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RESEARCH ARTICLE

Capturing the unseen: A low-cost method for stratified subterranean sampling of soil invertebrates in drylands

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Abstract

1. Drylands cover more than 40% of the earth's land surface and host unique soil meso- and macrofauna vital for ecosystem functioning. Conventional pitfall traps are widely used to assess surface-active invertebrates. However, they do not adequately sample subterranean invertebrates, especially in sandy, arid soils. This methodological gap limits our understanding of the ecological roles of soil fauna in drylands.
2. We aimed to: (i) design a low-cost, stratified subterranean trap for effectively capturing macrofauna in dryland soils, (ii) evaluate the sampling method by comparing invertebrate diversity and life-stage composition between subterranean traps and pitfall traps and (iii) assess temporal and spatial variation in richness, abundance and biomass within subterranean traps across sampling occasions, macrohabitats and soil depths.
3. We deployed the traps at 10 different transect sites within the three different land-use types at the study area in the southern Kalahari, South Africa. The traps captured invertebrates at multiple depths and in various macrohabitats with two distinct soil types (white calcareous and red dune sands).
4. Subterranean traps captured taxa and life stages that were not collected in pitfall traps, including termites (*Odontotermes*, *Microcerotermes*), Tenebrionidae larvae and hypogaeic ants (*Dorylus* spp.). The taxonomic overlap between the methods was low (12%), with pitfall traps that primarily captured epigaeic ants (79%). Subterranean traps revealed seasonal peaks in taxonomic richness, but there was no difference in the levels (strata) at which various species were captured. Across macrohabitats, there were differences in taxonomic abundance, with Tenebrionidae found more in red dunes compared to white calcareous sands.
5. *Practical implication*. Subterranean traps are a scalable tool and complementary method that improve the ability to monitor and determine soil macrofauna abundance and responses to land-use and climate change, offering insights for dryland conservation, diet studies and ecosystem management.

KEYWORDS
biodiversity monitoring, hypogaeic invertebrates, Kalahari, pitfall traps, soil macrofauna, soil mesofauna, stratified sampling

1 | INTRODUCTION

Drylands cover more than 40% of the global land mass and support a high level of biodiversity (Gross et al., 2024). Dryland soils are typically nutrient-poor, coarse-textured, with low organic matter and low water retention (Dougill & Thomas, 2004; Srinivasarao et al., 2023). Key but understudied components of the biotic communities in drylands are the soil invertebrates, which range in size from small-bodied mesofauna (often defined as 0.2–2 mm in length) to macrofauna (greater than 2 mm in length), although these size classifications may vary (Potapov, 2022; Lavelle, 1997; Lavelle et al., 2022; Swift et al., 1979). Many of these invertebrates spend all or part of their life cycle below-ground and respond strongly to fluctuations in soil moisture and temperature (Sohlenius & Boström, 2001; Thakur et al., 2018; Gongalsky et al., 2008). Responses include vertical movement and entering dormant stages below-ground (Ayal, 2007; Coyle et al., 2017; Iglesias Briones et al., 1997; Scholtz, 1988). Soil invertebrates accelerate litter decomposition, improve soil structure through bioturbation (increasing soil pore space, improving aeration and drainage) and support nutrient cycling in dryland soils (Filser et al., 2016; Lindberg & Bengtsson, 2005; Ruiz et al., 2023; Wall et al., 2010; Wilkinson et al., 2009). Many dryland vertebrates, such as meerkats, aardvarks and pangolins, rely on soil invertebrates as their primary food source, linking that below-ground biodiversity to above-ground food webs (Jubber et al., 2025; Phakoago et al., 2025; Panaino et al., 2022; Pietersen et al., 2015). Therefore, in the face of environmental change, the need to assess the spatiotemporal variation of soil fauna biodiversity is increasingly recognised (Bardgett & van der Putten, 2014; Nielsen & Ball, 2015).

A commonly used method to monitor soil macrofauna is pitfall trapping (Montgomery et al., 2021). However, pitfall traps may not capture species that spend most or all of their lives below the surface, as they rely on those invertebrates emerging and being active on the soil surface (Brown & Matthews, 2016; Pacheco & Vasconcelos, 2012). To assess the diversity of hypogaeic invertebrates (those that live and forage below ground), subterranean traps are required (Pacheco & Vasconcelos, 2012). Subterranean traps (including buried bait traps and subterranean pitfall traps) have been developed to assess the diversity of hypogaeic ants (Pacheco & Vasconcelos, 2012; Ryder Wilkie et al., 2007; Schmidt & Solar, 2010; Yamaguchi & Hasegawa, 1996) and have been deployed in forests, mainly in temperate or tropical ecosystems (Andersen & Brault, 2010; Pacheco & Vasconcelos, 2012). Other subterranean sampling methods include subterranean baited stations (buried baited chambers), soil core and extraction techniques (sifting, Winkler and Berlese extraction methods) (Sabu & Shiju, 2010) and subterranean tube-based traps that were developed for the mesovoid shallow substratum (consisting of an external tube with an internal tube that can be removed, leaving the external tube in place) (Culver & Pipan, 2014; López & Oromí, 2010; Ortuño et al., 2013; Wong & Guénard, 2017). Subterranean trapping can be time- and labour-intensive, and sampling outcomes can be influenced by trap design, bait or preservatives used, deployment duration and soil substrate. Subterranean trapping can also under-represent taxa that are inactive during the sampling window and invertebrates that occur in deeper horizons than the trap depth (Culver & Pipan, 2014; Ortuño et al., 2013; Wong & Guénard, 2017). Despite these challenges, subterranean traps are an important method for capturing hypogaeic taxa that are missed by surface-active sampling (Mammola et al., 2016; Wong & Guénard, 2017).

Few subterranean trap designs, however, have been explicitly adapted and evaluated for aeolian sandy soils in drylands. Sandy dryland soils present unique challenges for below-ground sampling, including structural instability, collapse of pitfall cavities and poor soil cohesion. Such factors can decrease the effectiveness and increase the maintenance demands of subterranean traps (Pacheco & Vasconcelos, 2012; Whitford & Duval, 2019). Drylands also often experience extreme temperature fluctuations and low soil moisture levels, conditions that complicate the establishment of stable subterranean sampling chambers (Bestelmeyer, 2000; Whitford & Duval, 2019). A subterranean trapping method that is effective under such conditions and appropriate for use given the behavioural adaptations of dryland soil invertebrates is therefore required (Lavelle et al., 2006; Raś et al., 2022).

We present a low-cost, stratified subterranean trapping method designed to sample soil invertebrates (hypogaeic macrofauna) across different life stages in drylands. We aim to provide a method tailored for unconsolidated aeolian sands, where preservative-filled traps and traps with removable internal tubes are often ineffective due to rapid sand ingress, contamination and instability of open cavities. Our method combines a stratified and a structurally stable trap in loose sand, which is an unbaited and a live-capture method. We further evaluated our sampling method by (i) comparing the diversity of captured invertebrates and the composition of life stages between our subterranean traps and pitfall traps, and (ii) assessing the temporal and spatial variation in richness, abundance and biomass within the subterranean traps across sampling occasions, macrohabitats and soil depths.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted at the Kalahari Research Centre (−26.978615°, 21.832148°, of approximately 7250 ha, including a fenced livestock camp that was excluded from the study) in the Kalahari, Northern Cape, South Africa (Russell et al., 2002). The area experiences hot summers, with rainfall typically occurring from November to April (the wet season) and cold winters from May to October (the dry season). Over the past 12 years, the mean annual rainfall has averaged 266 mm. In summer, the daily air temperature has averaged 30.3°C, reaching a maximum of 44.2°C. In contrast, in winter, the air temperature has averaged 10.1°C, with a minimum of −11.9°C (Jubber et al., 2025; Paniw et al., 2022). The soils in the study area are characteristic of the southern Kalahari and are acidic, nutrient-poor and dominated by sand (Wang et al., 2007).

Macrohabitats in the area include high and low duneveld (Van Rooyen et al., 2008), white calcareous river terraces and floodplains, calcareous pan flats with low grass cover interspersed with short dwarf shrubs and the diatomaceous fossil riverbed of the Kuruman River (Harrison et al., 2021; Thomas, 1981; Van Rooyen et al., 2008) (Figure 1).

The study area is divided into three distinct land-use types, with the main macrohabitats (Figure 1) found in each land-use type. The land-use types include: (1) Natural or rewilded area (excluding the fenced livestock camp), which spans 3000 ha and houses indigenous game species, including springbok (*Antidorcas marsupialis*), eland (*Tragelaphus oryx*), blue wildebeest (*Connochaetus taurinus taurinus*), red hartebeest (*Alcelaphus buselaphus*) and gemsbok (*Oryx gazella*); (2) Rotational grazing farm area (cattle-game integration), covering 2000 ha, which supports a combination of cattle and indigenous game species, including springbuck, kudu (*T. strepsiceros*) and ostrich (*Struthio camelus*), managed through a rotational livestock farming approach (Kong, 2012; Reinhard

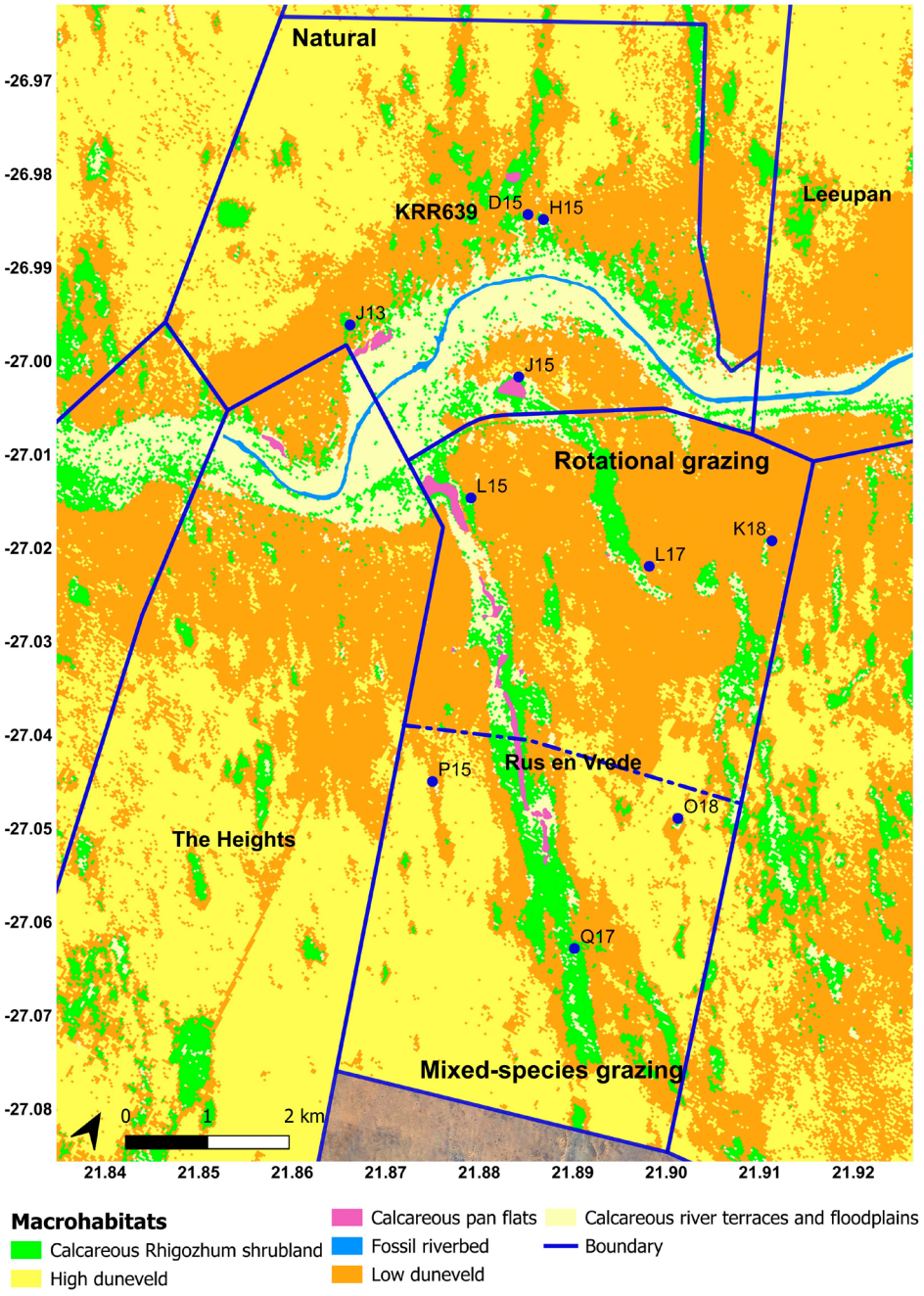

FIGURE 1 Macrohabitats (as shown in the key) of the study area, showing the three different land-use divisions: Natural, Rotational grazing and Mixed-species grazing. Neighbouring farm boundaries are in blue, with the name of the farm represented, and the blue dashed line indicates the boundary between the Rotational grazing and Mixed-species grazing areas. The blue points and code (e.g. P15) indicate the subterranean trap positions.

et al., 2022); and (3) Mixed-species grazing farm area (multiple livestock species-game integration), also 2000 ha, primarily used for mixed livestock farming that accommodates sheep, goats, camels, llama and cattle, with various game species both indigenous and non-indigenous to the area: springbuck, blue wildebeest, lechwe (*Kobus leche*), tsessebe (*Damaliscus lunatus lunatus*), roan (*Hippotragus equinus*) and impala (*Aepyceros melampus melampus*) (Figure 1). In addition, all three land-use areas have small mammal and bird species, which feed on invertebrates. The three distinct land-use areas are separated by game fencing (2.2–2.4 m in height), including predator-proof fencing extending 1 m below the ground and an additional 50 cm above ground.

2.2 | Subterranean trap design

The subterranean traps were made from polyvinyl chloride (PVC) pipes with a diameter of 160 mm and a wall thickness of 4.5 mm, each cut to a length of 600 mm (Figure 2). The handles were affixed to the top of each subterranean PVC trap to assist with pulling the traps out of the sand. The base was sealed with a glued end cap to prevent invertebrates from escaping from the bottom. Two designs were used for the subterranean traps to compare if one design was more efficient in sampling hypogaeic species: the triple-stratified subterranean trap (Figure 2a) and the double-stratified subterranean trap (Figure 2b). The triple-stratified subterranean trap was divided into three equal sections of 200 mm each, using metal tin plates supported by easy-to-remove steel wire pins. The upper part of each section (100 mm) was perforated with 14 mm diameter holes (24–28 holes) around the circumference of the pipe to allow invertebrate entry. The lower part of each section was not perforated to serve as a capture area (Figure 2c). The double-stratified trap consisted of two sections, each 300 mm long and divided similarly by a single metal tin plate. The double-stratified design had the first 150 mm upper section of each 300 mm section with perforation (same number of holes and diameter as the triple-stratified trap), followed by 150 mm of unperforated material below. We did not use an internal tube, as used in other tube-based subterranean traps, as there is a likelihood that the aeolian sands would pour into the tube cavity once the internal tube was removed.

2.3 | Deployment and sampling

Our sampling protocol was implemented in two stages between February and October 2024. We first deployed a single triple-stratified subterranean trap at three different sites (J13, J15 and H15) within the Natural area (Figure 1), as a pilot study from February to August 2024. In August 2024, we expanded the sampling effort at these three original sites by adding a double-stratified subterranean trap, totalling six subterranean traps across the original three sites. We also deployed both trap designs at three new sites: one in the Rotational grazing area (K18) and two in the Mixed-species grazing area (P15, Q17), resulting in six sampled sites. In October 2024, we added four additional sites (Natural—D15, Rotational grazing—L15 and L17 and Mixed-species grazing—O18), bringing the total to 10 sites across three land-use types. We continued our sampling efforts at all 10 sites until March 2025. At each site, the double- and triple-stratified subterranean traps were placed along a north–south transect, 80 m apart to avoid spatial autocorrelation, and we recorded the main soil and vegetation types (i.e. macrohabitat) at each location (Figure 1). GPS coordinates were recorded for each trap location.

To install the subterranean traps, a soil auger with a 25 cm diameter bit was used to excavate the holes. Each trap was inserted so that its open top (no end cap or lid) was flush with the soil surface,

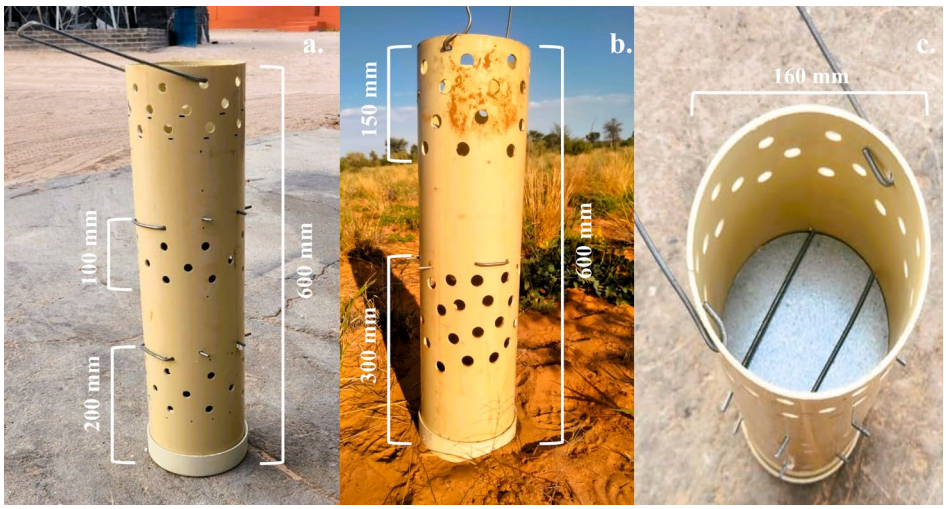

FIGURE 2 The two subterranean trap designs, (a) triple-stratified subterranean trap and (b) double-stratified design. Within each trap, strata (levels) are made using a tin plate (c) cut to fit the diameter of the PVC pipe and held in place with removable steel wire pins. The base of each trap is closed with a glued-on end cap.

allowing surface invertebrates to enter the subterranean trap (Figure S1). The stratified sections of the trap were then refilled with excavated sand (which was not defaunated) from the same excavation site up to ground level. The traps were left in place for 1 month, allowing soil invertebrates to naturally colonise the traps before retrieval. After 1 month, the traps were lifted out of the soil, and within each level, all the sand was sampled separately, aided by the internal metal divider plates that kept the sections distinct. The traps were then reinstalled at the exact same location and refilled with sand from the original site. The collected sand from each section was transported to a field laboratory, where it was sifted through a standard kitchen sieve with 0.2 mm aperture to extract predominantly macrofauna larger than the sieve openings.

2.4 | Comparison to standard pitfall trapping

Subterranean traps were placed 20 m adjacent to pitfall traps. The pitfall traps were placed along a transect line as part of ongoing conventional trapping that had begun in August 2023. Along the transect, pitfall traps were installed at 20 m intervals, resulting in a total of 10 traps per site across 10 sites ($n = 100$). Each trap consisted of a round plastic bucket (25 cm in diameter, 5 L volume), embedded with the top of the container level with the soil, allowing unobstructed entry by surface-active invertebrates (Figure S2). Traps were opened (bucket lid removed) for sampling every 14 days. On each sampling occasion, approximately 2 cm of local substrate (sand) was added to the base of each container, with a big enough piece of wood placed inside to provide shelter for captured organisms from direct sunlight. A transparent funnel with a 15 mm opening was inserted into each trap to facilitate the capture of invertebrates and reduce escape (Figure S2a). Invertebrates were collected from each trap at 4-h intervals throughout the daytime, starting at 07:00 in the morning, then 11:00, 15:00 and final collection at 19:00. The traps were left open overnight after sampling at 19:00. Final collection and closing (lid put back on) of the traps occurred the following morning (around 07:00). All collected specimens were transported to the laboratory for identification and weighing.

We employed a dry capture design for both subterranean traps and pitfall traps, where invertebrates were not killed, and most of the captured specimens were released (over 80%). Dry traps lessen soil invertebrate depletion, allowing for repeated sampling, biomass estimation and easier identification of taxa, without negatively affecting local biodiversity (Knapp et al., 2020; Montgomery et al., 2021).

2.5 | Invertebrate identification, biomass and preservation

The total number and the representative life stage of the collected invertebrates were recorded in each stratified section, and any evidence of predation (partly consumed invertebrates and any body parts remaining from obvious signs of being preyed upon) within the trap stratified sections was recorded. The collective invertebrate biomass was determined by weighing each organism using a precision balance (Mettler AC 100, manufactured by Mettler-Toledo, Columbus, United States of America; maximum mass of 100 g, 0.1 mg increment/accuracy), directly after sifting and sorting, to facilitate the quick release of invertebrates back at the collection site. Each invertebrate was identified at the lowest possible taxonomic level, and its life stage was noted. If an invertebrate was already part of the species catalogue at the Kalahari Research Centre, it was released back onto the surface at the capture site. An individual from any new species (for the study location) was collected, labelled and preserved in ethanol. To identify species, keys derived from the available literature were used (Borkent & Sinclair, 2017; Dippenaar-Schoeman et al., 2021; Penrith, 1984; Slingsby, 2017), and relevant experts were consulted (see Acknowledgements). Some invertebrates could not be identified (Table S1); therefore, a representative of each collected specimen was also preserved in sealable tubes containing 96%–99% ethanol to facilitate later DNA analysis. Collected specimens of rare or newly identified species were also made available to museums and experts for their collections. We provide a list of all captured invertebrates in the Supporting Information (Table S1).

2.6 | Ethics

Ethics clearance was obtained from the University of Witwatersrand Animal Research Ethics Committee (2022/07/05/B and AREC24-04-009B), and nature conservation permits (FAUNA 0041/2023 and 0455/2024) were secured from the Northern Cape Nature Conservation Department.

2.7 | Statistical analysis

2.7.1 | Comparisons of subterranean traps and conventional surface pitfall traps

We used qualitative analyses to compare species and life cycle stage differences between subterranean traps and conventional pitfall trapping methods for invertebrates caught between February 2024 and March 2025 (14 months). We used the number of captured specimens per grouped family and genus taxon as the frequency of captures. As the sampling effort between the two methods differed, we calculated the percentage of each family and its representative genera as a percentage of the total of individual invertebrates captured per method. We further grouped the captured family with their representative life stages to compare differences between the pitfall and subterranean life stages caught. We then generated Sankey diagrams to illustrate the percentual representation of the main sampled taxa and life stages between the two sampling methods. The analyses were carried out using R (version 4.4.1).

2.7.2 | Quantitative analyses of variation in species richness, biomass and abundances

We analysed variation in taxonomic richness (the number of different taxa grouped by family and genus taxa for each sampling occasion and trap; Jubber et al., 2025; Paniw & Jubber, 2026), total biomass (g) and abundance (number of captured individuals within different families, i.e. frequencies of captures) using data collected from October 2024 to March 2025, when all subterranean traps were deployed. We modelled richness and biomass using a zero-inflated generalised linear model with the *glmmTMB* package in R (version 4.1.2) (Brooks et al., 2017). We included trap type, month of sampling (Nov, Dec, Jan, Feb, Mar, where Nov includes the last week of October and the first week of November), land-use type (Natural, Rotational grazing, Mixed-species grazing) and main sand habitat (white sand, red sand) as predictor variables for the main effect on richness or biomass and for the zero-inflation term. For richness, we also tested whether the Poisson or negative binomial family better described the response variable. For total biomass, we assumed a Tweedie distribution (as the data were zero-inflated and continuous) (Gu, 2024). We used the AIC to determine whether a predictor explained more variance in the response variable ($\Delta AIC > 2$) than a null model containing no predictor terms. When two predictors were significant, we also tested their additive effect.

To explore the covariation of abundances of individuals caught in different soil meso- and macrofauna families, we used multivariate generalised linear mixed-effects models (Brommer et al., 2019), implemented using the *MCMCglmm* package in R (version 4.1.2) (Hadfield, 2010). Multivariate models have been suggested as appropriate tools to make inferences based on disaggregated data in biodiversity studies (Clark et al., 2011). Our multivariate GLMMs modelled the covariation in abundances as a function of categorical variables: month of sampling, land-use type and main sand habitat type (red sand on dunes and white calcareous sand). We considered abundances to be distributed as a Poisson variable and thus used the Poisson family link in the GLMMs. All models accounted for the multivariate response using a covariance matrix in which abundances covaried within sites. To incorporate the inherent non-independent relationships among species and differences in temperature sensitivity, we used a random site effect as a variance term on the mean abundance. The *MCMCglmm* package uses a Bayesian framework to fit models. We thus ran three independent chains using 50,000 iterations after a burn-in of 10,000 iterations. We used a 25-step thinning interval, resulting in 2000 posterior parameter samples per chain. We determined model convergence using standard Bayesian checks (i.e. traceplots and the Gelman-Rubin diagnostic; Brooks & Gelman, 1998). We considered differences in abundances and effects of predictors to be significant when the 95% credible interval (CI) of the respective parameters did not overlap 0. To avoid overfitting and allow the chains to converge, we focused our analyses on the most abundant families (caught in >5 traps on at least three occasions) of invertebrates. We grouped the other families into a single category (Other). We also performed additional analyses, in which we removed rarely caught families (instead of grouping), but the results did not change (see Supporting Information S1).

We also considered differences in richness, biomass and abundance between layers for each of the two subterranean trap types considered here (double-stratified vs. triple-stratified). The analysis was performed exactly as the above analyses but for a subset of data. We considered only sampling occasions where at least one animal was found in a given trap (to reduce the number of 0's in the data).

3 | RESULTS

Over a 14-month sampling period (February 2024 to March 2025), pitfall traps ($n = 100$) captured 12,458 individuals (89% of the total individuals captured by all traps), while subterranean traps ($n = 20$) captured 1538 individuals (11% of the total). Pitfall traps caught a greater diversity of taxa than subterranean traps, with 121 distinct taxa collected by pitfall traps compared to 32 taxa by subterranean traps. The recorded apparent predation records were less than 1% of captured prey. In addition, each pitfall trap collected more individuals, on average (125 individuals per trap), compared to subterranean traps (77 individuals per trap). Taxonomic overlap was low, with only 16 taxa (12%) collected by both methods. The main genera collected in both methods included the Arachnida genera *Ammoxenus*, *Asemesthes* and *Chelypus*; the Tenebrionidae genera *Calaharena*, *Stips* and *Zophosis*; and the Formicidae genera *Camponotus*, *Ocymyrmex* and *Tetramorium* (Figure 3). Pitfall traps caught taxa across 4 classes, 14 orders, 50 families, 36 subfamilies and 98 genera, while subterranean traps caught taxa across 4 classes, 12 orders, 21 families, 14 subfamilies and 21 genera (Table S1). Pitfall traps predominantly captured ants (Formicidae; 79% of total captured individuals). The most common Formicidae genera sampled by pitfall traps included *Tetramorium* ($n = 4073$; 33%) and *Ocymyrmex* ($n = 2820$; 23%) (Figure 3). In contrast, the subterranean traps caught the following invertebrates, which were absent from the pitfall traps: Formicidae genus *Dorylus* ($n = 501$; 33%), Blattodea (cockroaches and termites) members, including *Odontotermes* ($n = 358$; 23%), *Microcerotermes* ($n = 472$; 31%) and cockroach species from the genus *Tivia* ($n = 20$, 1%; Figure 3).

Life-stage representation varied in percentages and numbers caught between pitfall and subterranean traps (Table S1; Figure 4). Pitfall traps predominantly captured adult stages (>99% of captures, $n = 12,412$), with only 46 individuals in non-adult stages of development (<1%), namely 25 larvae (<0.1%), 14 immatures (<0.1%), 3 juveniles (<0.1%), 4 nymphs (<0.1%) and no pupae (Table S1). In contrast, subterranean traps captured 1437 adult stage invertebrates (93%), with 101 individuals in non-adult stages of development (7%), namely 93 larvae (6%), 5 pupae (0.3%), 2 juveniles (0.1%) and 1 nymph (<0.1%). The larval life stage in the subterranean traps was primarily represented by Tenebrionidae ($n = 38$), followed by Scarabaeidae ($n = 24$), Carabidae ($n = 18$) and Asilidae ($n = 5$); all of these invertebrate families were scarcely represented or absent in pitfall traps (Figure 4; Table S1).

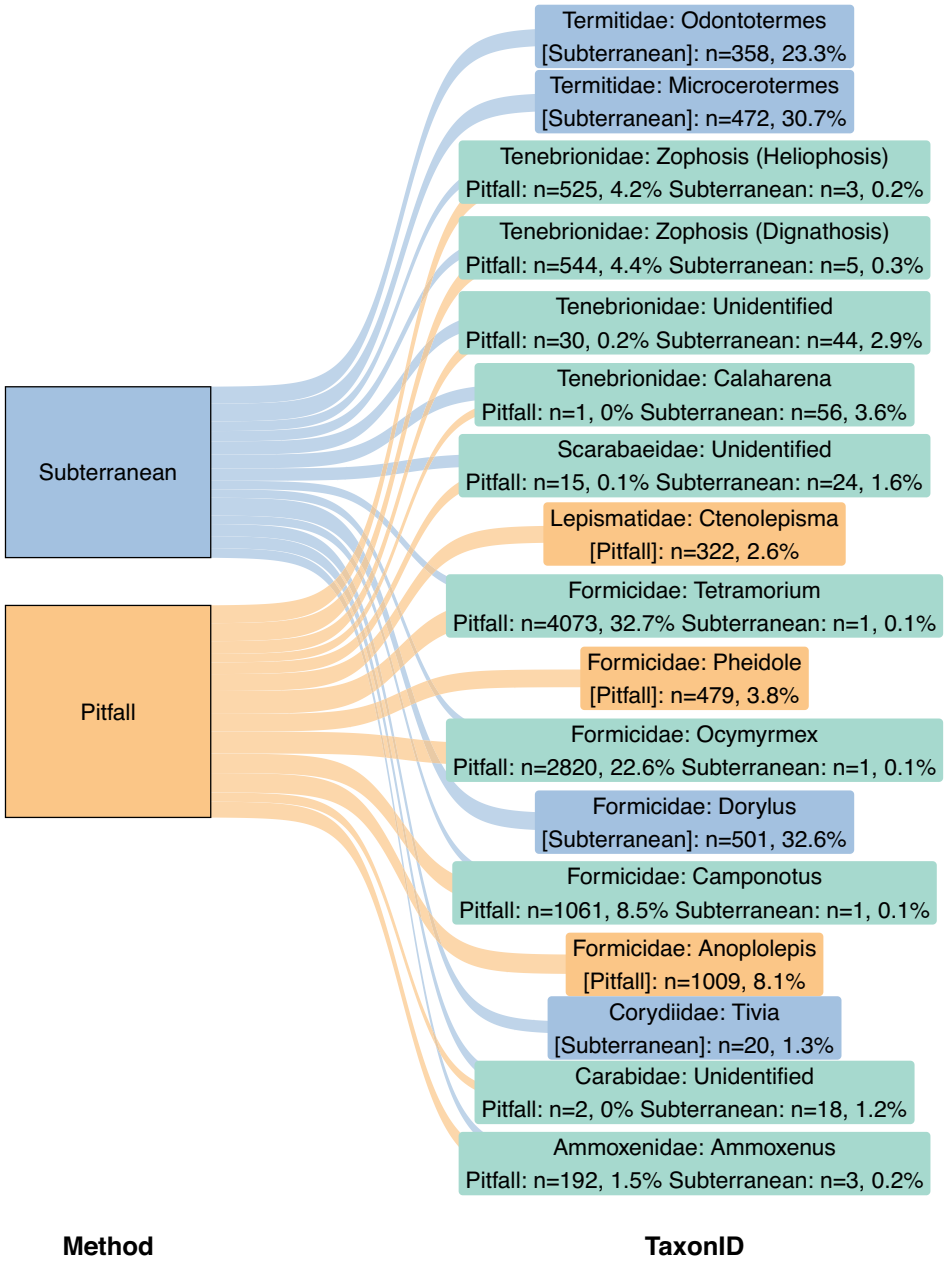

FIGURE 3 Sankey diagram illustrating the comparison of the most sampled invertebrate taxa captured by only subterranean (blue) or only pitfall (light orange) traps or taxa that were captured in both trap types (teal). The node labels indicate the taxon, the number of individuals captured (*n*) and their percentage (%) relative to each method's total catch.

Taxonomic richness was best described by the month of sampling, with the highest richness in January 2025 (1.37, ±0.41 SE; compared to November 2024; Figure 5; see Table S2 for all model parameters). The abundance (the number of individuals caught) of the main invertebrate families captured in the subterranean traps, Scarabaeidae and Tenebrionidae, covaried little between sites (Figure S3). However, we detected a positive covariation within the sites (Figure S4). At the same time, abundance was affected by both the month of sampling and the main macrohabitat sand type. Tenebrionidae were the most abundant family, but only in red dunes (Figure 6; Table S3). The abundance of Tenebrionidae decreased in white sands (model mean: −2.61; 95% credible interval: [−5.22, −0.51]) (Figure 6; Table S3) compared to red dune sands, while Scarabaeidae were caught mostly in white sands (compared to red dune sands; Figure 6). We did not detect an effect of any predictor on total biomass (Figure S5a). We also did not find differences in biomass (Figure S6), richness (Figure S8) or abundance (Figure S6) among the different layer designs of the subterranean traps.

4 | DISCUSSION

Our subterranean traps successfully captured hypogaeic taxa and invertebrate life stages within the soil, particularly certain termites

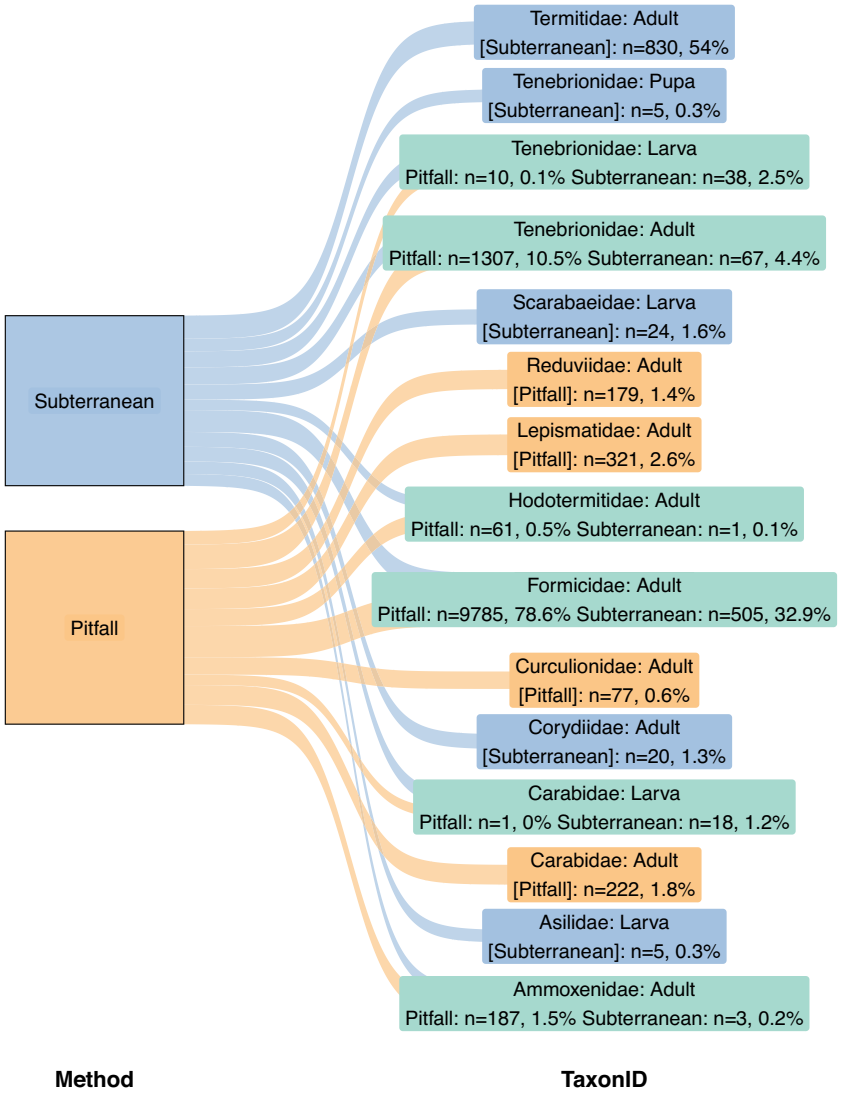

FIGURE 4 Sankey diagram illustrating the comparison in life-stage representation of the main invertebrate taxa captured by only subterranean (blue) or only pitfall (rust orange) traps, or taxa that were captured in both trap types (teal). Node labels indicate the taxon, life stage, number of individuals captured (*n*) and their percentage (%) relative to the total catch of each method.

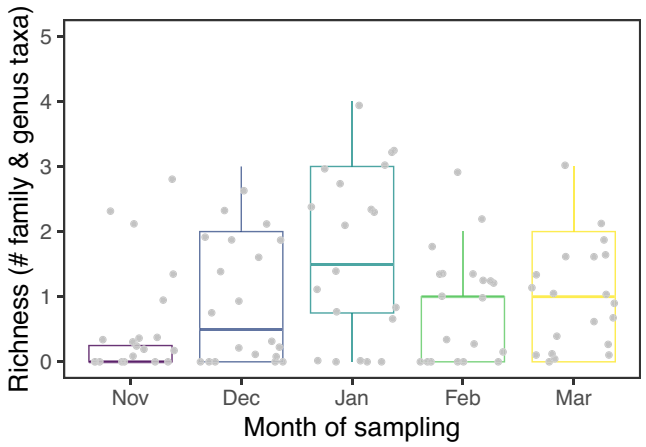

FIGURE 5 Box plot showing the distribution of the total number of specific taxa caught in subterranean traps in different months. The points on the *Y*-axis indicate the observed richness (number of distinct taxa grouped into families and genera) for each site ($n = 10$) and for each subterranean trap per site ($n = 2$) during individual sampling occasions.

(*Odontotermes*, *Microcerotermes*), sand cockroaches in the genus *Tivia*, *Dorylus* ants and larval stages in both Coleoptera (Tenebrionidae, Scarabaeidae, Carabidae) and Diptera (Asilidae). In addition, the subterranean traps revealed fine-scale spatiotemporal differences, with soil invertebrate richness peaking in January 2025 (wet summer month). The variation in invertebrate abundance was linked to soil type, with Tenebrionidae being more abundant in red dune sands and Scarabaeidae more prevalent in white calcareous sands. Although the overall variation between sampling sites was low, family-level abundance changed within the sites. Subterranean traps captured life stages other than adults, with larvae representing 6% of the total captures. These results support the use of unbaited and sand-filled subterranean traps as an effective and complementary method for sampling hypogaeic diversity. The traps allowed us to identify habitat-specific patterns in soil fauna and capture life stages that surface sampling and preservative subterranean traps alone may have missed (Mammola et al., 2016; Ortuño et al., 2013; Wong & Guénard, 2017).

We did not find differences in richness, biomass or abundance among the different vertical layers in the subterranean traps, which may be explained by the typical microclimatic uniformity of sandy

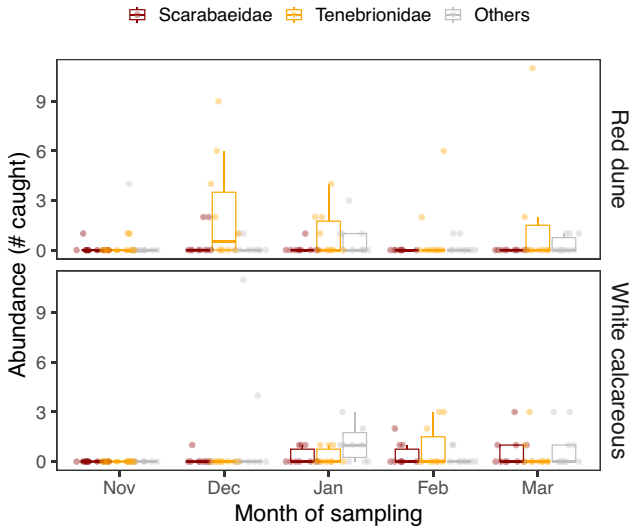

FIGURE 6 Box plot showing the abundances of the two main invertebrate families (Scarabaeidae and Tenebrionidae) caught in subterranean traps, with the remaining families categorised as 'Others'. Data are shown for each month of sampling and for the main macrohabitat sand types. Coloured circles indicate the observed abundance at each site ($n = 10$) for each sampling occasion.

soils in drylands. Surface soil temperatures can exceed 60°C during the day and drop as low as −12°C at night (Jubber et al., 2025), while temperatures at a depth of 30 cm often remain constant at 30°C (Seely & Mitchell, 1987; Bennett et al., 1988). Soil moisture, which increases with depth, is critical for dryland invertebrates. At high environmental heat loads, high soil surface temperatures and desiccation risk can lead to soil invertebrates burrowing deeper into the soil, and moisture-rich zones are essential for larval development in certain species (Knisley et al., 2018; Whitford & Duval, 2019). In many ecosystems, the vertical distribution of invertebrates is influenced by soil horizons (distinct layers within the soil profile that differ in structure, texture, organic matter and moisture content), because the horizons also create strong depth gradients in organic matter, root biomass and porosity that are selected by different faunal communities (Costantini & Mocali, 2022; Menta, 2020; Moradi et al., 2020; Potapov et al., 2017). However, these horizons are less well developed or absent in the loose, homogeneous sands (Doblas-Miranda et al., 2009) of our study area. The lack of such discrete layers likely reduces depth-related habitat differentiation, consistent with our finding of limited vertical differentiation of hypogaeic taxa. Our month-long trap deployment period, as well as mid-morning collection of invertebrates, before soils fully warmed, might also have influenced the detection of short-term vertical movements used by some invertebrates to escape high surface temperatures (Wang et al., 2011).

While our subterranean traps appear to offer a valuable tool for investigating biodiversity and ecosystem functioning, recognising areas for improvement may enhance their effectiveness. Some subterranean traps yielded no specimens despite being deployed across all seasons. One reason may be that our unbaited, live-capture design relied on invertebrates moving through the soil and being in the trap at the time of collection. Our reason for not using bait was that aeolian sand would easily and rapidly fill an open tube, contaminating liquid preservatives through the perforations. We chose a natural substrate and allowed intact live recovery of invertebrates and their life stages. Baited subterranean traps and pitfall traps with chemical lures may be more successful at capturing specific groups of locally present invertebrates, but they may also introduce bias, based on the species attracted (Andersen & Brault, 2010; Bestelmeyer et al., 2000; Pacheco & Vasconcelos, 2012). A direct comparison of the captures of sand-filled versus preservative-filled subterranean traps would be valuable in dryland conditions.

We also used a single trap per site to reduce disturbance, but increasing trap density may improve taxon detection (Knapp et al., 2020). Some species known to occur in the study area and eaten by meerkats, including *Hodotermes mossambicus* and other Diptera larvae (Bombylidae, Therevidae) (Jubber et al., 2025), were either caught in low numbers or absent from our samples. While we did not encounter excavation-related disturbances with our subterranean traps, installing additional traps could increase the risk of erosion and destabilise the surrounding substrate in unconsolidated sandy soils (Dougill & Thomas, 2004). We also considered using tube-based subterranean traps that would allow removal of internal tubes only (López & Oromí, 2010; Mammola et al., 2016; Ortuño et al., 2013); however, we reasoned that extracting the internal tube would disturb the surrounding sand and compromise the trap for repeatable approaches under our field conditions. Using such traps for longer acclimation periods would reduce possible disturbance effects, and we suggest that research should be undertaken to evaluate the benefits of trap sampling over extended acclimation periods. The physical design of traps like ours, with fixed depth intervals, also may restrict the ability of subterranean traps to capture fine-scale vertical patterns, especially in moisture-sensitive invertebrate groups (Lavelle et al., 2006). Further research to test the potential effects of trap fatigue or habitat disruption would also be valuable.

One advantage of subterranean traps is their ability to provide valuable insights into the recovery of soil fauna communities after habitat restoration. Since subterranean traps capture various hypogaeic taxa and life stages, they can provide indicators of recruitment, invertebrate community turnover and life-stage composition, which are key metrics to assess habitat quality and below-ground recovery (Bardgett & van der Putten, 2014). In restored sites, shifts in invertebrate community composition, abundance and diversity of life stages can reveal how well soil food webs are re-establishing when complemented with above-ground vegetation and faunal monitoring. The sensitivity of soil fauna to macrohabitat differences, such as those observed between red dune and white calcareous sands in our study, means they may also be useful in detecting whether restoration outcomes differ between soil types.

For long-term ecosystem monitoring, subterranean traps add a below-ground dimension to biodiversity assessments, enabling the detection of trends in hypogaeic community composition and abundance

over time. Soil fauna are highly responsive to changes in temperature and moisture, making them sensitive indicators of environmental shifts associated with climate change (Koehler & Melecis, 2010). Seasonal and macrohabitat sampling with subterranean traps can help distinguish natural variability from long-term trends, providing early warning of altered phenology and declines in key functional groups of soil invertebrates (Barnes et al., 2023; Potts et al., 2023). These insights are particularly valuable in drylands, where climate change is expected to increase aridity and temperature extremes, and where many species depend on below-ground refuges for survival during unfavourable conditions (Blanford & Thomas, 2000).

The subterranean trapping depth we used overlaps with the typical foraging depths (of about 20–30 cm) for meerkats and pangolins (Jubber et al., 2025; Pietersen et al., 2015; Swart et al., 1999) and therefore may be a useful tool for assessing prey availability for these digging mammals. However, greater depths may be needed to reveal the full vertical range of prey accessed by deeper-digging mammals such as aardvarks, which can dig as deep as 2 m in search of *Hodotermes mossambicus* (Taylor et al., 2002). Subterranean traps, however, offer a distinct advantage over conventional pitfall traps when evaluating prey availability. For meerkats at our study site, for example, Coleoptera account for 70% of dietary items, with Tenebrionidae and Scarabaeidae larvae contributing more than one-third of the prey consumed (Jubber et al., 2025). These larvae were frequently collected in our subterranean traps but were largely absent from the pitfall traps, which mainly captured adult beetles. Termites, such as *Odontotermes* and *Microcerotermes*, within the family Termitidae, recorded in the meerkat diet (although in low numbers), were captured only using subterranean traps. In other myrmecophagous species, including aardvarks and Temminck's ground pangolins, pitfall traps are effective in sampling foraging epigaeic ants but not the termites these species feed on (Panaino et al., 2022; Phakoago et al., 2025; Pietersen et al., 2015). Another limitation of pitfall traps is that they inherently bias results towards species with high surface activity, potentially underrepresenting those that are less active or dwell deeper within their nests or galleries (Knapp et al., 2020). Consequently, the actual diversity of potential prey items available might be underestimated, leading to a misrepresentation of prey selectivity in these mammals (Topping & Sunderland, 1992). An advantage of leaving subterranean traps in the ground over time is that they allow soil invertebrates, like termites, to colonise the traps, improving the likelihood of detecting these potential prey items.

5 | CONCLUSIONS

Our findings support the addition of a below-ground sampling method for assessments of biodiversity in drylands, particularly for detecting hypogaeic prey and life stages that are likely missed by surface-active trapping alone. Our proposed trap is low-cost and constructed from readily available materials, which makes the method more durable for long-term monitoring programmes and projects with limited resources. The subterranean trap design and structure address the problem of loose, low-cohesion sands, a common constraint of below-ground sampling in drylands. In addition, the subterranean trap design does not rely on chemical lures and preservative fluids in hot, arid field conditions. The subterranean trap design is suitable for comparative sampling across seasons, macrohabitats and land-use types. Future work should evaluate longer deployment durations and compare the trap to other subterranean trap designs, including those that extend deeper into the ground. Furthermore, expanding the approach to other dryland regions and soil types may enhance its usefulness for biodiversity monitoring, restoration assessment and studies linking below-ground prey availability to above-ground consumers.

AUTHOR CONTRIBUTIONS

Walter Jubber and Maria Paniw, conception and design of the study; Walter Jubber, acquisition of data; Walter Jubber, Andrea Fuller and Maria Paniw, analysis and interpretation of the data; Walter Jubber, Andrea Fuller and Maria Paniw, drafting and critically revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code have been made available and are deposited on GitHub (https://github.com/MariaPaniw/subterranean-invertebrate-trap) and Zenodo (https://doi.org/10.5281/zenodo.19300403).

STATEMENT OF INCLUSION

Our study was conducted in the Kalahari, with contributions from authors based both locally in South Africa (WJ, AF) and internationally (MP). All authors were involved early in the research process, from study design through to data interpretation, ensuring that diverse perspectives were incorporated from the outset. Wherever relevant, we cited literature produced by scientists working in the region and integrated South African research on soil fauna, invertebrate ecology and dryland systems.

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REFERENCES

Andersen, A. N., & Brault, A. (2010). Exploring a new biodiversity frontier: Subterranean ants in northern Australia. *Biodiversity and Conservation*, *19*(9), 2741–2750.

Ayal, Y. (2007). Trophic structure and the role of predation in shaping hot desert communities. *Journal of Arid Environments*, *68*(2), 171–187.

Bardgett, R. D., & van der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, *515*(7528), 505–511.

Barnes, A. E., Robinson, R. A., & Pearce-Higgins, J. W. (2023). Collation of a century of soil invertebrate abundance data suggests long-term declines in earthworms but not tipulids. *PLoS One*, *18*(4), e0282069.

Bennett, N. C., Jarvis, J. U. M., & Davies, K. C. (1988). Daily and seasonal temperatures in the burrows of African rodent moles. *South African Journal of Zoology*, *23*(3), 189–195.

Bestelmeyer, B. T. (2000). The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. *The Journal of Animal Ecology*, *69*(6), 998–1009.

Bestelmeyer, B. T., Agosti, D., Alonso, L. E., Silvestre, R., Brandão, C. R. F., Brown, W. L., Jr., & Delabie, J. H. C. (2000). Field techniques for the study of ground-dwelling ants: An overview, description and evaluation. In D. Agosti, J. D. Majer, L. Alonso, & T. Schultz (Eds.), *Ants: Standard methods for measuring and monitoring biodiversity* (pp. 122–144). Smithsonian Institution Scholarly Press.

Blanford, S., & Thomas, M. B. (2000). Thermal behavior of two acridid species: Effects of habitat and season on body temperature and the potential impact on biocontrol with pathogens. *Environtal Entomology*, *29*, 1060–1069.

Borkent, A., & Sinclair, B. J. (2017). 13. Key to Diptera families—Larvae. In A. H. Kirk-Spriggs & B. J. Sinclair (Eds.), *Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families* (pp. 357–405). South African National Biodiversity Institute.

Brommer, J., Class, B., & Covarrubias-Pazaran, G. (2019). Multivariate mixed models in ecology and evolutionary biology: Inferences and implementation in R. *EcoEvoRxiv*. https://doi.org/10.32942/osf.io/hs38a

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Mächler, M., & Bolker, B. (2017). GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378.

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics: A Joint Publication of American Statistical Association, Institute of Mathematical Statistics, Interface Foundation of North America*, *7*(4), 434–455.

Brown, G. R., & Matthews, I. M. (2016). A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity. *Ecology and Evolution*, *6*(12), 3953–3964.

Clark, J. S., Bell, D. M., Hersh, M. H., Kwit, M. C., Moran, E., Salk, C., Stine, A., Valle, D., & Zhu, K. (2011). Individual-scale variation, species-scale differences: Inference needed to understand diversity. *Ecology Letters*, *14*(12), 1273–1287.

Costantini, E. A. C., & Mocali, S. (2022). Soil health, soil genetic horizons and biodiversity. *Journal of Plant Nutrition and Soil Science*, *185*(1), 24–34.

Coyle, D. R., Nagendra, U. J., Taylor, M. K., Campbell, J. H., Cunard, C. E., Joslin, A. H., Mundepi, A., Phillips, C. A., & Callaham, M. A. (2017). Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biology & Biochemistry*, *110*, 116–133.

Culver, D. C., & Pipan, T. (2014). *Shallow subterranean habitats: Ecology, evolution, and conservation*. Oxford University Press.

Dippenaar-Schoeman, A. S., Haddad, C. R., Foord, S. H., & Lotz, L. N. (2021). *The Gnaphosidae of South Africa. Part 1 (A–D)*. South African National Survey of Arachnida Photo Identification Guide: The Gnaphosidae of South Africa.

Doblas-Miranda, E., Sánchez-Piñero, F., & González-Megías, A. (2009). Vertical distribution of soil macrofauna in an arid ecosystem: Are litter and belowground compartmentalized habitats? *Pedobiologia*, *52*(6), 361–373.

Dougill, A. J., & Thomas, A. D. (2004). Kalahari sand soils: Spatial heterogeneity, biological soil crusts and land degradation. *Land Degradation and Development*, *15*(3), 233–242.

Filser, J., Faber, J. H., Tiunov, A. V., Brussaard, L., Frouz, J., De Deyn, G., Uvarov, A. V., Berg, M. P., Lavelle, P., Loreau, M., Wall, D. H., Querner, P., Eijsackers, H., & Jiménez, J. J. (2016). Soil fauna: Key to new carbon models. *The Soil*, *2*, 565–582.

Gongalsky, K. B., Persson, T., & Pokarzhevskii, A. D. (2008). Effects of soil temperature and moisture on the feeding activity of soil animals as determined by the bait-lamina test. *Applied Soil Ecology*, *39*(1), 84–90.

Gross, N., Maestre, F. T., Liancourt, P., Berdugo, M., Martin, R., Gozalo, B., Ochoa, V., Delgado-Baquerizo, M., Maire, V., Saiz, H., Soliveres, S., Valencia, E., Eldridge, D. J., Guirado, E., Jabot, F., Asensio, S., Gaitán, J. J., García-Gómez, M., Martínez, P., … Le Bagousse-Pinguet, Y. (2024). Unforeseen plant phenotypic diversity in a dry and grazed world. *Nature*, *632*(8026), 808–814.

Gu, Y. (2024). Dispersion modeling in zero-inflated Tweedie models with applications to insurance claim data analysis. *arXiv*. http://arxiv.org/abs/2405.14990

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22.

Harrison, N. D., Maag, N., Haverkamp, P. J., Ganswindt, A., Manser, M. B., Clutton-Brock, T. H., Ozgul, A., & Cozzi, G. (2021). Behavioural change during dispersal and its relationship to survival and reproduction in a cooperative breeder. *Journal of Animal Ecology*, *90*, 2637–2650.

Iglesias Briones, M. J., Ineson, P., & Piearce, T. G. (1997). Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. *Applied Soil Ecology: A Section of Agriculture, Ecosystems & Environment*, *6*(2), 117–134.

Jubber, W. R., Manser, M. B., & Fuller, A. (2025). Feeding through the ages: Revisiting the diet of meerkats. *Journal of Arid Environments*, *227*(105331), 105331.

Knapp, M., Knappová, J., Jakubec, P., Vonička, P., & Moravec, P. (2020). Incomplete species lists produced by pitfall trapping: How many carabid species and which functional traits are missing? *Biological Conservation*, *245*, 108545.

Knisley, C. B., Gowan, C., & Wirth, C. (2018). Effects of soil moisture, vegetation and food on adult activity, oviposition and larval development in the tiger beetle, *Cicindela albissima* Rumpp. *Journal of Insect Conservation*, *22*, 443–449.

Koehler, H., & Melecis, V. (2010). Long-term observations of soil Mesofauna. In F. Müller, C. Baessler, H. Schubert, & S. Klotz (Eds.), *Long-term ecological research: Between theory and application* (pp. 203–220). Springer Netherlands.

Kong, T. M. (2012). *Understanding land management and desertification in the south African Kalahari with local knowledge and perspectives*. University of Arizona.

Lavelle, P. (1997). Faunal activities and soil processes: Adaptive strategies that determine ecosystem function. In M. Begon & A. H. Fitter (Eds.), *Advances in ecological research* (Vol. *27*, pp. 93–132). Academic Press.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., & Rossi, J.-P. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, *42*, S3–S15.

Lavelle, P., Mathieu, J., Spain, A., Brown, G., Fragoso, C., Lapied, E., de Aquino, A., Barois, I., Barrios, E., Barros, M. E., Bedano, J. C., Blanchart, E., Caulfield, M., Chagueza, Y., Dai, J., Decaëns, T., Dominguez, A., Dominguez, Y., Feijoo, A., … Zhang, C. (2022). Soil macroinvertebrate communities: A world-wide assessment. *Global Ecology and Biogeography*, *31*, 1261–1276.

Lindberg, N., & Bengtsson, J. (2005). Population responses of oribatid mites and collembolans after drought. *Applied Soil Ecology: A Section of Agriculture, Ecosystems & Environment*, *28*(2), 163–174.

López, H., & Oromí, P. (2010). A pitfall trap for sampling the mesovoid shallow substratum (MSS) fauna. *Speleobiology Notes*, *2*, 7–11.

Mammola, S., Giachino, P. M., Piano, E., Jones, A., Barberis, M., Badino, G., & Isaia, M. (2016). Ecology and sampling techniques of an understudied subterranean habitat: The milieu Souterrain Superficiel (MSS). *The Science of Nature*, *103*(11), 88.

Menta, C. (2020). Soil health and arthropods: From complex system to worthwhile investigation. *Insects*, *11*(1), 54.

Montgomery, G. A., Belitz, M. W., Guralnick, R. P., & Tingley, M. W. (2021). Standards and best practices for monitoring and benchmarking insects. *Frontiers in Ecology and Evolution*, *8*, 579193.

Moradi, J., John, K., Vicentini, F., Veselá, H., Vicena, J., Ardestani, M. M., & Frouz, J. (2020). Vertical distribution of soil fauna and microbial community under two contrasting post mining chronosequences: Sites reclaimed by alder plantation and unreclaimed regrowth. *Global Ecology and Conservation*, *23*, e01165–e01175.

Nielsen, U. N., & Ball, B. A. (2015). Impacts of altered precipitation regimes on soil communities and biogeochemistry in arid and semi-arid ecosystems. *Global Change Biology*, *21*(4), 1407–1421.

Ortuño, V. M., Gilgado, J. D., Jiménez-Valverde, A., Sendra, A., Pérez-Suárez, G., & Herrero-Borgoñón, J. J. (2013). The "alluvial Mesovoid shallow substratum", a new subterranean habitat. *PLoS One*, *8*(10), e76311.

Pacheco, R., & Vasconcelos, H. L. (2012). Subterranean pitfall traps: Is it worth including them in your ant sampling protocol? *Psyche; A Journal of Entomology*, *2012*, 1–9.

Panaino, W., Parrini, F., Phakaoago, M. V., Smith, D., Van Dyk, G., & Fuller, A. (2022). Do seasonal dietary shifts by Temminck's pangolins compensate for winter resource scarcity in a semi-arid environment? *Journal of Arid Environments*, *197*, 104676.

Paniw, M., Duncan, C., Groenewoud, F., Drewe, J. A., Manser, M., Ozgul, A., & Clutton-Brock, T. (2022). Higher temperature extremes exacerbate negative disease effects in a social mammal. *Nature Climate Change*, *12*(3), 284–290.

Paniw, M., & Jubber, W. R. (2026). Data and code from: Capturing the unseen: A low-cost method for stratified subterranean sampling of soil invertebrates in drylands. *Zenodo*. https://doi.org/10.5281/zenodo.19300403

Penrith, M. (1984). Two new species of Stizopina (Coleoptera: Tenebrionidae: Opatrini) from Namaqualand, southern Africa, and the relationships between the psammophilous genera. *Annals of the Transvaal Museum*, *33*(24), 353–363.

Phakoago, M., Panaino, W., Maloney, S. K., & Fuller, A. (2025). Prey preference and dietary overlap between the aardvark and Temminck's pangolin in the Kalahari. *Journal of Arid Environments*, *230*, 105422.

Pietersen, D. W., Symes, C. T., Woodborne, S., McKechnie, A. E., & Jansen, R. (2015). Diet and prey selectivity of the specialist myrmecophage, Temminck's Ground Pangolin. *Journal of Zoology*, *298*(3), 198–208.

Potapov, A. M. (2022). Multifunctionality of belowground food webs: Resource, size and spatial energy channels. *Biological Reviews of the Cambridge Philosophical Society*, *97*(4), 1691–1711.

Potapov, A. M., Goncharov, A. A., Semenina, E. E., Korotkevich, A. Y., Tsurikov, S. M., Rozanova, O. L., Anichkin, A. E., Zuev, A. G., Samoylova, E. S., Semenyuk, I. I., Yevdokimov, I. V., & Tiunov, A. V. (2017). Arthropods in the subsoil: Abundance and vertical distribution as related to soil organic matter, microbial biomass and plant roots. *European Journal of Soil Biology*, *82*, 88–97.

Potts, J., Brown, R., Jones, D. L., & Cross, P. (2023). Seasonal variation is a bigger driver of soil faunal and microbial community composition than exposure to the neonicotinoid acetamiprid within *Brassica napus* production systems. *Soil Biology and Biochemistry*, *184*, 109088.

Raś, M., Kamiński, M. J., & Iwan, D. (2022). Fossoriality in desert-adapted tenebrionid (Coleoptera) larvae. *Scientific Reports*, *12*(1), 13233.

Reinhard, J. E., Geissler, K., & Blaum, N. (2022). Grass and ground dwelling beetle community responses to holistic and wildlife grazing management using a cross-fence comparison in Western Kalahari rangeland, Namibia. *Journal of Insect Conservation*, *26*(4), 711–720.

Ruiz, S., Hallett, P. D., & Or, D. (2023). Bioturbation—Physical processes. In *Encyclopedia of soils in the environment* (Vol. *5*, 2nd ed., pp. 100–114). Elsevier.

Russell, A. F., Clutton-Brock, T. H., Brotherton, P. N. M., Sharpe, L. L., McIlrath, G. M., Dalerum, F. D., Cameron, E. Z., & Barnard, J. A. (2002). Factors affecting pup growth and survival in co-operatively breeding meerkats Suricata suricatta. *The Journal of Animal Ecology*, *71*(4), 700–709.

Ryder Wilkie, K. T., Mertl, A. L., & Traniello, J. F. A. (2007). Biodiversity below ground: Probing the subterranean ant fauna of Amazonia. *Naturwissenschaften*, *94*, 725–731.

Sabu, T. K., & Shiju, R. T. (2010). Efficacy of pitfall trapping, Winkler and Berlese extraction methods for measuring ground-dwelling arthropods in moist-deciduous forests in the Western Ghats. *Journal of Insect Science*, *10*(1), 98.

Schmidt, F. A., & Solar, R. R. C. (2010). Hypogaeic pitfall traps: Methodological advances and remarks to improve the sampling of a hidden ant fauna. *Insectes Sociaux*, *57*(3), 261–266.

Scholtz, C. H. (1988). Biology of *Sparrmannia flava* arrow (Coleoptera: Scarabaeidae: Melolonthinae). *The Coleopterists' Bulletin*, *42*(1), 57–62.

Seely, M. K., & Mitchell, D. (1987). Is the substrate environment of the Namib Desert dunes a thermal haven for chthonic beetles? *South African Journal of Zoology*, *22*, 57–61.

Slingsby, P. (2017). *Ants of southern Africa: The ant book for all*. Slingsby Maps Publishers.

Sohlenius, B., & Boström, S. (2001). Annual and long-term fluctuations of the nematode fauna in a Swedish scots pine forest soil. *Pedobiologia*, *45*(5), 408–429.

Srinivasarao, C., Kumar, G. R., Manasa, R., Pilli, K., Sahoo, S., Rakesh, S., Kundu, S., Nataraj, K. C., Rao, K. V., Prasad, J. V. N. S., & Malleswari, S. (2023). Dryland farming: Technological and management options for sustainable agriculture and food systems. In *Encyclopedia of soils in the environment* (pp. 113–124). Elsevier.

Swart, J. M., Richardson, P. R. K., & Ferguson, J. W. H. (1999). Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*). *Journal of Zoology*, *247*(3), 281–292.

Swift, M. J., Heal, O. W., & Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems*. Blackwell Scientific Publications.

Taylor, W. A., Lindsey, P. A., & Skinner, J. D. (2002). The feeding ecology of the aardvark *Orycteropus afer*. *Journal of Arid Environments*, *50*(1), 135–152.

Thakur, M. P., Reich, P. B., Hobbie, S. E., Stefanski, A., Rich, R., Rice, K. E., Eddy, W. C., & Eisenhauer, N. (2018). Reduced feeding activity of soil detritivores under warmer and drier conditions. *Nature Climate Change*, *8*(1), 75–78.

Thomas, M. A. (1981). *The geology of the Kalahari in the northern Cape Province (Areas 2620 and 2720)*. M.Sc. thesis, University Orange Free State, Bloemfontein.

Topping, C. J., & Sunderland, K. D. (1992). Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *The Journal of Applied Ecology*, *29*(2), 485.

Van Rooyen, M. W., Van Rooyen, N., Bothma, J.d. P., & Van den Berg, H. M. (2008). Landscapes in the Kalahari gemsbok National Park, South Africa. *Koedoe*, *50*. https://hdl.handle.net/10520/EJC139693

Wall, D. H., Bardgett, R., & Kelly, E. (2010). Biodiversity in the dark. *Nature Geoscience*, *3*, 297–298.

Wang, L., D'Odorico, P., Ringrose, S., Coetzee, S., & Macko, S. A. (2007). Biogeochemistry of Kalahari sands. *Journal of Arid Environments*, *71*(3), 259–279.

Wang, Y., Liu, X., Zhao, J., Rexili, K., & Ma, J. (2011). The rearing and biology of the desert beetle, *Microdera punctipennis*, under laboratory conditions. *Journal of Insect Science*, *11*, 39.

Whitford, W. G., & Duval, B. D. (2019). *Ecology of desert systems* (2nd ed.). Academic Press.

Wilkinson, M., Richards, P., & Humphreys, G. (2009). Breaking ground: Pedological, geological, and ecological implications of soil bioturbation. *Earth-Science Reviews*, *97*, 257–272.

Wong, M. K. L., & Guénard, B. (2017). Subterranean ants: Summary and perspectives on field sampling methods, with notes on diversity and ecology (Hymenoptera: Formicidae). *Myrmecological News*, *25*, 1–16.

Yamaguchi, T., & Hasegawa, M. (1996). An experiment on ant predation in soil using a new bait trap method. *Ecological Research*, *11*(1), 11–16.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Deployment of the subterranean traps where (a) the trap is placed into the soil and (b) covered completely and maintained in place for 3 weeks.

Figure S2. Example of a standard pitfall trap, which is (a) opened for the 24-h capture period or (b) remains covered otherwise.

Figure S3. Caterpillar plots of the distribution of posterior parameters from the Bayesian multivariate mixed effect model describing the covariance of abundances of individuals caught in subterranean traps belong to the families Scarabaeidae (S) and Tenebrionidae (T) and other families due to random site effects. Parameters where 50% credible intervals (C.I.) overlap 0 are indicated by open circles. Parameters where 50% C.I. do not but 95% C.I. do overlap 0 are indicated by closed grey circles. Parameters where 95% C.I. do overlap 0 are indicated by closed black circles. Thick lines represent 50% C.I.; thin lines represent 95% credible intervals.

Figure S4. Caterpillar plots of the distribution of posterior parameters from the Bayesian multivariate mixed effect model describing the covariance of abundances of individuals caught in subterranean traps belong to the families Scarabaeidae (S) and Tenebrionidae (T) and other families due to residual (within-site) error. Parameters where 50% credible intervals (C.I.) overlap 0 are indicated by open circles. Parameters where 50% C.I. do not but 95% C.I. do overlap 0 are indicated by closed grey circles. Parameters where 95% C.I. do overlap 0 are indicated by closed black circles. Thick lines represent 50% C.I.; thin lines represent 95% credible intervals.

Figure S5. Boxplot showing the distribution of the total biomass in subterranean traps in different months. Points indicate the observed richness in each site ($n = 10$) and subterranean trap per site ($n = 2$) in any given sampling occasion. Total biomass did not differ significantly among habitats, land-use types or month (see analyses_subterranean.R.).

Figure S6. Boxplot showing the distribution of the total biomass caught in different layers (L) of subterranean traps. Points indicate the observed richness in each site ($n = 10$) in any given sampling occasion. In (a) L01 = 0–300 mm below soil surface; L02 = 301–600 mm below soil surface; in (b) L01 = 0–200 mm below soil surface; L02 = 201–400 mm below soil surface; and L03 = 401–600 mm below soil surface. Biomass did not differ significantly among layers (see analyses_subterranean.R.).

Figure S7. Boxplot showing the distribution of abundance of individuals caught (belonging to the two main families that were caught or to other families) in different layers (L) of subterranean traps. Points indicate the observed richness in each site ($n = 10$) in any given sampling occasion. In (a) L01 = 0–300 mm below soil surface; L02 = 301–600 mm below soil surface; in (b) L01 = 0–200 mm below soil surface; L02 = 201–400 mm below soil surface; and L03 = 401–600 mm below soil surface. Abundances did not differ significantly among layers (see analyses_subterranean.R.).

Figure S8. Boxplot showing the distribution of the total number of grouped family and genus taxa caught in different layers (L) of subterranean traps. Points indicate the observed richness in each site ($n = 10$) in any given sampling occasion. In (a) L01 = 0–300 mm below soil surface; L02 = 301–600 mm below soil surface; in (b) L01 = 0–200 mm below soil surface; L02 = 201–400 mm below soil surface; and L03 = 401–600 mm below soil surface. Richness did not differ significantly among layers (see analyses_subterranean.R.).

Table S1. Taxonomic composition and life-stage representation of invertebrates collected by stratified subterranean traps and conventional surface pitfall traps (February 2024–March 2025). All data and analyses can be found on GitHub (https://github.com/MariaPaniw/subterranean-invertebrate-trap) and Zenodo (https://doi.org/10.5281/zenodo.19300403).

Table S2. Parameter estimates of the glmmTBM model assessing taxonomic richness as a function of month of sampling.

Table S3. Parameter estimates of fixed effects from multivariate GLMMs, modelling covariation of numbers of individuals (abundances) caught in subterranean traps as a function of month of sampling and main habitat sand type.

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