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Role of termites in the restoration of soils and plant richness on *bowé* in West Africa

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Abstract

Bowé (hardened ferricrete soils formed by erosion, drought or deforestation) are often associated with termite mounds, but little is known about these mounds and their role in the restoration of soils and plant biodiversity on ***bowé***. This study examined termite mounds on ***bowé*** and their effects on soil depth and plant richness. Sixty-four sampling plots were laid out randomly on ***bowé*** sites with mounds and on adjacent ***bowé*** sites without mounds. The height and circumference of each mound were measured. Species inventories were made and soil depth measured in each plot. Linear mixed effects and generalised mixed effects models with Poisson error distribution were used to assess the variation in soil depth and plant species richness in mound and nonmound microsites. Two types of mounds (small vs. large) associated with different termite species were observed on ***bowé***, with the small mounds being most common. Plots with either large or small mounds had deeper soils and higher plant richness than the adjacent plots without mounds. Conservation of termite mounds is important for restoring soils and plant richness on ***bowé***, and termite mounds should be taken into consideration in biodiversity and soil management strategies for ***bowé***.

Résumé

Les *bowé* (sols ferricrètes durcis formés par l'érosion, la sécheresse ou la déforestation) sont souvent associés aux termitières, mais on sait peu de choses sur ces monticules et leur rôle dans la restauration des sols et de la biodiversité végétale sur les *bowé*. Cette étude a examiné les termitières sur les *bowé* et leurs effets sur la profondeur du sol et la richesse végétale. Soixante-quatre parcelles d'échantillonnage ont été disposées au hasard sur les sites de *bowé* avec termitières et sur les sites de *bowé* adjacents sans termitières. La hauteur et la circonférence de chaque termitière ont été mesurées. Des inventaires des espèces ont été réalisés et la profondeur du sol mesurée sur chaque parcelle. Des modèles linéaires et généralisés à effets mixtes ainsi qu'une distribution des erreurs suivant une loi de poisson ont été utilisés pour évaluer la variation de la profondeur du sol et de la richesse en espèces végétales sur les microsites avec termitières et sans termitières. Deux types de termitières (petites par rapport à grandes) associées à différentes espèces de termites ont été observés sur les *bowé*, les petites termitières étant les plus courantes. Les sols des parcelles

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contenant à la fois de grandes et de petites termitières étaient plus profonds et la richesse végétale y était plus importante que sur les parcelles adjacentes sans termitières. La conservation des termitières est importante pour restaurer les sols et la richesse végétale des *bowé* et les termitières doivent être prises en compte dans les stratégies de gestion de la biodiversité et des sols pour les *bowé*.

KEYWORDS

Benin, *bowé*, plant diversity, soil restoration, termite mounds, West Africa

1 | INTRODUCTION

Bowé are a distinct form of degraded land on hardened ferruginous soils (ferricrete) found in tropical regions with unimodal precipitation. The name originates from the fulfulde language (Aubréville, 1947). *Bowalization* is a result of the exposure of ferricrete due to erosion of the soil surface or soil hardening caused by a combination of drought and deforestation (Padonou, Lykke, Bachmann, & Sinsin, 2015). *Bowé* are characterised by a reduced capacity to retain water, a shallow topsoil and a low content of organic matter, silt and nutrients (nitrogen and extractable phosphorus), but high amounts of exchangeable potassium (Padonou, Bachmann, Kakaï, Lykke, & Sinsin, 2015). *Bowalization* leads to a loss of biodiversity and changes in vegetation structure (Padonou, Assogbadjo, Bachmann, & Sinsin, 2013; Padonou, Bachmann, et al., 2015; Zwarg, Schmidt, Janßen, Hahn, & Zizka, 2012). The vegetation type on *bowé* is typically grassland or savannah, with few trees due to impeded root growth (Padonou et al., 2013). Termite mounds are often found on *bowé* (Aubréville, 1947). In general, many different termite species colonise semi-arid ecosystems in West Africa (Erpenbach & Wittig, 2016; Kaiser, 2014), building mounds of different shapes and colours (Jean-Pierre et al., 2015).

Termite mounds in tropical savannah ecosystems are microhabitats with a high biodiversity and important sources of heterogeneity in the landscape (Dossou-Yovo, Assogbadjo, & Sinsin, 2016; Erpenbach, Bernhardt-Römermann, Wittig, & Hahn, 2017; Joseph, Seymour, Cumming, Cumming, & Mahlangu, 2013). They increase the diversity of woody species in savannahs (Erpenbach & Wittig, 2016; Gbeffe et al., 2017) and likely increase resilience of ecosystems to drought and facilitate local-scale recovery after droughts (Bonachela et al., 2015; Jeltsch, Weber, & Grimm, 2000). The topsoil of plots with termite mounds has higher mineral, clay and silt contents (Erpenbach et al., 2017; Joseph et al., 2013; Konaté, Le Roux, Tessier, & Lepage, 1999; Seymour et al., 2014). The water storage capacity of termite mounds is higher than that of adjacent soils in arid and semi-arid ecosystems (Jouquet, Traoré, Choosai, Hartmann, & Bignell, 2011). However, in nutrient-rich systems, termite mounds may not always have a distinct influence on ecosystem processes and plant diversity (Muvengwi, Mbiba, & Nyenda, 2013; Muvengwi, Witkowski, Davies, & Parrini, 2017).

Termite mounds may play an important part in the prevention of desertification in arid regions and may be used in landscape restoration after severe droughts (Erpenbach & Wittig, 2016). Some studies in the Sahel have shown positive effects of active promotion of termites as part of rehabilitation of degraded landscapes (Kaiser, 2014; Kaiser, Lepage, Konaté, & Linsenmair, 2017; Sawadogo, 2011; Sawadogo, Bock, Lacroix, & Zombre, 2008). Termites promote formation of closed-canopy forest on formerly highly degraded land under the current precipitation regime (Kaiser, 2014; Kaiser et al., 2017). However, little is known about termite mounds on *bowé* and their impact on soil restoration and plant diversity. Termites are important for mineralising organic matter (Erpenbach et al., 2017; Erpenbach & Wittig, 2016; Kaiser et al., 2017), and therefore, sites with termites might have better soils and potentially deeper soils. Moreover, larger mounds would be associated with deeper soils. An understanding of the role of termite mounds in the restoration of soils and vegetation on *bowé* could be used to develop a successful restoration strategy. This work investigated the effects of termite mounds on soil conservation and plant species richness.

2 | MATERIALS AND METHODS

2.1 | Study area

Data were collected in the municipality of Banikoara (11°18′N, 2°25′E), located in the semi-arid zone of northern Benin (Figure 1). The climate is semi-arid with a single rainy season from mid-May to mid-October. The annual mean rainfall is 700–900 mm, and the relative humidity varies between 18% (February) and 99% (August). The annual mean temperature is 30–34°C. The major soil types are hydromorphic, well-drained ferruginous soils and lithosols. The natural vegetation is characterised by a mosaic of woodland, dry forest, tree and shrub savannah, and gallery forest. The area is dominated by *bowé*, on which termite mounds are abundant. The Bariba people are the main ethnic group, and the core economic activities are agriculture and livestock herding.

2.2 | Effect of termite mounds on plant diversity

2.2.1 | Sampling design and data collection

A total of 64 random sampling plots, each 10 m × 10 m in size, were located at seven sampling zones (Sampeto 1, 2 and 3; Samper peulh; Somsoro; Ankoamon; and the core of Park W). Thirty-two

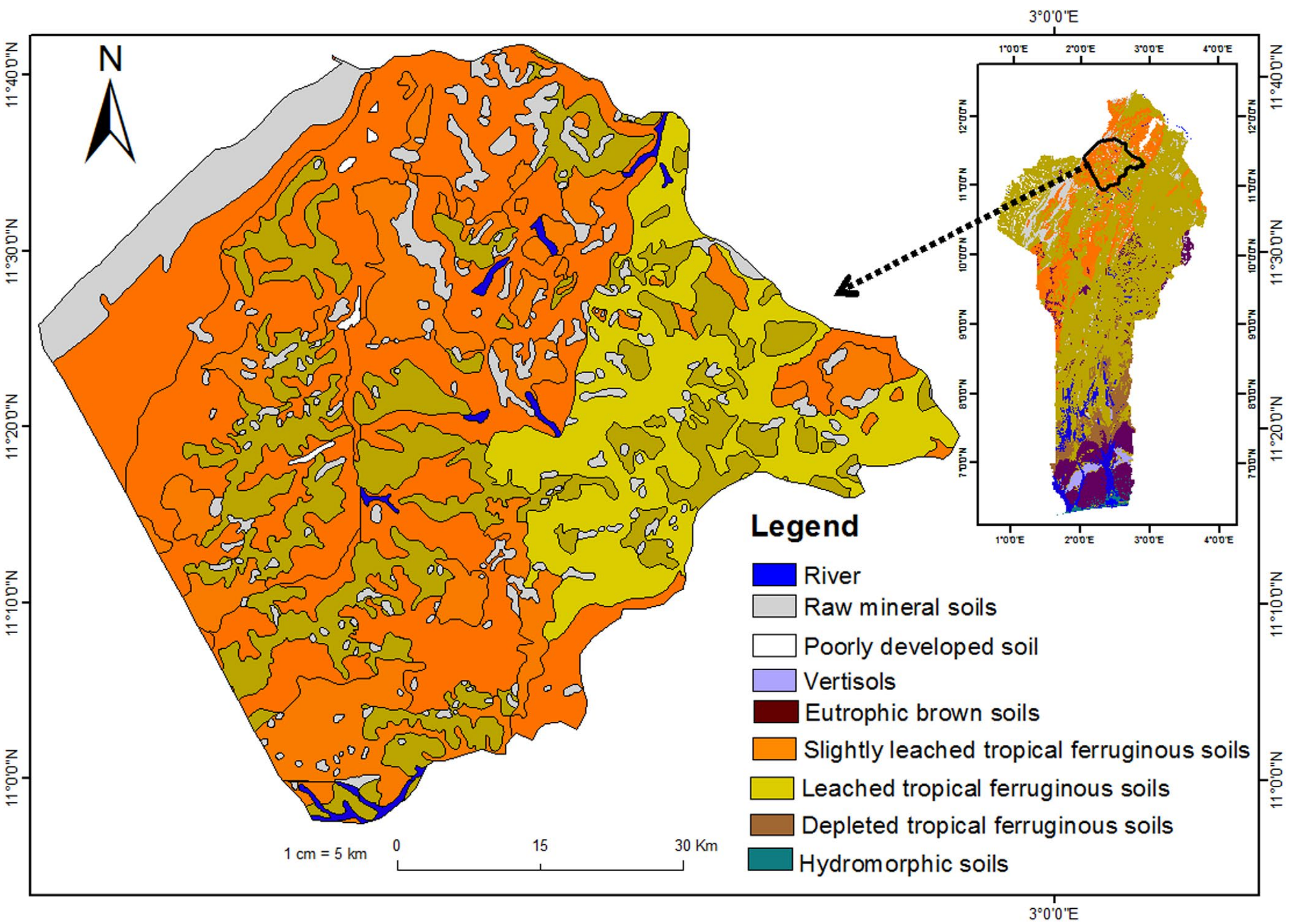

FIGURE 1 Soil characteristics and location of sampling sites in Banikoara, northern Benin

plots were located in areas with an abundance of both large and small termite mounds. For comparison, another 32 plots were located in areas without termite mounds, but within 5 m of the plots with termite mounds. Shape (height and circumference) of termite mounds was measured in each plot. The termite species in each mound were collected and identified at the museum of entomology of the International Institute of Tropical Agriculture in Benin.

Five sub-plots, each 1 m × 1 m in size, were located in the four corners, and the centre of each plot and diversity of herbaceous plant species were sampled using the point-intercept method (Strandberg, Lykke, & Padonou, 2016). The herbaceous plant species were sampled at grid points within a quadrat. At each position, a pin was lowered vertically onto the ground and the first point of contact with a plant species was recorded. The trees were counted and identified to species level in a 10 m × 10 m plot. The species were collected for further identification by botanists at the National Herbarium of Benin. The species nomenclature follows that of the African Plant Database version 3.4.0 (2020, February 3). To measure the depth of the topsoil, holes were dug in the four corners of each 10 m × 10 m plot until the ferricrete was exposed.

2.3 | Data analysis

Descriptive statistics (mean and standard deviation) were used to compare the height and circumference of the termite mounds. Linear mixed effects and generalised mixed effects models with Poisson error distribution were used to assess the variation in soil depth (continuous response) and species richness (count data). We tested the fixed effects of mound size (large vs. small) and presence (termite mound presence vs. control site) and the random effect (sampling zones). All analyses and graphics were implemented in the R 3.5.1 software environment (R Core Team, 2018). The analyses were conducted with the functions *lmer* and *glmer* of the *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017). The function *lsmeans* of the *lsmeans* package (Lenth, 2016) was used to extract the least-squares means of the response variables per level of fixed factors, which were then plotted using *ggplot2* (Wickham, 2016). Tukey's HSD test was used for post hoc test to show the differences between the dependent variables. The random intercepts were extracted using the *ranef* function of the *lmerTest* package to assess the pattern of the response variables across zones. Both marginal (only fixed effects) and conditional (both fixed and random effects)

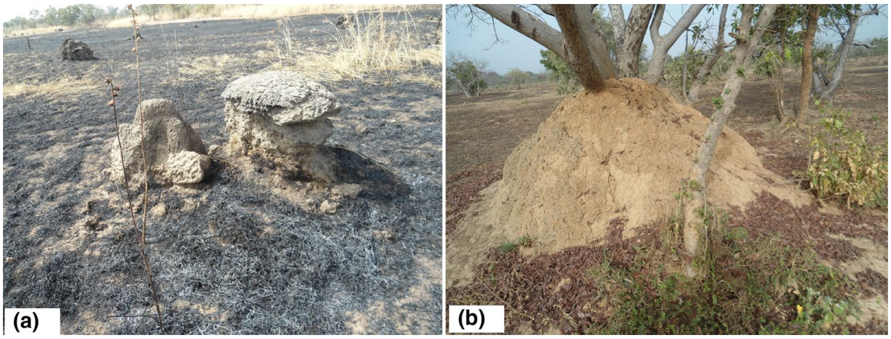

FIGURE 2 (a) Small termite mounds with and without a hat-shaped top. (b) Large termite mound

R-square values were calculated to determine the contribution of fixed and random effects in the explanatory power of the models.

Simpson's Index (D) was used to assess the plant species diversity in plots with presence/absence of termite mounds using the formula below

$$D=\sum (n/N)^2$$

n is the total number of organisms of a particular species, and *N* is the total number of organisms of all species.

The value of *D* ranges between 0 and 1; 0 represents infinite diversity and 1 no diversity. The bigger the value of *D* is, the lower the diversity. As this is not logical, *D* is generally subtracted from 1 to give: Simpson's Index of Diversity 1 − *D*. The value also ranges between 0 and 1, but now, the greater the value, the greater the sample diversity.

3 | RESULTS

3.1 | Morphological characterisation of termite mounds

A total of 84 termite mounds were measured and divided into two types (nine large and 75 small). On average, the large mounds were three times the height (146.78 ± 33.32 vs. 49.63 ± 17.51 cm) and four times the circumference (709.33 ± 350.17 vs. 169.18 ± 64.22 cm) of the small mounds (Figure 2). The small mounds, made by *Cubitermes* spp. and *Microcerotermes* spp., were of blackish colour and mushroom-shaped. *Trinervitermes geminatus* and *T. trinervius* formed small blackish mounds without a hat-shaped top. The large termite mounds were reddish in colour and formed by *Macrotermes bellicosus*. The mean density of small mounds ranged from 41 ± 22 to 68 ± 17 mounds/ha and that of large mounds from 2 ± 1 to 3 ± 0 mounds/ha (Table 1).

3.2 | Effect of termite mounds on soil depth and plant diversity

The presence of mounds had a significant effect on both response variables compared to nonpresence. In particular, the soil depth was higher (27.66 cm, $p < 0.001$) on sites with termite mounds than sites without termite mounds (1.43 cm). Similarly, sites with termite mounds had a higher plant richness (11.00, $p < 0.001$) than sites without termite mounds (4.00). The differences between sites where termites were found and control sites depended on the size of the termite mound, with a larger difference on sites with large mounds compared with sites with small mounds (Figure 3a vs. 3b).

Based on results from the Tukey's HSD tests, soil depth was significantly higher ($p = 0.026$) from plots with large mounds (28.40 ± 13.32 cm) when compared to plots with only small mounds (14.73 ± 8.51 cm). Species richness was higher where mounds were present (12 ± 3 and 10 ± 2 for large and small mounds, respectively) than in the control sites (3 ± 1 and 4 ± 2 for large and small mounds, respectively).

The random effect of sampling zone was significant on soil depth (R^2 conditional (0.7118) > R^2 marginal (0.6673)) and species richness (R^2 conditional (0.6824) > R^2 marginal (0.6544)). Figure 4 shows the random intercept of both responses per zone. Soil depth was highest at Samper peulh, followed by Somsoro, Ankoamon and Sampeto1 and lowest at Sampeto 2, Sampeto 3 and Parc W (Figure 4a). The species richness followed relatively similar pattern (Figure 4b).

There were differences in the plant species composition between the types of plot (Table 2). The plant diversity was higher on plots with mounds (*D* = 0.93 for big mounds and *D* = 0.92 for small mounds) compared to off-mound plots (*D* = 0.81 for off-big-mound plots and *D* = 0.72 for off-small-mound plots). A total of 29 plant species (21 forbs and 8 grasses) were recorded on mounds, whereas 18 species was recorded in off-mound plots. The most abundant species on mounds were *Eleocharis complanata*, *Perotis indica* and *Hyptis suaveolens* for big mounds and *Eleocharis complanata*, *Hyptis suaveolens* and *Alysicarpus*

TABLE 1 Variation of termite mounds in the study sites

	Small mound		Big mound	
Sites	Mean	Std deviation	Mean	Std deviation
Ankoamon	49	27	2	0
Parc W	74	6	3	0
SAMPER peulh	53	17	3	0
Sampeto 1	68	17	2	0
Sampeto 2	60	21	2	1
Sampeto 3	52	18	2	1
Somsoro	41	22	2	1

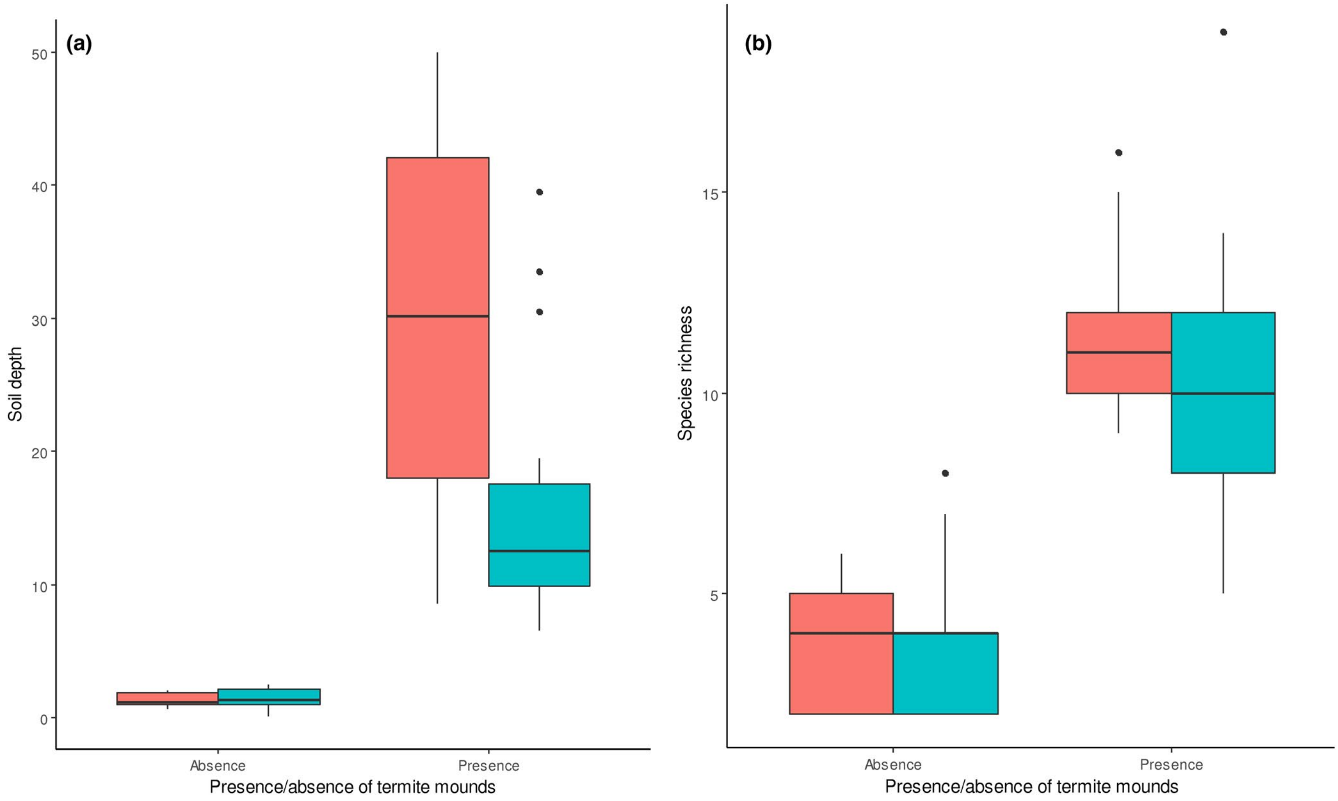

FIGURE 3 Variation in soil depth (a) and species richness (b) according to the presence or absence of termite mounds on *bowé*. Orange colour: big mound; green colour: small mound

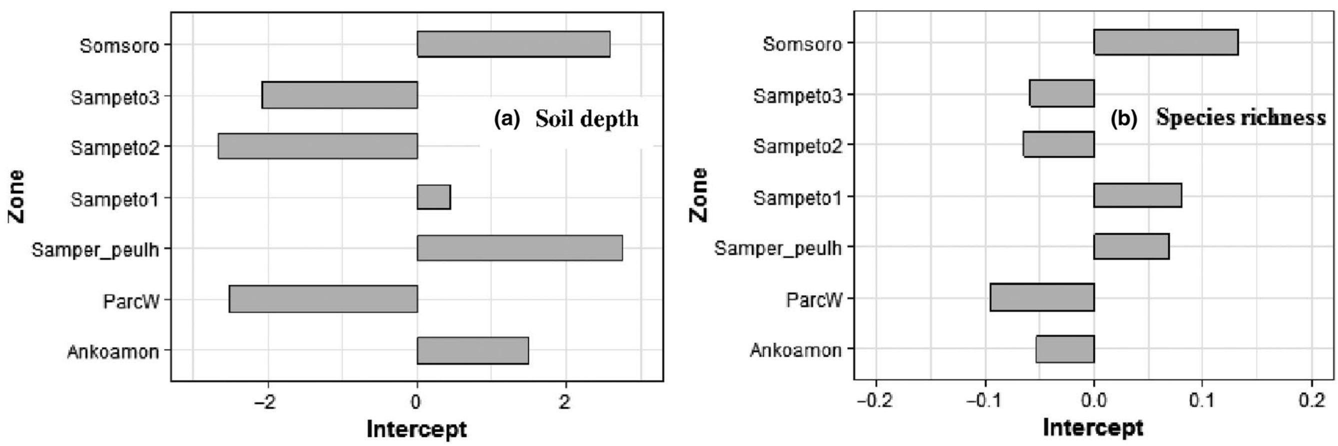

FIGURE 4 Random effect of zone on soil depth (a) and species richness (b)

ovalifolius for small mounds, while on off-mound plots *Eleocharis complanata* and *Andropogon pseudapricus* were most abundant in off-big-mound plots and *Eleocharis complanata*, *Perotis indica* and *Hyptis suaveolens* were most abundant in off-small-mound plots (Table 2).

4 | DISCUSSION

A significant difference in soil depth was observed between plots with and without termite mounds. The plots with termite mounds had deeper soil than the plots without mounds. Termites therefore have an important role in soil restoration, as reported by Kirchmair, Schmidt, Zizka, Erpenbach, and Hahn (2012) and Kaiser et al. (2017). The termite mounds are composed of clay and sand, which improve the soil structure and properties on *bowé*, thereby increasing the soil infiltration capacity, promoting microbial activity, and improving the composition and availability of nutrients to plants (Mills, Milewski, Fey, Groengroeft, & Petersen, 2009).

The plant richness increased in the presence of termite mounds, in agreement with previous reports of the effect of

TABLE 2 Abundance of plant species on sites with presence/absence of termite mounds

Plant species	Plots with big mounds	Off-mound plots adjacent to big mounds' plots	Plots with small mounds	Off-mound plots adjacent to small mounds' plots	Type of species
Abutilon abutiloides (Jacq.) Garcke ex Hochr.	13	0	15	1	Forb
Aeschynomene abyssinica Vatke	7	0	30	0	Forb
Alysicarpus ovalifolius (Schumach.) J.Léonard	70	44	240	72	Forb
Andropogon pseudapricus Stapf	0	75	39	127	Grass
Biophytum abyssinicum Steud. ex A.Rich.	16	0	20	0	Forb
Boerhavia erecta L.	25	0	8	0	Forb
Chamaecrista mimosoides (L.) Greene	69	0	24	0	Forb
Cissus quadrangularis L.	14	0	0	0	Forb
Commelina benghalensis L.	0	0	34	0	Forb
Commelina erecta L.	28	0	0	0	Forb
Corchorus olitorius L.	43	4	29	4	Forb
Corchorus trilocularis L.	80	64	141	7	Forb
Eleocharis complanata Boeckeler	151	188	381	725	Grass
Ethulia conyzoides Bojer ex DC.	0	0	8	0	Forb
Flueggea virosa (Roxb. ex Willd.) Royle	1	0	12	2	Forb
Hyparrhenia involucrata Stapf	0	0	39	1	Grass
Hyparrhenia rufa Stapf	7	21	139	58	Grass
Hyptis suaveolens (L.) Poit.	99	32	361	163	Forb
Ipomoea vagans Baker	0	0	1	0	Forb
Mitracarpus scaber Zucc.	73	0	29	0	Forb
Monechma ciliatum (Jacq.) Milne-Redh.	41	0	171	47	Forb
Ocimum americanum L.	37	0	141	0	Forb
Perotis indica (L.) Kuntze	122	66	124	202	Grass
Phyllanthus amarus Schumach. & Thonn.	12	0	31	2	Forb
Rhynchelytrum repens (Willd.) C.E.Hubb.	23	0	136	7	Grass
Spermacoce filifolia (Schumach. & Thonn.) J.-P.Lebrun & Stork	7	5	18	3	Grass
Spermacoce verticillata L.	39	7	5	2	Grass
Tephrosia purpurea (L.) Pers.	54	9	191	25	Forb
Wissadula amplissima R.E.Fr.	27	7	70	56	Forb

termite mounds on plant diversity in similar environments (Davies, Baldeck, & Asner, 2016; Dossou-Yovo et al., 2016; Erpenbach et al., 2017; Erpenbach & Wittig, 2016; Gbeffe et al., 2017; Kirchmair et al., 2012; Moe, Mobæk, & Narmo, 2009; Traoré, Nygård, Guinko, & Lepage, 2008). We found that termites participate in soil restoration and represent islands of richness on *bowé*. This is similar to what was found in semi-arid savannahs in general (Erpenbach et al., 2017; Erpenbach & Wittig, 2016; Kifukieto et al., 2016; Moe et al., 2009).

The result of the random effect of sampling zone on soil depth and species richness suggests that the location plays an important role on the influence of termite mounds. Soil depth and plant species richness with presence/absence of termite mounds were highest at Samper peulh, Somsoro, Ankoamon and Sampeto1 and lowest at Sampeto 2, Sampeto 3 and Parc W. Often differences among sites are larger than differences between presence/absence of termite mounds. This confirms the findings of Muvengwi et al. (2013 and 2017). However, the presence/absence of termite mounds has the same significant impact within each sampling site. Presence of termite mounds increases soil depth and plant species richness than absence of mounds in all sampling sites.

Five metre was considered as distance between plots with and without mounds despite some termites, particularly *Macrotermes*, having very large territories, which means that the plots without termite mounds might still be influenced by termite activity and therefore might not be independent. However, the mounds play a much bigger role than other termite building such as foraging tunnels and structures.

The density of large termite mounds on *bowé* was low compared to the density of small termite mounds. Similar results in the number of mounds per hectare were found by Tano and Lepage (1990) for Sudanian savannah in West Africa. Jean-Pierre et al. (2015) found 9–10 small and 8–12 large mounds/ha on ferralitic soils in humid forest in West Africa with a mean rainfall >1,800 mm and two rainy and two dry seasons in contrast to 41–68 small mounds/ha and 2–3 large mounds/ha in this study. The low density of large mounds on *bowé* in our study sites may be because the ecological conditions do not favour the activities of the *Macrotermes* genus. Moreover, trees struggle to grow on *bowé* and limit the amount of food available for savannah *Macrotermes* species (e.g., *Macrotermes bellicosus*). The termite species in the small mounds has a specific preference for grassland and savannah and is directly related to ferruginous, ferricrete and hydromorphic soils (Tano & Lepage, 1990).

Bowé represent an important part of degraded lands in the Sudanian region of West Africa. The Sudanian region covers 6.7 mill ha in Benin. The type of land where *bowé* occur (farmland and degraded savannah in the Sudanian zone) increased at a rate of 10 ha/year in the period 1990–2010 with 53% of the region converted to degraded savannah and farmland (Padonou, Lykke, Bachmann, Idohou, & Sinsin, 2017). *Bowalization* would persist and increase in the future if no restoration action is taken. It is therefore important to develop restoration measures on *bowé*. These measures should include the conservation of termite mounds on *bowé* due to their importance in plant diversity and soil restoration. Moreover, some native plant species are adapted to *bowalization* and are resistant to climate change in northern Benin (e.g., *Asparagus africanus*, *Andropogon pseudapricus* and *Combretum nigricans*) (Padonou, Teka, et al., 2015). These species could be used on *bowé* in association with the termites.

5 | CONCLUSIONS

The termite mounds significantly increased soil restoration, plant richness and plant diversity on *bowé*. The soil depth was significantly higher in sites with large mounds compared to sites with only small mounds. The conservation of termite mounds is therefore important for soil restoration and plant diversity management and should be taken into account in strategies of soil restoration and biodiversity conservation on *bowé*.

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CONFLICT OF INTEREST

The co-authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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