns, in relation to what would be expected from present-time regeneration processes, can be explained by these large-scale events which happened during the last few thousand years. © Elsevier, Paris

Holocene drought events / palaeofires / pioneer plant fluctuations / soil charcoals

1. INTRODUCTION

Tropical rain forests are made up of small juxtaposed units of vegetation corresponding to different stages of the regeneration process. This cyclic process is initialized by the fall of a large tree (opening of a gap), enabling the establishment of light-demanding short-lived pioneer species, which are then replaced little by little by mature forest species [16, 26, 57]. However, this process largely depends on the size of the gap, and redevelopment of pre-existing trees may also contribute, to various degrees, to the natural regeneration of the gap. In addition, when a tall emergent tree dies upright, other subtle replacement processes may take place [7, 27, 54]. The natural evolution of these units organizes the entire forest architecture around light availability [35, 37, 54]. The analyses of plant populations in undisturbed forests give a good picture of this general regeneration process, based on the repetitive succession of small events, distributed more or less evenly in space and time. However, some distributions of plant species and vegetation types, and some population and community structures, cannot easily be explained by these small-scale forest dynamic processes.

So far, the study of species distribution in tropical ecosystems has been based on two scales of time and space:

– on the local short-term scale (under 1 km^2, 1–100 years), the mechanisms of the forest regeneration processes and the key role of gap openings have been used to explain the structure and dynamics of the forest mosaic [24, 25, 28, 36, 39, 56].

– on the continental and regional long-term scale (10 000–100 000 000 km^2, 10 000–1 000 000 years), the Holocene refuge theory provides the theoretical framework for the interpretation of global species distributions [11, 15, 31, 32, 52, 55].

Both approaches can only bring satisfying answers at their own scale, and remain unable to explain abnormal population and community organizations. Our approach focuses on an intermediate scale and uses both functional arguments and local evidence for past events.

As different plant species have more or less delayed reactions after perturbations, the vegetation could retain scars left by major events even after a very long time. This hypothesis suggests that ancient perturbations of a much larger scale than ordinary gaps may have left long-lasting scars still visible in present-time forest ecosystems.

Evidence for such ancient large-scale perturbations has been discovered in soils and sediments, during the Ecofit research programme. This project includes geologists, ecologists, palynologists and climatologists who work together on the evolution of the intertropical ecosystems during the last ten thousand years. The tropical rain forest, thought to have remained stable since the last glacial event, has in fact undergone deep modifications.

2. MATERIAL AND METHODS

2.1. The study area

This study was undertaken on the Les Nouragues research station (French Guiana), in pristine tropical rain forest 100 km inland (4°5' N, 54°40' W). Annual rainfall totals over 3 000 mm distributed over about 280 days, with two drier periods of unequal duration: the main 'dry season' in September-October, and the much shorter 'little summer' around March. The rainfall data place French Guiana in the 'hyperhumid' forest zone [34], along with the Andean foothills between the Rio Negro, Putumayo and Maranon catchment areas.

The area had been inhabited by Nouragues Native Amerindians until the 18th century [12, pers. comm.], but on the actual research station grounds, the remains of human presence have all been dated between 1 000 and 1 500 BP [49]. It is possible that other more recent or older remains are still to be found. The area has been left untouched during the entire colonial era, until the creation of the research station in 1986.

The region is covered by primary forest to a canopy height of 30–45 m, with a few emergents reaching over 60 m. In some places, this high forest is punctually replaced by other vegetation types, such as the 'rock-savannas', the low forests found around inselbergs, the 'cambrouzes' bamboo thicket patches, and the sometimes extensive liana forests. The occurrence of markedly different vegetation types contributes to a high species diversity. So far, 1 250 higher plant species have been identified on the 3 km² surrounding the research station [30]. In the high forest sectors, botanical inventories have yielded between 160 and 260 tree species per hectare (trees above 10 cm DBH), and these values place Les Nouragues among the regions with the highest species diversities [30, 38, 41].

2.2. Methods

In order to locate the main forest types, the exploration of the area (covered by aerial photographs) was extended over several kilometres, using footpaths radiating from the camp (*figure 1*). Botanical inventories included one 87 ha core area [30], and several transects distributed on its periphery [18]. Each tree above 30 cm DBH (10 cm for focal species) was marked, measured, mapped and identified to species, genus or family level. Botanical samples were collected in order to complete the identifications and were deposited in the Orstom herbarium (Cayenne) and in the National Museum of Natural History herbarium (Paris).

A vibration core drill [23] was used for the core boring. Core samples were processed for seed and pollen contents following the usual method [19]. Charcoal fragments were collected by sifting the soil of 50 × 50 cm pits in successive 5 cm-thick layers, to depths of 60 to 90 cm. The fragments were identified by studying vessel anatomy and comparing with a reference collection [49]. The fragments (charcoal and seeds) were dated at Beta Analytic (Miami) and Utrecht University, and ages converted into conventional ^{14}C ages.

3. RESULTS

Overall, the Guianan forest is relatively homogeneous at the scale of the main vegetation types, and is organized as a mosaic of functional units evolving from one stage to another. This spatial organization fits well with the general mechanisms of natural regeneration studied locally [7, 36], but a number of small units, enclosed in the extent of the forest, appear to undergo distinct processes (rock savannas, low forests, liana forests, bamboo thickets). These vegetation types are considered 'atypical' because they display particular structures and are relatively uncommon (they are sometimes absent over 50 to 100 km). Some species local distributions, which do not conform to the general pattern found in the forest, are also termed 'atypical'. The interpretation of such 'anomalies' must take into account past situations, and this is why we have attempted, through sediment analyses, to retrace the past events which may have deeply modified the dynamics of the forest ecosystem.

Results will be presented in two sections. The first will focus on past events as they appear through the analyses of sediments (which record past events). The second will examine how atypical vegetation types can give evidence for environmental conditions which have since disappeared (traces of the past in the organization of present living organisms).

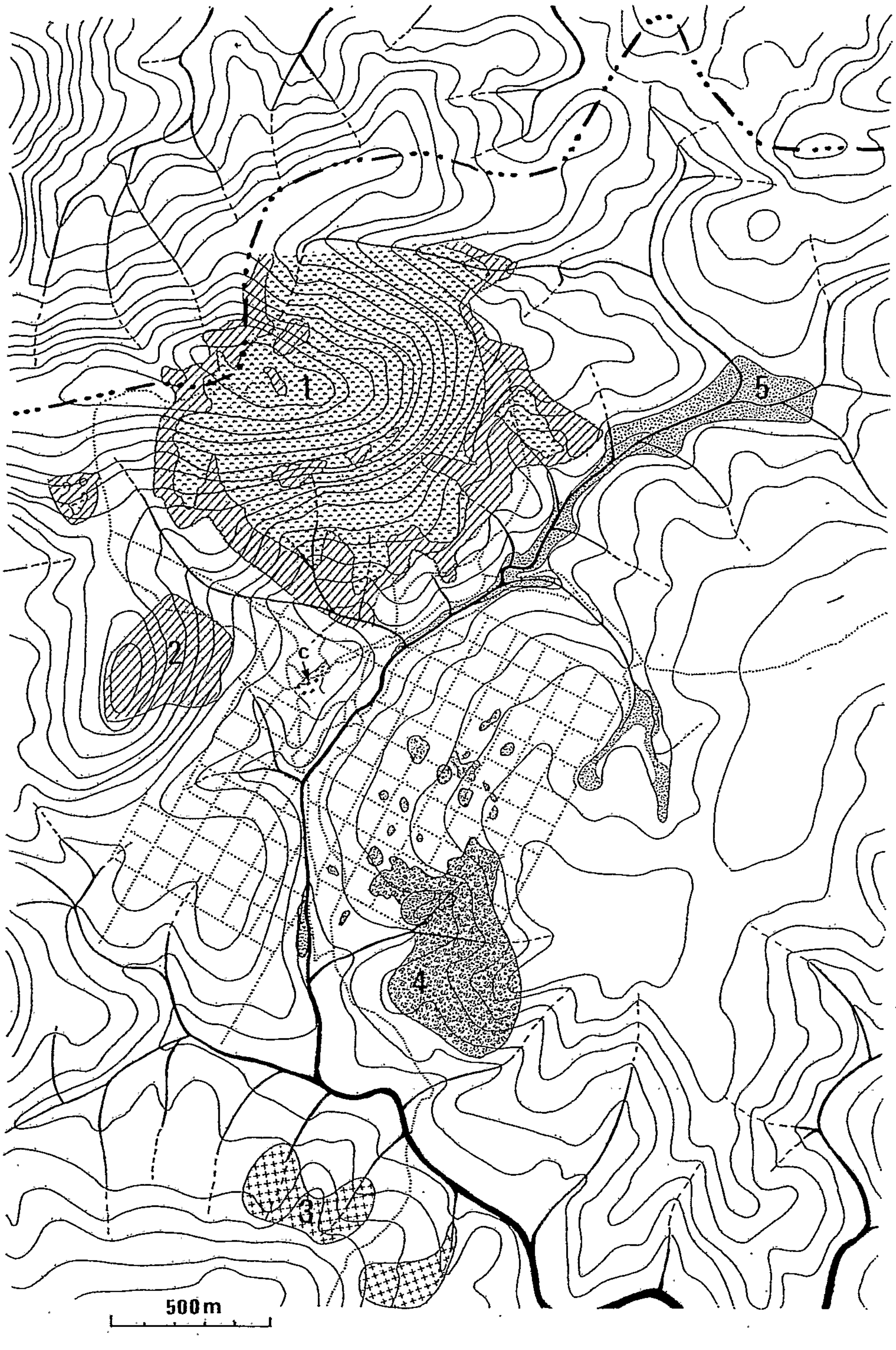

Figure 1. Map of the study area - c: camp; 1: Rock savanna; 2: Low forest; 3: Bamboo thickets; 4: Liana forest; 5: Pino palm swamp; dotted lines: trails and paths; continuous lines: level curves (every 20 m, from 60 to 400 m), large dotted line: separation of hydrologic basins.

3.1. The main ancient large-scale perturbations of the forest

3.1.1. *Palaeofires*

The charcoal layers found in the soil are the most obvious indicators of palaeofires. They were first found by Soubies [47] in Southern Amazonia, and have been recently discovered in French Guiana on many sites. They appear to be independent of human occupation levels: Tardy et al. [49] showed that palaeofire levels may occur underneath human occupation levels, antedating these by several thousand years. The presence of Man in America is attested since 30 000 BP at least, and agriculture since 6 000 BP [9], but evidence for tropical rain forest agriculture is only found since 2 500 BP in Meso-America [20]. In French Guiana, intensive archaeological searches undertaken in the Petit Saut area over 275 archaeological sites [33] have not yielded any remains anterior to 2 000 BP, while palaeofires appeared a long time before this, during the periods 10 000–8 000 BP, 6 000–4 000 BP and 2 000 BP to the present time.

3.1.2. *Erosion*

Today, the physical erosion of the forest floor is minimal under primary forest cover (under 1 mm·year^{-1} on average, [40]). The 30–45 m stratified vegetation considerably reduces the impact of heavy rains. Moreover, the forest floor is entirely colonized by a dense mat of surface roots which form a protective mesh under the litter. Most of the rain water drains into the ground through the soil. Chemical dilution (24 kg·ha·year^{-1}) and the export of fine particles (190 kg·ha·year^{-1}, [13, pers. comm.]) are the main pathways of soil erosion. Heavy rains notably intensify the flow of small streams and rivulets, but very small amounts of solid matter are actually torn from the forest floor, and the water flow merely reorganizes ancient sediments. Large-size elements are never driven from the forest floor into the stream beds. However, remains of alluvial terraces that could only have been formed during periods of intensive erosion were found in Les Nouragues, during recent studies undertaken along a small river with a 8 km^2 catchment area [4]. The lower terrace (1 m high) sits on a bed of clay and sand containing charcoal fragments, seeds and dead leaves, dated 530 ± 70 BP (Beta 89824). The examination of the seeds reveals a great abundance of pioneer species: *Henriettea spp*, *Miconia spp* (Melastomataceae), *Cecropia obtusa*, *C. sciadophylla* (Cecropiaceae), *Goupia glabra* (Celastraceae), etc. which suggests a period of important disturbance of the forest cover during this time. The second terrace (3 m high), situated higher up and older, has not been dated for the time being.

The study of a pino palm swamp, a little further upstream and lodged in a plateau depression, also displays traces of several periods of intensive erosion. In this case, layers of sand and gravel several centimetres thick have been found included within clay-organic sediments or peat. The reconstitution of the soil profiles reveals up to three such layers one above the other, with a slight slope towards the center of the swamp, suggesting the transport of material by surface water. One of these layers, with its upper limit at –85 cm, has been dated under 1 390 BP (UT86). Another, located between –131 and –140 cm [19], would be about 3 000 years old (OBDY 1416). Today, the swamp does not receive any coarse particles during heavy rains, and these sand and gravel alluvions could only have been deposited during intensive soil erosion periods, as in large open areas after massive simultaneous destruction of the forest cover. The same goes for the alluvions accumulated further down along the stream bed. At the scale of such a small catchment area, such erosion/alluvion cannot be explained outside extensive deforestation, such as those generated by palaeofires .

3.1.3. *Human versus climatic origin of palaeofires*

In all tropical rain forests, air humidity remains high and does not allow the development of forest fires. The traditional agriculture in these habitats uses the ‘slash-and-burn’ method, i.e. the felling of trees and then the burning of the dead dry matter at the end of the dry season. Sometimes, the dry season is too subdued to allow the dead wood to dry and no fire can be ignited, whereby the piece of land is temporarily lost for cultivation. In contrast, on exceptionally dry years, the fires set to clear the dead wood may propagate into the surrounding forest, as it happened in southern Brazilian Amazonia in 1988, when over 80 000 km^2 were destroyed [Ronchail pers. comm.]. Such incidents have not, in recent history, been recorded in hyperhumid forests. However, the widespread presence of charcoal layers indicate that several large-scale forest fires have occurred.

One possibility is that the great forest fires recorded in the Guianan soils have been the consequences of intensive slash-and-burn agricultural activities. But the presence of charcoal layers older than 2 000 years old (without agricultural evidence) show that natural processes alone may very well cause rain forest fires. Additionally, in order to explain the sedimentary deposits, one must consider openings large enough to entail intensive soil erosion. Even today, areas under slash-and-burn agriculture in French Guiana do not particularly suffer from erosion, and in pre-colombian times, when stone axes must have limited the size of the cleared areas [17], the impact of agriculture on soil erosion must have been even less than today. Many charcoal fragments are found along with the coarse sediments, but their ages vary, and it is possible that the sediments were reorganized when the deposits were formed [49].

In South America, the water deficit is most pronounced during the dry season, which is cloudless and very sunny. This is when trees may suffer important water losses and become inflammable if the water table is too low. Forest fires in Guiana would thus indicate the repetition of abnormally long dry seasons over a number of years, with a consequent severe lowering of the water table.

3.1.4. The vegetation since 3 000 years ago

Identification of pollen [19] and seeds from peatbog cores [4], as well as charcoal fragments [49], have given insights into what the past vegetation must have looked like. The peatbog cores go back 3 000 years BP for pollen and 1 400 years BP for seeds, and the charcoal fragments can be dated over a period of 10 000 years. Overall, between 3 000 and 2 000 BP, the forest appears to have been more humid than today, with a greater taxonomic diversity. Between 1 800 and 1 200 BP, the swamp must have somewhat dried up, and large areas, favourable to pioneer species (*Cecropia spp, Solanum spp, Piper spp*), must have opened up with a peak around 1 600–1 300 BP. Between 1 200 and 900 BP, the forest progressively regained ground, and between 900 and 600 BP, new disturbances arose, allowing the development of pioneer plant assemblages (in particular the family Melastomataceae). These subsided from 600 to 300 BP, and today's pollen and seed assemblages appeared around 300 BP.

The apparitions of pioneer species during several consecutive centuries suggest that, during each of these periods, brief disturbances must have occurred every 10–30 years, impeding the establishment of mature forest species and maintaining a widespread secondary vegetation.

No traces of herbs such as Poaceae and Cyperaceae have been found in the pollen profile, which rules out altogether open vegetation types such as savannas or woodland-savannas. Moreover, the analyses of the charcoal remains have yielded some forest species ever since 10 000 BP, although diversity is much lower during the two older periods (8 000–7 000 BP and 6 000–4 000 BP) than from 2 000 BP onwards [49]. From the sole examination of pollen and seeds, it appears that the forest must have undergone two series of severe perturbations during the last 3 000 years: the first between 1 800 and 1 200 BP, and the second, less important, between 900 and 600 BP.

3.1.5. Concluding remarks on past events

The study of the charcoal layers in the soils, the traces of ancient erosion and alluvions, and the pioneer plant explosions, suggest that climatic perturbations with severe droughts must have favoured the occurrence of large-scale forest fires, long after the last glacial period and in a region now classified as hyperhumid. The scale excludes a solely human origin, particularly before 2 000 BP, hence, a climatic origin appears more likely. Data from other areas of the Amazonian region indicate that this was no mere local phenomenon, but that it ranged over the entire continent. In Carajas, in less humid forests (6° S), the charcoal layers in the soils have been dated between 2 880 and 2 080 BP, and layers of minute charcoal remains have been found in lake sediments, peaking between 7 000 and 4 000 BP and between 900 and 400 BP [48]. In the Roraima, beyond the northern boundary of the rain forest, pollen analyses indicate that the environment changed from semi-deciduous forests to the actual mosaic of dry forests and savannas around 2 000 BP [1]. Lastly, in the hyperhumid Andean foothills of Peru, the geomorphologists Dumont and Fournier [6] concluded that river flows declined around 1 900–1 500 BP and again around 900–600 BP.

In the course of the last decades, particularly dry years have been recorded in Amazonia, in correlation with increases in the surface temperature of the Eastern Pacific, off the coasts of Peru ('El Niño' phenomenon [29, 51]). By analogy with these recent climatic events, some authors have suggested that the dry periods of the Middle and late Holocene could be explained by very intense and frequent 'El Niño' events and/or by the prevalence of high temperatures in the waters of the Eastern Pacific [22, 53].

3.2. Atypical vegetation types

3.2.1. Rock savannas

The open vegetation on rocky outcrops, locally called rock savannas, are mostly distributed in the southern part of French Guiana, 100–300 km inland (but some occur as little as 20 km from the coast), and are generally found on inselbergs. De Granville [10] and Sarthou [42] showed that some rock savanna plant species were also common to coastal savannas, but that others were only found in these particular habitats. Overall, during the current humid period, the forest is slowly expanding and gaining over the rock savannas on its borders. This expansion is sometimes held back on the steepest slopes where surface water flow is strong. Rock savannas have their own regeneration mechanisms: the bare rock is first colonized by nitrogen-fixing cyanobacteria [44], initiating the formation of a soil substrate [43] and the establishment of a herbaceous xerophytic vegetation cover, finally invaded by shrubby thickets [42].

It is difficult to estimate the age of rock savannas, but it is likely that they have been around for a long time since they harbour specific plant species. They probably expanded and receded over time, with maximum extensions during the glacial periods, when forest soils were drastically eroded down. More recent erosion phases initiated by droughts and fires must have allowed rock savannas to expand periodically and maintain themselves over time since the last glacial event.

3.2.2. *Low forests*

The low forest, so-called 'transition forest' is an original low thickety forest vegetation generally found on the outside borders of rock savannas. They are established on porous soils where water stress is often more important than in the soils of high moist forest [18]. Today, they tend to gain over the rock savanna vegetation with the help of seed-dispersing birds [18, 50]. This tendency may be locally reversed in favour of rock savanna species when the ecotone is disturbed. High forest similarly gains on the low forest, on the outside, at a very slow pace. Low forests have an original flora: in Les Nouragues, almost 200 species are found only in this type of vegetation. This indicates that this so-called low forest is not a mere ecotone between rock savannas and high forest, but actually a distinct vegetation entity. These forests are well adapted to xeric conditions, and may have known greater extensions in the past. Nowadays, they could represent relict patches, like the enclosed savannas found near the borders of the large forest blocks.

Two other types of vegetation, the liana forests and the bamboo thickets ('cambrouzes'), materialize a stagnation in the regeneration process [2] and may also constitute relict patches. Data are not sufficient as yet to conclude on this point, and a human origin cannot be ruled out, in particular for the bamboo thickets [8]. In French Guiana, the mammalian faunas, especially bats, often display sibling species which only differ by minute cranial or dental characters. Typically, one of the species lives in high forest and the other in marginal areas such as coastal savanna and swamp borders or certain types of low forests [3]. These 'marginal habitats' must have existed for a long time to have allowed speciation to take place. The origin of these formation types is probably unrelated to the palaeofires which have occurred during the last milleniums. However, their surface area may have been affected by these events.

3.2.3. *Zoochory and autochory*

Zoochory is widespread in French Guiana, and this dispersal mechanism using fruit-eating vertebrates allows quick recolonization. Today's plant assemblage is mainly made up of quick-spreading species, suggesting frequent small-scale forest perturbations. A small number of slow-spreading autochorous trees exists nonetheless, and these frequently follow a very patchy distribution pattern, which cannot be explained by today's forest dynamics. A current hypothesis is that these patches are relics from ancient distributions reorganized by the latest palaeofires, and in expansion since then. Tree mapping in Les Nouragues (87 ha) has outlined possible small-scale refuge patches around swamps and springs. More detailed studies on *Eperua falcata* (Caesalpiniaceae) show that the older individuals are situated in the center of the patches, while the younger are distributed mainly on the periphery, as if the population was currently spreading from the swampy lowlands onto the plateau [38]. The species was present on the plateau before, as is attested by charcoal remains [49].

4. DISCUSSION AND CONCLUSION

Exceptional events occurring at several centuries intervals should be taken into account as well as all the common constraints organisms have to face. Their exceptional nature explains that they have frequently been ignored in functional ecology models, which generally use climatic parameter averages. Connell [5], however, considered that perturbations occurring at a moderate rate could be favourable to the maintenance of a high species diversity. Sporadic catastrophes could give a new impulse to the dynamics of forest ecosystems, maintaining biotopes and species which would otherwise tend to disappear.

Forest fires seem to have been the only type of catastrophic event to have affected French Guiana in the course of the last milleniums. The region is located away from the cyclone routes and does not exhibit volcanic or seismic activity. Fires in tropical hyperhumid forests can only develop beyond a certain water stress threshold, and have probably been triggered by climatic fluctuations which intensified the effects of the dry season.

Studies undertaken on the Guianan forest ecosystem, which have focused on functional aspects as well as on spatial organization at species or vegetation type levels, show that present environmental conditions by themselves cannot fully explain the situation prevailing today. This is particularly noticeable in the case of species and vegetation types which exhibit long turnover rates or slow colonization rates. Understanding the mechanisms of forest processes calls for the integration of several scales of time and space, and, in particular, scales adapted to slow-evolving biological systems (100 to 10 000 years, and local to regional scales). The collection and carbon-dating of sediments (in particular charcoal fragments) can constitute a sound basis for this type of approach, providing invaluable information towards the validation of hypotheses.

Comparisons made between Amazonia and western Equatorial Africa underline a fundamental difference between these two regions: in Amazonia, the dry season is cloudless and imposes important water stresses on the vegetation [14], while in Africa (in particular southern Cameroon, Gabon and the Congo), the dry season is overcast and misty, although rainless, and plants are less exposed to water stress [21, 46]. This characteristic of the west African dry season is thought to be caused by the upwelling of cold polar water in the Golf of Guinea. In contrast with the abundant charcoal fragments found in Amazonian and Guianan soils, remains of forest fires are rare in west Africa and are generally associated with human settlements [45, pers. comm].

The tropical rain forests of Amazonia and the Guianas thus appear to be relatively exposed to fire if the dry season lengthens or intensifies beyond a certain threshold. Today, this type of catastrophe is prevented by the high air humidity and the short duration of the dry season, but it must be reconsidered in the current context of global warming and increasing human pressure.

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