

1 **Seed dispersal by animals influences the diverse woody plant community on**
2 **mopane woodland termite mounds**

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10
11 **ABSTRACT**

12 In African savannahs, mound-building termites induce higher diversity in plant
13 communities. Biotic and abiotic filters, such as nutrients and disturbances (e.g., herbivory

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14 or fire), may influence the distinct vegetation on termite mounds; however, seed dispersal
15 has not yet been evaluated as a filter in this ecosystem. This study examined the effects
16 of seed dispersal, particularly animal seed dispersal, on the distinct woody plant
17 community on termite mounds in a mopane woodland in north-western Namibia. We
18 compared the functional traits of woody plants related to dispersal, as well as responses
19 to resource availability and disturbance, between plant communities on and those off
20 termite mounds. We conducted vegetation surveys of woody plants in 13 paired mound–
21 savannah plots and measured their functional traits. Soil samples were also collected from
22 10 of the 13 plots for soil chemical analysis to compare the differences between mound
23 and savannah plots. Drupe-type fruits and dispersal by animals, including mammals and
24 birds, were more dominant in plant communities on termite mounds, whereas pod and
25 winged fruits and wind-dispersed species were typical in matrix communities. Termite
26 mounds were rich in soil nutrients compared with the surrounding matrix, and soil
27 phosphorus was associated with mound soil. We conclude that dispersal mechanisms
28 contribute to the distinct and diverse woody plant community on termite mounds. Seed
29 dispersal by animals is likely to be more common in the distinct woody plant community
30 of the mounds, whereas the community in the surrounding matrix was characterised by
31 wind dispersal.

32

33 **Key words:** animal seed dispersal; ecosystem filters; functional traits; *Macrotermes*;
34 mopane woodland; Namibia; termite mound.

35

36 INTRODUCTION

37 In savannah ecosystems, spatial heterogeneity plays an important role (Scholes 1990) in
38 maintaining a high level of biodiversity (Mittermeier and others 1998; Scholes and Biggs
39 2005). This heterogeneity is found at different spatial scales and is driven by different
40 abiotic and biotic factors (Pickett and others 2003). At the continental to regional scales,
41 spatial and temporal variations in precipitation drive vegetation dynamics (Wiegand and
42 others 2005), whereas fire, geology and soil factors (Scholes 1990; Higgins and others
43 2000; Bond and others 2005) and herbivory (Cromsigt and Olf 2008) become more
44 important at the regional to landscape scales. The landscape -scale heterogeneity
45 positively affects species richness, especially in severe environments (Yang and others
46 2015), by providing niche space for species that have different ecological strategies
47 (Bergholz and others 2017).

48 In African savannahs, mound-building termites are important agents producing
49 fine-scale heterogeneity through the reallocation of nutrients and subsoil particles (Sileshi

50 and others 2010; Gosling and others 2012). Termite-induced heterogeneity often creates
51 a distinct woody plant assembly, with high species richness and woody biomass
52 (Loveridge and Moe 2004; Traore and others 2008) compared with the surrounding
53 savannah. However, why plant communities on termite mounds are so different from the
54 surrounding savannah is poorly understood.

55 Plant species differ in their environmental requirements for successful
56 establishment and survival; thus, the environment acts as a filter, removing species that
57 lack traits allowing their persistence under a particular set of conditions (Keddy 1992).
58 The process of seed dispersal determines which species reach a site (i.e., dispersal
59 limitation, Nathan and Muller-Landau 2000; Kraft and others 2015). Then biotic and
60 abiotic filters determine which species establish under conditions formed by the
61 environment and other organisms (Weiher and Keddy 1995; Belyea and Lancaster 1999).
62 The observed community composition is an outcome of the sum of these filters, which
63 sort the species by functional traits.

64 Numerous abiotic and biotic filters contribute to the unique vegetation on termite
65 mounds. Enriched soil (Sileshi and others 2010; Erpenbach and others 2013), higher soil
66 moisture (Dangerfield and others 1998; Konate and others 1999; Sileshi and others 2010),
67 and elevated topography, which acts as a refugium from fire (Moe and others 2009;

68 Joseph and others 2011; Joseph and others 2013), and savannah flooding (Dangerfield
69 and others 1998; McCarthy and others 1998) have been suggested as causes for the
70 distinct plant communities found on termite mounds. Herbivory acts as a biotic filter to
71 the plant community on mounds. Herbivores prefer to browse plants on mounds, which
72 results in higher deposition of urine and dung on mounds as a result of longer or more
73 frequent visits, creating a positive feedback loop (Holdo and McDowell 2004; Loveridge
74 and Moe 2004). Furthermore, the higher browsing activity alters herbaceous and woody
75 plant communities (Okullo and Moe 2012b; Stoen and others 2013). In addition to these
76 herbivores, small vertebrate (Fleming and Loveridge 2003) and avian species (Joseph and
77 others 2011) also frequently visit termite mounds for browsing and nesting spots, which
78 leads to seed deposition on mounds. However, the effects of dispersal on the distinct plant
79 assembly of termite mounds have not been sufficiently evaluated.

80 In north-eastern Namibia, large *Macrotermes* (Isoptera) termite mounds are
81 sparsely distributed (Coaton and Sheasby 1972). The vegetation in this region is classified
82 as mopane, *Colophospermum mopane* ((J. Kirk ex Benth.) J. Kirk ex J. Léonard)
83 woodland (White 1984). Although *C. mopane* is a dominant species both on and off
84 termite mounds, there is higher density and species richness of woody plants on these
85 mounds than in the surrounding savannah matrix (Yamashina 2013). Avian seed dispersal

86 may contribute to this unique woody plant community (Yamashina 2014); however, clear
87 evidence is lacking.

88 We examined the effects of seed dispersal, particularly by animals, on the
89 community composition of termite mound vegetation by exploring woody plant
90 functional traits related to dispersal. The plant community on termite mounds will also
91 reflect the effects of filters other than dispersal; therefore, we assessed the effects of traits
92 related to soil resource use and disturbance. The soil nutrient environment, a well-studied
93 factor affecting termite mound vegetation, was also analysed as an underlying factor. We
94 used community-weighted mean (CWM) trait values (i.e., the mean of the trait values
95 weighted by the relative abundances of species), which are adequate to summarise shifts
96 in mean trait values within a given community (Ricotta and Moretti 2011).

97 We examined three questions by measuring plant traits, including the traits
98 related to seed dispersal and other processes, and analysing the relationship between soil
99 components and woody species composition on and off mounds: 1) Do the functional
100 traits of woody plant communities differ between termite mounds and the surrounding
101 savannah matrix? 2) If so, which traits differ in woody plant communities between the
102 mound and savannah matrices? 3) Does seed dispersal by animals contribute to the
103 distinct woody plant community on termite mounds?

104

105 **METHODS**

106 **Study site**

107 Fieldwork was conducted in the Muyako Community Forest (17.88°S, 24.40°E) in the
108 Zambezi region of Namibia in November 2012, November 2014, January 2015 and
109 November 2015. The altitude is approximately 1000 metres above sea level and the
110 topography is nearly flat. The annual precipitation is greater than 650 mm (Mendelsohn,
111 2002), with most rain falling between October and March. The average temperature
112 ranges between 20 and 22°C. September is the warmest month (range, 14.1–33.8°C) and
113 June is the coolest (range, 6.1–24.5°C) (Namibia Meteorological Service 2013). Large
114 areas of the landscape are covered by eutric Fluvisols and fertile soils with high base
115 saturation are found along large river margins and valleys (Mendelsohn 2002). The
116 research site lies between the Zambezi and Chobe Rivers, downstream from the Kwando
117 River. The site is located on the boundary between the Kwando and Zambezi drainage
118 basins; some areas were inundated during the rainy season. Lyambezi Lake, which
119 contained water all year round during the study period, lies to the west of the study site.
120 The local vegetation contains mopane woodland, acacia woodland, riparian forest, and
121 floodplains, which cover small areas of the landscape (Mendelsohn and Roberts 1997).

122 The understory vegetation of mopane veldt, including grasses and herbs, is poorly
123 developed (Werger and Coetzee 1978); therefore, we only surveyed woody plants.

124

125 **Field sampling**

126 This study included 13 paired mound–savannah plots (20 × 20 m). Within our study site,
127 there were several types of mound shapes: 1) mostly active cone-shaped mounds; 2)
128 sometimes active cone-shaped areas with surrounding erosion skirts; and 3) mostly
129 inactive dome-shaped mounds without a prominent cone-shaped area. Our plots focused
130 on the latter two types, and we selected mounds at least 20 m in diameter, based on
131 accessibility in the forest and low human impact due to far distances from residential
132 areas. Termite samples, including soldiers and workers, were collected from two mounds
133 and were identified as *Macrotermes michaelseni* (Sjöstedt) by a termite expert in the
134 National Museum of Namibia. Although we could not identify the builders of all of the
135 mounds in our samples, a previous study conducted in a floodplain in Botswana suggested
136 that dome-shaped mounds with a large diameter originated from the cone-shaped mounds
137 built by *M. michaelseni* (McCarthy and others 1998). Savannah plots were set in the
138 surrounding savannah matrix at least 50 m from each mound.

139 In each plot, all woody plants taller than 1 m were counted and identified by their

140 leaves, flowers and fruit, using Wyk and Wyk (1997) as a reference. Leaf, fruit/pod and
141 twig samples were collected for trait measurements. We collected 10 paired mound–
142 savannah soil cores (> 200 g per core) between 0 and 10 cm in depth for soil chemical
143 analysis.

144

145 **Trait selection and measurement**

146 To examine if functional traits of woody plants differ between termite mounds and the
147 surrounding matrix, we selected 16 traits related to seed dispersal, and responses to soil
148 nutrient availability or disturbance (Table 1) including growth form, plant height,
149 phenology, specific leaf area (SLA), leaf area (LA), leaf thickness, leaf dry matter content
150 (LDMC), twig dry matter content (TDMC), leaf palatability (for mammal herbivores),
151 spinescence, seed mass, fruit/pod palatability, fruit type (drupe, pod, winged), dispersal
152 mode (mammal, bird, wind), nitrogen (N)-fixing ability, leaf N content and leaf carbon
153 (C) content. We followed standardised protocols to measure functional traits (Cornelissen
154 and others 2003; Perez-Harguindeguy and others 2013). To determine LA and leaf
155 thickness, 10 leaves from 3–6 individuals (n=157) were collected from each species (n=
156 31). Each leaf was weighed fresh and photographed using a reference scale in the field.
157 LA was measured using the Photoshop CS6 software. Leaf thickness was measured using

158 a digital micrometre (Mitsutoyo, Tokyo, Japan). Leaves were oven-dried at 75°C for at
159 least 48 h, and dry weight was measured to 0.001 g precision. SLA was expressed as the
160 ratio of fresh LA to dry mass of the leaf sample ($\text{mm}^2 \text{mg}^{-1}$). LDMC was expressed as the
161 ratio of dry mass to fresh mass. Leaf samples were collected at both mound and savannah
162 plots where possible. Other traits including N-fixing ability, phenology, growth form and
163 fruit type were obtained from the literature (Defaria and others 1989; Campbell 1996;
164 Jacobs and others 2007; Roux and Muller 2009; Cramer and others 2010).

165 We measured three traits related to seed dispersal: seed mass, fruit type, and
166 dispersal mode. Seed mass is related to dispersal and establishment, with smaller-seeded
167 species producing more seeds per reproductive bout to increase the chance of dispersal,
168 whereas species with larger seeds are more likely to establish in competitive environments
169 (Westoby 1998). Dispersal agents can be inferred from seed morphology (Levin and
170 others 2003). In this study, we classified the plant seeds as either drupes, pods, or winged.
171 Seeds with wings are dispersed by wind. Drupes are fleshy fruits dispersed by birds and
172 mammals (Perez-Harguindeguy and others 2013). Pods occur mostly in the Fabaceae
173 family and are eaten and dispersed by livestock, ungulates, elephants, and other wildlife
174 (Miller 1996; Dudley 1999). Species with a higher LDMC tend to be resistant to physical
175 damage, such as herbivory and fire, and are associated with low-nutrient environments

176 (Perez-Harguindeguy and others 2013; Wigley and others 2016). The leaf C:N ratio and
177 SLA also reflect the soil resource, *i.e.* a higher leaf C:N ratio tends to be associated with
178 a low-nutrient environments, whereas lower C:N ratio tends to be associated with
179 productive environments (Wigley and others 2016). N fixation is a costly process that
180 consumes carbon (Vitousek and Howarth 1991), and N fixing ability reduces the need for
181 this in rich environments (Van der Plas and others 2013).

182

183 **Soil and leaf analysis**

184 Soil samples were analysed for pH (H₂O), conductivity (EC), calcium carbonate
185 equivalent (% CaCO₃), organic C, organic matter, phosphorus (P), sodium (Na),
186 potassium (K), magnesium (Mg), calcium (Ca) and total N at the Analytical Laboratory
187 Services in Namibia. Soil pH was measured in a supernatant suspension with a 2:5
188 soil:water ratio using a hydrogen-selective electrode and pH meter (WTW MultiLab 540,
189 Weilheim, Germany). Conductivity (with a soil:water ratio) was measured using a
190 specific conductivity meter (WTW MultiLab 540). The calcium carbonate equivalent was
191 measured by neutralising the 2:5 soil:HCl (1M) suspension with standardised 1 M sodium
192 hydroxide and titrating the supernatant. The determination of soil organic C was based on
193 the Walkley–Black chromic acid wet oxidation method. P was measured by the Olsen

194 method using a spectrophotometer (UVmini-1240, Shimadzu, Kyoto, Japan). Soil organic
195 C was converted to soil organic matter using a van Bemmelen factor of 1.724. Soil
196 exchangeable bases (Na, K, Mg and Ca) were analysed using 1 M ammonium acetate (pH
197 7.0) by inductively coupled argon plasma optical emission spectroscopy (Optima 7000
198 DV, Perkin Elmer, Waltham, MA, USA). The Kjeldahl method was used to determine the
199 total N content in soil samples. Soil particle analyses were also performed using a pipette
200 method. Leaf C and N were measured using an NC Analyser at a laboratory in Kyoto
201 University (Sumigraph NC-22F Sumika Chemical Analysis Service, Tokyo, Japan) with
202 ground-dried leaves processed after dry weight measurements had been taken.

203

204 **Statistical analysis**

205 All statistical analyses were performed using R software (version 2.15.2 for Windows,
206 Vienna, Austria). To compare the plant communities on termite mounds with those in the
207 surrounding matrix, we calculated the density, species richness and species diversity
208 index (alpha diversity, evenness and beta diversity) of the woody plant community on
209 each plot. Species richness was expressed as the total number of species in each plot. For
210 alpha diversity, we used the Shannon–Wiener index, calculated as $H' = -\sum P_i(\ln P_i)$,
211 where P_i is the proportion of each species ‘ i ’ in the sample. Evenness was calculated as

212 $H'/\ln S$, where ' S ' is the total number of species in each plot. Beta diversity was assessed
213 as among-plot dissimilarity in community composition. We used the Bray–Curtis index,
214 computed using the 'vegdist' function in the 'vegan' R-package (Oksanen and others
215 2016). To test for differences in these indices, the CWMs of each functional trait and the
216 soil components between mound and matrix plots, we used paired t -tests or the Wilcoxon
217 signed-rank test following Shapiro–Wilk tests. Functional traits and soil components were
218 standardised, and multicollinearity of functional traits and soil components were assessed
219 using a correlation matrix of all of the functional traits and soil parameters (Pearson's
220 correlation coefficient) to examine possible linkages between variables before subsequent
221 analyses.

222 To assess differences in dispersal-related traits between mound and matrix plots,
223 we defined an 'indicator species' for each site using typical species and their dispersal
224 mode. To identify indicator species, an indicator value (Dufrene and Legendre 1997) was
225 calculated using the '*labdsv*' package (Roberts 2016) in R with 100,000 iterations.

226 We conducted a detrended correspondence analysis (DCA), which indicated that
227 the gradient length of the first axis was long (5.2 standard deviation), suggesting a
228 unimodal distribution response of species assemblages to environmental variables (ter
229 Braak and Smilauer 2002). To explore whether differences in woody plant communities

230 can be explained by soil nutrients and functional traits, we used a canonical
231 correspondence analysis (CCA). CCA is a constrained ordination method that detects key
232 variables accounting for the variation (ter Braak, 1995). Variables that significantly
233 explained the variance in species assemblages ($p < 0.05$) were selected using the ‘ordistep’
234 function in the ‘vegan’ package (Oksanen and others 2016) of R. A separate CCA was
235 used to evaluate the influence of soil components and functional traits on species
236 composition. Explanatory variables with $p < 0.05$, P and Na for soil components and
237 dispersal mode (endozoochory, bird, and wind) for functional traits, were selected for a
238 separate CCA analysis. A permutation of 1000 iterations was used to evaluate significance
239 in CCA. The CCA and DCA were also conducted using the ‘vegan’ package.

240

241 **RESULTS**

242 Termite mounds exhibited higher density of woody plants ($t = 3.6, p < 0.01$), species
243 richness ($t = 7.2, p < 0.0001$), alpha diversity ($t = 5.4, p < 0.0001$) and evenness ($t = 3.6,$
244 $p < 0.001$) of woody plants than the matrix; however, beta diversity did not differ between
245 the mound and matrix plots (Table 2). We extracted 10 indicator species ($p < 0.05$) to
246 represent the mound plots. Species with significant indicator values ($> 60\%$) were
247 considered characteristic mound species (McGeoch and others 2002). Thus, the top six

248 indicator species were characteristic of mounds; *Salvadora persica* had the highest
249 indicator value of 92% (Table 3). Four indicator species were extracted to represent
250 matrix plots; however, the indicator values were not significant (Table 3). All of the
251 indicator species in mound plots were bird- and/or mammal-dispersed, whereas matrix
252 plots were characterised mostly by wind-dispersed species and one mammal-dispersed
253 species (Table 3).

254 CWMs of woody species exhibiting traits related to mammal ($W = 128, p < 0.05$)
255 and bird dispersal ($W = 159, p < 0.001$) were higher on mounds, whereas wind-dispersed
256 species ($W = 38, p < 0.05$) were more common in the matrix (Table 4). CWMs of woody
257 species bearing drupe-type fruits were higher on mounds ($W = 160, p < 0.0001$), whereas
258 those of pod and winged seeds were higher in the matrix ($W = 14, p < 0.001$; $W = 41, p <$
259 0.05 , respectively). Woody species in the matrix plots had heavier seeds than the species
260 in mound plots ($t = -2.6, p < 0.05$). Leaf traits with high CWMs in the matrix included
261 leaf palatability ($W = 14, p < 0.0001$), LA ($t = -2.1, p < 0.05$), LDMC ($W = 37, p < 0.05$),
262 leaf C content ($W = 0, p < 0.0001$) and leaf C:N ($W = 23, p < 0.01$), whereas SLA ($W =$
263 $124, p < 0.05$) and leaf thickness ($W = 150, p < 0.001$) had high CWMs on mounds. There
264 were no differences in CWM of leaf N content between mound and matrix plots. The
265 CWM of evergreens was higher on mounds than in the matrix ($W = 165, p < 0.0001$), and

266 the CWM of deciduous species was conversely higher in the matrix than on mounds (W
267 = 4, $p < 0.0001$); CWMs of plant height ($W = 40$, $p < 0.05$) and N-fixing ability ($W = 13$,
268 $p < 0.001$) were higher in the matrix. The tree growth form was common in the matrix (W
269 = 15, $p < 0.001$), whereas shrubs and climbers were typical on mounds ($W = 155$, $p <$
270 0.0001 ; $W = 118$, $p < 0.05$, respectively). The CWMs of TDMC and spinescence showed
271 no difference between the mound and matrix plots.

272 Values of soil pH, EC, total N, P, K, Ca, CaCO₃, organic C and organic matter
273 were higher on mounds than in the matrix (all $p < 0.05$). The soil on mounds contained
274 more silt than the matrix (Appendix 1). In the evaluation of the effect of soil components
275 on species composition, the first two axes explained 58% of the species composition (Fig
276 1a; ANOVA: $F = 3.8$, $p < 0.01$; eigenvalues for axes 1 and 2: 0.361 and 0.219,
277 respectively). The first axis separated mound plots from matrix plots. P values tended to
278 be associated with mound plots, whereas Na was associated with *Terminalia* spp. and
279 *Acacia* spp., which produce winged or pod fruits. In the evaluation of the relationship
280 between functional traits and species composition, the first two axes explained 64% of
281 the species composition (Fig 1b; ANOVA: $F = 5.1$, $p < 0.05$; eigenvalues for axes 1 and
282 2: 0.475 and 0.161, respectively). The first axis was separated by traits related to
283 endozoochory or wind. Mound plots were strongly associated with traits related to

284 endozoochory and bird dispersal, whereas matrix plots tended to be associated with traits
285 related to wind dispersal. Indicator species on termite mounds were also strongly
286 associated with traits related to bird dispersal.

287

288 **DISCUSSION**

289 We used woody plant functional traits related to seed dispersal to understand the
290 contribution of seed dispersal by animals in determining the woody plant community
291 species composition on termite mounds in an African savannah. We found that termite
292 mounds in the savannah have a diverse woody plant community, which is consistent with
293 the findings of previous studies (e.g. Joseph and others 2014). Many functional traits of
294 woody plants and soil components differed between the mound and matrix.

295 Seed dispersal by animals, including mammals and birds, and drupe-type fruits
296 were defined as the traits of the community composition on the mounds, whereas woody
297 species with winged seeds dispersed by wind were common in the matrix. These results
298 would indicate the contribution of animal seed dispersal in forming the distinct woody
299 plant community found on termite mounds. In the indicator species on these mounds, *S.*
300 *persica* and *Capparis tomentosa* bear drupes at the beginning of the rainy season, and
301 many avian species visit fruiting plants and consume these fruits (Yamashina 2014). In

302 addition, many mammal species were observed on termite mounds; African elephants
303 (*Loxodonta africana*) fed on the leaves of *Commiphora* sp., vervet monkeys (*Chlorocebus*
304 *pygerythrus*) ate the fruits of *Ximenia americana*, and aardvarks (*Orycteropus afer*)
305 hunted termites (personal observation using automatic sensor cameras in October for 1
306 month). Genets (*Genetta genetta* or *Genetta maculata*), common warthogs
307 (*Phacochoerus africanus*), cape porcupines (*Hystrix africaeaustralis*), and mongoose
308 (species unknown) were also observed on termite mounds (same method as above), and
309 their nests were also found on mounds, except for genets (personal direct observation on
310 mounds). Studies have suggested that large herbivores and small mammals utilise termite
311 mounds, more than the surrounding matrix, as browsing and nesting sites (Loveridge and
312 Moe 2004; Okullo and others 2013). Avian species nesting in woody species on termite
313 mounds may disperse seed among the mounds (Joseph and others 2011). Of the animal
314 species observed at our site, the genet, vervet monkey, elephant and mongoose have been
315 suggested to act as seed dispersers (Jackson and Gartlan 1965; Debussche and Isenmann
316 1989; Clevenger 1996; Barnes 2001; Tews and others 2004). Additional observational
317 studies on matrix need to compare the relative abundance of potential seed dispersers
318 between mounds and surrounding matrix. However, these mammals, in addition to avian
319 species, visited *S. persica* and *C. tomentosa*, possibly dispersing seeds that shape the

320 unique vegetation on termite mounds, because some of them feed on the indicator species
321 on mounds and utilise the mounds as nesting sites.

322 Soil components would contribute to the differences in the species compositions
323 of distinct vegetation on mounds. As many studies have shown (e.g. Sileshi and others
324 2010), *Macrotermes* mounds are relatively resource-rich islands with higher total N, P, K,
325 Ca and organic matter contents compared with the surrounding matrix. Of these
326 components, P was associated with mound plots, and indicated the difference in species
327 composition between mound and matrix plots. We also found that N-fixing ability, LDMC,
328 LA and leaf C:N were higher in the resource-poor matrix, whereas SLA and leaf thickness
329 were higher on resource-rich mounds. These results are consistent with the findings of
330 previous studies, which showed that species growing in resource-rich environments
331 generally have higher SLA and lower LDMC values (Cornelissen and others 2003),
332 whereas species growing in resource-poor environments have higher leaf C:N and LDMC
333 values and larger leaves (Perez-Harguindeguy and others 2013; Wigley and others 2016).
334 Van der Plas and others (2013) suggested that the presence of fewer N fixers in mounds
335 indicates the role of the mounds as refugia for woody plant species that are less adapted
336 to environments with relatively poor nutrient availability, which is consistent with our
337 results.

338 We found more evergreen species on mounds and more deciduous species in the
339 matrix. In recent studies, termite mounds have been shown to act as buffers against
340 drought by enhancing revegetation and plant growth (Bonachela and others 2015) and
341 woody species associated with the mounds have been shown to exert cooling effects,
342 which modulate temperature and humidity in African savannahs (Joseph and others 2016).
343 Deciduous species have traits associated with drought avoidance, whereas evergreen
344 species are less well adapted to drought (Lebrija-Trejos and others 2010). Therefore, these
345 mound-induced environments would be advantageous for the establishment of drought-
346 sensitive evergreen species and act as revegetation foci during drought periods, resulting
347 in non-uniform distributions of evergreen and deciduous species and further distinction
348 of the vegetation patterns on mounds and the surrounding matrix. Termite mounds might
349 also act as refugia for fire-prone evergreen species (Van der Plas and others 2013). The
350 vegetation on termite mounds experiences less fire damage due to low fuel load (Joseph
351 and others 2013), high water availability (Konate and others 1999) and elevated
352 topography (Moe and others 2009; Sileshi and others 2010). Although grass cover did not
353 differ significantly between termite mounds and the surrounding matrix at this site
354 (Yamashina 2013), water availability, elevated topography and fire frequency should be
355 examined to assess their filtering effects.

356 Large herbivores have been suggested to influence the vegetation community of
357 termite mounds, as a disturbance factor (Okullo and Moe 2012a), and have been shown
358 to negatively affect mound woody plant diversity at high densities, with browsers having
359 a greater impact than grazers (Joseph and others 2015). In miombo woodland, termite
360 mounds provide preferred forage for large herbivores (Loveridge and Moe 2004; Mobaek
361 and others 2005) because of their nutrient-rich foliage (Holdo, 2004), although the reverse
362 pattern, in which the plants on mounds are less preferred by mammal herbivores, was
363 found in mosaic vegetation in South Africa (Van der Plas and others 2013). Davies and
364 others (2016) found that the importance of termite mounds for herbivores as foraging sites
365 varied with nutrient availability and season, and is likely to be more important in nutrient-
366 poor environments in the wet season, and more important in nutrient-rich environments
367 in the dry season. In this study, we found no differences in leaf N content, fruit/pod
368 palatability, or spinescence between mound and matrix, and leaf palatability was higher
369 in the matrix plots. Thus, we found no evidence from functional traits that termite mounds
370 should act as browsing hotspots, which may be explained by the fact that the leaves and
371 pods of *C. mopane*, the sole dominant species at the site, are the most important resource
372 for herbivores in mopane vegetation ecosystems. The lack of difference in spinescence,
373 which acts as physical protection against herbivores, also indicates no difference in

374 browsing pressure on the woody species on the mound and in the matrix. Therefore, we
375 found no filtering effects due to herbivory in this study.

376 This study suggested that dispersal processes, especially animal seed dispersal,
377 contribute more to the distinct and diverse woody plant community found on termite
378 mounds than that in the surrounding matrix. Certainly, this non-uniform distribution of
379 woody species with animal dispersal traits could be an incidental result of other filters
380 rather than dispersal mechanisms. Actually, soil can act as a filter of vegetation from the
381 soil P in mound plots. This study, however, found a clear association only between soil P
382 and woody species composition on mounds, despite of the significant differences in many
383 soil components between mounds and matrix. Then animal seed dispersal was suggested
384 as a filter. The seed-dispersal process, including direct measurement of seed dispersal,
385 during the creation of diverse plant assemblies on the termite mounds (Pringle and others
386 2010; Sileshi and others 2010; Erpenbach and others 2013) should be evaluated in future
387 studies, in addition to biotic and abiotic filters, such as the soil environment (e.g. Konate
388 and others 1999; Sileshi and others 2010), topography (Dangerfield and others 1998;
389 McCarthy and others 1998) and disturbance (Holdo and McDowell 2004; Loveridge and
390 Moe 2004; Moe and others 2009; Joseph and others 2013). Animals contribute to the
391 development of this hotspot via nutrient input (Holdo and McDowell 2004; Loveridge

392 and Moe 2004) and seed deposition, whereas termite mounds act as browsing and nesting
393 hotspots for mammals and birds (Holdo and McDowell 2004; Loveridge and Moe 2004;
394 Joseph and others 2011). Therefore, more studies are needed to explore the interaction
395 between animals and the plant community on termite mounds to understand the
396 heterogeneity induced by mound-building termites (Sileshi and others 2010; Erpenbach
397 and others 2013).

398

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595 **Table 1.**

Traits	Response to dispersal	Response to soil resource	Response to disturbance (fire, herbivore)
Dispersal mode (Mammal, Bird, Wind)	✓		
Fruit type (Drupe, Pod, Winged)	✓		
Seed mass	✓		
Leaf palatability (for herbivore)			✓
Fruit/pod palatability			✓
LDMC		✓	✓
Leaf thickness		✓	
LA		✓	
SLA		✓	
Spinescence			✓
Leaf N		✓	
Leaf C		✓	
LeafC:N		✓	
N-fixing		✓	
Growth form (Tree, Shrub, Climber)		✓	✓
Phenology (Deciduous, Evergreen)		✓	
596 Tree height		✓	✓

597

598 **Table 2.**

	Mound	Matrix	<i>p</i> -value
Tree density (/400m ²)	81.1 ± 39.1	38.7 ± 16.2	**
Species richness (/400m ²)	11.9 ± 2.4	4.1 ± 3.1	***
Alpha diversity (Shannon-Wiener index)	2.8 ± 0.7	1.0 ± 0.9	***
Evenness (Shannon evenness index)	1.0 ± 0.2	0.5 ± 0.4	**
Beta diversity (Bray-Curtis)	0.6 ± 0.2	0.6 ± 0.3	

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602 **Table 3.**

Mound					Matrix				
Family	Species	Indicator value	Individuals %	Dispersal vector	Family	Species	Indicator value	Individuals %	Dispersal vector
Salvadoraceae	<i>Salvadora persica</i>	92***	12.24	bird	Fabaceae	<i>Colophospermum mopane</i>	46 n.s.	64.02	wind
Fabaceae	<i>Acacia nigrescens</i>	89***	5.50	mammal	Fabaceae	<i>Dichrostachys cinerea</i>	30 n.s.	21.27	mammal
Tiliaceae	<i>Grewia</i> spp.	81***	3.98	bird/mammal	Combretaceae	<i>Combretum imberbe</i>	23 n.s.	1.59	wind
Burseraceae	<i>Commiphora glandulosa</i>	66**	4.55	bird	Combretaceae	<i>Combretum hereroense</i>	15 n.s.	1.39	wind
Olacaceae	<i>Ximenia americana</i>	62**	5.22	mammal					
Braginaceae	<i>Cordia</i> spp.	62**	3.22	bird/mammal					
Braginaceae	<i>Ehretia</i> spp.	53**	4.17	bird					
Capparaceae	<i>Capparis tomentosa</i>	49*	3.13	mammal					
Rhamnaceae	<i>Berchemia discolor</i>	44*	1.90	bird/mammal					
Anacardiaceae	<i>Lannea discolor</i>	38*	0.66	bird					

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605 **Table 4.**

		Mound	Matrix	<i>p</i> -value
Dispersal mode (<i>b</i>)	Endozoochory	0.69 ± 0.27	0.34 ± 0.36	*
	Bird	0.43 ± 0.18	0.08 ± 0.17	***
	Wind	0.28 ± 0.26	0.65 ± 0.36	*
Fruit type (<i>b</i>)	Drupe	0.45 ± 0.19	0.08 ± 0.17	***
	Pod	0.51 ± 0.20	0.86 ± 0.19	***
	Winged	0.30 ± 0.24	0.66 ± 0.36	*
Seed mass (g)		0.26 ± 0.14	0.44 ± 0.21	*
Leaf palatability (for herbivore) (<i>b</i>)		0.93 ± 0.06	1.00 ± 0.01	***
Fruit/pod palatability (<i>b</i>)		0.91 ± 0.05	0.94 ± 0.10	
LDMC (mg/g)		393.94 ± 20.87	412.91 ± 13.55	*
Leaf thickness (µm)		239.00 ± 23.94	209.05 ± 10.88	***
LA (mm ²)		1932.36 ± 493.80	2436.24 ± 726.89	*
SLA (mm ² /mg)		10.76 ± 1.08	10.07 ± 0.75	*
Spinescence (<i>b</i>)		1.35 ± 0.73	0.99 ± 1.09	
Leaf N (%)		2.73 ± 0.27	2.53 ± 0.31	
Leaf C (%)		43.12 ± 2.86	47.41 ± 0.54	***
LeafC:N		18.27 ± 1.82	21.08 ± 2.51	**
N-fixing (<i>b</i>)		0.53 ± 0.17	0.87 ± 0.19	***
Growth form (<i>b</i>)	Tree	0.67 ± 0.17	0.94 ± 0.15	***
	Shrub	0.29 ± 0.15	0.06 ± 0.14	***
	Climber	0.03 ± 0.04	0.01 ± 0.01	*
Phenology (<i>b</i>)	Deciduous	0.81 ± 0.14	0.99 ± 0.01	***
	Evergreen	0.19 ± 0.14	0.01 ± 0.01	***
606	Tree height (m)	3.91 ± 0.37	4.35 ± 0.64	*

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610 **Table legends**

611 **Table 1.** Woody plant functional traits reflecting their responses to dispersal, soil

612 resources and disturbances (fire and herbivores).

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614 **Table 2.** Woody plant community species on termite mounds and in the surrounding

615 matrix (average±standard deviation).

616 Student's t-test or Wilcoxon signed rank test. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

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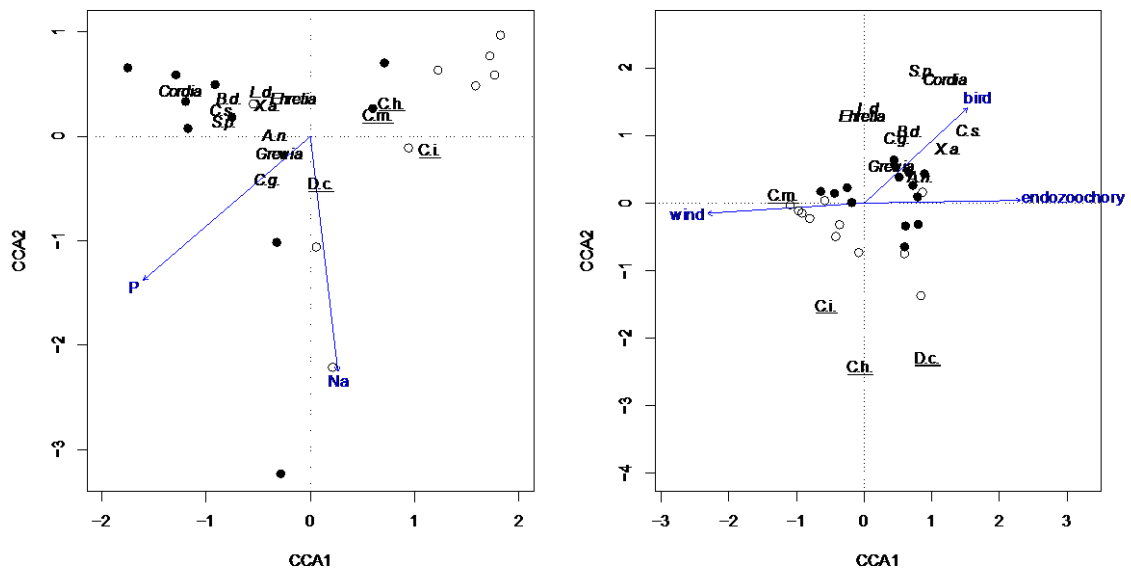
618 **Table 3.** Indicator species on termite mounds and in the surrounding matrix.

619

620 **Table 4.** Community-weighted mean (CWM) values of each functional trait in woody
621 plants on termite mounds and in the surrounding matrix (average±standard deviation).

622 Student's t-test or Wilcoxon signed rank test. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

623 (b): binary data (yes=1, no=0)



624

625 **Figure 1.**

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636 **Figure Legends**

637 **Figure 1.** CCA of woody plant species composition with statistically significant

638 explanatory variables for (a) soil components and (b) functional traits. Abbreviations

639 indicate the indicator species names of woody plants: A.n., *Acacia nigrescens*; B.d.,

640 *Berchemia discolor*; C.g., *Commiphora glandulosa*; C.h., *Combretum hereroense*; C.i.,

641 *Combretum imberbe*; C.m., *Colophospermum mopane*; C.t., *Capparis tomentosa*; Cordia,

642 *Cordia* sp.; D.c., *Dichrostachys cinerea*; Ehretia, *Ehretia* sp.; Grewia: *Grewia* sp.; L.d.,

643 *Lannea discolor*; S.p., *Salvadora persica*; X.a., *Ximenia americana*. Italics indicate the

644 indicator species of the mounds, and underline indicates the indicator species of the

645 matrix.

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654 **Appendix 1.** Soil contents on termite mounds and in the surrounding matrix.

	Mound	Matrix	<i>p</i> -value
pH	7.84 ± 0.38	6.99 ± 0.71	**
EC (mS/m)	100.79 ± 103.97	38.24 ± 46.49	**
Total N (mg)	2063.42 ± 1412.64	652.07 ± 366.21	*
P (mg/kg)	18.60 ± 10.35	3.44 ± 1.76	***
K (cmol _c /kg)	1.94 ± 1.39	0.44 ± 0.34	***
Ca (cmol _c /kg)	24.31 ± 3.60	7.57 ± 9.35	***
Mg (cmol _c /kg)	3.64 ± 1.45	2.36 ± 2.86	
CaCO ₃ (%)	1.28 ± 0.69	0.29 ± 0.17	***
Organic C (%)	1.41 ± 0.68	0.57 ± 0.33	**
Organic matter (%)	2.44 ± 1.17	0.98 ± 0.57	**
Na (cmol _c /kg)	2.42 ± 5.32	0.52 ± 0.65	
Sand (>53 μm %)	62.30 ± 10.79	73.15 ± 28.67	
Silt (53-2 μm %)	20.34 ± 9.04	10.27 ± 7.36	*
655 Clay (< 2 μm %)	17.36 ± 4.79	16.58 ± 22.12	

656 Student's t-test or Wilcoxon signed rank test. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

657