A phylogenetic community approach for studying termite communities in a West African savannah

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Termites play fundamental roles in tropical ecosystems, and mound-building species in particular are crucial in enhancing species diversity, from plants to mammals. However, it is still unclear which factors govern the occurrence and assembly of termite communities. A phylogenetic community approach and null models of species assembly were used to examine structuring processes associated with termite community assembly in a pristine savannah. Overall, we did not find evidence for a strong influence of interspecific competition or environmental filtering in structuring these communities. However, the presence of a single species, the mound-building termite *Macrotermes bellicosus*, left a strong signal on structuring and led to clustered communities of more closely related species. Hence, this species changes the assembly rules for a whole community. Our results show the fundamental importance of a single insect species for community processes, suggesting that more attention to insect species is warranted when developing conservation strategies.

1. Introduction

In terrestrial tropical ecosystems, termites are believed to play a key role in ecosystem functioning [1–4]. As keystone species, large mound-builders foster species richness as their ‘termittaria’ harbour unique flora [5] and increase even vertebrate diversity [1]. Although this important role of termites is now well established, it is still unclear which factors govern the assembly of termite communities and whether they are also influenced by large mound-builders.

Within a habitat, termites have very similar ecological requirements, and only four feeding groups are distinguished [6]. In African savannahs, almost all species are wood-litter feeders [7]. Ecological analyses allow a further differentiation of specialist grass-feeders (*Trinervitermes*) and fungus-growing termites (*Macrotermi- tinae*) [8]. These ecological similarities raise the question about the importance of interspecific competition and environmental filtering compared with neutral processes (ecological drift) in structuring such communities.

Addressing this question is challenging, because complex interactions are difficult to unravel, even more so in termites for which few ecological data exist. Phylogenetic community analyses that use phylogenetic information to infer ecological processes can help in deducing assembly mechanisms [9,10] (see §2). They cannot replace ecological studies and require careful interpretation [10,11]: for instance, the evolutionary ‘speed’ (i.e. whether traits are conserved or labile) of niche-relevant traits (such as feeding-habits) must be known and environmental filtering effects must be separated from interspecific competition.

We applied phylogenetic community analyses and tested the importance of interspecific competition and environmental filtering in structuring termite communities in a pristine African savannah. Here, feeding-habits are phylogenetically
2. Material and methods

(a) Taxon sampling and identification

Termites were systematically collected when they were most active during the beginning of the rainy season in the Pendjari National Park (10°30′–11°30′ N, 0°50′–2°00′ E, Benin), a typical savannah of the West Sudanian biome [13]. We were specifically interested in local community assembly within a single habitat. Hence, we purposefully excluded obvious environmental gradients and choose plots with similar vegetation of medium dense bush savannah, so that all species could potentially occur in all study plots. The plot scale was selected to reflect the Darwin–Hutchinson zone [14], i.e. the scale where interactions among species occur. It depends on the ecology of the study species. For the termites we studied, the interactions among species occur at a scale of about 1 ha, because the foraging range of colonies is around 100 m [15]. Hence, we choose 1 ha as our plot size.

We sampled nine 1 ha plots (electronic supplementary material, figure S2), three in 2008 (P1–P3) and six in 2009 (P4–P9), using a standardized belt transect protocol first developed for sampling termites in forests [16] and then adapted to savannahs [7] (for details see electronic supplementary material). All samples of a plot were used to characterize the local species composition.

All samples were identified to species level either by morphological and/or genetic means (see electronic supplementary material) [17–19].

(b) Community analyses

The regional species pool of the study area contains 20 species (electronic supplementary material, table S1) [7]. We found 18 species (electronic supplementary material, table S1), showing that sampling was efficient. The phylogenetic community structure was analysed with PHYLOGEN v. 4.1 [17] (for details see the electronic supplementary material). Using the net relatedness index (NRI), we tested whether co-occurring species are more (phylogenetically clustered; high positive values) or less closely related (phylogenetically overdispersed; low negative values) than expected compared with null models in which species occurrences are randomized. As closely related species share niche-relevant traits such as feeding habits (electronic supplementary material, figure S1), competitive interactions between species are expected to result in phylogenetic overdispersion, whereas phylogenetic clustering indicates environmental filtering [9,17]. A lack of pattern indicates random community assembly.

To test whether any of our nine communities significantly differed from random assemblages, 999 random communities were generated from null models using the independent swap algorithm on presence/absence data [18,19] (see the electronic supplementary material). Non-significance indicates that local communities do not differ from random communities, implying that environmental filtering or interspecific competition do not have strong effects and that ecological drift (e.g. random dispersal, migration or extinction) is important.

To test the effect of M. bellicosus on community composition, we compared NRIs between plots with and without M. bellicosus. To assess whether this is a species-specific effect, we did similar analyses using the fungus-growing Coptotermes sp. 1 and Odontotermes sp. 2, as well as Adaiptotermes sp. 1. These were the only species for which such analyses were possible (see the electronic supplementary material). No effect of any of these species on community composition was found (electronic supplementary material, figure S3).

Additionally, we tested for potentially confounding influences of abiotic environmental factors on community composition using logistic regressions as suggested by Helmus et al. [20] (for details see electronic supplementary material, table S2). These analyses help us to detect ‘hidden’ environmental effects that might have escaped our attention when choosing similar plots. Second, they allow testing for an effect of environmental filtering separate from interspecific competition [20]. We found no evidence for an influence of abiotic environmental factors, nor was there any signal after accounting for environmental variables (electronic supplementary material, figure S4).

3. Results

Seventeen of the 18 species in our study were Termitidae (exception: Rhinotermitidae: Coptotermes sp. 1; electronic supplementary material, table S1). Among them, the fungus-growing termites (Macrotermiteinae) dominated, with nine species (electronic supplementary material, table S1). These fungus-growers all belong to the same feeding group, nevertheless up to eight coexisted locally (electronic supplementary material, table S1). This implies that interspecific competition among fungus-growers is too weak to result in competitive exclusion of species at the local level.

In addition, we did not find evidence of either strong interspecific competition or environmental filtering from the phylogenetic community composition analyses; the NRIs ranged from −2.36 to 1.02, and none significantly deviated from random assemblages generated by null models (p > 0.05; figure 1a). NRIs also did not significantly correlate with species richness (Spearman’s rank correlation: r = 0.496; figure 1a). However, the mound-building species M. bellicosus had a significant effect on phylogenetic structuring, when M. bellicosus was present, NRIs were significantly higher (i.e. more phylogenetically clustered communities) than when it was absent (Mann–Whitney U-test: n = 9, Z = −2.45, p = 0.016; figure 1b). This was mainly owing to the occurrence of many Trinervitermes species (electronic supplementary material, table S1). Using the number of samples found within a plot as a proxy for abundance (encounter; electronic supplementary material, table S1), there was a trend that Trinervitermes occidentalis was more frequent when M. bellicosus was present (Mann–Whitney U-test: n = 9, Z = −1.88, p = 0.060) but not Trinervitermes ocononcus (n = 9, Z = −0.51, p = 0.612).

4. Discussion

We found no evidence for either interspecific competition or environmental filtering in structuring our local termite communities: the composition of none of our studied communities differed significantly from random communities (figure 1a). Also, when we accounted for environmental variables, the studied communities did not differ from random assemblages of the regional species pool (electronic supplementary material, figure S4). This implies that, across all localities, random events such as random dispersal and/or mortality are important in...
determining local community composition. However, the presence of *M. bellicosus* led to a signal of environmental filtering (figure 1b), indicating that more closely related species co-occur when this keystone species was present. This effect was significant, even though the sample size was rather small.

This effect of *M. bellicosus* could be direct or indirect, for instance, through restricting species with niche requirements similar to those of the mound-builder, to specific savannah types. Such an indirect effect is less likely: *M. bellicosus* occurs in all kinds of savannahs from open grass to dense bush savannahs with highly variable soil types [21]. Its often patchy distribution rather results from stochastic effects such as spatiotemporally highly variable rainfalls that restrict successful colony foundation [15].

Hence, direct effects are more likely, either through (i) direct ‘filtering’ or (ii) removal of competition. *Macrotermes* mounds provide homes for a broad range of species, among termites, *Macrotermes* and *Trinervitermes* [22,23]. In our study area, *T. occidentalis* and *T. oconumus* often inhabit *M. bellicosus* mounds (electronic supplementary material, table S1), and at least the former seems to occur more commonly when *M. bellicosus* was present. Further filtering of termite species may occur through soil processes as *Macrotermes* creates habitat heterogeneity [1,3,4]. Alternatively, *M. bellicosus* may cause filtering by reducing interspecific competition among (closely related) termite species (*Trinervitermes*) that are outcompeted when it is absent (similar to an indirect ‘competitive release’ effect). *M. bellicosus* is a dominant species [21] and there is limited evidence from confined subsets of only a few termite species for other ecosystems to show that interspecific competition can occur [21,24,25]. Our current understanding of the ecology of savannah termites is too limited and requires further ecological studies to test between these alternative hypotheses that we have generated using the phylogenetic approach.

To summarize, our data imply that large *Macrotermes* mounds not only affect the diversity of other taxa [1], but are also a key element in structuring termite communities. *M. bellicosus* may function as a direct environmental filter or through changing ecological dominance hierarchies. The randomness of termite communities across localities may reflect the fact that the occurrence of this mound-builder is largely determined by stochastic factors. In several West African regions, *M. bellicosus* is threatened by climate change and land use (J.K. 2008–2014, unpublished data). Hence, such crucial insect ecosystem engineers deserve more attention, also in conservation debates.

**Ethics.** This work was performed according to laws of the respective countries.

**Data accessibility.** DNA sequence data are available at GenBank accession JF923148–JF923412. Other datasets supporting this article have been uploaded as part of the electronic supplementary material.

**Authors’ contributions.** J.K. designed the study, obtained funding, contributed to data sampling and data analyses. B.H did data sampling, species identification and data analyses. Both authors wrote the paper.

**Competing interests.** The authors declare no competing interests.

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**References.**


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**Figure 1.** Phylogenetic structure of local termite communities measured by net relatedness index (NRI). *(a)* NRI varied and did not significantly correlate with species richness (Spearman’s rank correlation: $p = 0.496$). *(b)* Plots with *M. bellicosus* mounds were significantly more clustered (higher NRI values) than plots lacking this species.


