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Phylogenetic Community Structure of Southern African Termites (Isoptera)

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Abstract

The processes that structure communities are still largely unknown. Therefore, we tested whether southern African termite communities show signs of environmental filtering and/or competition along a rainfall gradient in Namibia using phylogenetic information. Our results revealed a regional species pool of 11 species and we found no evidence for phylogenetic overdispersion or clustering at the local scale. Rather, our results suggest that the assembly of the studied termite communities has as strong random component on the local scale, but that species composition changes along the climatic gradient.

Introduction

The mechanisms that structure communities are still highly debated (Chase & Leibold, 2003; Chave, 2004; Zhou & Zhang, 2008; Holt, 2009). Environmental factors such as temperature and rainfall can act as filters that limit, for instance, the distribution of species and define part of a species niche, especially over larger geographic scales. An understanding of the importance of local versus regional processes depends on the spatial scale, divided into spatial grain (the size of the sample unit) and the spatial extent (the total area of the study), at which species communities are defined and studied, and the scale at which actual processes operate (Graham & Fine, 2008; Emerson & Gillespie, 2008; Weiher et al., 2011).

Classically, interspecific competition was thought to be a major driving force in structuring communities of ecologically similar species (members of the same guild, functional analoga) (Diamond, 1978; Schoener, 1982). The resulting concept of limiting similarity states that species can only co-exist if they differ in their niche axes (Abrams, 1983). There is supporting evidence, for example, when striking patterns of size or morphological differences were found for co-existing guild members (Bowers & Brown, 1982; Leibold, 1998). Yet, in many cases the concept was taken for granted and local communities were not tested against the null hypothesis of random assemblages from the regional species pools. In more recent years the development of the unified neutral theory of biodiversity and biogeography challenged the classical niche theory and considered niche differences less important (Hubbell, 2001). According to this theory, trophically similar species are demographically equivalent and ecological communities are mainly structured by 'ecological drift' (*i.e.* stochastic factors such as birth, death, random migration and extinction) (Hubbell, 2001; Volkov et al., 2009). A 'niche versus neutrality' debate is largely unproductive and attempts exist to incorporate elements of both theories into more general explanations (Holt, 2009; Weiher et al., 2011).

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The high species diversity of tropical ecosystems, where many species of seemingly identical niches coexist, is a challenge for classical niche theory. The fact that tropical insect communities have even less specialists than those of temperate regions (Schleuning et al., 2012; Ollertonet al., 2012) supports the theory that niches may not play such an important role in the tropics. Yet, data that explicitly test structuring processes in tropical animal communities are scarce (Vamosiet al., 2009). This applies especially for insects whose sheer species richness can hardly be explained by niche differences.

Many termite species occupy apparently very similar niches: they have similar abiotic requirements and are decomposers of organic matter. Currently, four feeding groups are recognized by analysis of gut content (Donovan et al., 2001), representing different stages of decomposition from sound wood to soil organic matter. This classification is also reflected in the four feeding types; wood-, leaf litter-, soil- and true soil- feeders (Eggleton & Tayasu, 2001). Recent stable isotope analyses of a termite assemblage from a forest implied that there is subtle niche differentiation within feeding groups (Bourguignon et al.,2009). Yet, they cannot explain how more than 20 species of leaf litter feeders can co-exist in African savannas that all forage from the same dead plant material (Hausberger et al., 2011).

We tested whether local termite communities in southern Africa differ from random assemblages of the regional species pool with regard to phylogenetic composition, by looking at communities across a north/south rainfall gradient in Namibia. The northern region is characterized by higher precipitation and therefore more diverse vegetation than the more arid southern region with less vegetation (Jürgens et al., 2010; Grohmann et al., 2010). We investigated whether ß-diversity between sites is related to distance along this gradient.

To do this, we applied phylogenetic community analyses (Webb et al., 2002, 2008; Cavender-Bares et al., 2009; Kembel et al., 2010), which allowed us to explicitly test real communities against null models of random assemblages. By using phylogenetic information, we tested whether local communities are more or less closely related than assemblages drawn randomly from the regional species pool. As ecological traits are phylogenetically conserved for the species studied here (Inward et al., 2007), related species share ecological traits, and therefore assemblages of less closely related species (i.e. phylogenetic overdispersion) indicate interspecific competition because these similar traits prevent species from coexistence. The reverse (i.e. phylogenetic clustering) suggests environmental filtering due to similar ecological preferences (temperature, rainfall, vegetation density, soil type) (Webb et al., 2002, 2008). Combined with analyses of species turnover between localities (ß-diversity; Whittaker, 1972) and its phylogenetic signal (phylogenetic ß-diversity; Bryant et al., 2008; Kembel et al., 2010), and an analysis of the impact of environmental variables (Helmus et al., 2007a, 2007b), we tested whether these southern African termite communities differed from random assemblages.

Materials and methods

Termite sampling

Termites were collected in January 2010 from 6 sampling sites (22°50’ to 26°11’N; 18°5’ to 16°8’E; Namibia; Fig 1) when they were most active, that is, at the beginning of the rainy season, using a standardized transect sampling protocol (Hausberger et al., 2011). This protocol developed for termite diversity assessments consists of soil sampling and a thorough search of dead plant material on the ground, in trees, and in mounds (Jones & Eggleton, 2000). Such transect sampling is recommended to assess termite diversity in regions of intermediate to moderately low rainfall (Davies et al., 2013). A plot size of one ha was chosen because the foraging range of termite colonies is within 100m (Korb & Linsenmair, 2001) and hence one ha represents the local scale where interactions among colonies occur, i.e. it reflects the Darwin-Hutchinson-Zone, which is most relevant to study the assembly of local communities (Vamosiet al., 2009). Three transects each measuring 2 m x 50 m, divided into ten 2 m x 5 m sections, were arbitrarily located within each plot. Each transect section was searched thoroughly for termites for 15 minutes by a trained person; additionally, we sampled eight soil pits per transect section, each measuring 12 cm x 12 cm x 10 cm. All encountered samples were stored in pure ethanol for subsequent molecular analysis. Due to limitations of the study, additional sampling along the climatic gradient was not possible. However, this transect method is designed to obtain the best possible ‘snapshot’ of conditions in a site and has been tested and used frequently in termite diversity studies (Jones & Eggleton, 2000; Donovan et al., 2002; Eggleton et al., 2002; Inoue et al., 2006) and our study design is comparable to other termite studies (Houston et al., 2015; Dahlsjö et al., 2015).

All samples were identified to species level. First, samples containing soldiers were identified to the genus level using the keys by Webb (1961) and Uys (2002). Then these morphological identifications were confirmed by molecular genetic analyses (see below). For samples with workers only, morphological identification was difficult, they were genetically analysed (see below). The presence/absence of each species within a plot was documented as well as the encounter rate (i.e. the number of samples per species and plot), which is used as a surrogate of species abundance (Davies, 2002).

Genetic analyses

To allow unambiguous species identification, we isolated DNA and sequenced fragments of three genes as described elsewhere (Hausberger et al., 2011) (see also Supplementary

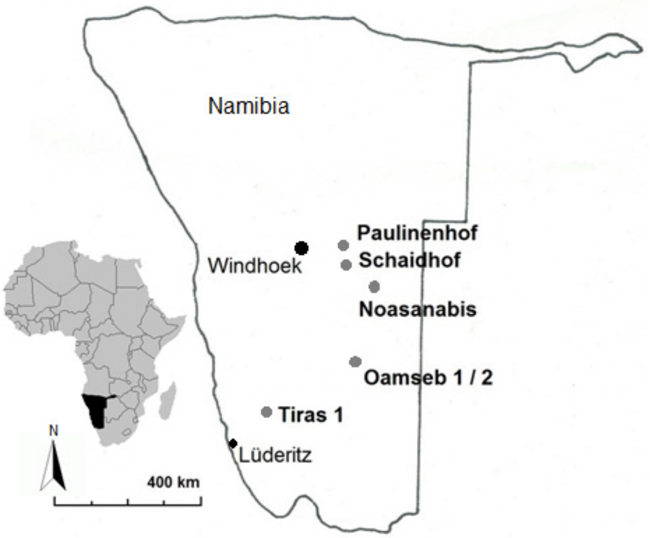

Fig 1. Map of the six sampling sites in Namibia. One sampling site (plot) represents one community with one ha in size.

Material, Table S1): *cytochrome oxidase subunit I* (*COI*; total length 680bp), *cytochrome oxidase subunit II* (*COII*; total length 740 bp), and *12S* (total length 350 bp). These sequences were used to re-construct phylogenetic trees using three approaches (Bayesian method, maximum-parsimony analysis, and maximum-likelihood analysis) to delimitate and identify species (for more details and GenBank accession numbers see Supplementary Material, Table S2). As in former termite studies (Legendre et al., 2008; Hausberger et al., 2011), *COII* was most useful for 'barcoding' (i.e., assigning species to samples) because it amplified well and gave appropriate resolution for species identification. All collected samples were sequenced for identification.

Phylogenetic community structure analyses

We analysed the local community structure with PHYLOCOM 4.2 (Webb et al., 2008). As input tree for the phylogenetic community structure analyses we used the *COII* gene tree, which was pruned prior to analysis so as to have only species of the regional species pool included and only one representative per species in the tree. We calculated the net relatedness index (NRI) that measures whether locally co-occurring species are phylogenetically more/less closely related than expected by chance. It uses phylogenetic branch length to measure the distance between each sample to every other terminal sample in the phylogenetic tree, and hence the degree of overall clustering (Webb et al., 2008). The NRI is the difference between the mean phylogenetic distance (MPD) of the tested local community and the MPD of the total community (regional) divided by the standard deviation of the latter. High positive values indicate clustering; low negative values overdispersion (Webb et al., 2002).We chose the NRI and not the nearest taxon index (NTI) because the NRI quantifies overall clustering of taxa on a tree and takes deep-level clustering into account. The NTI quantifies terminal clustering, independent of deep-level clustering and gave qualitatively the same results as the NRI. We tested whether our data significantly deviated from 999 random communities derived from null models using the independent swap algorithm on presence/absence data (Gotelli & Entsminger, 2003; Hardy, 2008). The swap algorithm creates swapped versions of the sample/species matrix and constrains row (species) and column (species' presence or absence) totals to match the original matrix. The regional species pool consisted of all species from all studied localities. As suggested by Webb et al. (2008), we used two-tailed significance tests based on the ranks that describe how often the values for the observed community were lower or higher than the random communities. With 999 randomizations, ranks equal or higher than 975 or equal and lower than 25 are significant at $P < 0.05$ (Bryant et al., 2008).

Comparison between study sites

We quantified the compositional similarity (ß-diversity) between all localities using the Sorensen and Bray-Curtis index, which were calculated in EstimateS version 8.2.0 (Colwell, 2013). High values indicate high similarities between plots with regard to species composition and low values the reverse. A Mantel test was used to analyse whether the similarity correlates with distance between plots using XLSTAT, version 2013.2.06. The PhyloSor index quantified the phylogenetic ß-diversity (Bryant et al., 2008). It ranges from 0 (two communities only share a very small root, which means they consist of phylogenetically very different taxa) to 1 (both communities are composed of related taxa). Equivalent to the Phylocom analyses it was tested whether phylogenetic similarities between plots deviated from random by using 'independent swap' null models with 999 runs and applying rank tests. Analyses were done with Picante 1.2.0 (Kembel et al., 2010) as implemented in R 3.0.3.

Influence of environmental variables

We also tested if environmental factors influence the assemblage of termite communities using logistic regressions as suggested by Helmus et al. (2007a, b). We retrieved monthly data for the bioclimatic variable mean annual precipitation for our study areas from the WorldClim database (www.worldclim.org; Hijmans et al., 2005), which is a set of global climate layers (climate grids) with a spatial resolution of $1km^2$. We only used one variable because of the small sample size and precipitation seems the most influential variable in arid regions. As termite colonies are perennial and sedentary this data seems more appropriate than recordings for a certain year. We correlated co-occurrence of species pairs with phylogenetic co-occurrence of species pairs, both before and after accounting for environmentally caused variability (mean annual precipitation), and calculated the change in occurrence correlations when including mean annual precipitation as implemented in the R-package "Picante" (Kembel et al., 2010).

Results

Diversity

The phylogeny revealed a regional species pool of 11 species in nine genera (Fig 2). Nine species belonged to the higher termites (Termitidae), with two Macrotermitinae (*Allodontotermes* sp., *Microtermes* sp.), four Termitinae (*Microcerotermes* sp., *Angulitermes* sp., *Promirotermes* sp., *Amitermes* sp.), and three Nasutitermitinae *(Trinervitermes bettonianus, Trinervitermes trinervoides* and *Trinervitermes* sp.). From the lower termites *Hodotermes mossambicus* (Hodotermitidae) was sampled as well as one representative of the genus *Psammotermes* (Rhinotermitidae). The phylogenetic analyses for the gene *COII* showed appropriate resolution, which was not the case for the genes *COI* and *12S*. Here sequencing of all samples was difficult and the phylogenetic trees did not give appropriate resolution for all species (Fig 2, Supp. Fig S1 and S2). This similarly applied for the other phylogenetic methods used.

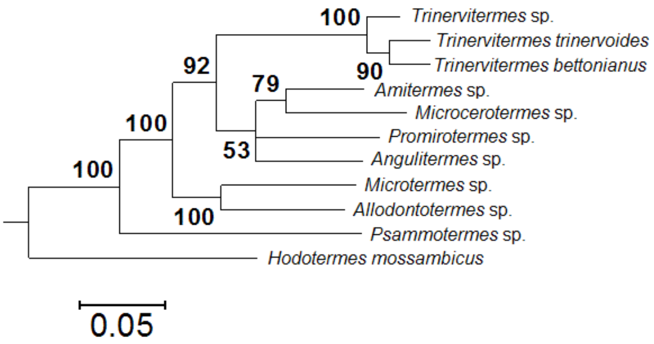

Fig 2. Input Bayesian phylogeny for Phylocom based on the gene cytochrome oxidase II using Mr Bayes v3.1.2. Analysis was done with 10^7 generations, as well as a number of chains=4, sample frequency=1000 and a finalizing burn-in of 2500.

Phylogenetic community structure

There were no significant signals of overdispersion or clustering within local communities. The NRI indices ranged from 0.21 to 1.12. They never deviated from random communities generated with the 'independent swap' algorithm (always p>0.05). Species richness per plot did not correlate with NRI either (Spearman-rank correlation: NRI: r= 0.313, p= 0.545) (Fig 3).

Comparison between study sites

The compositional similarity between plots varied, with the Sorensen index ranging from 0.40 to 1.00, the Bray-Curtis index ranging from 0.19 to 0.74 (Supp. Fig S3 and S4) and the PhyloSor index ranging from 0.53 to 1.00 (Supp. Fig S5). The Sorensen and Bray-Curtis indices correlated significantly with the PhyloSor indices (Spearman-rank correlation: Sorensen: r= 0.742, p= 0.002; Bray-Curtis: r=0.717, p=0.003). The PhyloSor and Sorensen index showed that the community pairs located in the arid, southern region were more similar to each other compared to the remaining community pairs. Tiras1 and Oamseb 1, with a PhyloSor and Sorensen index of 1, were significantly more similar with regard to phylogenetic composition than expected by chance and had identical species composition (Fig S3 and S5; Supp. Table S3). Community pairs Tiras1 / Oamseb2 and Oamseb1 / Oamseb2 had PhyloSor values of 0.89 and Sorensen index value of 0.86. The remaining community pairs had index values ranging from 0.53 – 0.75 (PhyloSor index) and 0.40 – 0.67 (Sorensen index). The geographical distance between plots did not significantly correlate with ß-diversity (Mantel-test: Sorensen index: r= -0.144, P=0.611; Bray-Curtis index: r = -0.050, p= 0.861) or phylogenetic ß-diversity (Mantel-test: r=-0.341, p = 0.205) (Supp. Fig S6).

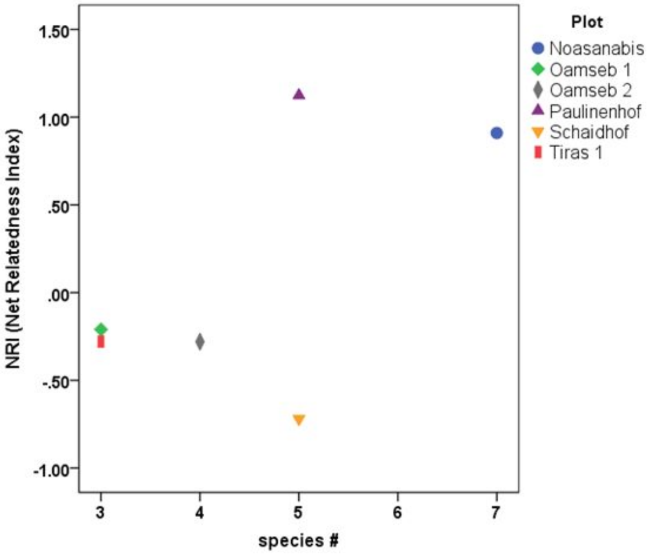

Fig 3. Indices of the phylogenetic community structure using the null model independent swap with the presence/absence data showing the NRI for all plots with the number of species per plot. The number of species did not correlate significantly with the NRI.

Environmental variables

The observed pairwise correlations between plots did not correlate significantly before and after including mean annual precipitation with the phylogenetic correlations (always p> 0.05) (Fig 4a, b). Further, the change in occurrence correlations, when including mean annual precipitation, did not significantly correlate with the pairwise phylogenetic correlations (p> 0.05) (Fig 4c), indicating that it is not a major variable influencing species co-occurrences.

Discussion

Local community assembly

This study aimed at uncovering processes that structure termite communities in Namibia at a local scale, along a

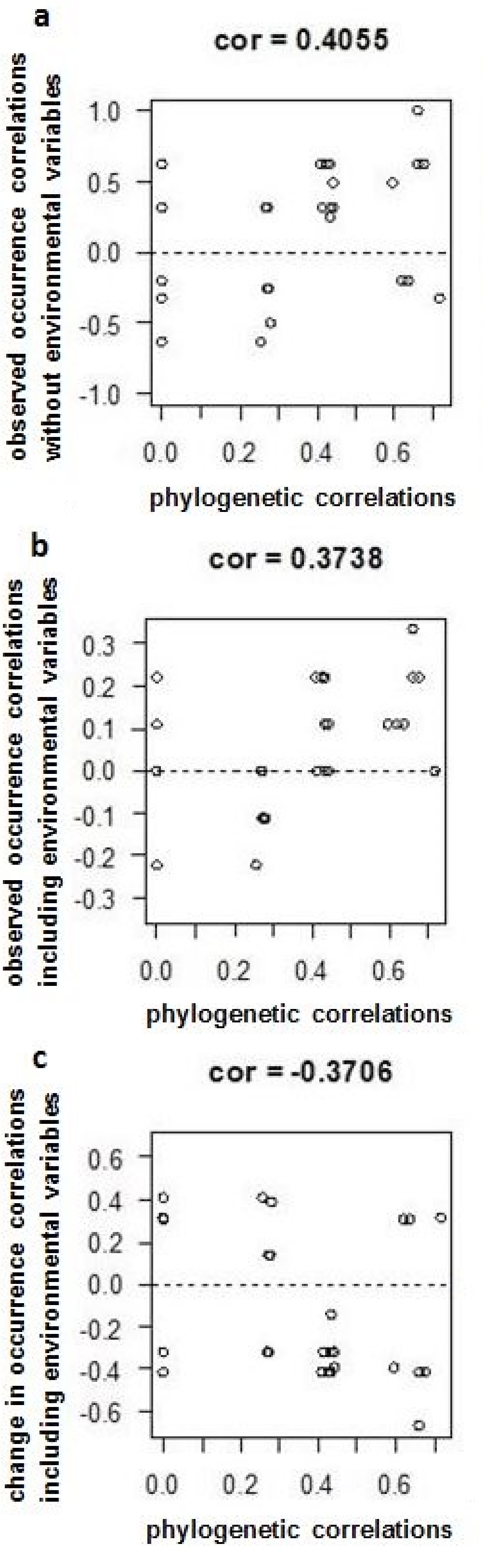

Fig 4. Influence of environmental factors on community structure. Shown are correlations of pairwise species co-occurrence and pairwise phylogenetic correlations a) without environmental variables, b) including environmental variables,and the c) change in species co-occurrence once environmental variables are taken into account. There were no significant results a) without and b) with environmental variables included (P > 0.05). Also c), the changes in correlation were not significant either (P > 0.05).

climatic gradient (Supp. Table S4). We did not find evidence that habitat filtering or interspecific interactions play major roles in structuring these communities locally.

The highest termite diversity is located in African tropical forests (Eggleton et al., 1994; Davies et al., 2003). Compared to forests, savannas harbour much lower species diversity. In West African savannas at least 20 species were identified, mostly fungus-growing Macrotermitinae (Hausberger et al., 2011). This is higher than the uncovered regional species pool of 11 species from nine genera in this study (Supp. Table S3). This might be due to the more arid conditions in Namibia as previous studies revealed less species under drier conditions (de Bello et al., 2006; Traill et al., 2013). For Namibia, a total of 17 termite genera have been identified (Jürgenset al., 2010). This is considerably more than what we found, but our study covered a smaller area and did not include all vegetation zones (e.g. woodland savanna). We concentrated on analysing local community assembly, which supplements the work of Jürgens et al. (2010), which monitored regional species occurrence and distribution. When comparing overlapping regions between both studies we had similar species occurrences (Supp. Table S2).

This is the first study investigating the phylogenetic community structure of southern African termite communities and explicitly testing their composition against a null model of random assemblages. Termites are mainly sessile organisms in that the colonies stay on one site over many years.Therefore, they may be more prone to certain local environmental conditions and interspecific competition than highly mobile species that can (temporarily) escape unsuitable conditions, for example birds (Canales-Delgadillo et al., 2012; Harmon-Threatt et al., 2013). Nest building in termites can be beneficial, in that it makes them less sensitive to abiotic environmental conditions. However, our results did not reveal significantly clustered or overdispersed communities according to the NRI, indicating a random component to local species assembly.

It has been shown that the opposing forces of habitat filtering and interspecific competition can counteract one another (Lessard et al., 2009), resulting in seemingly neutral communities. In order to test for such effects the environmental regression analyses were done that tested for and ‘statistically’ removed environmental effects to reveal potentially hidden patterns of competition (Kembel et al., 2010). Assuming that rainfall is the major environmental factor in arid regions, including mean precipitation still could not reveal such a hidden pattern. For other tropical species, a variety of assembly patterns have been found, ranging from phylogenetic overdispersion to phylogenetic clustering along an environmental gradient (Graham et al., 2009; Webb, 2000; Gòmez et al., 2010; Cavender-Bares et al., 2004). Several reasons may explain these differences such as the studied taxon, its ecological requirements and sampling effort as well as the geographic history and conditions of the respective region.Sampling effort could influence the results of community structure analyses as there might be a minimal diversity needed to detect a certain pattern. Other studies had a termite species diversity of around 20 species and here community structure was detectable, even in local sites harbouring only 3-5 species (Hausberger & Korb, 2015, 2016).

Community structure along the climatic gradient

The analysis of environmental variables showed that the effect of annual precipitation on community structure along the north / south gradient does not seem to be clear, despite the climatic gradient covered (annual precipitation in the north: 303 mm and south: 144 mm; Supp. Table S4). This may be due to a small sample size and the fact that other factors influencing community structure may compensate for the low rainfall in the arid region. This should be investigated in future studies. By contrast, other community studies have shown that broad-scale variation in climate, along latitudinal or altitudinal gradients, influences both the structure of species communities and the activity rates of certain species, which can modify species interactions and influence the degrees to which food resources are accessible (Lessard et al., 2011; Graham et al., 2009; Gòmez et al., 2010; Machac et al., 2011).

As the ß-diversity and phylogenetic ß-diversity of the sampling sites revealed that communities are more similar in the southern part of the sampling area, some environmental or historical processes seem to influence species assembly, although we did not find an effect of the rainfall gradient. Species diversity was higher in the northern area and next to a few other species, only *Trinervitermes* sp. and the 'desert'-species *Psammotermes* sp. were sampled frequently in the arid southern region. This is similar to what has been shown in previous studies (Coaton & Sheasby, 1972) and can be explained by the fact that *Trinervitermes* sp. are grass-feeders and occur more frequently in open grass savannas with little other vegetation. Although more research is clearly needed, our study contributes to the identification of African termite species with the goal to understand their distribution and species assembly processes.

Authors contribution

J. Korb obtained funding, conceived and designed the experiments. J. Korb and B. Hausberger carried out the fieldwork. J. Schyra performed the laboratory work and data analyses. J. Schyra, B. Hausberger and J. Korb wrote the manuscript.

Supplementary material

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