




Research Article

Small-scale variations in spider and springtail assemblages between termite mounds and the surrounding grassland matrix

Hannelene Badenhorst¹, Charles Richard Haddad¹, Charlene Janion-Scheepers²

¹ Department of Zoology & Entomology, University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa

² Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch, Cape Town, 7701, South Africa

Corresponding author: Charles Richard Haddad (HaddadCR@ufs.ac.za)



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Abstract

The snouted harvester termite (*Trinervitermes trinervoides* (Sjöstedt, 1911)) is a widespread grass-eating termite species that constructs thermoregulated dome-shaped mounds. However, little is known about the influence of these mounds on the arthropod assemblage structure in the surrounding grassland matrix, and whether the mounds represent ecological islands. Spiders and springtails are two ecologically important arthropod groups often associated with termites or their mounds. We investigated their assemblage composition inside and around active and abandoned *T. trinervoides* mounds in a central South African grassland. In total, 838 spiders (59 spp., 22 families) and 217 857 springtails (24 spp., 9 families) were collected from 96 pitfall traps, placed at four microhabitats in and around each of 12 active and 12 abandoned mounds during March 2019. The most abundant and species-rich spider families include the Gnaphosidae (n = 270, 10 spp.), Zodariidae (n = 86, 7 spp.), Lycosidae (n = 86, 6 spp.) and Salticidae (n = 77, 5 spp.), whereas the springtail fauna was dominated by Brachystomellidae (n = 56 521, 1 species), Bourletiellidae (n = 49 573, 7 species), Sminthuridae (n = 44 491, 3 species), Isotomidae (n = 32 288, 1 species) and Entomobryidae (n = 26 216, 7 species). Indicator analysis showed that the spiders *Zelotes sclateri* Tucker, 1923, *Heliocapensis termitophagus* (Wesołowska & Haddad, 2002) and *Scytodes elizabethae* Purcell, 1904 are associated with abandoned mounds, but no springtails showed an association based on the IndVal analysis of the eight microhabitats (lumped data), even though the undescribed *Cyphoderus* sp. were mostly collected inside active mounds. The mounds thus had a negligible influence on the spatial distribution of springtails in the surrounding grassland. The different spider and springtail assemblages sampled indicate that both active and abandoned mounds function as ecological islands in grasslands, but that mound size does not affect their abundance or species richness in the different microhabitats sampled.

Key words: Araneae, Collembola, diversity, pitfall trap, termitophile, *Trinervitermes trinervoides*

Introduction

Termitaria are a common sight throughout the savannas and grasslands of Africa (Uys 2002). Aside from serving as the nests for the organisms constructing them, they play a significant role in these ecosystems by creating nutrient

islands (Dangerfield 1991) and providing refuge, food and spatial resources to a range of animals, including a variety of termitophilous arthropods (Warren 1919), mammals (Fleming and Loveridge 2003) and predacious ants (Tuma et al. 2020), amongst others. Furthermore, termite mounds constructed in savannas can often have very strong effects on the soil nutrients and vegetation on and surrounding them (e.g. Dangerfield 1991; Joseph et al. 2013; Davies et al. 2014).

Trinervitermes trinervoides (Sjöstedt, 1911) is a widespread termite species within the semi-arid grasslands and savannas of South Africa, where it predominantly feeds on grass litter (Adam et al. 2018) and constructs characteristic dome-shaped mounds (Coaton 1948; Uys 2002; Field and Duncan 2013). The mounds are used to store grass fragments that not only act as a constant food supply, but aid in thermoregulation, helping maintain a narrow range in core nest temperature (Field and Duncan 2013). Even though many studies have focused on *T. trinervoides* ecology (Potts and Hewitt 1973, 1974; Adam et al. 2005, 2008, 2012, 2018; Adam and Mitchell 2009; Field and Duncan 2013; Conlon et al. 2016; Mills and Sirami 2018; Nampa and Ndlovu 2019; Ndlovu et al. 2021), as well as mound degradation and opportunistic occupation/invasion of the abandoned *T. trinervoides* mounds by many vertebrates and some invertebrates (Smith and Yeaton 1998; Haddad and Dippenaar-Schoeman 2002, 2006; Wesolowska and Haddad 2002; Gosling et al. 2012), there is relatively little known of the arthropods that cohabit the active nests and their dynamics in the surrounding grasslands.

As in savanna landscapes, *T. trinervoides* mounds in central South African grasslands have a direct influence on the grassy and shrubby vegetation around them, with clear compositional differences between active and abandoned mounds (Smith and Yeaton 1998). These vegetation changes inevitably provide different resources to the arthropods dependent on them, which will likely cause changes in the composition of phytophagous and detritivorous arthropods feeding on the plant material (as found by Leitner et al. 2020 in savanna), as well as predators of those arthropods, such as spiders, which are affected by vegetation structure on and around mounds (Nduwarugira et al. 2016). Furthermore, active and abandoned mounds' internal temperatures are independent of (more stable) and dependent (fluctuating) on ambient temperatures, respectively (Ndlovu et al. 2021), which would directly impact the organisms occupying each mound. We were therefore interested in assessing whether *T. trinervoides* mounds fulfil the role of ecological islands within a grassland matrix, similar to other termitaria elsewhere (Fleming and Loveridge 2003; Joseph et al. 2013; Chen et al. 2021), and how different mound types affect the organisms occupying them and their surroundings.

Spiders (Araneae) and springtails (Collembola) are two very ecologically significant arthropod groups that function as predators and detritivores in terrestrial ecosystems, respectively (Janion-Scheepers et al. 2016). Spiders are the most diverse group of terrestrial predators, with more than 52 300 species described globally (World Spider Catalog 2024), of which around 2 265 species are known from South Africa (Dippenaar-Schoeman et al. 2023). They contribute significantly to the natural limitation of terrestrial arthropod populations, particularly insects (Nyffeler and Birkhofer 2017), with springtails often forming a considerable portion of the diet of generalist spiders (e.g. Birkhofer et al. 2008, 2011), or even being exclusively fed on by specialists (Korenko et

al. 2014). Some South African spider species have adapted their behaviour and activity patterns to specialise and mainly feed on termites (e.g. Wesołowska and Haddad 2002; Pekár et al. 2020), with *Ammoxenus amphalodes* Dippenaar & Meyer, 1980 being a true predator specialist of *Hodotermes mossambicus* (Hagen, 1853) (Dippenaar-Schoeman et al. 1996; Petráková et al. 2015; Haddad et al. 2016; Pekár et al. 2018; Henschel et al. 2023).

In contrast, springtails are a small hexapod order with about 9500 described species worldwide (Bellinger et al. 2023), and only 133 species have been recorded from South Africa (Janion-Scheepers 2021). Despite their comparatively low species richness, they are widely recognised as being one of the most important groups of terrestrial detritivores in soil mesofaunal assemblages, playing a key role in the breakdown of decomposing organic material, while also serving as food to many predators, including spiders (Rusek 1998). Springtails from the tribe Cyphoderini are commonly collected in association with ants and termites. They move freely in termite mounds and are presumed to be scavengers, and their abundance could be attributed to the narrow ranges in humidity and temperatures maintained in the host species' nests (Kistner 1982).

The aim of this study was to characterise the springtail and spider assemblages that occur inside and around the mounds of the snouted harvester termite *T. trinervoides* in central South African grasslands. As living mounds are closed off from the surrounding environment by their continuous exterior crust (Field and Duncan 2013) that is inaccessible to most macroarthropods, we hypothesised 1) that both spider and springtail abundance, species richness and diversity would increase from inside the mounds to 3 m away from the mounds, and 2) that the assemblages in the grassland matrix and around the edges of mounds would be the most similar, indicating that mounds have a limited influence on assemblages in the surrounding grassland habitat. Consequently, 3) that the assemblages inside or on the outer crust of mounds would support the concept of *T. trinervoides* termitaria as islands, as has been proposed for *Macrotermes* and *Odontotermes* termites in savanna and forests (e.g. Fleming and Loveridge 2003; Joseph et al. 2013; Chen et al. 2021). Lastly, considering the frequently obligate association of Cyphoderini springtails with colonies of social insects (e.g. Paclt 1967; Kistner 1982; Janion-Scheepers et al. 2015; Parmentier and Braem 2024), we hypothesised 4) that *Cyphoderus* springtails would be collected exclusively from the inside of living *T. trinervoides* mounds.

Material and methods

Study area

This study was conducted in the grassland areas on the western side of the main campus of the University of the Free State in Bloemfontein, South Africa (29°06'43.7"S, 26°10'43.9"E). The study area had a dense grass litter cover on the soil surface due to annual mowing. The vegetation mostly consists of a mixture of grass species (mainly *Themeda triandra*, *Eragrostis lehmanniana*, *Eragrostis curvula*, *Digitaria eriantha* and *Aristida congesta*), a variety of herbaceous plant species (including *Nidorella resedifolia*, *Hibiscus pusillus*, *Pentzia globosa* and *Selago densiflora*), dwarf-shrubs (including *Felicia muricata*) and trees (Dingaen and Du Preez 2013). The tree species consist of mostly

indigenous species, such as *Searsia lancea* and *Olea europaea* subsp. *africana*, as well as a few alien species such as *Quercus stellata*, *Fraxinus angustifolia* and *Pinus taeda*. Bloemfontein is a summer rainfall area with an annual average of 550 mm of rain, mainly in the form of thunderstorms (Dingaen and Du Preez 2017). Bloemfontein experienced above average rainfall (± 602 mm) during 2019 (Moeletsi et al. 2022), of which 46 mm fell during the 21-day study period, indicated below.

Sampling Araneae and Collembola

A total of 96 pitfall traps (volume 350 ml, mouth diameter 60 mm) were placed in and around 12 active and 12 abandoned *T. trinervoides* mounds from 5–26 March 2019 (21 days). A KML (Keyhole Markup Language) file for viewing the locations of each of the 24 mounds interactively in Google Earth (<http://earth.google.com/>) is available as a Suppl. material 1. At each of the studied termite mounds, four pitfall traps were placed in specific microhabitats: the first was placed inside, the second trap on the top of the mound outside, the third at the base of the mound in the soil (0 m away), and the final pitfall trap at 3 m from the mound in the natural grassland matrix (Fig. 1). We considered active and abandoned mounds to represent different abiotic conditions, as they have contrasting internal thermal and structural conditions and effects on the surrounding vegetation, so considered the four trap positions of each mound type to represent a different microhabitat, i.e. eight in total. For abandoned mounds, we scored the degree of perforation of the external crust following the scale proposed by Haddad and Dippenaar-Schoeman (2002).

To avoid spatial pseudoreplication and account for any potential movement of arthropods, mounds were separated by a minimum of 25 m; most inter-mound distances, however, exceeded 50 m. As termite mound size can affect the number of organisms sampled (e.g. Haddad and Dippenaar-Schoeman 2002; Leitner et al. 2020), we improved the comparability of the mounds sampled by only selecting well-established mounds with a height of >25 cm and basal diameter >50 cm (Suppl. material 2).

We used a spade to dig a $\sim 25 \times 25$ cm square into the outer crust of the mound on the top of the northern side in order to plant pitfalls inside the mound structure, and gently removed the excavated material before using an augur to dig a hole into the tunnel structure before placing the bottle flush with the bottom of the cavity. After filling the bottle with preservative, the square crust was returned to its position, the cracks filled with loose sand from the base of the mound on the southern side, and water dripped onto the crack to seal it and (in the case of active mounds) facilitate repair by the workers. For traps placed on the outer surface, we used the augur to excavate the required cavity on the top of the southern side (about 30–50 cm from the northern excavation), placed the bottle, and filled any cracks as described above. Traps at 0 m were planted at the base of the mound and those at 3 m were planted in natural *Themeda triandra*-dominated grassland, both on the northern side of each mound and flush with the soil surface (Fig. 1).

Each pitfall trap was filled with 50 ml ethylene glycol as a preservative. The traps were inspected daily and those that were filled more than halfway by heavy rainfall during the sampling period were emptied and the preservative replaced.

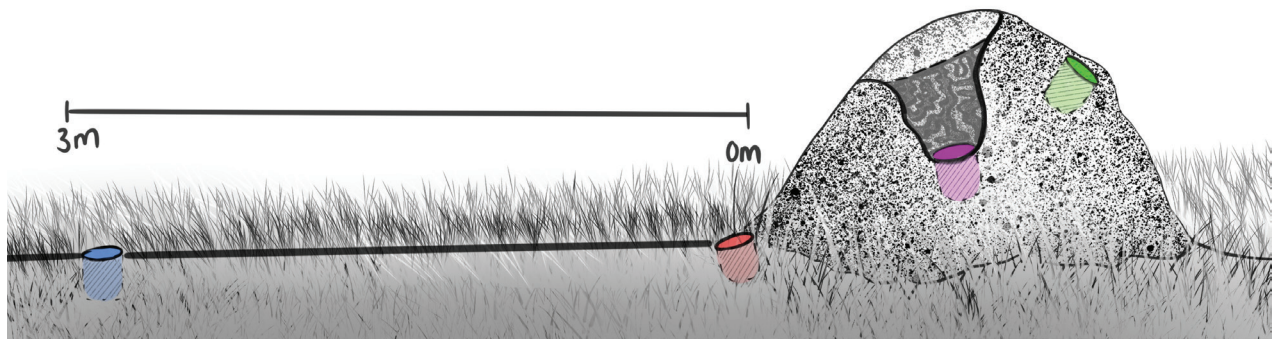


Figure 1. Study arrangement, showing the placement of the four pitfall traps in the microhabitats associated with an active *Trinervitermes trinervoides* mound: inside (purple), on top (green), at 0 m (red) and 3 m away (blue) from a mound. Illustration: M. Peach.

All the replaced samples were merged with their replacement traps after the sampling was concluded. The contents of the traps were washed from the ethylene glycol into a 70% ethanol solution. Springtails were quantified and sorted to morphospecies by the first author and identified to genus level by the first and third authors using a provisional key (Janion-Scheepers 2021). Spiders were sorted and identified to species level by the second author using literature available on the World Spider Catalog (2024).

Statistical analysis

For some of the statistical analyses, the 96 replicates were lumped to represent the four microhabitats sampled in and around the active or abandoned mounds. The spider and springtail data were analysed using Microsoft® Excel® v.2311 (Microsoft Corporation 2021), PRIMER v7 statistical software (PRIMER-e 2017) and RStudio (RStudio Team 2020). Data processing and visualisation in RStudio required additional installation of multiple software packages, including *vegan* (Oksanen et al. 2019), *indicspecies* (De Caceres and Legendre 2009) and *ggVennDiagram* (Gao et al. 2021). Rarefaction curves were prepared in RStudio, based on the eight microhabitats for each of the focus arthropod groups. Sample completeness was calculated as the ratio between observed species richness (S_{obs}) and Chao1 estimated species richness (S_{Chao1}) with the below formula, as described by Chao et al. (2009):

$$\text{Sample completeness} = \frac{S_{obs}}{S_{Chao1}}$$

and S_{Chao1} (estimated species richness) was calculated with the following formula:

$$S_{Chao1} = S_{obs} + \frac{f_1^2}{2f_2}$$

where f_1 is the number of species only represented by one individual (singletons) and f_2 the number of species only represented by two individuals (doubletons). Chao et al. (2009) further stipulated that when $f_1 = 0$ or the undetected number of species is less than 0.5, sampling is deemed complete. However, if $f_2 = 0$, S_{Chao1} is calculated with the following modified formula:

$$S_{Chao1} = S_{obs} + \frac{f_1(f_1 - 1)}{2(f_2 + 1)}$$

Sample coverage (C_n) was determined for both the spider and springtail assemblages of each microhabitat by means of the formula below:

$$C_n = 1 - \frac{f_1}{n} \left[\frac{(n-1)f_1}{((n-1)f_1) + 2f_2} \right]$$

where n is the abundance, f_1 is the number of singletons, and f_2 is the number of doubletons (Chao and Jost 2012).

Alpha diversity (species abundance, species richness, Shannon's diversity index and Pielou's evenness) was calculated for each of the microhabitats, with differences between the groups tested by means of the Kruskal-Wallis rank sum test and post hoc testing done using the pairwise Wilcoxon rank sum test. To assess whether mound size (volume and circumference) affected abundance and species richness of the two orders, we used linear regression for each of the microhabitats for active and abandoned mounds separately. Mound circumference was measured in the field (Suppl. material 2), with the estimated volume of each mound being calculated using the equation for the volume an ellipsoid, divided by two, following Ndlovu et al. (2021). Beta diversity analyses were conducted by performing non-metric multi-dimensional scaling (NMDS) analyses based on the Bray-Curtis distance using PAST version 2.07 (Hammer et al. 2001).

An analysis of similarities (ANOSIM) was performed with RStudio on the NMDS datasets (Bray-Curtis dissimilarity measure, permutations = 9999) to test whether there were statistical differences between the assemblages in the eight microhabitats. Indicator species analyses were performed to identify species that were statistically more abundant in specific microhabitats. Similarity percentage (SIMPER) analyses were done in PRIMER to determine the contribution of individual species towards the dissimilarities observed between the four microhabitat types, as well as between the colony activity status. Venn diagrams were constructed in RStudio to illustrate the sharing of species and hierarchical cluster dendrograms based on Bray-Curtis similarity distances were constructed in PRIMER to illustrate the clustering of microhabitats with similar assemblage structures. Only clusters with a similarity percentage of higher than 60% are considered ecologically important. Microsoft Excel was used to calculate Sørensen's quotient of similarity (C_s , range between 0 and 1) with the below formula:

$$C_s = \frac{2ab}{a+b}$$

where ab is the number of shared species between two samples, a is the species richness of Sample 1 and b is the species richness of Sample 2. In the current study, Sørensen's quotient of similarity was used to compare the springtail and spider assemblages, respectively, between the eight different microhabitats. Values closer to 1 indicate higher similarity in faunal assemblages between the compared microhabitats and values closer to 0 indicate a more unique faunistic composition.

Results

The rarefaction curves for both Araneae (Suppl. material 3: fig. S3A) and Collembola (Suppl. material 3: fig. S3B) collected from eight microhabitats tapered off, indicating that sampling was sufficient for evaluating the species richness of the spider and springtail assemblages from these microhabitats. Coverage values for both spiders and springtails from the eight microhabitats were all above 0.7 (Suppl. materials 4, 5).

Assemblage composition and structure

Araneae

A total of 838 spider individuals, representing 59 species from 22 families, were collected from eight microhabitats situated in and around the 24 *Trinervitermes trinervoides* mounds (Suppl. material 4). The most abundant and species-rich spider families include the Gnaphosidae (n = 270, 10 spp.), Zodariidae (n = 86, 7 spp.), Lycosidae (n = 86, 6 spp.) and Salticidae (n = 77, 5 spp.). Spider abundance, species richness and diversity were higher in the traps situated at 0 m and 3 m away from both the active and abandoned mounds, than inside or on top of mounds.

The Kruskal-Wallis rank sum test showed significant differences for the spider abundance, species richness and Shannon's diversity (all $P < 0.001$). Pairwise comparisons using Wilcoxon rank sum test revealed that the spider abundance inside the active mounds was significantly lower than that of the other microhabitats. The spider abundance was also significantly lower on the outside of the active termite mounds than in most of the other microhabitats (Fig. 2, Suppl. material 6). The spider abundance at the foot of the abandoned mounds, at 0 m away, was significantly higher than that of most of the other microhabitats (Fig. 2, Suppl. material 6).

Spider species richness of the pitfalls inside and outside (on top of) mounds was lower than those at 0 m and 3 m away from mounds for both active and abandoned mounds (Suppl. material 7). Similarly, the Shannon's diversity values of the inside and outside microhabitats was significantly lower than that of the pitfalls 0 m and 3 m away from mounds, whether active or abandoned (Fig. 2, Suppl. material 8). Pielou's evenness was consistent in seven of the eight microhabitats and showed that no one species dominated any of these microhabitats. The linear regression showed that mound size (circumference and volume) did not have a strong effect on either abundance or species richness, irrespective of microhabitat, with the exception of species richness at the base of abandoned mounds, which decreased slightly with mound size; most R^2 values were <0.1 (Suppl. material 9).

Collembola

In total, 217 857 springtail individuals representing 24 species in nine families were collected from the eight microhabitats (Suppl. material 5). Brachystomellidae (n = 56 521, 1 species), Bourletiellidae (n = 49 573, 7 species), Sminthurididae (n = 44 491, 3 species), Isotomidae (n = 32 288, 1 species) and Entomobryidae (n = 26 216, 7 species) were the most abundant families. *Cyphoderus* sp. (n = 18 065)

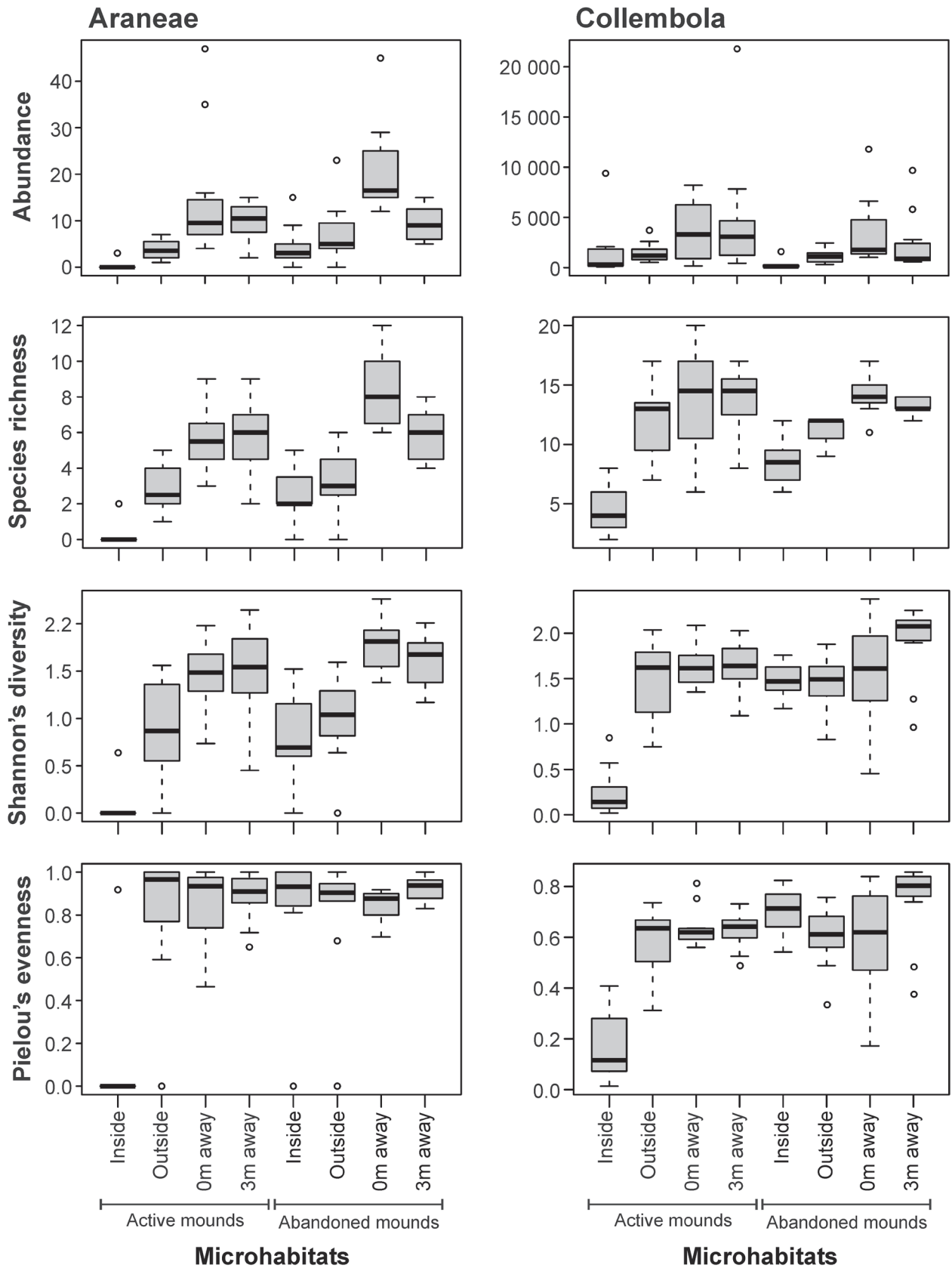


Figure 2. Abundance and alpha diversity of the spider (Araneae) and springtail (Collembola) assemblages sampled at each of the eight microhabitats (12 replicates), illustrated by means of box-and-whisker plots.

was a major contributor to the Entomobryidae abundance and 96.5% of these individuals were collected from inside the active mounds. The families Orchesellidae (n = 5 887, 2 species), Neanuridae (n = 2 537, 1 species), Mackenziellidae (n = 336, 1 species) and Katiannidae (n = 8, 1 species) were less abundant.

Springtail abundance was higher in traps that were situated at 0 m and 3 m away from both the active and abandoned mounds, than on the inside or on top of the active and abandoned mounds, respectively (Fig. 2). The Kruskal-Wallis rank sum test showed significant differences in springtail abundance, species richness and Shannon's diversity between microhabitats (all $P < 0.001$). Pairwise comparisons using the Wilcoxon rank sum test revealed that springtail abundances inside the abandoned mounds were significantly lower ($P < 0.001$) than in six of the other seven microhabitats (Fig. 2, Suppl. material 10). As in the case of the spiders, the linear regression found no association between mound size (circumference and volume) and springtail abundance and species richness, with all the R^2 values below 0.2 (Suppl. material 9).

The differences in springtail species richness were due to the lower species richness inside the active mounds, as well as inside and on the outside of the abandoned mounds (Suppl. material 11). Springtail diversity was the lowest inside the active mounds, which was the main cause of the significant difference observed in Shannon's diversity values between the microhabitats (Suppl. material 12). Overall, Pielou's evenness showed moderate to high evenness values, except for the inside of the active mounds, which were dominated by an undescribed *Cyphoderus* sp. (Fig. 2).

Assemblage comparisons

The abundance-based NMDS analyses of both the spider (stress: 0.116, good representation) and springtail (stress: 0.046, strong representation) assemblages showed that assemblages from the inside of the active mounds were different from those occupying the other microhabitats (Fig. 3A, B). The ANOSIM results comparing the spider assemblages between active and abandoned mounds ($R = 0.1979$, $P = 0.1151$), as well as the different microhabitats ($R = 0.3542$, $P = 0.0863$) showed that there were no statistically significant differences in the spider assemblages based on these factors when tested independently. The ANOSIM results for springtail assemblage comparisons also found no statistical differences between assemblages associated with active or abandoned mounds ($R = 0.04167$, $P = 0.3943$), nor between the four different types of microhabitats ($R = 0.1667$, $P = 0.1945$), irrespective of mound status.

Indicator species analysis of the spider abundance data (lumped according to eight microhabitats) showed that *Zelotes sclateri* Tucker, 1923 (Gnaphosidae), *Heliocapensis termitophagus* (Wesołowska & Haddad, 2002) (Salticidae) and *Scytodes elizabethae* Purcell, 1904 (Scytodidae) are associated with abandoned mounds and their surroundings. These findings were supported by the SIMPER analysis (Suppl. material 13). The springtail abundance data (lumped according to eight microhabitats) did not show any statistically significant species as indicators of a specific microhabitat or the status of the mounds. However, SIMPER analyses showed that the unidentified *Cyphoderus* sp. contrib-

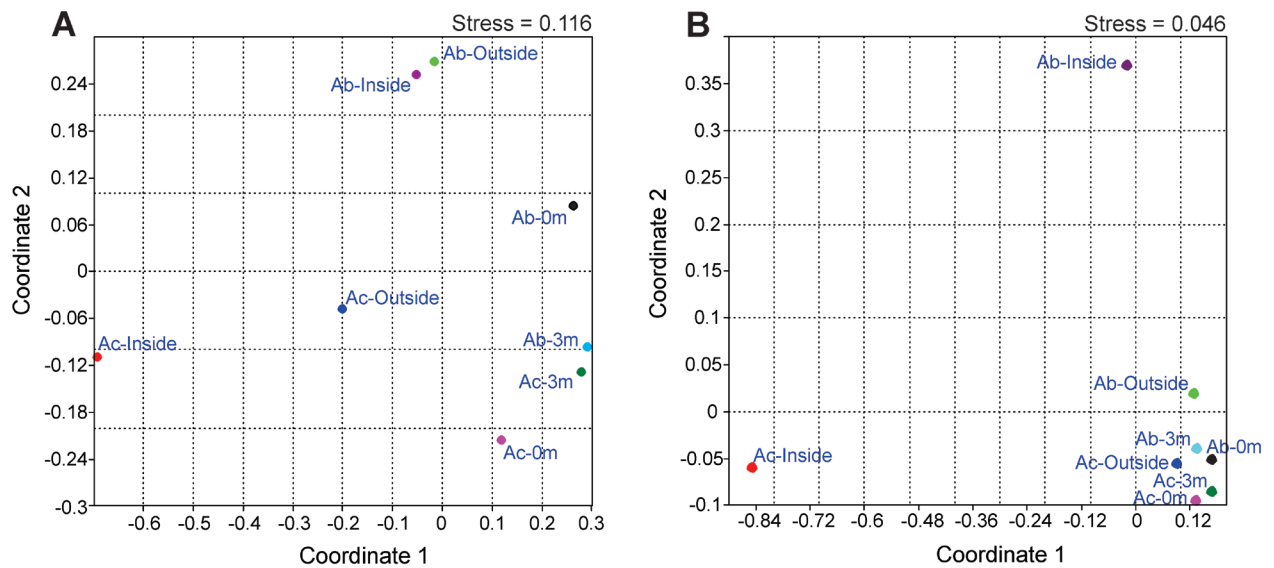


Figure 3. Non-metric multidimensional scaling (NMDS) analyses on the abundance-based datasets of spider (A) and springtail (B) assemblages collected from eight microhabitats associated with active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds and the surrounding grassland, based on the Bray-Curtis similarity index.

uted to the differences observed between the active and abandoned mounds, as well as between the inside of active mounds and the other microhabitats (Suppl. material 14).

Venn diagrams only consider the presence and absence of species in the specific microhabitats and exclude their abundance, which could provide valuable insights into the success and level of specialisation of a species in a specific microhabitat. All the microhabitats showed the presence of unique spider species, except the inside of active mounds (Fig. 4A). Only two spider species were collected from inside a single active mound, viz. *Theuma fusca* Purcell, 1907 (Prodidomidae; n = 1) and *Enoplognatha molesta* O.P.-Cambridge, 1904 (Theridiidae; n = 2), which were commonly recorded from all the other microhabitats. It was noted that nearly half of the total springtail species richness was shared between all eight microhabitats (Fig. 4B). None of the springtail species were exclusively collected from the inside or outside of either active or abandoned mounds. Only three microhabitats showed the presence of unique springtail species with respect to the mound status-specific analysis and include the 0 m away (4 species) and 3 m away (1 species) from abandoned mounds, as well as 0 m away (2 species) from active mounds.

The hierarchical cluster dendrograms based on the Bray-Curtis similarity of the springtail and spider assemblages showed that the similarities between spider assemblages of the eight microhabitats were mostly less than 60% similar (Fig. 4C). The habitats that were away from the mounds, both active and abandoned, showed the highest similarity (Fig. 4C, Suppl. material 15). The springtail assemblage showed high levels of similarity (> 60%) between most assemblages, with only the assemblage inhabiting the inside of active mounds showing a moderate level of uniqueness (Fig. 4D, Suppl. material 16).

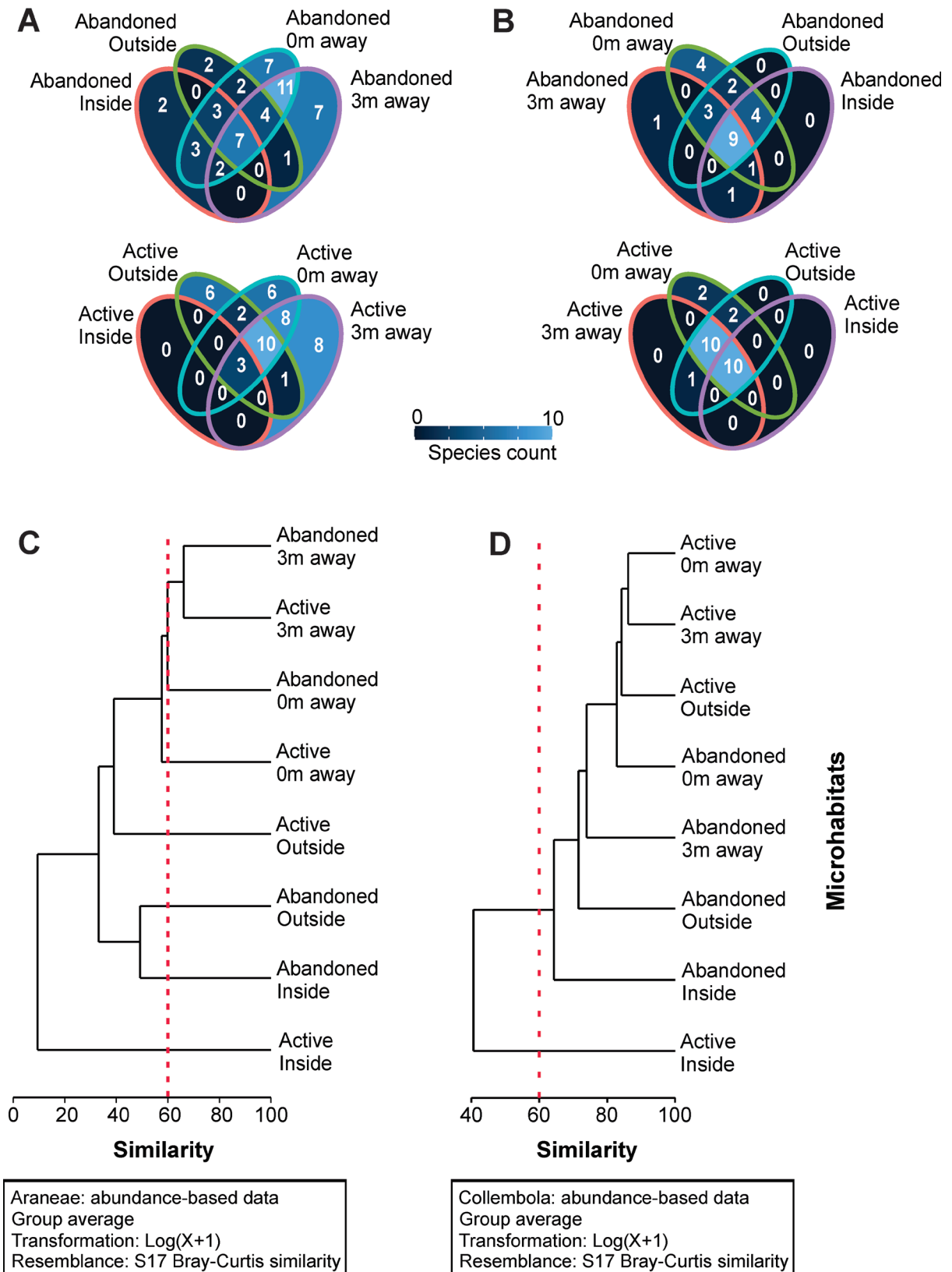


Figure 4. Venn diagrams (**A, B**) and hierarchical cluster dendrograms (**C, D**) illustrating the similarities between the spider (**A, C**) and springtail (**B, D**) assemblages from the different microhabitats. Cophenetic correlation values close to 1 indicate that the cluster dendrograms represent the data very well; these values are 0.948 and 0.960 for the spiders and springtails, respectively.

Discussion

This is the first study in South Africa to investigate the spider and springtail assemblages both inside and around the mounds of the snouted harvester termite, *T. trinervoides*, and how their composition differs. The sampling coverage values per mound for spiders were very high for both the active (0.733–0.931) and abandoned mounds (0.896–0.952). These values suggest that most of the expected species for this site and the specific sampling period were collected, but that additional sampling could provide a few additional species, especially at 0 m away from the active mounds. The sample coverage for the springtails of all eight microhabitats was all equal to 1, indicating that the sampling effort was sufficient and all the epedaphic springtail species that were present in these microhabitats during the sampling period were collected. The addition of other sampling methods and seasonal surveys could, however, contribute more species for both taxa.

Spider assemblages

Spiders play an important role in arthropod population dynamics in terrestrial environments (Nyffeler and Birkhofer 2017) and are abundant terrestrial predators in the Free State Province's grassland ecosystems (Haddad et al. 2013). The present study found the Gnaphosidae, Zodariidae, Lycosidae and Salticidae to be the most abundant and species-rich families sampled, which according to Dippenaar-Schoeman et al. (2023), represents four of the six most species-rich spider families in South Africa (Table 1). These four families primarily consist of ground-dwelling spiders. The absence of Araneidae and scarcity of Thomisidae was expected, as both families primarily live on plants (Dippenaar-Schoeman 2023). Sampled spider assemblages are greatly influenced by sampling methods and this study only made use of pitfall trapping, which mainly collects active ground-dwelling spiders (Haddad et al. 2013). Many of the spider species sampled during this study are ground-dwellers that are commonly collected in pitfall traps in the Grassland Biome, as well as in association with different termite species (e.g. Haddad and Dippenaar-Schoeman 2006; Haddad et al. 2015; Haddad and Butler 2018).

Alpha diversity (abundance, species richness and Shannon's diversity) showed a significant decrease in the spider assemblages that were inside or

Table 1. The six most species-rich spider families from South Africa (Dippenaar-Schoeman et al. 2023), with four of them also being the most abundant and species-rich in the present study (indicated by *).

Six most species-rich families in RSA	South Africa (RSA)		Present study	
	Genera	Species	Genera	Species
Salticidae*	80	354	4	5
Gnaphosidae*	28	195	7	9
Thomisidae	38	143	3	3
Lycosidae*	24	113	6	6
Araneidae	40	100	0	0
Zodariidae*	21	97	7	7

on top of both the active and abandoned termite mounds compared to those occurring at 0 m and 3 m away from the mounds, only partly supporting hypothesis 1. Spider abundance, species richness and diversity were, in fact, the highest at 0 m away, suggesting that the mounds may serve as a structural barrier that disrupts the running activity of spiders while foraging, increasing their pitfall capture rates in this microhabitat. This microhabitat had similar spider assemblages to the pitfalls 3 m away from mounds, as it is situated in the edge area between the mounds and the grassland.

However, none of the microhabitats supported statistically different spider assemblages, as the grassland assemblages (3 m away from active and abandoned mounds) and those at the mound periphery (0 m away) shared many species (Fig. 4), supporting hypothesis 2. This would indicate that the considerable effects that the mounds have on soil characteristics and vegetation composition and productivity between active and abandoned mounds of different ages (Smith and Yeaton 1998) have little effect on higher trophic levels, such as active ground-dwelling predators. The assemblages in the surrounding grassland also did not differ significantly from those on top of or inside the mounds, contrary to hypothesis 3. This seems somewhat contradictory to expectations, as the only three indicator species were specifically associated with the abandoned mound structures. Additionally, the nMDS analysis clearly indicated that the assemblages of the inside and outside of abandoned mounds were very similar, but different from those of the surrounding grassland and of active mounds; this was likely biased by the low spider numbers inside active mounds ($n = 3$). So, although the ANOSIM results do not support hypothesis 4, i.e. that *T. trinervoides* termitaria function as ecological islands, the nMDS results do support this hypothesis, at least in the case of spiders.

This is further supported by the very low spider abundance and species richness on and inside active mounds. This is most likely related to the chemical defence exhibited by *Trinervitermes* species, whose soldiers have a nasutiform head and release repellent terpene compounds when disturbed (Nel 1968; Prestwich et al. 1976a, b; Prestwich 1977). These chemicals evidently have no effect on particular nest associates such as *Cyphoderus* sp. and specialist mammalian predators such as the aardwolf and armadillo (Richardson 1987; Richardson and Levitan 1994; Taylor and Skinner 2000; De Vries et al. 2011), but our results suggest that they may effectively deter spiders inside active mounds. This may also explain why the mound specialist jumping spider, *H. termitophagus*, is only found associated with abandoned and not active mounds (Wesołowska and Haddad 2002) and likely displays euryphagous specialist habits rather than stenophagy on the host termites (Michálek et al. 2021). This suggests that the mounds are generally unsuitable as foraging grounds for ground-dwelling spiders, despite the obviously plentiful food source, and that they represent nude barren islands that are not suitable for occupation by predominantly generalist predators.

Abandoned mounds play an important role as refuge for many arthropods, including spiders, which also makes these mounds prey-rich areas for many opportunistic spiders (Haddad and Dippenaar-Schoeman 2006). According to Theron (2013), these abandoned mounds are also inhabited by ants, which form part of the diet of predators that visit the mounds, such as ant-eating spiders (all of the Zodariidae sampled except *Cydrela* sp.), or serve as models

of ant-mimicking spiders (Gnaphosidae: *Micaria* spp.), which were collected inside and around the studied mounds. However, only three species (*Z. sclateri*, *H. termitophagus* and *S. elizabethae*) were statistically linked with abandoned *T. trinervoides* mounds and their nearby surrounding grassland. Of these, *H. termitophagus* is the only one that has previously been found specifically associated with abandoned *T. trinervoides* mounds (Wesołowska and Haddad 2002); the other two are widespread in South Africa and have no specific habitat associations (Haddad and Dippenaar-Schoeman 2006; Butler and Haddad 2011; Haddad et al. 2015; Dippenaar-Schoeman et al. 2021a, b).

Springtail assemblages

Springtails are abundant terrestrial arthropods with a global distribution, inhabiting a wide range of terrestrial environments that include the nests of ants and termites (Bellini et al. 2023; Oliveira et al. 2023). Springtails are important prey items for many ants and spiders (Basset et al. 2020). Studies by Wesołowska and Haddad (2002) and Michálek et al. (2021) showed that *H. termitophagus* does not only feed on termites, but on a broader spectrum of arthropods, including springtails.

Alpha diversity (abundance and species richness) showed a significant decrease in the springtail assemblages that were inside or on top of both active and abandoned termite mounds with respect to those inhabiting the 0 m and 3 m microhabitats. However, similar to spiders, abundance and species richness were highest at 0 m, thus only partly supporting hypothesis 1. Most of the springtail species were present in the majority of the microhabitats, indicating little to no habitat selection taking place. This was evident in the high collembolan diversity values observed in most microhabitats, excluding the inside of the active mounds that were mainly inhabited by *Cyphoderus* individuals (Fig. 4); thus, hypothesis 2 was not supported. As in the case of spiders, there is evidence that supports *T. trinervoides* mounds being ecological islands (nMDS analysis), although this is contradicted by the ANOSIM results. There is thus partial support for hypothesis 3.

The high number of *Cyphoderus* individuals showed that it was influenced by the mound activity, as their abundance ratio between the active and abandoned mounds are 147.7:1 individual. Although *Cyphoderus* was collected from the other microhabitats, their abundance on the inside of the active mounds was far higher than that of any of the other microhabitats, including the inside of abandoned mounds. This indicates that these springtails either have a relationship with the termites or exploit the living conditions created inside the mounds by active harvester termite colonies, which supports hypothesis 4. According to Kistner (1982), members of the tribe Cyphoderini, including *Cyphoderus* spp., are associated with ants and termites, and can occasionally be observed in sampling data away from ant and termite nests, as it is suggested that they can follow chemical trails of their host species.

This study also contributed important new springtail genus records for the Free State Province and South Africa (species absent from the species lists available in Thibaud (2013), Janion-Scheepers et al. 2015 and Janion-Scheepers 2021)), from which undescribed species will be described by the respective taxonomists. Interesting new springtail family records for the Free State Province

include the families Orchesellidae (genera *Capbrya* Barra, 1999 and *Nothobrya* Arlé, 1961) and Mackenziellidae (genus *Mackenziella* Hammer, 1953). This is the first record of *Nothobrya* for South Africa, and although *Capbrya* was thought to be a genus endemic to South Africa, a new species from this genus was recently described from Brazil (Nunes et al. 2020). The family Mackenziellidae currently only has one described species worldwide, *M. psocoides* Hammer, 1953 (Bellinger et al. 2023), and was redescribed by Fjellberg (1989). Fjellberg extracted this species from moss in an area that experiences periods of drought during the summer and suggested that it has a well-adapted life strategy to overcome these conditions. The addition of these new records to the Free State play an important role in understanding the distribution and ecology of springtails.

Suggestions for sampling termitophiles in *T. trinervoides* mounds

Although Collembola (especially Cyphoderini) were very effectively sampled from the interior of active mounds, the scarcity of spiders therein was somewhat surprising. Costa et al. (2009) reported 34 species of spiders from the mounds of *Cornitermes cumulans* (Kollar, 1832) in Brazil, whereas Lawrence (1952) and Benoit (1964, 1976) described numerous species of spiders from termite nest interiors in tropical Africa. One would thus expect *T. trinervoides* mound interiors to be ideal environments in which termitophilous spiders could survive, particularly as the internal environment of these termitaria is generally stable compared to ambient temperature fluctuations (Field and Duncan 2013; Ndlovu et al. 2021) and provides an effective barrier against other external factors such as rainfall and extreme heat.

As such, two factors may potentially be of importance in explaining the results of our study. Cristaldo et al. (2012) found that nest size was a crucial factor shaping the occupation of *Constrictotermes cyphergaster* (Silvestri, 1901), with particular critical lower limits in nest volume affecting the establishment of termitophiles and inquilines. Similarly, Marins et al. (2016) found an increase in the abundance and richness of co-inhabitants with increasing *Cornitermes cumulans* mound size. The nests sampled in our study (Suppl. material 2; 27–76 cm high) could be considered as moderately large for *T. trinervoides* when compared to other studies in the literature (heights of 20–80 cm in the central Free State in Smith and Yeaton 1998; 12–64 cm in the central Free State in Adam et al. 2018; approximately 1 m in KwaZulu-Natal Province in Ndlovu et al. 2021). Nest size thus seems unlikely to explain the lack of termitophilous spiders.

More likely, therefore, is the inadequacy of the sampling approach. Most of the pitfalls inside the active mounds were filled with termites by the time the sampling period of 21 days was completed, which may have reduced the capture of both springtails and spiders. As this was the first time such trapping had been attempted in *T. trinervoides* mounds, its efficacy in capturing termites could not have been foreseen. Replacing the pitfalls intermittently was not an option, as this would disturb the interior conditions of the mound and undo the repairs to the mound crust effected by the worker termites. A more plausible solution to effectively sampling termitophiles in active mounds in future would be the excavation of the mounds, as done by Haddad and Dippenaar-Schoeman (2002, 2006) for abandoned mounds. This would enable sampling arthropods from the deepest parts of the nest that are inaccessible to pitfall trapping.

Conclusion

This study provided insights into the biodiversity patterns of springtail and spider assemblages that co-inhabit active and abandoned *T. trinervoides* mounds, as well as the surrounding grassland. It showed that the spider assemblages inside and on top of the mounds were different from those at the foot of the mounds and 3 m away from the mounds in the grassland, although ANOSIM analysis found no significant differences in assemblage composition. Springtail species were more generally distributed outside mounds and in grasslands, with only the inside of the active and abandoned mounds showing signs of selection for these specific microhabitats, as indicated by their lower species richness. This study shows that both active and abandoned mounds should be treated as islands in the grassland matrix, as their spider and springtail assemblages differed from that of the surrounding area. This study further provides a baseline dataset for future research to focus on the diversity of termitophilous springtails in southern Africa, which remain very understudied.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

Ethical clearance was obtained from the University of the Free State Animal Ethics Committee (UFS-AED2017-006101).

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Author contributions

H.B. conducted field work, did initial sorting of samples, did morphospecies sorting and identification of Collembola, conducted analyses, and wrote the first draft of the manuscript; C.R.H. conceptualized the study, conducted field work, identified the Araneae, and prepared the publication draft of the manuscript; C.J.-S. identified some of the Collembola and helped with analyses. All authors contributed to the writing of the publication draft of the manuscript. This work forms part of the Ph.D study of H.B. under the supervision of C.R.H. and C.J.-S.

Author ORCIDs

Hannelene Badenhorst  <https://orcid.org/0000-0001-6012-3043>

Charles Richard Haddad  <https://orcid.org/0000-0002-2317-7760>

Charlene Janion-Scheepers  <https://orcid.org/0000-0001-5942-7912>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

KML (Keyhole Markup Language) file for viewing the locations of each of the 24 mounds interactively in Google Earth

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: kml

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl1>

Supplementary material 2

Summary of the structural characteristics of the 12 active (Ac) and 12 abandoned (Ab) *Trinervitermes trinervoides* mounds sampled

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: pdf

Explanation note: Degree of perforation follows the scale proposed by Haddad and Dippenaar-Schoeman (2002).

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl2>

Supplementary material 3

Rarefaction curves of the spider (A) and springtail (B) species richness for each of the eight microhabitats.

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: pdf

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Supplementary material 4

Spider species collected from four microhabitats associated with the active (Ac) and abandoned (Ab) mounds of the snouted harvester termite, *Trinervitermes trinervoides*, and the surrounding grassland.

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: pdf

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl4>

Supplementary material 5

Springtail species collected from four microhabitats associated with the active (Ac) and abandoned (Ab) mounds of the snouted harvester termite, *Trinervitermes trinervoides*, and the surrounding grassland.

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers
Data type: pdf

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl5>

Supplementary material 6

Results from the Wilcoxon rank sum test analysis performed for spider abundance collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds, with significant differences ($P < 0.05$) indicated by an asterisk

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers
Data type: pdf

Explanation note: Microhabitats: In = inside mounds; Out = outside, on top of mound;
0m = 0 m away from mound; 3m = 3 m away from mound.

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl6>

Supplementary material 7

Results from the Wilcoxon rank sum test analysis performed for spider species richness collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds, with significant differences ($P < 0.05$) indicated by an asterisk

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers
Data type: pdf

Explanation note: Microhabitats: In = inside mounds; Out = outside, on top of mound;
0m = 0 m away from mound; 3m = 3 m away from mound.

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl7>

Supplementary material 8

Results from the Wilcoxon rank sum test analysis performed for the Shannon's diversity index values of the spider assemblages collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds, with significant differences ($P < 0.05$) indicated by an asterisk

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: pdf

Explanation note: Microhabitats: In = inside mounds; Out = outside, on top of mound; 0m = 0 m away from mound; 3m = 3 m away from mound.

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl8>

Supplementary material 9

Results of simple linear regression of spider and springtail abundance and species richness collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds relative to mound volume and circumference

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: pdf

Explanation note: Only R^2 values above 0.25 are indicated in bold. Microhabitats: In = inside mounds; Out = outside, on top of mound; 0m = 0 m away from mound; 3m = 3 m away from mound.

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl9>

Supplementary material 10

Results from the Wilcoxon rank sum test analysis performed for springtail abundance collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds, with significant differences ($P < 0.05$) indicated by an asterisk

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: pdf

Explanation note: Microhabitats: In = inside mounds; Out = outside, on top of mound; 0m = 0 m away from mound; 3m = 3 m away from mound.

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl10>

Supplementary material 11

Results from the Wilcoxon rank sum test analysis performed for springtail species richness collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds, with significant differences ($P < 0.05$) indicated by an asterisk

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: pdf

Explanation note: Microhabitats: In = inside mounds; Out = outside, on top of mound; 0m = 0 m away from mound; 3m = 3 m away from mound.

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl11>

Supplementary material 12

Results from the Wilcoxon rank sum test analysis performed for the Shannon's diversity index values of the springtails assemblages collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds, with significant differences ($P < 0.05$) indicated by an asterisk

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers
Data type: pdf

Explanation note: Microhabitats: In = inside mounds; Out = outside, on top of mound;
0m = 0 m away from mound; 3m = 3 m away from mound.

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Supplementary material 13

Results obtained from the similarity percentage (SIMPER) analyses showing the percentage dissimilarity between spider assemblages of different microhabitats in and around active and abandoned *Trinervitermes trinervoides* termite mounds, presented as average abundance (Av. Abun) per group, average dissimilarity (Av. Diss), contribution percentage (Contrib %) and cumulative percentage (Cum. %) of spider species towards these dissimilarities

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers
Data type: pdf

Explanation note: The list only includes the species contributing up to a cumulative percentage (Cum. %) of 70% of the observed dissimilarity.

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Supplementary material 14

Results obtained from the similarity percentage (SIMPER) analyses showing the percentage dissimilarity between springtail assemblages of different microhabitats in and around active and abandoned *Trinervitermes trinervoides* termite mounds, presented as average abundance (Av. Abun) per group, average dissimilarity (Av. Diss), contribution percentage (Contrib %) and cumulative percentage (Cum. %) of spider species towards these dissimilarities

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers
Data type: pdf

Explanation note: The list below only includes the species contributing up to a cumulative percentage (Cum. %) of 70% of the observed dissimilarity.

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Supplementary material 15

Sørensen's quotient of similarity of the spider assemblages collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers
Data type: pdf

Explanation note: Microhabitats: In = inside mounds; Out = outside, on top of mound; 0m = 0 m away from mound; 3m = 3 m away from mound.

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Link: <https://doi.org/10.3897/AfrInvertebr.65.139404.suppl15>

Supplementary material 16

Sørensen's quotient of similarity of the springtail assemblages collected from eight microhabitats inside and around active (Ac) and abandoned (Ab) *Trinervitermes trinervoides* mounds

Authors: Hannelene Badenhorst, Charles Richard Haddad, Charlene Janion-Scheepers

Data type: pdf

Explanation note: Microhabitats: In = inside mounds; Out = outside, on top of mound; 0m = 0 m away from mound; 3m = 3 m away from mound.

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