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RESEARCH ARTICLE

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The biogeography of Gabonese savannas: Evidence from termite community richness and composition

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Abstract

Aim: The mosaic of savannas that persists in the forest-dominant Congo Basin is thought to be palaeoclimatic relics, but past biogeographical processes that have formed and maintained these systems are poorly understood. Here, we explored the post-Pleistocene biogeography of Gabon's savannas using termites as biological indicators to understand historical and mechanistic factors influencing present-day termite communities in the country's extant savannas.

Location: Gabon, Central Africa.

Taxon: Blattodea: Termitoidae.

Methods: Using standardised transect methods, we sampled termite communities in four disjunct modern savanna areas of Gabon: the centre (Lopé), the southeast (Batéké) and the south (Mayombe North and South). Termites at Lopé were collected in three habitats (annually burned savannas, savannas with a depressed fire regime and forest). We used DNA barcoding of the COII region to identify termite species and compared abundance, species richness and community composition across areas and habitats.

Results: Community composition differed greatly between Lopé and both Batéké and Mayombe savannas with Lopé being exceptionally depauperate and lacking characteristic savanna species. Within Lopé, termite abundance and diversity was highest in forests and lowest in annually burned savannas, with a gradual change in species composition across the forest–savanna gradient associated with fire history.

Main Conclusions: The absence of savanna typical species in Lopé savannas challenges current assumptions that these savannas were linked to the south/southeastern savannas during the Pleistocene and suggests a different evolutionary history. Lopé savannas may instead have opened as an isolated grassland and never have been contiguous with neighbouring savannas, or were isolated soon after forest expansion began and have now lost savanna-typical species. Furthermore, the patterns of

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termite community composition in fire suppressed savannas support a hypothesis of rapid change driven by fire frequency where either fire suppression or infrequent burning over 23 years has meant savannas have become ecologically much more forest-like.

KEYWORDS
biogeography, Central Africa, DNA barcoding, fire, forest, Gabon, savanna, termites

1 | INTRODUCTION

The C4 grasses that dominate tropical grasses biomes (savannas and grasslands) emerged in the late Oligocene some 30 Mya. Their expansion in Africa between 10 and 15 Mya during the Miocene (Charles-Dominique et al., 2016; Davies et al., 2020) was a major driver of grass diversification (Spriggs et al., 2014). This expansion is thought to have been linked to increased aridity, declining atmospheric CO_2 levels and enhanced fire activity (Charles-Dominique et al., 2016; Hoetzel et al., 2013). There has been a constant dynamic between forest and savanna cover on the African continent ever since. During the last glacial maximum, previously forested areas of the continent including the Congo basin rainforests, retreated and shrank, with grassland expansion facilitated by fire (Keeley & Rundel, 2005), low CO_2 (Cerling et al., 1997) and mammalian herbivory (Charles-Dominique et al., 2016), making savannas the most extensive vegetation cover in Africa throughout the Pleistocene (Bond & Zaloumis, 2016).

In contrast, post-Pleistocene climatic conditions have favoured forest expansion, and what is commonly termed the 'Congo Basin' (but includes both the Congo and Ogooue river basins) now holds the second largest tropical rainforest on the planet and is one of the world's most biodiverse ecosystems (Myers et al., 2000). These forests cover about 2.4 million km^2 (Schwartz et al., 2000). The biogeographical contexts in which tropical grassy and forest systems have evolved, and how they have responded to climatic changes and anthropogenic impact remains poorly understood. This study uses termites as biological indicators to understand past and present interactions between forest and savanna biomes, focusing on savanna and forest systems in Gabon.

Today, although the Congo Basin region is mainly dominated by tropical forests, almost 40% of its vegetation cover is savanna grasslands (de Wasseige et al., 2009; Solbrig et al., 1990). These grasslands can be divided in two categories: savannas located at the edges of the equatorial forest block (South Congo and North Cameroon), and savannas enclosed within forests (White, 1983). These grassy formations are an important habitat for a significant number of faunal and floral species (Vande Weghe, 2011). Nevertheless, the continued existence of such savannas in humid tropical environments where forests currently dominate has raised questions and controversial debates on their ecological drivers.

The savannas now present in Central Atlantic Africa were first thought to be ecosystem anomalies because they occur in climatic conditions known to be favourable to humid tropical forests (Aubréville, 1949, 1967). Archaeological findings lend support to the anthropogenic origin of Congo Basin savannas, caused by human-originated fires (Aubréville, 1967; Schnell, 1976). However, subsequent palaeoecological studies showed that these savannas emerged and extended in the Congo Basin region during the glacial period, specifically during the last glacial maximum between 20,000 and 10,000 years BP (Aubréville, 1962; Dupont et al., 2000; Edwards et al., 2010; Giresse et al., 2020; Lanfranchi et al., 1990; Maley, 1996; Oslisly et al., 2006; Schwartz et al., 2000) and thus provided evidence supporting their palaeoclimatic, rather than anthropogenic, origin. δC^{14} and δC^{13} analysis of sediments found a significant presence of C4-type vegetation characteristic of tropical grasses (Aubréville, 1962; Dupont et al., 2000; Edwards et al., 2010; Giresse et al., 2020; Lanfranchi et al., 1990; Maley, 1996; Oslisly et al., 2006; Schwartz et al., 2000) implying that the vegetation of Central Atlantic Africa was largely dominated by grassy biomes during the last glacial maximum. The landscapes differed from now, with savannas covering large areas, and forests confined to a few refuges (Aubréville, 1962; Dupont et al., 2000; Edwards et al., 2010; Giresse et al., 2020; Lanfranchi et al., 1990; Maley, 1996; Oslisly et al., 2006; Schwartz et al., 2000). At the end of the last glacial maximum, around 12–18,000 years BP, the forest began to expand, a process which continues today, with a maximum forest expansion between 9000 and 3000 years BP (Maley & Brenac, 1998). The forest expansion progressively reformed the landscape of the Congo Basin into mosaics of forest–savanna (Dupont et al., 2000; Leal, 2001; Oslisly et al., 1996; White, 2001; White & Abernathy, 1996). Today, to the west of the Central African forest basin, the middle Ogooué savannas of Gabon (Aubréville, 1967) represent a reduced model of the forest and savanna mosaic landscapes thought to be previously widespread and typical of the region. Just how the expansion and contraction of forest and savanna has influenced the biota of this region remains poorly known. Exploring differences in biota across this region enable past biogeographical processes to be understood better.

Gabon is situated on Africa's west coast on the south-western edge of the Congo Basin Forest block and bisected by the Equator (Figure 1). Savannas cover less than 10% of the country while forest cover occupies 88% (Sannier et al., 2014). The most extensive expanses of savannas are in the south (Mayombe) and southeast (Batéké Uplands) of Gabon. These two zones are the most northwesterly extents of the Anglolan savannas to the south which link to southern Africa (White, 1983). Smaller areas of savanna are found along the Gabonese Atlantic coast and around Lopé in the

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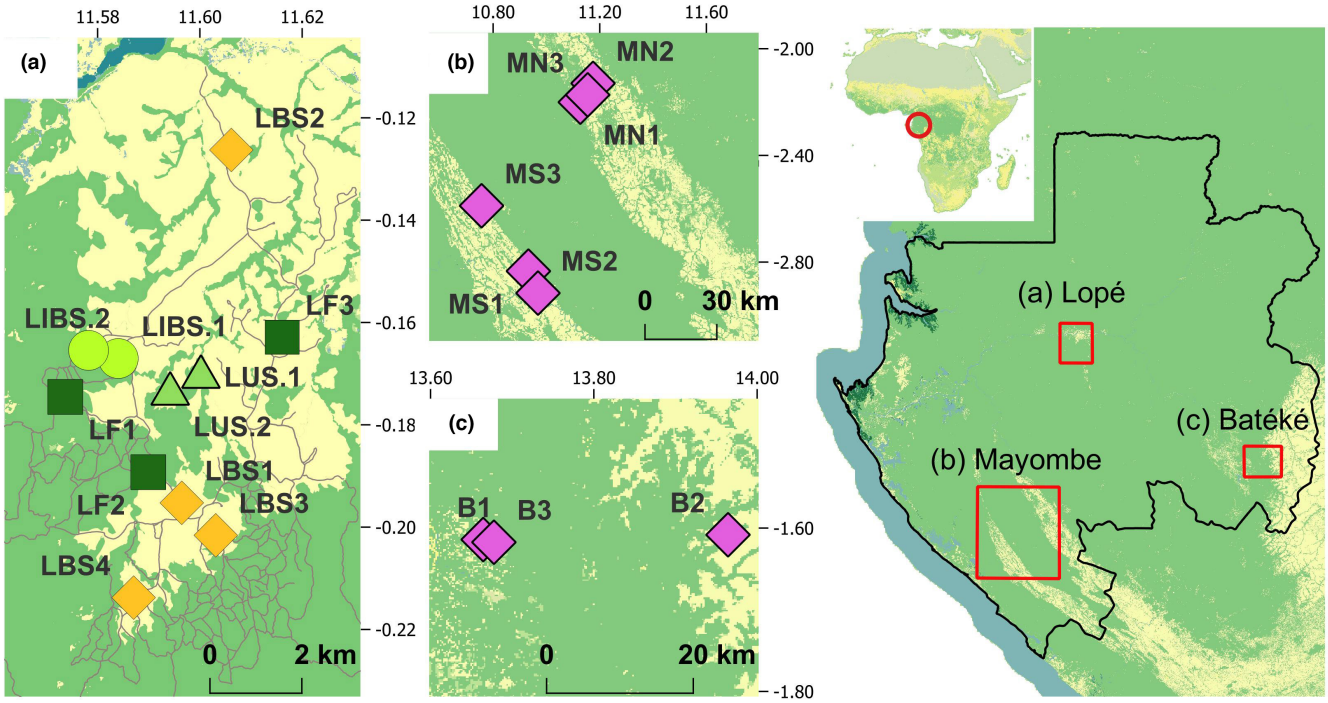

FIGURE 1 Sampling locations of termites in Gabon, with detail of the four main sampling areas as follows: (a) Lopé (b) Mayombe North (MN) and Mayombe South (MS) and (c) Batéké. Green = forest; pale yellow = savanna, blue = water, coloured symbols = transect locations, where for Lopé, orange diamonds = burned savannas, pale green circles = infrequently burned savannas, green triangles = unburned savannas and dark green squares = forest, and for all other sites purple diamonds = burned savannas. Decimal degrees of latitude–longitude are shown on the inset map borders.

middle Ogooué valley in central Gabon, where small pockets of enclosed savannas are present (Aubréville, 1967). All of Gabon's savannas have been considered to be palaeoclimatic relics of the Quaternary (Oslisly & White, 2000). Yet from the most recent glacial fluctuations (2800 and 2000 years BP) to today, these savannas have continued to shrink, gradually increasing in tree cover (Mitchard et al., 2009; Mitchard & Flintrop, 2013). Despite this tendency, recolonisation of savannas by forests has been retarded by frequent anthropogenic fires for hunting and agriculture, made possible by an annual dry season across the region (Oslisly et al., 2013).

Bantu peoples have been present in Gabon since at least 2400–2300 years BP (Oslisly & Peyrot, 1992); a population hiatus between 1400 and 700 BP coincided with the absence of fire and accelerated expansion of forests into savannas (Oslisly et al., 2013; Sankaran et al., 2005; White et al., 1995). Currently, a prescribed annual burning plan in the savannas of Lopé NP National Park (begun in 1993) contributes to the maintenance of these savannas (Jeffery et al., 2014). All other savannas in the country are burned by local people, following various adapted traditional fire regimes but typically an annual or even bi-annual burn is applied, although regimes are variable between and within years (Vande Weghe et al., 2016; Walters, 2015). The regular and documented burning of the Lopé savannas make it the ideal site to study fire impacts on the forest–savanna dynamic. Beyond the use of fire, savanna persistence at Lopé is also supported by the local microclimate, characterised by low rainfall, with levels now around 1450 mm/year, which is well below the minimum thought necessary to support rainforest cover (Bush et al., 2020).

Particular biotic indicators, markers of the evolution of ecosystems, could allow us to better understand past biogeographical contexts and determine how these ecosystems responded to climatic changes on a millennial scale (Davies, 2001; Eggleton, 2000; Eggleton et al., 1994). Termites play a fundamental functional role in tropical ecosystems (Ashton et al., 2019; Jouquet et al., 2011). They play key roles in terrestrial ecosystems through the decomposition of dead plant matter (Jouquet et al., 2011), the decomposition of much of the litter (Ashton et al., 2019; Eggleton, 2000; Griffiths et al., 2019), and bioturbation and enhancing soil drainage (Jouquet et al., 2011). In short, as ecosystem engineers, they contribute to the redistribution of organic matter and minerals in ecosystems, and therefore to the growth and diversity of vegetation (Fox-Dobbs et al., 2010; Jouquet et al., 2006). Termites are relatively easy to sample (Jones & Eggleton, 2000), and sensitive to ecosystem disturbances (Dibog et al., 1999; Eggleton, 1997; Eggleton et al., 1996; Gathorne-Hardy & Eggleton, 2001). They have been shown to have limited dispersal ability across biome boundaries (Gathorne-Hardy, Collins, et al., 2000; Gathorne-Hardy, Jones, & Mawdsley, 2000). The composition of termite communities can therefore reflect historical ecosystem patterns, making them ideal bioindicators for studying Quaternary environmental change (Davies, 2001; Eggleton et al., 1994; Jones & Eggleton, 2000).

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Previous studies have shown that termites are more diverse in forests than in savannas (Eggleton et al., 1996; Jones & Eggleton, 2000). Termite abundance and diversity in African savannas are not greatly affected by fire (Davies et al., 2012; Kouakou, 2015) with savanna species more resistant to fire than those whose biogeographical history is linked to forests (Davies et al., 2010). However, there is some suggestion that species in mesic savannas are more sensitive to fire as different fire regimes can result in very different vegetation (Beale et al., 2018; Davies et al., 2012). The effect that fire has on the diversity and composition of termite communities can therefore provide us with additional evidence to understand what biogeographical changes have occurred.

Research on termite ecology in central Africa has been limited to date; however, some surveys have been undertaken in the Batéké Uplands in the Democratic Republic of Congo (Kifukieto et al., 2014), and a few non-exhaustive studies have also been conducted in Gabon. Studies have focused on soil-feeding termites in Gabonese forests, particularly emphasising the dominance of two Termitidae sub-families, the Apicotermitinae and Cubitermitinae (Harry, 1998; Scholtz, 2010). All of this previous work was conducted in forest ecosystems and identification was not undertaken beyond genus level. The abundance, composition and variability of the termite communities in Gabonese savannas therefore remain undocumented.

The main aim of this study was to explore the biogeographical history of Gabonese savannas using the termite communities as biological indicators, and to understand how certain factors (habitat, fire and age of ecosystems) could influence termite distribution. We focused specifically on the following research questions:

Question 1: How does the abundance and richness of the termite community differ among regularly burned Gabonese savannas?

Question 2: Does the termite species composition of the isolated savannas at Lopé indicate a possible past link to one or other of the larger savanna areas?

Question 3: What influence do long-term fire regimes have on the abundance, richness and composition of termite communities in forest–savanna mosaic type savannas?

Across mesic savannas in Gabon that are broadly similar in fire and climatic conditions, we expected that there would be no significant difference in termite abundance or richness, but that the areas might differ in species composition due to their geographical distance and biogeographical barriers (Q1). We expected that the species composition of the Lopé savannas might associate more closely with one or other of the larger savanna areas, indicating possible contiguity between them when savannas were more widely spread in the region (Q2). Under this general hypothesis, we predicted that a closer link was more likely between Lopé and Batéké than between Lopé and the Mayombe savannas, because the latter are separated by the Chaillu Mountain range which retained forest cover during the last glacial maximum (Lanfranchi & Schwartz, 1990; Sosef et al., 2004). We also expected a much higher richness and composition of termites in forests than in savannas, but to see no impact of fire on termite abundance or richness within savanna communities, because savanna species tend to be adapted to fire, that is, little difference between regularly burnt and long unburnt (Q3).

2 | MATERIALS AND METHODS

2.1 | Sampling sites

Termite sampling was undertaken in four distinct savanna systems that occur across Gabon: Mayombe North, Mayombe South, Batéké and Lopé (Figure 1 and Table S1). All form part of the West Congolian Forest–Savanna Mosaic (White, 1983), and while influenced by an equatorial climate, a climatic gradient occurs between the equator and the southern part of the country.

- **Mayombe North** forms part of a large finger of savanna that extends into south-eastern Gabon from the much larger savannas of southern Republic of Congo and Angola (Vande Weghe, 2012). The area is under the influence of a transitional equatorial climate regime, with a long dry season between July and September. Average annual rainfall is 2198 mm (range: 1468–2937 mm) and annual average temperature is 26°C (Ministère de l'Education Nationale de la République Gabonaise et al., 1983; Vande Weghe, 2012). Savannas are customarily burned each year by local communities who practice swidden agriculture, grazing and hunting (Vande Weghe, 2008; Walters, 2015). However, fires are set irregularly and savannahs may be burnt once or several times a year as burning is not managed or controlled (King et al., 1997). Sampling in the Mayombe N area was conducted near the town of Mouila, where three transects were established in frequently burned savannas (Table S1; Figure 1b).
- **Mayombe South** forms part of a second finger of savanna that runs parallel to the MN savannas, also connected to the larger savannas of southern Republic of Congo and Angola (Vande Weghe, 2012). The area is considerably drier than Mayombe N, with average annual rainfall is 1489 mm (range 1937–1230 mm) but temperatures are similar. Savanna burning practices are the same as for Mayombe N (Vande Weghe, 2008, 2012; Walters, 2015). Sampling in the Mayombe S area was conducted near the town of Tchibanga, where three transects were established in frequently burned savannas (Table S1; Figure 1b).
- **Batéké** is located in the extensive open grassy savanna systems and forest–savanna mosaics of the Batéké Plateaux in the SE of Gabon, which extend east and south into the Republic of Congo and the Democratic Republic of Congo. The area has a transitional tropical regime with a well-defined, long dry season from June to August and a long rainy season between September and May. Average annual rainfall is 2015 mm (range 2000–2250 mm/year: [Ministère de l'Education Nationale de la République Gabonaise et al., 1983; Vande Weghe, 2008]) and average annual temperature is 25°C (Vande Weghe, 2008). Savanna burning practices are the same as for Mayombe N and Mayombe S (Walters, 2015). Three transects were established in savanna in the Batéké area,

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near the towns of Franceville and Bongoville: a forest belt approximately 10 km wide separates the two towns (Table S1; Figure 1c).

- **Lopé** is characterised by a forest–savanna mosaic flanked by continuous forest to the south and east of the study area, and the middle reaches of Gabon's principal river, the Ogooué, to the north (Figure 1a). The enclosed savannas of Lopé date from at least 9000 years BP (Henga, 2021; Oslisly et al., 1996). They are separated from the Mayombe savannas by the forested Massif du Chaillu Mountain range to the south (Lanfranchi et al., 1990), and from the Batéké Uplands savannas in the east by extensive forests (Aubréville, 1967; White, 1983). Lopé is one of the driest areas in Gabon, with an average annual rainfall of 1466 mm (range 1265–1667 mm) (Bush et al., 2020). Average annual temperatures are 25°C in the forest and 26.8°C in the savannas. Fire practices inside Lopé National Park differ from those at the other sampling sites (which were outside protected areas). Here savannas are burned annually, and burning is controlled by the park authorities under a management plan (Jeffery et al., 2014). Some savannas are actively protected from fire; these are more susceptible to the growth of woody vegetation than those that are burned annually (Jeffery et al., 2014). Unburned or infrequently burned savannas therefore represent 'intermediate' vegetation types between frequently burned savannas and forests. To address Question 3, a more detailed sampling strategy was implemented in Lopé. Here, three distinct habitat types representing a gradient from old growth forest to open savanna were sampled: four transects were established in annually burned savannas; four in savannas with a depressed fire regime and three in forests (LF). Of the savannas with a depressed fire regime, two had not been burned for at least 23 years (LUS) and two had an attenuated fire regime, with burns only occurring in between 10% and 50% of the past 23 years (LIBS; Jeffery et al., 2014). Of the forests, two were continuous forest and one was a natural forest fragment (Table S1; Figure 1a).

2.2 | Sampling approach

Termites were sampled using standardised transect methods (Davies et al., 2021; Jones & Eggleton, 2000). Two protocols were used depending on habitat: the first was developed for forest ecosystems and has been widely used in tropical forests around the world (Gathorne-Hardy et al., 2002), and the second was developed for savannas (Davies et al., 2021; Jones & Eggleton, 2000).

At each selected sampling site, transects were established at a minimum distance of 50 m from the nearest forest–savannah edge or any human infrastructure. Transects were marked on the ground with a measuring tape. Each transect measured 200 m^2 (100 m × 2 m) and was separated into twenty 10 m^2 (5 m × 2 m) sub-sections which were marked with a tape before being sampled.

In each sub-section, all microhabitats where termites may be found (e.g., soil, termite mounds, tree trunks, tree buttresses, dead stumps, tree nests, branches and twigs) were manually searched for a set sampling period. In the forest, the complexity of microhabitats necessitated a more intensive sampling effort than in the savannas (Eggleton et al., 1996; Jones & Eggleton, 2000). In the forest each 5 × 2 m sub-section was sampled for 30 min by two people, whereas in savannas, a 10 person-minute search per sub-section was implemented, as described in Davies et al. (2021). Each time termites were encountered, a maximum representative sample of 10 workers and 3 soldiers were collected. In addition, a number of soil pits of 5–10 cm deep were dug (between 6 and 12 per section) and searched for termites during the sampling period. Termites were placed immediately into individual Eppendorf tubes containing 70% alcohol for identification in the laboratory.

2.3 | Termite identification

Termites were identified by DNA barcoding. To extract DNA, individual termites were selected at random from the Eppendorf tubes collected in the field. Each tube, containing termites in ethanol, also had a small identification label inside, which was recorded onto a grid reference template, mirroring the wells of a 96-deep well plate. On removal from the tubes, specimens were first blotted onto tissue to remove excess ethanol and placed into each well using sterilised tweezers. 180 μL of ATL tissue lysis buffer (Qiagen Ltd) and 20 μL proteinase K solution {40 mAU/mg protein} (Qiagen Ltd) were added to each well using a multi-channel pipette and left to digest overnight on a shaking incubator (Corning LSE benchtop shaking Incubator) at 56°C with agitation. After digestion was complete, the lysate was removed using a multi-channel pipette and transferred into a clean 96-deep well plate. DNA extraction clean-up on the lysates was performed on a Qiagen BioSprint 96, using the BioSprint 96 DNA Blood kit (384), following the manufacturer's instructions (Qiagen Ltd).

Polymerase chain reactions (PCRs) were carried out in a 25 μL reaction volume, using the BIOLINE-MYTAQ method, comprising of 15.5 μL sterile water, 5 μL 10× buffer (supplied with *Taq* polymerase) containing 1.5 μL magnesium chloride {50 mM} and 0.2 μL dNTP mix {25 mM}: 1 μL of each primer (Forward primer: MODA_5'-CAGAT AAGTGCATTGGATTT) and (Reverse primer: ILYSB_5'-GTTTAAGA GACCAGTACTTG) at 10 μM, 0.5 μL MyTAQ BIOLINE (Bioline) and 2 μL of gDNA template. PCR cycling conditions for MODA/ILYSB were as follows: 40 cycles at 95.0°C for 30 s, 45.0°C for 30 s, 72.0°C for 45 s and 72.0°C for 10 min.

PCRs were amplified using a GeneAmp PCR system 9700 (Applied Biosystems). All PCR products were separated on a 2% agarose gel and successful amplified PCR products purified using Appleton Woods AxyPrep PCR Magnetic Beads. DNA concentrations of each purified extract were measured using a Nanodrop 8000 DNA spectrophotometer. Any samples outside the concentration required for the fragment size being amplified (700 base pair fragment) were normalised. Forward and reverse samples were set up in separate plates for sequencing using Applied Biosystems BigDye Terminator kit V3.1, and cycled using a GeneAmp 9700 dual block thermal cycler (Applied Biosystems) following the manufacturer's

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guidelines. Samples were then further purified to remove unincorporated dye using Appleton Woods AxyPrep DyeClean Magnetic Beads. Purified reactions were sequenced on an AB 3730xl capillary DNA Analyser (Applied Biosystems) at the Natural History Museum London—Sequencing Facility.

Sequences were aligned using Geneious Prime Software version 2021.2 and identified to species level using the BLAST algorithm in the National Center for Biotechnology Information (NBCI) Genbank database (https://blast.ncbi.nlm.nih.gov/Blast.cgi). The pairwise percentage similarity of each sequence was examined; species-level identity was accepted at 97% and generic-level identity at 95%. Where samples could not be assigned to a species, genus and sequential novel species numbers (i.e. 'sp 1', 'sp 2', etc.) were assigned. Sequence data for each specimen are available at Genbank (Accession codes: ON952588- ON953141). This applied especially to the soldierless Apicotermitinae, where the taxonomy is poorly developed, and many species have not been described or sequenced.

2.4 | Data analysis

DNA barcoding cannot determine the number of individuals contributing to the genetic signature of a species detected in a sample (i.e., Eppendorf tube); thus, a detection was recorded as a single occurrence of each species per sample (Longino et al., 2002). Therefore, to compare the abundance of termites between the four study areas, the total number of samples (Eppendorf tubes) collected per transect was used as an index of relative, rather than absolute, abundance.

Because sampling success differed between habitats, rarefaction (Pearson & Rosenberg, 1977) was used to estimate the number of species expected for each sample, by calibrating to a standard number of individuals ($n = 16$, the smallest number in the whole sample). This method allowed us to obtain comparable species richness values among sites with different sampling effort (Sanders, 1968). Generalised linear models (GLMs) were used to estimate mean abundance and mean rarefied species richness for each habitat and site. GLMs for rarefied species richness were fitted with a Gaussian (identity-link) distribution. Abundance data were overdispersed and were therefore fitted with a negative binomial (log-link) distribution. Model fit was assessed following Zuur et al. (2010). To compare mean rarefied species richness and abundance between habitats and sites, we estimated marginal means with *P*-values adjusted using the Tukey method (emmeans R package) (Lenth et al., 2021).

To visually compare taxonomic similarities in the termite community among sites and habitats, we used non-metric multidimensional scaling (NMDS) and agglomerative hierarchical clustering applied to a Bray–Curtis dissimilarity site × species matrix. Statistical analysis was performed using RStudio version 4.1.1 (R Core Team, 2021). Negative binomial GLMs were fitted using the MASS R package (Venables & Ripley, 2002). Clustering was performed using the vegan, cluster and dendextend R packages (Galili, 2015; Mächler et al., 2012; Oksanen et al., 2020).

3 | RESULTS

3.1 | Relative abundance and species diversity (Question 1)

A total of 1336 termite samples (i.e., individual Eppendorf tubes containing termites) were collected (Table 1). Species-level identification of these samples revealed 108 species (see Table S2), 107 of which were Termitidae, with one species of Rhinotermitidae. Seven subfamilies of Termitidae were present, the most common being the Apicotermitinae (57 species) followed by Cubitermitinae (19) and Termitinae (15).

Rarefied species accumulation curves revealed a clear difference between habitat types in sampling completeness (Figure 2). The curve almost reached its asymptote for the burned savannas particularly at Lopé, suggesting that the sampling here was successful at capturing most species. However, more generally the forest transects and long unburned savanna transects had species accumulation curves that

TABLE 1 Summary of collection effort at each sampling area.

			Abundance		Diversity	
Sampling area	Habitat type	No. of transects	No. of samples	Median per transect	No. of species[a]	Median per transect
Mayombe North (MN)	Burned Savannas	3	197	66	26	16
Mayombe South (MS)	Burned Savannas	3	166	56	17	11
Batéké (B)	Burned Savannas	3	122	41	27	12
Lopé (L)	Burned Savannas	4	131	34	8	4
	Unburned (2) and infrequently burned (2) Savannas	4	155	38	43	12
	Forest	3	565	178	65	28
	Total	20	1336		108	

[a]Note that some species were found at multiple sites, so the total number of species identified does not equal the sum of the number of species found at each site.

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clearly did not reach an asymptote (Figure 2). This means that species richness estimates were not complete in these study areas, and species richness differences between burned savannas and other habitats are thus likely to be underestimated by our analysis (Figure 2).

A total of 616 samples were collected across all burned savannas: 131 at Lopé, 197 at Mayombe N, 166 at Mayombe S and 122 at Batéké (Table 1). The mean relative abundance of termites differed among the burned savannas, and Lopé had significantly lower mean abundance than the two Mayombe savannas (Figure 3a; Table S3). Mean abundance for the Batéké savanna was intermediate between the Lopé and the Mayombe savannas (Figure 3a).

In all, 52 species were identified in Gabon's frequently burned savannas: 8, 26, 17 and 27 were found at Lopé, Mayombe N, Mayombe S and Batéké, respectively (note that as individual species were found at multiple sites, the total number of species identified for any combination of sites does not equal the sum of those sites). This indicated that Lopé burned savannas were species poor compared to other burned savannas. Rarefied richness analysis (Figure 3b) of all burned savanna sites showed Lopé had significantly lower rarefied species richness than Mayombe N but species richness was otherwise similar among the burned savannas (Figure 3b; Table S4). Not only were Lopé burned savannas species depauperate compared with the other burned savanna areas, but characteristic savanna taxa found at other sites (such as *Trinervitermes* sp and *Nitiditermes sankurensis*) were also absent at Lopé (Table S2).

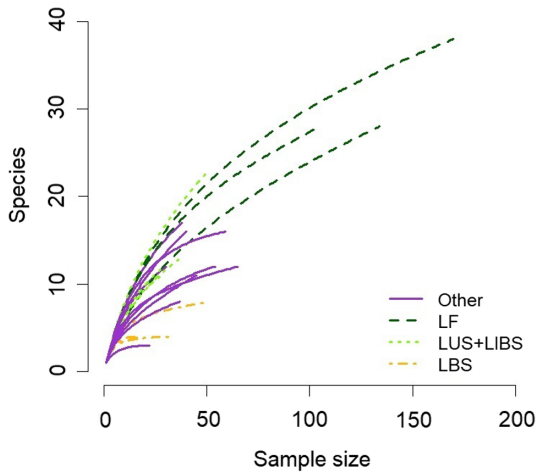

FIGURE 2 Species richness rarefaction curve for termites in Gabon, organised by habitat type. Green forest dotted line = Lopé Forest (LF); green dotted line = Lopé Unburned and Infrequently burned Savanna (LUS + LIBS); orange dotted line = Lopé (annually) Burned Savanna (LBS); purple solid line = all other burned savannas (Mayombe N, Mayombe S, Batéké).

3.2 | Community composition in different savanna areas (Question 2)

To examine variation in the composition of the termite communities and possible groupings between different sampling areas, we created a hierarchical clustering dendrogram (Figure 4). Based on species similarities, three main clusters are apparent, with Batéké and Mayombe sites forming one group, and Lopé savannas grouping into two different clusters, depending on the fire history. Not only are Lopé savannas distinct from the other savanna areas, but within Lopé species similarity groupings are in accordance with savanna fire history. Here, savannas that have not burned for at least 23 years group with forests, whereas savannas the intermediate fire regime group with those that are burned annually.

3.3 | Termite abundance responses to fire in Lopé (Question 3)

We recorded 851 termite samples across all Lopé sampling sites. The forest habitat (LF) produced 565 termite samples, while unburned savannas (LUS) and burned savannas (LBS) had 155 and 131

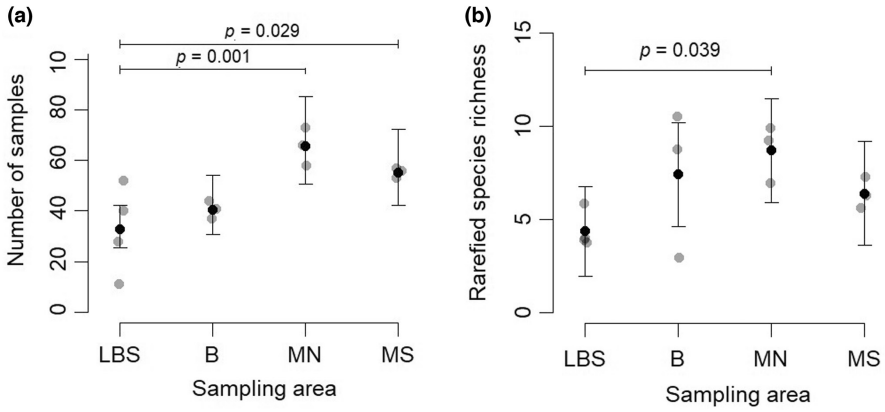

FIGURE 3 (a) Estimated mean termite abundance (black filled circles), 95% confidence intervals and p values (where $p < 0.05$) from the GLM comparing burned savannas across Gabon. Grey filled circles show the raw data for each transect (offset randomly on the x-axis to improve visibility); (b) Estimated mean rarefied species richness (black filled circle) and 95% confidence intervals of termites in burned savannas across Gabon. Grey filled circles show the raw data for each transect. B, Batéké; LBS, Lopé burned savannas; MN, Mayombe N; MS, Mayombe S.

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termite samples, respectively. Mean abundance in the forest habitat was significantly higher than both burned and unburned savannas (Figure 5a; Table S5).

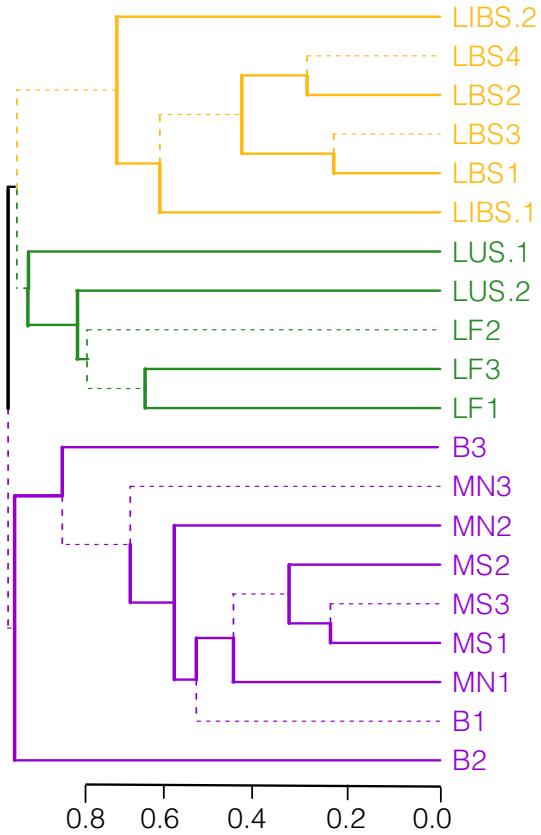

FIGURE 4 Dendrogram of termite species composition similarity between all sampled sites in Gabon. Codes refer to individual transects, where B, Batéké; LBS, Lopé (annually) Burned Savanna; LF, Lopé Forest; LIBS, Lopé Infrequently burned savanna; LUS, Lopé Unburned Savanna; MN, Mayombe N; MS, Mayombe S. The colours distinguish the different habitat types/burn regimes.

3.4 | Species richness in different habitats (Question 3)

Total species richness in the three Lopé habitats was 84 species, 65 of which were found in forests, 43 in infrequently burned and unburned savannas and only 8 in frequently burned savannas (Table 1). Analysis of rarefied specific richness (Figure 5b) confirmed that there was a highly significant difference in richness between LBS and forests but savannas unburned for 13–20 years had a similar richness to forests (Figure 5b; Table S6). Sample sizes were too small to separately compare differences between recently and long-unburned savannas.

3.5 | Community composition across the fire gradient in Lopé (Question 3)

Of the 84 species found in Lope, 65 were found in forests and 46 in savannas; 27 (32%) of these were in common between the two habitat types. Comparing forests with the different savanna categories, 31% of the Lopé species were shared between forest and savannas with a depressed fire regime (LUS and LIBS); for LUS savannas, LIBS savannas and annually burned savannas (LBS) this was 20%, 15% and 4%, respectively.

NMDS showed a strong distinction in community composition between the three Lopé habitats (Figure 6). Unburned savannas clearly make up an intermediate stage between forests and burned savannas and the NMDS also revealed a progressive sequence across the forest–savanna gradient with LIBS savannas being more similar to those that are burned annually, whereas LUS savannas display a termite composition closer to that of forests.

4 | DISCUSSION

At the outset of our study, we asked: (Question 1) How does the relative abundance and richness of the termite communities differ

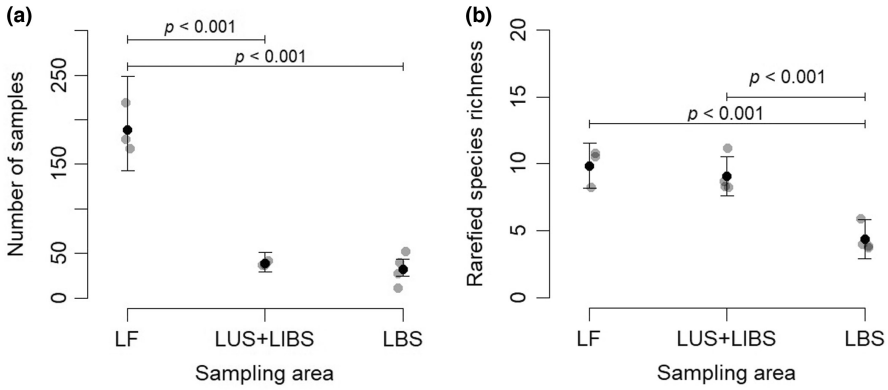

FIGURE 5 (a) Estimated mean termite abundance (black filled circles), 95% confidence intervals and p values (where $p < 0.05$) from the GLM for the three Lopé habitats. Grey circles show the raw data for each transect (offset randomly on the x-axis to improve visibility); (b) Estimated mean termite rarefied species richness in Lopé, from the GLM (black filled circles) with 95% confidence intervals. Grey filled circles show the raw data for each transect (LF, Lopé Forest; LUS + LIBS, Lopé Unburned and Infrequently Burned Savannas; LBS, Lopé Burned Savanna).

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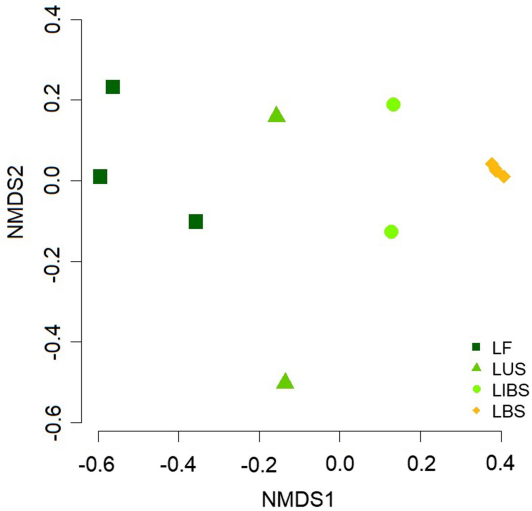

FIGURE 6 Non-metric multidimensional scaling plot of termite communities in Lopé, Gabon (LBS, Lopé (annually) Burned Savanna (yellow diamond); LF, Lopé Forest (green square); LIBS, Lopé Infrequently Burned Savanna (pale green circle); LUS (green triangle), Lopé Unburned Savannas).

among Gabonese savannas (under the same fire regime)? (Question 2) Does the termite species composition of the isolated savannas at Lopé indicate a possible past link to one or other of the larger southern Savanna areas? (Question 3) What influence does the long-term fire regime of frequent fires have on the abundance and richness of termite communities in the savannas of Lopé?

In answer to Question 1, we found that of the four burned savanna areas sampled in Gabon, Lopé had a significantly lower relative abundance (Figure 3a) and rarefied richness of termite communities (Figure 3b) than Mayombe and Batéké. When we compared the termite community compositions across the frequently burned savannas, we found that species found at Lopé did not group closely to either Batéké, Mayombe N or Mayombe S communities. Instead, we found that the species identified in Lopé savanna communities were more different to the other savanna areas than they were to the adjacent forests within the Lopé site (Figure 4), so geographical distance had more of an effect than apparent habitat similarity. Lopé savanna communities were especially species depauperate compared with other similar savannas in Gabon. Strikingly, the low termite diversity in Lopé savannas is also a continental anomaly. Even though termite diversity is generally predicted by rainfall, the species richness of the Lopé savannas is lower than that in comparable high rainfall savannas elsewhere in Africa (Donovan et al., 2002) and just equal to, or lower than, the richness recorded in much more arid savannas elsewhere in Africa (e.g., in Kruger National Park, South Africa), which receives 550 mm per annum, or one-third of the Lopé rainfall (Davies et al., 2012). Within Gabon, species richness broadly followed the predicted rainfall gradient, with the most species found in the higher rainfall savannas (Batéké and Mayombe N), and fewer species found in the lower rainfall savannas (Mayombe S and Lopé). Nevertheless, species richness in Lopé's frequently burned savannas was less than half of that of Mayombe S, which receives similar rainfall.

In answer to Question 2, our data suggest that the four savanna areas in Gabon (Mayombe N, Mayombe S, Batéké and Lopé) have probably experienced differing histories. Mayombe N, Mayombe S and Batéké savannas are linked to the extensive savannas of southern Africa, whose very ancient origins have been proven by numerous studies (Aubréville, 1962; Edwards et al., 2010; Lanfranchi et al., 1990; Maley, 1996; Oslisly et al., 2006). The presence of characteristic savanna taxa *Trinervitermes* sp (Emerson, 1966) and *Nitiditermes sankurensis* (Hellemans et al., 2021), in the Mayombe and Batéké savannas supports the hypothesis of their continuous, long-term connection to extensive savanna systems to the south where savanna-typical termite species have evolved under relatively higher habitat stability than has been the case in Central Africa. However, despite their presence in these savannas, characteristic savanna taxa were notably absent from Lopé (Table S2). The lower species diversity in Lopé savannas was unexpected because previously these savannas have been shown to be relatively ancient dating from at least 9000 years BP (Henga, 2021; Oslisly et al., 1996; Peyrot et al., 2003) and comparable savannas elsewhere in Africa have higher richness (Donovan et al., 2002). However, we note that Lopé savannas are not biogeographically similar to the other Gabonese savannas, despite having similar palaeoclimatic origins rooted in the Quaternary (Oslisly & White, 2000). Those in Mayombe and Batéké are located along the southern edge of the equatorial forest block. In contrast, Lopé's savannas are enclosed within large forest blocks. Lopé savannas are also fragmented (forest–savanna mosaics) by gallery forests and small forest groves (Hiol et al., 2014). In addition, the soils of the Lopé savannas are very low in organic content (Chiti et al., 2018; Cuni-Sanchez et al., 2016).

The lack of specialist savanna termites in Lopé (Table S2) suggests that either (1) the Lopé savannas form an 'island' in a sea of forest that was never connected to a greater savanna extent and never colonised by savanna-adapted species or (2) past connections were short-lived and the savanna specialist species that may have found themselves isolated in the Lopé area have since stochastically died out through a process of island species attrition (Benchimol & Peres, 2015; Jones et al., 2016). Dating to at least 9000 BP (Henga, 2021), it is possible that the enclosed Lopé savannas are younger than those of the Mayombe and the Batéké Plateaus, which may have persisted for up to 40,000 years (Dechamps et al., 1988). However, the extent of savanna cover in these greater savanna areas is thought to have fluctuated considerably with climatic changes and human activity, making it problematic to define an exact age for them (Nieto-Quintano et al., 2018). Given that termites (as slow dispersers) are likely to require lengthy periods to adapt to and successfully colonise savanna environments, if a savanna island appeared in the forest and was never connected to a source of savanna specialist species, it is possible that not enough time has passed to allow the termite dispersal and speciation to fully run its course. Termite dispersal by flight is limited, as termites are poor fliers (Hu et al., 2007) and are limited by their biparental colony foundation (Nobre et al., 2010). Analysis of the composition of termite communities demonstrates that Lopé savannas and those in the south (Mayombe) or southeast (Batéké) do not share a recent common historical relationship. The hypothesis of a recent biogeographical link between Lopé and either of the two other grassy biome areas therefore appears to be unlikely.

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The composition of the forest termite communities at Lopé was also relatively different from those found in savannas (Table S2). For example, some species such as *Aderitotermes* sp 5, *Anenteotermes* sp 2 and *Odontotermes* sp 2, which are classified functionally and biogeographically as forest species (Kanvaly, 2012), were also found in Lopé savannas.

In answering Question 3, we showed that the fire regime of the Lopé savannas appeared to have a strong influence on community species composition. Annual fires suppress termite abundance and diversity, but both can rapidly increase if burning is stopped. Our NMDS analysis revealed a gradual change in species composition across the forest–savanna gradient, indicating savannas with a depressed fire regime (LUS and LIBS) as an intermediate phase between frequently burned savannas (LBS) and forests (Figure 4). Furthermore, both the NMDS and dendrogram showed that savannas that have not been burned at all for at least 23 years exhibited a species composition much closer to that of forests, whereas even with a reduced fire frequency over the last 23 years (LIBS) savannas with some burning more closely resembled annually burnt savannas than forests (Figures 4 and 6). These results suggest that there may be a 'tipping point' of fire suppression, between savannahs with intermediate burning frequencies (LIBS) and those unburned for at least 23 years (LUS), where savannas become ecologically more forest-like. This result is supported by previous observations showing that unburned savannas in Lopé can rapidly thicken into colonising forest-like habitat around 15 years after burning (Jeffery et al., 2014).

Eliminating fires in Lopé has had the direct effect of shifting the termite community to a forest-associated profile, by forest colonisation of the unburned habitat (Cuni-Sanchez et al., 2016; White, 2001). The development of mid-successional habitats offers not only an altered microclimate through increased woody cover, but also greater diversity in the food sources termites depend upon.

While we might expect that fire has a stronger effect on the abundance and diversity of termite communities in this mesic savanna because fire has a greater effect on vegetation (Beale et al., 2018), the depauperate nature of the burned savanna termite community supports a hypothesis of a migration of forest termite species into the savannas at Lopé, rather than the persistence of a different, savanna specialist and fire-adapted community in the savanna biome.

5 | CONCLUSIONS

Lopé savannas are species depauperate compared with other burned savannas in Gabon, and are biogeographically distinct from either the Batéké or Mayombe areas. It is possible that Lopé savannas opened as an isolated grassland and have never been contiguous with neighbouring savannas, or that they were isolated soon after forest expansion began and have now lost savanna-typical species. Although forest termite species appear to be adapting to use the empty savanna habitat, these forest species have not yet evolved to cope with the fire regime. Eliminating fires, however, allows rapid colonisation of the structurally and functionally more diverse young forest habitat by forest termite species. The patterns of termite community composition in both fire-suppressed and fire-attenuated savannas support a hypothesis of rapid change driven by fire frequency where no burning over 23 years let savannas become ecologically much more forest-like than under an intermediate fire regime. Work on other animal taxa is needed to confirm to what extent similar patterns hold for other groups.

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CONFLICT OF INTEREST STATEMENT

No, there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All biological samples collected for this study are stored at the Natural History Museum of London and remain the property of the Gabonese government. Research authorisation from Gabon's Centre National de la Recherche Scientifique et Technologique (CENAREST) will be required for use of these samples for any other research. R scripts and raw data are archived on Zenodo (DOI: 10.5281/zenodo.6475429). Sequence data have been submitted to the GenBank database under accession numbers ON952588-ON953141.

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BIOSKETCH

Fidèle Evouna Ondo obtained his doctorate degree from the University of Montpellier in France and is a research scientist for Gabon's National Parks Agency. He is interested in models of diversity and ecosystem processes in Gabonese savannas. The SoFIA consortium (Soil & Fauna In Africa) team is interested in the role of soil fauna in African ecology, with a focus in Gabon on the biogeography of termites in savanna and forest ecosystems, their contribution to ecosystem processes and interaction with soils (https://royalsociety.org/grants-schemes-awards/grants/dfid-parr/).

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