CORRESPONDENCE

Termite mounds alter the spatial distribution of African savanna tree species: artefacts and real patterns

ABSTRACT

In a recent issue (vol. 43) of the *Journal of Biogeography*, Davies *et al.* (2015) presented novel analyses of the spatial distribution of tree species around termite mounds in a South African savanna. However, some of their conclusions are not supported by the data. My aim in this correspondence is to point out some limitations of their analyses, stimulate cautious interpretation of their results and suggest better methods for future use.

There is a growing body of evidence demonstrating that termite mounds are hotspots of soil nutrients, plant diversity and safe sites for the regeneration of woody plants compared with surrounding savannas (Sileshi *et al.*, 2010; Sileshi & Arshad, 2012; Joseph *et al.*, 2013). In a recent article published in this journal, Davies & co-workers (2015; hereafter referred to as D&Cw) make strong conclusions that are not supported by their data and analyses. In this correspondence, I will highlight the main problems in the interpretation of some of their results. More specifically, I highlight limitations of their analyses, suggest a more cautious interpretation of their results and propose better methods for future use.

LACK OF CLEAR DEFINITION OF THE 'MATRIX VEGETATION'

The first major problem is the lack of clear definition of the 'matrix' vegetation. In some places D&Cw describe it as 20–25 m from the mound centre, in others 15–20 and 10–15 m elsewhere. The description of the 'matrix' vegetation merely based on

measured distance ignores the size-dependence of mound effects. Termite mounds in a given locality may not be of the same origin, age or size. D&Cw assumed that the mounds in both landscapes were built by *Macrotermes falciger*. However, detailed field studies in the northern Kruger National Park show that *M. falciger* mounds are less abundant than those of other species; in decreasing order of mound densities *Macrotermes natalensis* > *Macrotermes ukuzii* > *Macrotermes michaelseni* > *M. falciger* (Meyer *et al.*, 1999). Even *M. falciger* mounds also vary widely in size and age (Mujinya *et al.*, 2014; Ernes *et al.*, 2015). For example, Mujinya *et al.* (2014) found mounds with basal diameters ranging from < 10 m to > 25 m and heights ranging from < 2 m to > 6 m. Similarly, Joseph *et al.* (2013) found *Macrotermes* mounds with surface area (SA) ranging from 0.4 to 1220 m^2. Large *Macrotermes* mounds are often ancient structures built over decades or centuries. For instance, the age of *M. falciger* mounds ranged from 680 years for those with heights of *c.* 3.2 m to > 2300 years for mounds of > 6 m in height (Ernes *et al.*, 2015). Compared to younger mounds, older mounds provide woody plants more time to establish and potentially expand their effects much further than the mound's physical location. In addition, nutrient redistribution by erosion of the mound may lead to more enrichment of the outwash pediment and thus expand the mound influence. Thus, mound influence on vegetation could extend up to 2.5 times the radius of mounds (Levick *et al.*, 2010). In that sense, even the 30-m distance from the mound centre may not qualify for 'matrix vegetation' in some situations.

## ANALYSES AND INTERPRETATION OF OVERALL TREE DENSITY

D&Cw aggregate densities of all tree species (hereafter called 'overall tree density') and analyse the data using distance classes

as 'fixed effects'. However, their analysis does not account for variation in mound size and the correlation between various distance classes. D&Cw conclude that termite mounds reduce tree densities over distances up to 10 m and acknowledge that this finding contrasts with previous studies. But the reasons they cite to explain what they call 'tree suppression' on mounds are not convincing. For example, D&Cw mention heavy herbivory and formation of grazing lawns as possible reasons for the suppression of tree densities around mounds. However, D&Cw's analysis does not provide direct evidence for suppression of trees on mounds. It merely suggests that mounds have lower densities of woody species up to 10 m from the mound centre. It is not clear whether the 10-m distance accurately circumscribes the mound or the outwash pediment. For example, in the case of large mounds, 10 m is likely to be within the area occupied by mounds. This is especially the case for mounds with surface areas of up to 1220 m^2 (Joseph *et al.*, 2013) or basal diameters of up to 25 m (Mujinya *et al.*, 2014) typical of *Macrotermes* species in African savannas. According to Joseph *et al.* (2013) small mounds were predominantly (75%) characterized by species typical of matrix savanna but woody plant composition changes gradually as mound size increased until only species restricted to mounds (called 'indicators') dominated on the very large mounds. Therefore, if data were analysed for small and large mounds separately, the outcome could have been different from fig. 2 of D&Cw.

Another complication with D&Cw's analysis emerges from the aggregation of densities. Although aggregation of data is a common practice in ecology, there are situations where it can lead to unexpected patterns. For example, different trends may be visible when data are analysed by species but such trends may disappear or reverse signs when the data are aggregated. In statistics this phenomenon is called Simpson's paradox (Steven & Mullee,

1994; Pearl, 2014). In the case of D&Cw, aggregating the data into overall tree density seems to oversimplify more complex patterns by ignoring the underlying differences in species responses to mounds. A more appropriate approach for D&Cw's data would be to analyse large and small mounds separately and to model the species response using multivariate analysis of variance (MANOVA). Aggregation of the data into overall tree density will be valid only if the assumptions of MANOVA (i.e. parallelism and coincidence) are satisfied.

Furthermore, the statistical model [i.e. quasi-Poisson generalized linear model (GLM)] D&Cw use for data analysis does not fully account for autocorrelation and overdispersion evident in the data. The main problem is the treatment of distance classes as 'fixed effects' in the model. In reality, distance classes are not discrete. Thus, observations in distance classes that are closer together will be more correlated than those in other classes. This creates a strong spatial structure around mounds (see Sileshi & Arshad, 2012 for details). For spatially structured data such as those in figs 2–5 of D&Cw, the distance-decay framework is more appropriate (Sileshi & Arshad, 2012) because it is based on first principles (i.e. quantitative law-like postulates), which are also the bedrock of biogeography (Soininen et al., 2007; Nekola & McGill, 2014). The advantage of the distance-decay models over GLMs is that they are predictive and can reveal insights into emergent patterns and underlying mechanisms. In order to illustrate this, I fitted the power-law and exponential distance-decay models (Nekola & McGill, 2014) to C. imberbe densities and community similarity data from figs 4 & 5 of D&Cw. As expected, both models fit the data very well (Fig. 1a–d) even though the distance classes were limited to 30 m. Figure 1(a–d) also show that the responses are monotonic functions of distance. This indicates that distance classes are not discrete, so the use of GLMs is not ideal for identifying underlying patterns. Both models predicted that the community similarity between lowland and mound vegetation at 30 m is 32–33% at Nwaswitshaka and 48% at Shingwedzi (Fig. 1c,d). When extrapolated to 50 m, community similarity declined to 21–28% at Nwaswitshaka and 38–44% at Shingwedzi. This indicates that even the vegetation located 50 m away from the mound shares substantial similarity (> 20%) with the lowland tree community.
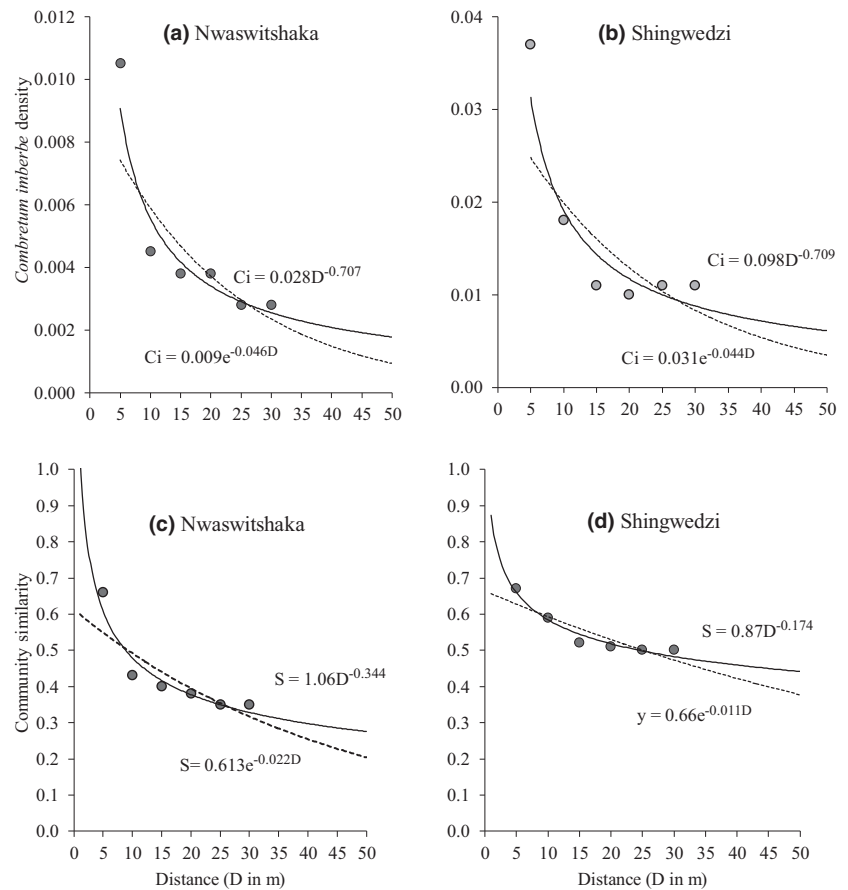
Figure 1 Agreement between the observed (solid circles) and predictions (Y) from the power-law ($Y = \alpha D^{-\beta}$) model (solid lines) and the exponential ($Y = \alpha e^{-\beta D}$) distance-decay model (broken lines) for densities of *Combretum imberbe* (upper panel) and community similarity (lower panel) at two sites in the Kruger National Park, South Africa. The observed densities of *C. imberbe* (Ci), community similarity (S) and distance (D in metres) from centre of mound were extracted from figs 3–5 of Davies et al. (2015).

DEFINITION OF THRESHOLDS OF CHANGE

In order to detect thresholds of change in tree density around termite mounds, D&Cw fitted quasi-Poisson GLMs. Based on the statistical significance from the GLM they then defined the threshold of change as 10 m. However, D&Cw state that they made adjustments of the baseline where differences between distance intervals were non-significant. It is not immediately clear how they adjusted the baseline but obviously they were searching for a significant difference between neighbouring zones. Such approaches are subjective and are based on the assumption that statistical significance is equivalent with ecological reality. The statistical tests applied are also inconsistent with potential processes that might generate observed patterns (i.e. the distance-decay of spatial interaction). From

Fig. 1 and earlier work (see details in Sileshi & Arshad, 2012) it is evident that mound influence decays monotonically with distance. This indicates that the effects of mounds on soil properties and tree distributions are spatially structured, and response profiles will be continuous rather than discrete. Therefore, dividing a continuous response variable into discrete classes artificially and then claiming that boundaries have been discovered using significance tests is incorrect. Their method also ignores the size-dependence of mound effects on patterns. Unless all the mounds studied are of the same size, setting the same threshold will lead to incorrect inferences about mound influence.

Interestingly, D&Cw used the 10-m radius to calculate the landscape scale influence of mound on tree densities. For reasons that are not made clear, they also used thresholds of 15 and 20 m to

calculate the landscape scale influence of mound in Nwaswitshaka and Shingwedzi respectively. Given the large size of some mounds, the use of these thresholds could lead to underestimation of the total area influenced by mounds.

INTERPRETATION BASED ON INCOMPLETE ANALYSES

The header of their paper 'Termite mounds harbour assemblages of lowland trees' and their conclusion that 'mounds increase the abundance of tree species typically associated with lowland habitats' give the impression that mounds create communities dominated by lowland species on hill crests. On the other hand, a growing body of literature (references in Sileshi et al., 2010) demonstrates that mounds create unique vegetation assemblages with affinities to savannas and other forest types including lowland/riparian vegetation. The floristic composition may consist of a mixture of species exclusive to mounds (called 'indicator' species), savanna vegetation and species imported from elsewhere (references in Sileshi et al., 2010; Joseph et al., 2013). Indeed, Joseph et al. (2013) demonstrated that on medium to large mounds, the great majority are indicator species. My predictions (see Fig. 1) from the limited data (in fig. 5 of D&Cw) indicate that a sizable proportion of the lowland/riparian species that occur on mounds also occur in the matrix savanna. The contradiction between their conclusion and our current knowledge appears to emerge from their focus on the analysis of community similarity between the mounds and the lowlands. In the absence of equivalent comparisons of community similarity between matrix and mound vegetation, and between lowland and matrix vegetation, this kind of analysis may lead to spurious conclusions. To complete the picture, therefore, I appeal to the authors to provide analyses of community similarity between lowland and matrix vegetation as well as matrix and mound vegetation for small and large mounds separately.

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