

Pulsing hydrology and topography determine the structure and spatial distribution of *Cubitermes* mounds in a savanna ecosystem



Justice Muvengwi^{a,b,*}, Monicah Mbiba^{a,b}, Hilton.G.T. Ndagurwa^{c,d}, Nomatter Kabvuratsiye^b

^a School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits, 2050, South Africa

^b Department of Environmental Science, Bindura University of Science Education, Private Bag, 1020, Bindura, Zimbabwe

^c Forest Ecology Laboratory, Faculty of Applied Sciences, National University of Science & Technology, P.O. Box AC 939, Ascot, Bulawayo, Zimbabwe

^d Department of Forest Resources and Wildlife Management, Faculty of Applied Sciences, National University of Science & Technology, P.O. Box AC 939, Ascot, Bulawayo, Zimbabwe

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ABSTRACT

Spatial patterns are important to understanding factors that shape many ecological processes in natural plant and animal communities. However, the spatial patterns of *Cubitermes* mounds remain poorly understood despite their importance in many ecological processes in savanna ecosystems. We assessed the structural characteristics and spatial patterns of *Cubitermes* mounds in 25 × 25 m plots along a catena sequence i.e. upper, middle and bottom in a seasonal savanna wetland. A density of 1317 mounds ha⁻¹ was estimated for this savanna system. Mound density decreased whereas mound size increased down the catena, and mounds were absent in the floor region of the catena due to prolonged inundation. Spatial analysis showed that mounds were randomly distributed in the upper section of the catena and either random or clustered in the middle and bottom sections. True segregation between large and small mounds only occurred in the upper section of the catena; otherwise small mounds were either randomly distributed or clustered in relation to large mounds in the middle and bottom sections of the catena. With increase in spatial scale, however, mounds were independent indicating the absence of interaction between mounds. In the bottom region of the catena, mounds were independent at small spatial scales but positively correlated with increase in spatial scales a result consistent with low mound density and mutual stimulation, respectively. In conclusion, along the catena sequence, mound size and spatial distribution are a function of competition in the upper regions, whereas in the bottom regions these characteristics appear to be regulated by inundation. The study highlights the importance of hydrology, topography and competition for the structure and spatial patterning of *Cubitermes* mounds, and consequently for the spatial heterogeneity of ecological processes in savanna ecosystems.

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1. Introduction

Ecosystem spatial and temporal dynamics are often influenced by resource availability and timing, a phenomenon called 'resource pulse'. The term resource pulse can be defined as "brief episodic events of high resource availability" (Levi et al., 2015). Resource pulse has been studied in different ecosystems, including riparian floodplains (Nakamura et al., 2005), tropical forests (Lodge et al., 1994; Woolbright, 1996), lakes and rivers (Carlton and Goldman, 1984) and coral reefs (McCormick, 2003). Resource pulse can take different forms, for example precipitation (Jaksic, 2001), insect outbreaks (Carlton and Goldman, 1984; Yang, 2004), increases in small mammal population (Jaksic et al., 1997; Schmidt and Ostfeld, 2003), and has the potential to influence ecological processes at individual, population

and community level (Yang et al., 2008). Some pulses are recurrent and predictive whereas others are highly stochastic (Yang et al., 2010). Although the cascading effects of resource pulse have been demonstrated (Yang et al., 2008, 2010), general insights and theory linking resource pulses to community level processes are still poorly understood (Levi et al., 2015).

One major influencing resource on seasonal wetlands is precipitation, which is normally variable in timing and quantity particularly in southern Africa (Fauchereau et al., 2003). This variation results in a pulsing hydrology. Indeed hydrology has been shown to regulate the distribution of termite mounds in many savanna landscapes (Davies et al., 2014). For example, termites avoid areas with greater risk of inundation which result in clustered patterning in termite mound distribution (Levick et al., 2010). Effects of hydrology on mound distribution are also evident when drainage line effects are considered, and generally there is increase in distance to the nearest termite mound as drainage line size increases (Davies et al., 2014). Additionally, hydrology influences the amount of clay and colloids in soils, elements which

* Corresponding author at: School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits, 2050, South Africa.

E-mail address: justicemuvengwi@yahoo.co.uk (J. Muvengwi).

determine nest construction (Khomu et al., 2011; Levick et al., 2010). Although there are studies elucidating how termite diversity and activity varies along rainfall gradients (Buxton, 1981; Davies et al., 2012), little has been done to understand how pulsing hydrology influences the structure and spatial distribution of termite mounds more so for *Cubitermes* species.

As well as pulsing hydrology, topography can influence the spatial distribution of termites through their effects on landscape properties that determine termite distribution such as vegetation cover, soil structure and hydrological conditions (Davies et al., 2014; Levick et al., 2010). For example, clear shifts in vegetation structure and composition, underlying soil and hydrological conditions along catenal gradients are common in many savanna landscapes. Usually termite mounds are clustered on crests and barely present on the lower regions of the catena (Davies et al., 2014) because, unlike the well-drained shallow soils of the upper regions of the catena, the bottom sections are heavily loaded with clay and prone to inundation (Davies et al., 2014; Levick et al., 2010). The increased drainage associated with elevated sites may thus have a positive influence on termite mound spatial distribution, and those landscapes with elevation characteristics have higher numbers of termite mounds (Davies et al., 2014; Levick et al., 2010). Additionally, upper catena regions have a higher vegetation cover with more litter, coarse woody debris and soil nutrients, and thus support more termites than the predominantly grassy lower regions of the catena (Davies et al., 2014). As a result, these topographical factors may explain the structure and spatial distribution of termite mounds across a catena. While the spatial distribution of termite mounds has been examined in savanna landscapes, most studies have focused on *Macrotermes* mounds (Grohmann et al., 2010; Korb and Linsenmair, 2001) despite the importance of other species such as *Cubitermes* in many ecosystem processes (Donovan et al., 2001; Wood, 1988).

Cubitermes construct small conical epigeal mounds (Mitchell, 1980; Uys, 2002), which may as well have cascading effects on plant and animal communities in ecosystems where they occur and hence are part of the 'ecosystem engineers guild'. *Cubitermes* mounds occur on vleis and grasslands and are often aggregated around small springs or moist places along drainage lines (Mitchell, 1980). *Cubitermes* mounds also house other species of termites, for example *Fulleritermes*, *Crenetermes*, *Ancistrotermes latinotus*, *Allodontermes* spp. and *Noditermes* spp. (Mitchell, 1980). Additionally, similar to other termite species, *Cubitermes* mounds are associated with improved soil physical and chemical properties as well as aeration and drainage (Donovan et al., 2001; Wood, 1988), which in turn increase the robustness of dryland ecosystems, especially in this era of climate change (Bonachela et al., 2015). Despite wide distribution, high species diversity and ecosystem engineering role (Brauman, 2000; Donovan et al., 2001), the influence of topography and resource supply on *Cubitermes* mounds spatial distribution remains poorly understood. Therefore, the understanding of such organisms' distribution in space and time is fundamental for ecosystem management.

The present study examines the influence of hydrological pulse and topography on *Cubitermes* mound size and spatial distribution on a seasonal wetland catena in a savanna ecosystem. We hypothesized that *Cubitermes* mounds would be: (i) larger (both in diameter and height) on the wetland floor (drainage line) to avoid inundation, and (ii) randomly distributed in the lower sections of the catena due to establishment by chance as a result of prolonged flooding.

2. Materials and methods

2.1. Study area

The study was carried out on a seasonal wetland located (latitude: 17° 59'–18° 00'S, longitude 30° 56'–30° 57'E) in Mhondoro, 30 km south west of Harare. The average rainfall is 750 mm per annum, and mean annual temperatures are 9 °C for winter and 40 °C for summer

(Bulton, 1995). The wetland flows from south to the north and falls within the Manyame catchment. The wetland comprise of a catena which was divided into upper, middle, bottom and floor (Fig. 1). The upper and middle sections of the wetland dry out in winter (June–July) and the bottom section and floor usually between August and October. The wetland is dominated with grasses such as *Hyperthelia dissoluta*, *Sporobolus pyramidalis*, *Sporobolus ioclados*, *Eragrostis rotifer* and *Eragrostis inamoena*, and some sedge species, which include *Nymphaea* sp., *Scirpus raynalianii*, and *Scirpus sinutus*. The upper section of the wetland catena borders with a woodland comprising of *Brachystegia spiciformis*, *Terminalia sericea*, *Combretum zeyheri*, *Swartzia madagascariensis*, *Lannea discolor* and *Ochna pulchra* (Fig. 2a–b). The wetland is used for grazing cattle by the community nearby and signs of heavy grazing are visible (Fig. 2a).

The geology of the area was described following Food and Agriculture Organization guidelines (FAO, 2006). The area is characterised by unjointed to weakly jointed granitic and gneissic rocks of the basement complex. The soils of this unit show a catenary association with upper slopes comprised of moderately well drained sands, with a thickness >50 cm spreading over bedrock or yellowish brown to reddish yellow, frequently mottled sometimes concretionary, coarse-grained sandy loams to sandy clay loams (Anderson et al., 1993). These pass down slope to a vlei edge, yellow over very pale brown coarse sand (>100 cm), mottled and concretionary at depth, passing into more variable but usually medium textured, imperfectly to poorly drained vlei soils, some of which are sodic (Anderson et al., 1993). The upper to middle slopes comprise of ferric-haplic, lixisols or sometimes reffic-haplic and acrisols whereas the lower slope can be described as ferralic-haplic and arenosols. The wetland bottom and floor comprise of gleyic lixisols and haplic solonetz (Anderson et al., 1993).

2.2. Soil sampling and analyses

The wetland was divided into four catena sections, upper, middle, bottom and floor (Fig. 1). Five soil samples were randomly collected in each stratum at a depth of 20 cm using a soil auger. Soils were tested for physical (% sand, % silt and % clay) and chemical (calcium: Ca, magnesium: Mg, sodium: Na, potassium: K and pH) properties. Soil pH was obtained using the CaCl₂ method (Okalebo et al., 2002; Thomas, 1996). Exchangeable Ca, Mg, Na, and K were extracted using the aqua regia digestion method (Anderson and Ingram, 1993). The resulting compound was then dissolved in concentrated HCl, filtered, and the resulting solution was diluted with distilled water. Total Ca and Mg were determined at 0.460 nm and 0.595 nm using a spectrophotometer, respectively, and flame emission was used for K and Na.

2.3. Mound mapping and measurement

A transect 125 m wide cutting across all section of the catena was marked. In each stratum a 25 m × 25 m plot was marked at the centre of the transect and the location of mounds was recorded as Cartesian coordinates (x, y). For each mound, height, long and short perpendicular diameters were measured. Other variables, basal and lateral surface areas were calculated using measured variables. Since this was part of

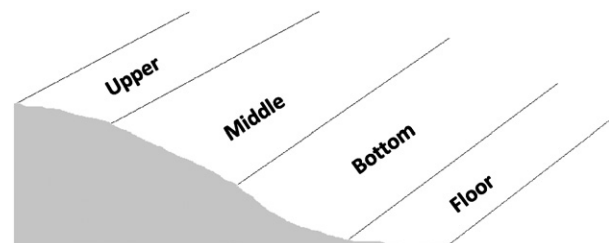


Fig. 1. Illustration of wetland catena at the study site showing the four sampled sections.

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