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Bryophytes associated with termite mounds on the northeastern Nigerian highlands

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ABSTRACT
Eighteen termite mounds on a stretch of undulating continuously grazed and burnt grasslands on the Mambilla Plateau, Eastern Nigeria, were surveyed for bryophytes. Bryophyte mats were present on all mounds investigated except one. The bryophyte mats were located at the base of the mounds, on a depression etched by raindrops and apparently serving to keep erosion at bay. We suggest that on grasslands with frequent fire episodes, the bryophyte mats may also play a role in fireproofing the mounds. In all, eight bryophytes species across five families were collected on the termite mounds. All species were new to the region but had been collected elsewhere from different substrates in Nigeria, except *Fissidens ezukanmae* Brugg.-Nann., which is a new species collected for the first time from termite mounds on Eastern Nigerian Highlands. Two species, *Campylopus obrutus* Thér. & P. de la Varde and *Fissidens intramarginatus* (Hampe) A.Jaeger, with estimated frequency of 24% each, were the most abundant species on the termite mounds.

KEY WORDS
Africa, Archidium, grassland, Mambilla Plateau, mosses, Nigeria.

MOTS CLÉS
Afrique, Archidium, prairies, Plateau Mambilla, mousses, Nigéria.


RÉSUMÉ
Bryophytes associés aux termitières dans les hauts plateaux du nord-est du Nigéria.
INTRODUCTION

In the tropics, naked undisturbed soil is a seldom-used substrate for bryophytes (Richards 1984), apparently due to the absence of a well-developed humic layer on the forest floor as a result of the high rate of decomposition, which renders the soil almost bare of bryophytes (Gradstein 1992; Frahm 2003). Conversely, disturbed soil has a unique bryoflora dominated mostly by species of Fissidens Hedw. (Pócs 1982; Richards 1984). Termite structures may have the appearance of bare soil but they are not entirely equivalent to naked soil. The termite structures present a durable surface with an elevated nutrient profile due to the enriched organic substances from termites, like saliva and faeces used during the construction of these structures (Harris 1956; Ackerman et al. 2009).

Termite mounds are known to have remarkable impact on their surroundings (Yamashina 2010). In Kenya and Australia, several species of plants are known to thrive on termite mounds and support the herbivore populations which prefer to feed on plants growing on the mounds (John & Stein 2004; Ragnhild et al. 2005). The rich nutrient contents of the soil on the mounds enhance its use as fertilizer for field cultivation in South Africa (Coaton 1950) and Amazonia (Batalha et al. 1995). In Kenya and Zambia, the soil of termite mounds is a rare delicacy, especially for pregnant women, and is eaten and exchanged as a precious and expensive food because of its rich mineral content (Yamashina 2010).

In most cases, the termite mound is not a fortuitous heap of earth but a construction mediated by an intricate interplay of species behavior, available material, climate and elevation (Harris 1956). The soil that is available at any particular location determines the shape of the mound. Tall, thin mounds have a sand to clay ratio of 1:1 to 3:1, while larger dome-shaped mounds range from 2:1 to 18:1 (Hesse 1955). Coaton (1947) observed an inverse proportion of mound size of the termite Macrotermes bellicosus Smeathman with increasing elevation. At the upper limits of its range in the Highlands of East Africa at approx. 1800 m above sea level, the mounds are low, rounded domes with a gradual increase in size as one descends to lower elevations. The most profound effect of climate on termite mounds is caused by rainfall (Harris 1956). Falling rain erodes away turrets and pinnacles, which are constructed mostly during the rains, thereby producing a dome-shaped mound. Harris (1956) suggested that the intensity of precipitation is more important than overall annual rainfall.

Some bryophyte species are associated with the termite mounds which serve as surrogate substrate for species that preferentially dwell on disturbed soil (Reese & Pursell 2002). The shingling effect provided by the flattened, overlapping fronds of the tiny moss plants and the soil-binding effect of the moss rhizoids facilitate drainage of the raindrops. In addition, the springy stems of the moss plants attenuate the impact of raindrops, depleting their energy and dissipating their impact. These add to the long-term stability of the termite structure (Reese & Pursell 2002). Species of the genus Fissidens are the most common associates with termite mounds in tropical America (Churchill 1998), but Reese (2001) and Lisboa (1993) listed several species of Calyptraceae and Pilotrichaceae associated with termite mounds in Amazonia. Likewise, in parts of Africa, various Fissidens species have been collected from termite mounds (Potier de la Varde 1928, 1936; Bizot & Pócs 1979; Bizot et al. 1990; Bruggeman-Nannenga 1993). However, we are not aware of any account of bryophyte species associated with termite mounds in Nigeria. This study therefore aims to determine which bryophyte species are associated with termite mounds and the influence of the species on the stability of the structures.

MATERIAL AND METHODS

STUDY SITE

The study area is a stretch of grassland on the outskirts of Yelwa village on the path to Ngel Nyaki Forest Reserve, Mambilla Plateau, Taraba State, Nigeria. The Mambilla Plateau as described by Chapman & Chapman (2001) is a mid-altitude, submontane region ca. 1500 m above sea level located in the southeast corner of Taraba State, between 11°00’ and 11°30’E, and 6°30’ and 7°15’N. The plateau is a mainly open grassland of approximately 3100 km². Only fragments of forest limited to the stream valley remain (Akinsoji 2013; Ihuma et al. 2011b). The plateau is drained by numerous water courses which unite to form the main rivers to discharge eventually into River Benue, Nigeria’s second biggest river. The plateau is delineated on its northern and western sides by a steep escarpment rising to 1070 m above the surrounding lowlands. To the east Mambilla is connected with the Cameroon highlands, which extend southwest towards Bamenda and northeast to the Massif de L’Adamaoua.

Geologically, the largest portion of the Plateau is basement rock (2630 km²), whereas lava occupies 570 km² (Chapman & Chapman 2001). The part of Mambilla Plateau underlain by volcanic rocks is characterized by rolling grassland, becoming more hilly towards the western border where columnar jointing of the basalt gives rise locally to low cliffs and crags. Generally, the landscape is undulating with numerous dome-shaped hills and steep valleys which rarely exceed 1680 m. The soils of the grassland section of the plateau as described by Chapman & Chapman (2001) are humic ferrisols, slightly acidic (pH 5.6-6) and mainly silty loamy in texture. Mean annual precipitation exceeds 1780 mm, spread across 250 rainy days from April to October (Ihuma et al. 2011a) with June/July and September as the rainiest months (Chapman & Chapman 2001). The dry season is from November to March; during this period, less than 80 mm of rain may be recorded. Daily mean temperature usually does not exceed 30°C and frost has been recorded in the past at Mayo Ndaga in February (Chapman & Chapman 2001).

The Mambilla plateau is a high grassy upland with palatable grasses dominated by Hyparrhenia Andersson ex E. Fourn. sp. (Richard 2014), high rainfall, and low veterinary disease challenge that present the plateau as an ideal grazing terrain attracting large pastoralists and large herds of cattle (Blench 2013). Overgrazing and annual burning, perhaps to induce
regrowth, is common on the plateau. Low dome-shaped termite mounds dot the grassland landscape and are readily visible, especially during the dry season.

**Sampling**

Field work was carried out in November 2015. Starting with the nearest mound about 60 m outside the fence of the Ngel Nyaki Forest Reserve and heading towards Yelwa village (approx. 5 km away), eighteen termite mounds were selected along a transect (Fig. 1; Table 1). After inspecting a mound, the next visible mound from the thicket at least 20 m apart was approached while walking towards the village. We mostly kept off the road to the village during the selection and inspection of the mounds for the presence of bryophytes, but the road was crisscrossed at various points. The height and diameter of each mound were recorded and distribution of mounds plotted using a GPS unit (Yamashina 2010). Bryophyte species occurring on the mounds were collected and processed following the method of Vanderpoorten et al. (2010). Estimated frequency of species was calculated and scored according to Frahm (2003) and Andersson & Gradstein (2005):

- I = 0-5%
- II = 6-20%
- III = 21-40%
- IV = 41-60%
- V = 61-80%
- VI = >80%

**Species Distribution Range Analysis**

The distributional range of each species was determined from O’Shea (2006) and TROPICOS (2018) to generate a species-countries/territories distribution matrices and scored for presence or recorded (1) and absence or not recorded (0). The generated matrices were used to conduct a neighbour joining clustering with similarity index and root set at Kimura (1980). The matrices were transposed for hierarchical clustering with similarity index and root set at Kimura (1980). The distributional range of the eight species were predominantly Palaeotropic and Neotropical except Archidium ohioense Schimp. ex Müll.Hal. and Splachnobryum obtusum, which are also known from North America (Southern United States) and Western Europe (United Kingdom). The combined distributional range of the eight species is 66 countries/territories with New Caledonia as the farthest range of a species (A. ohioense) collected from the termite mounds.

The hierarchical clustering of the recorded species indicates that two pairs of species: Fissidens intramarginitus and Wijkia trichocoleoides (Müll.Hal.) H.A.Crum. and Splachnobryum obtusum and Campylopus savannarum (Müll.Hal.) Mitt. share very similar distributional patterns, > 80%, while Fissidens ezukanmae (Müll.Hal.) H.A.Crum. and Splachnobryum obtusum share very similar distributional patterns, > 80%. The other mounds that gave a thud sound when struck, the mound without bryophytes emitted a hollow sound when struck, suggesting the structure may have been abandoned by termites.

**Results**

The mean diameter and height of the termite mounds were 175.61 ± 32.14 cm and 39.83 ± 10.46 cm, respectively (Table 2). Bryophytes usually occurred at the base of the mound and tended to align with a shallow depression etched by cascades of rain and flood water (Fig. 2;3). Bryophytes were found on all sampled termite mounds except one (Table 1). Unlike...
sidens inflatus (and the new species F. ezukanmae) share the least similarity, < 1%, with other species (Fig. 4). Similarly, the neighbour joining clustering of the countries/territories indicates that Nigerian termite mound flora based on these eight species were most related to species known from DRC (Zaire), Tanzania, Ivory Coast, Central African Republic, Bioko, Cameroon, Rwanda, Gabon, Kenya, and Mexico (Fig. 5).

**DISCUSSION**

The absence of bryophytes on the ‘abandoned’ mound suggests that the bryophyte species occurring on mounds were not chance occurrences. Instead, these species may have been deliberately selected and cultivated by the termites. Although it is not so clear if all the mounds were constructed by the same termite species, it is obvious that the occupants of the mounds have an intrinsic relationship with the grasses and the grassland. It is likely that the termite species on the grassland are grass feeders, like Trinevervitermes spp. (Nasutitermitinae) (Duponnois et al. 2005), rather than litter-feeders or fungus-growing termite species such as Macrotermes Holmgren and Odontotermes Holmgren spp. (Macrotermitinae) (Contour-Ansel et al. 2000; López-Hernández et al. 2005; Coaton & Sheasby 1972). Although the mounds were positioned on an incline, with an increased likelihood of being washed off by...
the torrents, the size of the termite structures with a mean diameter and height of 175.6 and 39.8 cm, respectively, is not likely due to reduction in size caused by erosion.

The bryophytes on the mounds seem to be strategically placed to abate the accelerated floodwater as it cascades down the incline of an undulating landscape. But in a continuously grazed grassland with frequent episodes of fire outbreak, the bryophyte mats on the mounds may have additional roles like fire mitigation, due to their moisture-holding ability. It appears that the bryomass at the base is ‘placed’ to contend with the smoldering splinters. Perhaps there are morphological adaptations of bryophyte species on the mound to attenuate both raindrops and floodwater impact and to serve as fireproofing for the mound. However, this is beyond the scope of the present study and is worth considering in future studies that include experimental work. For the bryophytes,

**FIG. 2.** — Termite mound with bryophyte mats at the base. Mambilla Plateau, Nigeria.
the mounds may provide special conditions that are favorable, including shading, enhanced nutrients, favorable pH, and greater retention of moisture. These parameters need to be measured and manipulated experimentally to determine their role in bryophyte establishment.

It is not clear whether the different positions of the bryophyte mat on the mounds in the present study as compared with mounds on the Amazonian forest floor, where mosses are elevated above the forest floor, leaf litter and pooling rainfall (Reese & Pursell 2002), may reflect the local microclimatic conditions. It seems that air humidity towards the crests of the mounds in the open grassland is usually too low and unfavorable for bryophyte growth. A related trend is observed among epiphytic bryophytes on isolated trees which are often restricted to the base of the tree and are unable to grow higher up the trunk (as opposed to the more desiccation-tolerant lichens). In rain forests, however, where humidity conditions are less constrained, bryophytes may freely grow higher up the trunks. This may explain why bryophytes on termite mounds in Amazonian rain forest areas are not restricted to the base of the mound. However, we are not aware of any correlations between bryophyte
Mosses on termite mounds in Nigeria

Just like on the Amazonian forest mounds studied by Reese & Pursell (2002), *Fissidens* species traditionally associated with termite mounds were similarly present on the mounds in this study. The genus *Fissidens* is widely distributed in Africa with about 90 species out of the estimated 450 species distributed worldwide and has a very wide altitudinal amplitude (Bruggeman-Nannenga 2013a, b). The discovery of a new species on the termite mounds from the Eastern Nigerian Highlands may suggest marked preference of this *Fissidens* for termite mounds.

All the bryophyte species in the present study are new records on the termite mounds from the Eastern Nigerian Highlands may suggest marked preference of this *Fissidens* for termite mounds.

All the bryophyte species in the present study are new records on the termite mounds from the Eastern Nigerian Highlands but had been collected from other substrates from different parts of Nigeria. For instance, Egunnyomi (1984) reported *Archidium ohioense*, *Campylopus obrutus*, and *C. savannarum* on rocky substrates and exposed inselberg in Southwest Nigeria. This suggests that these species are widely distributed in Nigeria and are common in open and exposed surfaces. The distributional patterns of the species differ markedly. Four species: *Campylopus obrutus*, *Fissidens ezukanmae*, *F. inflatus*, and *Wijkia trichocoleoides* are exclusively African in distribution, while the other species: *Archidium ohioense*, *Campylopus savannarum*, *Fissidens intramarginatus*,
and Splachnobryum obtusum are known from various parts of Africa and are widely represented in the Neotropics and elsewhere (TROPICOS 2018).

Egunyomi (1984) attributed the Afro-American bicontinental distribution of species to remnants of the time on Gondwana during the Jurassic, about 135 million years ago when the continents were connected (Frahm 2003). However, recent molecular studies have shown that bryophyte species are not that old and that continental disjunctions of bryophyte species are more likely due to long-distance dispersal (Devos & Vanderpoorten 2009; Gradstein 2013; Laenen et al. 2014).

The hierarchical clustering of the eight species distribution ranges (Fig. 4) highlights two pairs of species with over 80% distribution similarity: Splachnobryum obtusum + Campylopus savannarum and Fissidens intramarginatus + Wijkia trichocoleoides. These species are likely to have developed over time similar successful adaptation strategies, efficient reproduction and dispersal mechanisms to enable them to colonize diverse substrates over wide geographical range.

The Eastern Nigerian Highlands is currently a bryophyte under-collected region but preliminary records of bryophytes from the region (Ezukanma et al. 2017) found greater distribution affinities with flora from eastern and southern Africa and the Neotropics (Fig. 5) than that found for the neighbouring West Africa countries like Chad, Benin, Togo, Ghana, and Niger Republic. Similarly, Keay (1953) observed a related pattern in the phanerogam flora on the Jos-Bauchi Plateau, where many species were found not to occur elsewhere in West Africa but are identical with those from eastern and southern Africa. Likewise, the liverwort collection on the Jos Plateau gathered by E. A. Drew in 1962 were consistent with Keay’s (1953) phanerogam distributional pattern on the Jos-Bauchi Plateau. (Harrington & Jones 2004). It might be helpful to get familiar with flora from eastern and southern Africa and the Neotropics for future studies of bryophytes of Eastern Nigerian Highlands.

In all, the bryophyte mats on termite mounds on grassland on the highland of Northeastern Nigeria may represent a unique and mutually beneficial co-evolutionary association. While the mounds avail a surrogate stable nutrient-enriched substrate for the bryophyte species ‘cultivated’ by the termites, the bryophyte mat may act to attenuate the impact of the falling raindrops and cascading floodwater on the mounds, thereby reducing erosion and enhancing the long-term stability of the termite structures. We also suggest that the bryophyte mats may play a role in fireproofing the termite mounds. The history and mechanisms of termite-bryophyte coevolution are still poorly understood and present opportunities for future investigation.

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