The effects of *Heuweltjies* and *Microhodotermes viator* (Isoptera: Hodotermitidae) on invertebrate assemblages and species turnover in the succulent Karoo, Western Cape

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Picture: frass of *Microhodotermes viator* (left) and the larger faecal pellets of the scarab larvae that inhabit and consume the frass (photo author's own).

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ABSTRACT

Species turnover is a measure of β-diversity that attempts to quantify the change in species composition along a spatial, temporal or environmental gradient. One such environmental gradient that has been shown to affect species turnover is local edaphic variation. This is seen in the Western Cape Province of South Africa, where the unique edaphic character of large earth mounds, known as *heuweltjies,* support distinct plant communities. The aim of this study is to assess whether these mounds, and the termite *Microhodotermes viator* commonly associated with them, also support distinct invertebrate communities, thereby contributing to invertebrate species turnover in the region. Pitfall and emergence traps were set on *heuweltjies* and in the surrounding matrix in the Karoo Desert National Botanical Gardens, Worcester, Western Cape Province. On- and off- mound community contrasts were assessed by means of a cluster analysis, and species turnover was measured using the Jaccard distance. Invertebrates were more abundant on the *heuweltjies,* which also had distinct communities when compared to the matrix. Spiders (Aranaea) were more abundant on the *heuweltjies,* as were in the invertebrates emerging from the frass, suggesting a trophic cascade. Invertebrates commonly associated with *M. viator* were found more commonly on the *heuweltjies.* The Jaccard distances indicated that environmental homogenisation of the *heuweltjies* resulted in homogenisation of the on-mound invertebrate communities. Heuweltjie soil enrichment was most similar to that of termite frass when compared to the matrix, supporting a termite origin for the heuweltjies.

Introduction

Beta diversity, at its core, is the extent of variation in a community of species among study sites. Originally proposed by Whittaker (1960, 1972), it is a component of diversity that links the species richness of an isolated locality (α-diversity) with the overall richness of a region (γ-diversity). Numerous indices have subsequently been used to assess β-diversity (see Tuomisto 2010a), with no clear consensus as to the most appropriate methods or the exact relationship of β-, α- and γ-diversity (Anderson *et al.* 2011).

One important concept of β-diversity is species turnover. As a subset of β-diversity, it can be thought of as follows: in any given community, there will be a variety of species occupying a distinct set of niches. These niches are composed of many different variables, such as environmental characteristics and interspecific interactions (Whittaker 1972). As one moves along a gradient of these variables, the niches will change, resulting in a change in the species inhabiting these niches and thus the overall community composition. Species turnover is therefore inherently linked to environmental change, and will theoretically be greater across areas of greater environmental contrast (Anderson *et al.* 2011; Vellend 2001).

The importance of environmental variation in driving species turnover is shown across many different scales, and in many different systems. Across more than 4000 km of three different Chinese grassland types, species composition change was more strongly related to environmental divergence than geographic difference (Tang *et al.* 2012). Dornelas *et al.* (2006) found that environmental heterogeneity was a major driver of diversity on coral reefs. On a smaller spatial scale, Guèze *et al.* (2013) found that soil Ca, Mg and C:N ratio were important environmental factors explaining floristic diversity in Amazonian rainforest.

Species turnover in the CFR

The Cape Floristic Region (CFR) of the Western Cape Province of South Africa is an area of exceptionally rich plant diversity at the regional scale, broadly encompassing the fynbos biome (Cowling *et al.* 1992). Within the fynbos, however, α-diversity is not recorded as being significantly greater than other southern African biomes (Cowling 1990). This apparent disparity between richness at the local and regional scale is explained by very high species turnover. Cowling (1990) found high levels of species turnover along soil fertility gradients and between similar soils derived from different substrata, reflecting specialisation of the CFR flora to narrow edaphic niches. The diversity of soils in the CFR (see Deacon *et al.* 1992) thus facilitates many diverse plant communities within the region, leading to high γ-diversity (Cowling *et al.* 1992). Indeed, the soil diversity does not only support different plant communities, but was considered at least partly responsible for rapid speciation of the flora in the region (Richardson *et al.* 2001).

The high levels of plant diversity in the CFR are reflected in the fauna of the region, with high levels of diversity and endemism seen in many taxonomic groups (Colville *et al.* 2014; Linder *et al.* 2010; Jonathan 1992). For invertebrates, the drivers of diversity in the region have been shown to be similar to that of the flora (Procheş *et al.* 2009), with the fynbos biome subsequently displaying relatively high levels of invertebrate α- and β-diversity (Procheş and Cowling 2006; Pryke and Samways 2009). However, the invertebrate diversity of the CFR has received far less research attention than the plants.

Termites as ecosystem engineers, and their influence on species turnover

An organism is considered to be an ecosystem engineer if, through their presence, they alter either the abiotic conditions or the availability of resources. Direct trophic effects are, however, excluded. (Jones *et al.* 1994 and Lawton 1994 in Dangerfield *et al.* 1988). Termites are an archetypical example of this, particularly *Macrotermes* (Isoptera: Termitidae). They have been shown to enhance the local nutrient content, cation exchange capacity and water availability of soil through the building of their large earth mounds (Arshad 1982; Dangerfield *et al.* 1998; Griffioen and O'Connor 1990; Holdo & McDowell 2004; Jones, 1990; Fox-Dobbs *et al.* 2010). In turn, these termite-altered soils support distinctive plant communities. *Macrotermes* mounds represent discrete niches, allowing species to persist that may be at a competitive disadvantage in the surrounding soils (Griffioen and O'Connor 1990). The mounds support more productive communities of larger, nutrient-enriched grasses and trees, with plant species composition often different from the surrounding matrix (Arshad 1982; Griffioen and O'Connor 1990; Holdo & McDowell 2004; Steinke 1989; Moe *et al.* 2009). This in turn influences utilization of the mounds by animals, including increased browsing by elephants (Holdo & McDowell 2004; Levick *et al.* 2010) and ungulates (Mobæk *et al.* 2005) and increased on-mound occupancy by arthropods, geckos and small mammals (Fleming & Loveridge 2003; Pringle *et al* 2010).

The *heuweltjie* debate

Heuweltjies (meaning "little hills" in Afrikaans), are large earth mounds found exclusively in South Africa. They occur nearly continuously from south of the Orange River in the Northern Cape to the eastern limit of the Cape Peninsula in the Western Cape, with some intrusion into the interior of the province (Lovegrove & Siegfried 1986). They are often observed to have a layer of calcrete through the base of the mound, and are commonly associated with the southern harvester termite, *Microhodotermes viator* (Lovegrove & Siegfried 1986; Moore & Picker 1991). The mounds can reach 30m in diameter and 2m in height, though this can vary drastically across their range (Picker et al. 2007) (see Appendix 1).

The origin of *heuweltjies* is a contentious topic, with many hypotheses being put forward. Lovegrove & Siegfried (1986, 1989) hypothesised that these mounds were produced as a result of the mole rat *Cryptomys hottentotus* burrowing into and colonising the mounds of *M. viator.* However, in other studies, no evidence could be found for the colonisation of mole rats, and the mounds were described as 4000 year old nests of *M. viator* (Moore & Picker 1991). Subsequently it was proposed that the mounds are in fact up to 30 000 years old and were produced in the Late Pleistocene by an unknown, now extinct, species of termite, with the mounds then later colonised by *M. viator* (Midgley *et al.* 2002). It has since been contested that termites could not have been responsible for the formation of *heuweltjies* and that the mounds were produced as a result of differential erosion around regularly spaced, extinct bush-clumps (Cramer *et al.* 2012). More recently, however, it has been hypothesized that the mounds of *M. viator* are centres of nutrient enrichment supporting denser vegetation, thus increasing the accretion of aeolian sediments and the growth of the *heuweltjie* (McAuliffe *et al.* 2014). Further supporting this, Francis *et al.* (2013) found evidence of previous *M. viator* activity in mounds that did not currently appear occupied. There is currently no clear consensus as to the origins of these regularly-spaced geological features, though most authors acknowledge that termites are likely to at least contribute to their genesis.

Irrespective of the origins of *heuweltjies*, they share many edaphic characteristics with termite mounds , such as an enhanced nutrient status, water-holding capacity and organic matter content (Lovegrove 1991). Subsequently, like *Macrotermes* mounds, *heuweltjie* soils are more fertile than the intervening matrix (Kunz *et al.* 2012; Midgley & Musil 1990) and support a distinct plant community when compared to surrounding soils (Armstrong & Siegfried 1990; Knight *et al.* 1989; Kunz *et al.* 2012; Midgley & Musil 1990; Rahlao *et al.* 2008), thus increasing β- and γ-diversity (Lovegrove 1991). There is, however little literature on the response of faunal communities to *heuweltjies* - it is broadly suggested that *heuweltjies* "attract a great diversity of animals" (Milton & Dean 1990), and that livestock preferentially graze on *heuweltjies* (Armstrong & Siegfried 1990).

With the altered soils on *heuweltjies* supporting a unique floral community, it is of interest to see if this is reflected by the fauna as well. Thus, the main aim of this study is to determine whether *heuweltjies* contribute to β-diversity and species turnover of invertebrates in the Succulent Karoo. If mounds do support a unique invertebrate community, there are a number of possible explanations. Firstly, invertebrates could be responding directly to the unique on-mound floral community and its effects on soils through trophic cascades. Secondly, termite faeces (frass) concentrated on these mounds might represent a nesting site and food source for various larvae. Frass nutrients have also been examined to see if this enrichment is of a similar nature and magnitude to that of the *heuweltjies,* and if it could be used to further support the termite origin hypothesis.

Methods and Materials

Study Site

The study took place in the Karoo Desert National Botanical Gardens, Worcester, Western Cape, South Africa (approximately 33°36'52.50"S, 19°27'11.61"E). The local climate is typically Mediterranean (Fuggle 1981), with a mean annual rainfall of approximately 250 mm (South African National Biodiversity Institute 2014). The region forms part of the Succulent Karoo Biome (Rutherford and Westfall 1986), with the local soils derived from the Bokkeveld and Witteberg groups (Harmse 1978 in Midgley & Musil 1990). The vegetation in this area is part of the Succulent Karoo Biome, within which there are many rare and endemic species (Hall *et al.* 1980; Werger 1978). There were large accumulations of termite frass on the *heuweltjies* at this site, but very little was present in the matrix. Although not measured, it is estimated that at least 25 L was present on each *heuweltjie.*

Pitfall traps

Pitfall traps were used to sample the epigaeic fauna. Each trap consisted of a 150 ml centrifuge tube, approximately 15 cm deep with a 3 cm opening diameter. Tubes were filled to 2cm deep (approximately 7.5 ml) with a 50% solution of ethylene glycol (antifreeze) and placed in the ground with the lip of the opening flush to the surface and not protruding. Each transect was made up of 10 traps placed 1m apart. Trap lines were set on 10 randomly selected *heuweltjies* and at 10 randomly selected sites in the matrix. Traps were set in such a way that a *heuweltjie* transect would not enter the matrix and a matrix transect would not enter a *heuweltjie.* There were four trapping periods of four trap days each, commenced on April 30, June 16, July 30 and September 4 of 2014. Trapped samples were collected in plastic jam jars and kept in the trapping fluid during transport to the lab, where they were rinsed with water and then stored in 70% alcohol until analysis.

Emergence traps

Emergence traps were made as an inverted cone of 50% green shade cloth with an open circular base 1.5 m in diameter. The apex of the cone had 5 cm opening, through which a plastic u-bend (lined with an adfixed layer of coarse sand) was forced. A plastic jam jar half-filled a 50% solution of ethylene glycol was attached to the end extending from the trap. One of each of these was placed near each of the pitfall transects as the emergence trap associated with that site. They were initially set on April 30, with the contents collected and the traps reset each time the pitfalls were collected (May 4, June

20, August 3 and September 8, 2014.) The emergence traps were therefore continuously collecting from April 30 to September 8. The contents were treated in the same manner as the pitfall traps, but were analysed separately.

Sieving

A once-off frass sieving survey was conducted on September 8, where 10 L of frass from different locations on each *heuweltjie* was pooled and sieved through a 2 mm sieve. Any invertebrates found were collected. Adults were stored in 70% alcohol while larval or pupal stages were reared in frass according to their dietary needs in order to identify their adult stages.

Additional one-off surveys were undertaken at Malmesbury (approximately 33°26'47.24"S, 18°42'54.26"E) on July 22 and south of Vanrhynsdorp on July 28 (approximately 31°39'40.68"S, 18°43'32.52"E), both in the Western Cape Province of South Africa. The methods as above were applied.

Throughout the fieldwork, any larval or pupal invertebrates observed in the frass were collected to be used in compilation of a species list.

Species identification

Invertebrates trapped were examined under a compound microscope where they were separated to morphospecies and photographed for further reference. All species were identified to at least order. All ants were identified to genus and morphospecies.

Soil data

Soil was collected from the top 10 cm soil profile on each of the 10 matrix and *heuweltjie* sites associated with an emergence trap at the Karoo Desert National Botanical Gardens. Each sample was pooled from four randomly selected subsamples on each site to ensure equal sampling. Frass samples were also collected on each *heuweltjie,* each sample pooled from four different mounds on the respective *heuweltjie.*

Samples were sieved through a 2 mm mesh, air dried and then sent to the Soil Sciences Department at the University of Stellenbosch for analysis, where total N, C and Ca was determined.

Organic matter content was determined by loss on ignition. Samples were first air dried and sieved through a 2 mm mesh. Approximately 5 g of each sample was then weighed and placed in a muffle furnace at 400 °C for 24 hours. Samples were then re-weighed and percent organic matter was calculated as follows:

$$\frac{W_{INITIAL} - W_{FINAL}}{W_{INITIAL}} \times 100$$

The coefficient of variation of the total N, C, Ca and percent organic matter were calculated as follows:

$$\frac{Standard\ deviation}{Mean} \times 100$$

Anoplolepis ant analysis

As the ant *Anoplolepis custodiens* was too numerous to count without great difficulty, five subsamples, each over 500 individuals, were counted and then dried in an oven at 45 °C for 5 hours. The subsamples were subsequently weighed to determine a weight to abundance conversion factor of 2.4 ants.g^{-1}. The rest of the samples were then oven dried and weighed to determine approximate abundances in each sample. This was only necessary for the first trapping session, as this species of ant was relatively inactive during winter. The mean abundance of *A. custodiens* on and off mound was then calculated and compared using a Mann-Whitney U test.

Statistical analysis

The species data for the four trapping sessions was pooled, so that for both the emergence and the pitfall data there were 10 *heuweltjie* and 10 matrix transects. Any very rare species with a total count of less than seven was removed from the statistical analyses. *Microhodotermes viator* were also excluded as they are already known to utilize *heuweltjies* and may thus mask possible trends of the invertebrate community.

Plymouth Routines in Multivariate Ecological Research (PRIMER) (PRIMER-E version 6. Clarke & Gorley 2006) was used to investigate community similarity for abundance data. A resemblance matrix was used to create a Bray-Curtis similarity matrix, which was used to construct a non-metric Multi-Dimensional Scale (MDS) plot for the ants (Hymenoptera: Formicidae). Because there was no clear separate clustering of the *heuweltjies* and the matrix ant communities, ant communities were considered as uniform across the site contrasts and excluded from further statistical analysis to prevent them masking any ecological trends.

PRIMER was used to calculate the abundance, richness, Pielou's J evenness, Shannon H' diversity index and the Gini-Simpson 1-λ diversity index for each transect. This was done for the pitfall and emergence separately and together, as well as for spider species alone. The means of these data for matrix and *heuweltjie* transects were then compared using a Mann-Whitney U test in the statistical computing environment R (R Development Core Team, 2011).

The Jaccard distance among *heuweltjies,* among the matrix sites and between *heuweltjies* and the matrix was calculated using PRIMER. A one-way analysis of variance test was applied in R in combination with Tukey's Honest Significant Difference test to reveal means that were significantly different from one other. All assumptions for normality were met.

The mean C:N ratios of the matrix and *heuweltjie* soils and frass were determined. The means of total N, C and Ca, percent organic matter and C:N ratio were determined and compared using a Mann-Whitney U test in R. An MDS plot was created from a Bray-Curtis similarity matrix using PRIMER to determine how the samples clustered based on the percent organic matter and the amount of C, N, and Ca in each sample. The statistical significance of groupings observed was tested using a one-way analysis of similarity (ANOSIM) in PRIMER.

In PRIMER, MDS plots were created from a Bray-Curtis similarity matrix to examine community structure of *heuweltjie* and matrix transects for (a) the pitfall traps, (b) the emergence traps, (c) both of these combined and (d) the spiders caught in the pitfall traps. The statistical significance of groupings observed was tested using a one-way analysis of similarity (ANOSIM) in PRIMER. The species contributing most to this similarity were determined using a similarity percentage (SIMPER) analysis based on the Bray-Curtis similarity.

Results

Anoplolepis custodiens (Hymenoptera: Formicidae) was the single most dominant species, with 14908 individuals recorded. They did not appear preferentially on either *heuweltjies* or in the matrix, with means (±SD) of 742.3 ± 1168.8 and 748.5 ± 884.7 respectively. More than 96 % of all individuals were caught in the first late autumn trapping session.

Overall invertebrate abundance was significantly higher on *heuweltjies* than in the matrix for all trap types (Table 1). This trend was the same for species richness, though none of the differences were significant. Pielou's evenness was significantly higher in the matrix than on *heuweltjies* for all trap types. Shannon's diversity index was only significantly greater in the matrix than on *heuweltjies* for the emergence traps, with none of the other trap types showing any significance differences. Simpson's index was significantly higher in the matrix than on *heuweltjies* for all trap types except pitfall traps.

Table 1: The mean ± standard deviation of the abundance (S), richness (N), Pielou's eveness (J'), Shannon index to the base e (H') and Simpson index (1-λ) of invertebrates recorded on heuweltjies and in the matrix. Displayed are the results for the two different trapping methods and the combination of both, as well as only spiders (Arachnida: Araneae) caught in pitfalls. A significant difference between the respective heuweltjie and matrix values for each measure, as tested using a Mann-Whitney U test, is denoted * ($p < 0.05$).

Trap type	Site	S	N	J'	H'	1-λ
Pitfall	Heuweltjie	23.2±2.69	**57.5±13.9***	**0.86±0. 08***	2.7±0.32	0.90±0.06
	Matrix	18.5±5.70	**35.0±11.7***	**0.93±0.02***	2.7±0.34	0.94±0.03
Emergence	Heuweltjie	12.5±3.27	**118.7±133.82***	**0.54±0.28***	**1.4±0.73***	**0.54±0.30***
	Matrix	10.8±3.46	**22.7±15.87***	**0.89±0.09***	**2.1±0.20***	**0.89±0.07***
Combined	Heuweltjie	17.9±6.2	**88.1±97.8***	**0.70±0.25***	2.0±0.87	**0.72±0.28***
	Matrix	14.7±5.06	**28.9±14.9***	**0.91±0.07***	2.3±0.41	**0.92±0.06***
Araneae	Heuweltjie	8.9±1.4	**25.8±7.0***	**0.81±0.11***	1.8±0.31	**0.78±0.12***
	Matrix	6.7±2.6	**11.8±5.2***	**0.93±0.05***	1.7±0.43	**0.88±0.09***

The pitfall, emergence and combined samples all followed the same trend for the Jaccard distance (d_j) (Table 2). There was no difference between the matrix and matrix vs *heuweltjie* comparisons. However, the mean value of the *heuweltjie* comparison was significantly smaller than both the matrix and the matrix vs *heuweltjie* comparisons.

Table 2: The mean (±SD) of the Jaccard distance (d_J), quantifying % dissimilarity among matrix samples, among heuweltjie samples and between matrix and heuweltjie samples. Results are for each trapping method, as well as the combination of both. Significance of the differences within each sample was tested using an ANOVA and Tukey post-hoc test. Within each sample, significant differences are shown by different alphabetic superscripts ($p < 0.05$).

	Jaccard distance (% similarity)		
Comparison	**Pitfalls**	**Emergence**	**Combined**
Heuweltjie	60.8±6.65$^{\mathbf{a}}$	65.8±9.78$^{\mathbf{c}}$	57.1±6.89$^{\mathbf{e}}$
Matrix	69.8±7.97$^{\mathbf{b}}$	71.7±10.13$^{\mathbf{d}}$	65.7±7.69$^{\mathbf{f}}$
Matrix vs *heuweltjie*	68.9±7.64$^{\mathbf{b}}$	72.5±7.64$^{\mathbf{d}}$	65.2±7.33$^{\mathbf{f}}$

The frass of *M. viator* had a higher C:N ratio and contained significantly more nitrogen, carbon and organic matter when compared to *heuweltjie* or matrix soils (Table 3a). There was significantly more Ca in frass than matrix soils, but no difference when frass was compared to *heuweltjie* soils. *Heuweltjie* soils had a higher C:N ratio and contained significantly more N, C, Ca and organic matter when compared to matrix soils. For all the soil characteristics measured, the coefficient of variation of the nutrients and the organic matter was lowest in the frass and highest in the matrix (Table 3b).

Table 3a: The mean ± standard deviation of the nutrient and organic matter contents of termite frass and matrix and *heuweltjie* soils. Means were compared using a Mann-Whitney U test. Within each analysis, significant differences are shown by different alphabetic superscripts ($p < 0.05$)

	Analysis				
Sample	**N (mmol.kg^{-1})**	**C (mmol.kg^{-1})**	**C:N ratio**	**Ca (mmol.kg^{-1})**	**Organic matter (%)**
Frass	534.7 ±65.9$^{\mathbf{a}}$	22921.2±3040.0$^{\mathbf{d}}$	37.2±1.87$^{\mathbf{g}}$	156.2±18.1$^{\mathbf{j}}$	59.6±7.57$^{\mathbf{l}}$
Heuweltjie	356.3±94.3$^{\mathbf{b}}$	9505.9±3338.0$^{\mathbf{e}}$	22.5±0.748$^{\mathbf{h}}$	144.3±33.64$^{\mathbf{j}}$	29.7±10.0$^{\mathbf{m}}$
Matrix	57.8±25.3$^{\mathbf{c}}$	1322.2±672.0$^{\mathbf{f}}$	19.3±0.905$^{\mathbf{i}}$	10.7±7.0$^{\mathbf{k}}$	4.3±1.54$^{\mathbf{n}}$

Table 3b: The coefficient of variation ((standard deviation/mean)*100) of the nutrient and organic matter contents of termite frass and matrix and *heuweltjie* soils.

	Coefficient of variation			
Sample	**N**	**C**	**Ca**	**Organic Matter**
Frass	12.32	13.26	5.03	12.70
Heuweltjie	26.31	35.12	23.31	33.67
Matrix	43.77	50.82	65.42	35.81

The species that contributed most to within-*heuweltjie* similarity from the emergence traps was Chrysomelidae 1, a flea beetle (Alticinae) (Table 4). It was also the most abundant non-ant species recorded, and contributed the most (53.16%) to between-sample dissimilarity within the emergence samples. Araneae 1 contributed the most to intra-*heuweltjie* similarity in the pitfall traps, as well as the most to inter-sample dissimilarity. The same was true in the spider sub-samples.

Table 4: The morphospecies that contributed most to intra-sample similarity, calculated from a SIMPER analysis in PRIMER. Species were identified as far as possible. For a full morphospecies list see Appendix 3.

Trap target	Sample	Identity	Average abundance	Average Similarity	Similarity contribution (%)
Pitfall	Heuweltjie	Araneae 1	9.8	10.96	27.42
		Acari 13	7.3	4.36	10.92
		Araneae 35	3	3.02	7.56
	Matrix	Acari 10	2.4	4.07	13.51
		Thermophilum spp.	2.7	2.81	9.34
		Acari 6	1.6	2.76	9.17
Emergence	Heuweltjie	Chrysomelidae 1	93.7	21.32	67.64
		Nymphal spiders	3.2	2.89	9.16
		Araneae 6	1.8	1.15	3.66
	Matrix	Coleoptera 6	2.7	6.5	21.91
		Chrysomelidae 1	3.9	4.79	16.14
		Araneae 5	1	3.66	12.34
Spiders (Araneae)	Heuweltjie	Araneae 1	9.8	23.11	47.32
		Araneae 35	3	6.69	13.7
		Araneae 8	2.1	3.85	7.89
	Matrix	Nymphal spiders	2.6	15.44	41.63
		Araneae 8	1.1	3.82	10.3
		Aranea 4	1.1	3.36	9.06

When an MDS plot was constructed based on community composition, the *heuweltjie* subsamples clustered separately form the matrix subsamples for the pitfall (Fig. 1a) and emergence (Fig. 1b) trap. For the combined MDS plot (Fig. 1c), pitfall and emergence trap communities clustered separately from one another. Within these separate clusters, *heuweltjie* and matrix subsamples clustered separately. The Araneae showed distinct clustering of *heuweltjie* subsamples, while the clustering of the matrix subsamples was less distinct. All groupings were significant at the 5 % probability when tested using an ANOSIM in PRIMER. Ants *(*Hymenoptera: Formicidae) (excluding *Anoplolepis custodiens*) did not show any clear clustering, and no groupings was were significant when tested using an ANOSIM in PRIMER.

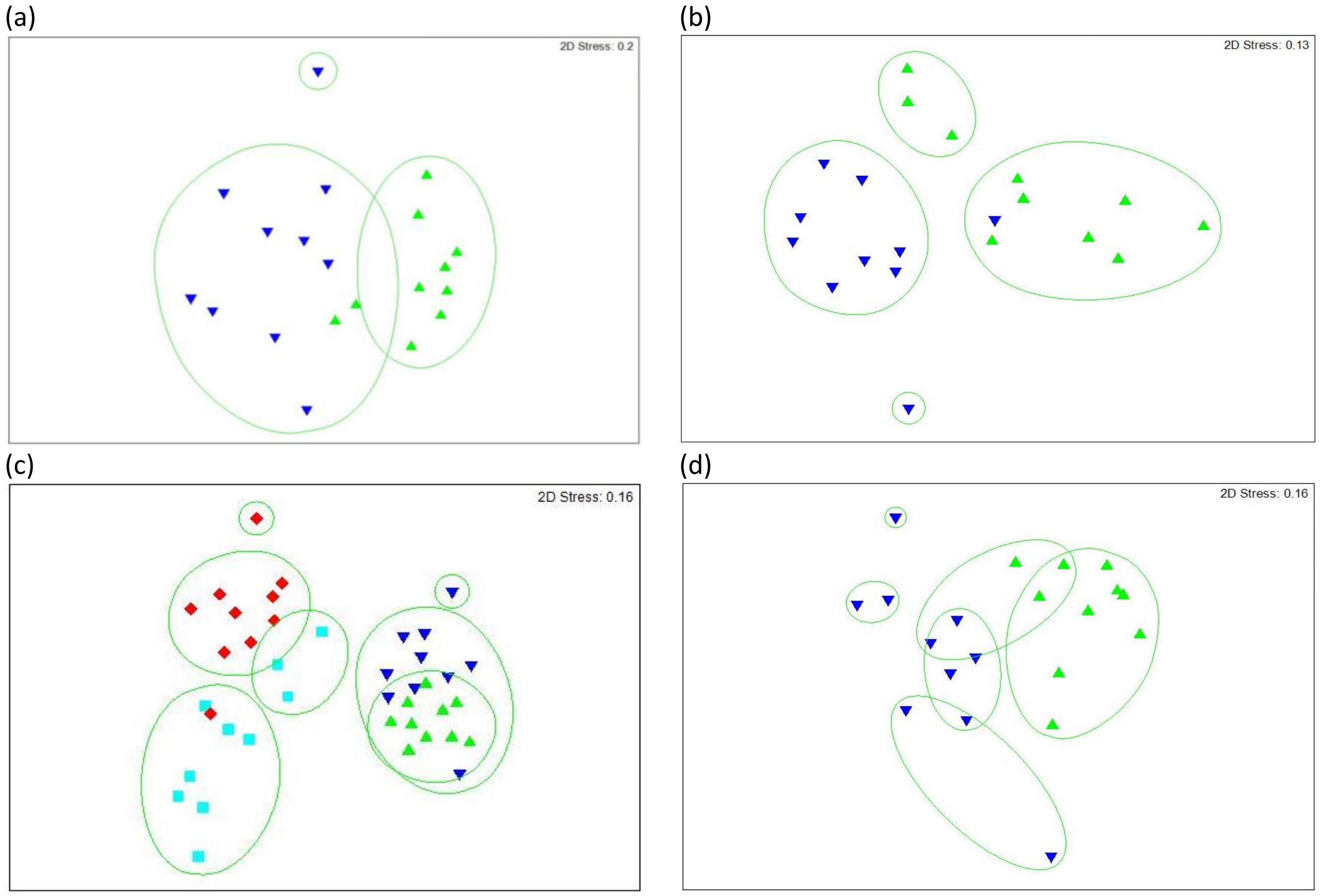

Figure 1: Bray Curtis similarity Multidimensional Scaling (MDS) plot clustering the community composition of invertebrates caught in **(a)** pitfall traps (Global R = 0.473, $p < 0.005$; 2D stress = 0.2; similarity at 29%), **(b)** emergence traps (Global R = 0.528, $p < 0.005$; 2D stress = 0.13; similarity at 30%) **(c)** pitfall and emergence traps combined (Global R = 0.129, p = 0.011; similarity at 30%) and **(d)** spiders (Araneae) (Global R = 0.609, $p < 0.005$; similarity at 48%). For (a), (b) and (d) *heuweltjie* = green and matrix = dark blue. For (d), *heuweltjie* pitfalls = green, matrix pitfall = dark blue, *heuweltjie* emergence = light blue and matrix emergence = red. Significance was tested using an ANOSIM in PRIMER

The species that contributed most to within-*heuweltjie* similarity from the emergence traps was Chrysomelidae 1, a flea beetle (Alticinae) (Table 4). It was also the most abundant non-ant species recorded, and contributed the most (53.16%) to between-sample dissimilarity within the emergence samples. Araneae 1 contributed the most to intra-*heuweltjie* similarity in the pitfall traps, as well as the most to inter-sample dissimilarity. The same was true in the spider sub-samples.

The nutrient profiles of frass, *heuweltjie* soils and matrix soils were distinct from one another, with the subsamples from each clustering tightly together in an MDS plot (Fig. 2). However, the nutrient profile of the frass and *heuweltjie* samples were more similar to one another (all at least 55% similar) than either were to the nutrient profile of the matrix samples (less than 20% similar).

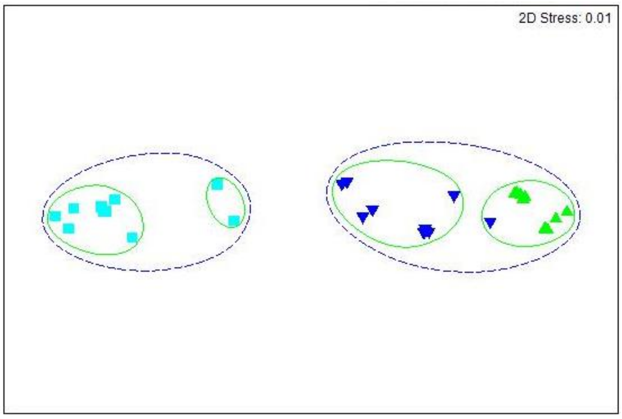

Figure 2: Bray Curtis similarity Multidimensional Scaling (MDS) plot clustering the soil nutrient properties (C, N , Ca content and % organic matter) of termite frass (green), *heuweltjie* soils (dark blue) and matrix soils (light blue). Similarity is drawn at 74% (solid green line) and 55% (dashed blue line). Significance was tested using an ANOSIM in PRIMER (Global R = 0.919, p < 0.005).

Discussion

The present findings clearly demonstrate an invertebrate community shift between matrix and *heuweltjie* that is matched by enriched nutrient profiles on heuweltjies. It is highly plausible that this community change is driven by some combination of the distinct edaphic characteristics of *heuweltjies* found in this and other studies (Kunz *et al.* 2012; Midgley & Musil) as well as the subsequent altered *heuweltjie* plant communities (Armstrong & Siegfried 1990; Knight *et al.* 1989; Kunz *et al.* 2012; Midgley & Musil 1990; Rahlao *et al.* 2008).

Heuweltjie soil enrichment

Heuweltjies are more clayey, better aerated and more alkaline than the surrounding soils (Kunz *et al.* 2012; Midgley & Musil 1990; Moore & Picker 1990). They can be further distinguished from matrix soils on the basis of their nutrient profile, as seen in this and other studies (see Table 5). However, the degree of C and N enrichment in the present study is far greater than found by Midgley & Musil (1990) (whose study also took place in the Worcester valley) and Kunz *et al.* (2012). One explanation is that our study site is more productive. This is likely the case with the Soebatsfontein site which has a mean annual rainfall of 129 mm (Kunz *et al.*) compared to the annual rainfall of approximately 250 mm at Worcester (South African National Biodiversity Institute 2014). It is unlikely that this accounts for the differences observed between this study and that of Midgley & Musil (1990), as both took place within the same valley. It is also doubtful that this difference comes from an error in calculations, as both sites had similar off-mound N concentrations and similar on- and off-mound Ca concentrations. The disparity may be because Midgley & Musil (1990) employed different methods to this study. Whereas they selectively avoiding soils below canopy and made 5 pairs of samples (each made of 3 subsamples) we sampled randomly on 10 pairs of samples (each made of 4 subsamples) in this study. Secondly, Midgley & Musil do not give the exact site within the Worcester-Robertson valley. Therefore differences may be due to changes in local environment or because of environmental stochasticity over the 25 years between studies. They do not mention termite occupancy or frass outputs at their site. If termites were less active at their study site or packed the frass away below ground (Moore and Picker 1991), then the upper soil layers would not be as enriched, explaining the differences observed here.

Table 5: Comparison of the mean (this study and Midgley & Musil 1990) and median (Kunz *et al.* 2012) concentrations of N, C and Ca measured on *heuweltjies* and in the matrix in three different studies. For each nutrient in all studies the *heuweltjie*-matrix comparison was significant. ND means not determined in that study.

			Concentration (mmol.kg-1)		
Author	**Site**	**Sample**	**N**	**C**	**Ca**
This study	Worcester	*Heuweltjie*	356.3	9505.9	144.3
		Matrix	57.8	1322.2	10.7
Midgley & Musil (1990)	Worcester-Robertson	*Heuweltjie*	84.6	ND	146.7
		Matrix	62.0	ND	11.2
Kunz et al. (2012)	Soebatsfontein	*Heuweltjie*	78.5	1124	ND
		Matrix	35.7	549.5	ND

Biotic response to *Heuweltjies*

Midgley & Musil (1990) recorded more deciduous plants on-mound than in the matrix which, along with the frass input, would account for the elevated levels of organic matter recorded on-mound in this study. Although not measured here, it has been shown that on-mound plant communities consist of more deciduous shrubs and annual floras (Knight *et al.* 1989; Midgley & Musil 1990). Plants on *heuweltjies* are also more productive than those of the surrounding matrix (Picker *et al.* 2007) and have higher foliar nutrient content (Midgley & Musil 1990). Similar processes are seen in the fynbos (Cowling 1990) and on termite mounds (Dangerfield et al., 1988; Holdo & McDowell, 2004), where stark changes in parent geology and the activities of termites, respectively, increase plant β-diversity and local species turnover.

The invertebrate community on *heuweltjies* is clearly distinct from that of the matrix. The species that contributed most to intra-site similarity were generally different for *heuweltjies* and the matrix, further illustrating the community separation. Greater invertebrate abundance on *heuweltjies* reflects the higher on-mound plant productivity (Picker *et al.* 2007), suggesting greater utilization of the denser, nutrient rich foliage on the mounds by herbivorous invertebrates. This increased abundance is not a direct consequence of termite occupancy of the mounds because *M. viator* were excluded from this analysis. This process is similar to what is seen on termite mounds where, for example, the altered and enriched soils and plant communities on mounds of *Macrotermes* induce a trophic cascade, increasing faunal productivity and abundance (Holdo & McDowell 2004; Levick *et al.* 2010; Pringle *et al.* 2010). In the fynbos, invertebrate species turnover is likely due to the same abiotic factors driving high plant species turnover (Procheş and Cowling 2006; Procheş *et al.* 2008). Using these examples, it is likely that the community change on *heuweltjies* is due to some combination of the presence of termite frass, an invertebrate response to altered soils and a trophic cascade induced by the changes to the plant community.

Community change in response to termites

At this study site, the abundance of nutrient-rich *M. viator* frass represents a niche that is unique to *heuweltjies*. The detritivorous and predaceous larvae from numerous families observed living in the frass, with some directly consuming it, show that it is utilized by invertebrates. Scarab (Coleoptera: Scarabaeidae) and dipteran (Order: Diptera) were present in relatively high abundances in the frass at Vanrhynsdorp, Malmesbury and Worcester (Appendix 2). As the frass does not appear to occur in large volumes in the matrix, the frass mounds contribute towards habitat heterogeneity and species turnover. The relative immobility of larvae means it is likely that female insects are choosing to lay in frass mounds and not that the larvae present have migrated over metres into the frass. While some of the invertebrates that are utilizing the frass may also be found in the leaf litter of the matrix or the *heuweltjies*, the frass is a theoretically important breeding site for a number of reasons. Although the factors involved in oviposition preference are complex, site nutrient quality directly affects fecundity, and thus site choice (Awmack and Leather 2002). Fresh frass is nutrient rich, high in organic matter, uncompacted and enhanced with termite body-moisture after defecation, making it a potentially attractive nesting site in in the semi-arid environment. Additionally, termite faecal pellets have been shown to have an anti-fungal effect (Rosengaus *et al.* 1998), possibly reducing egg loss. Predaceous larvae caught in the frass (e.g. Diptera, Coleoptera) indicate that there is a trophic cascade induced by the presence of the termite faeces. Additionally, the above-ground predators may also be responding to the increased numbers of detritivores emerging from the frass and *heuweltjie* soils.

This study also illustrates how *M. viator* impacts the local species composition through facilitative and trophic interactions. Both the histerid species (Coleoptera: Histeridae) and staphylinid species (Coleoptera: Staphylinidae), caught via sieving and in emergence traps, respectively, are known to be termitophilous with *M. viator* (see Helava *et al.* 1985 and Kistner 1970), while the Ammoxenid spider (caught in pitfalls) (Araneae: Ammoxenidae) is a termite-predator (Dean 1988; Dippenar and Meyer 1980) (see Appendix 3). The fruit chafer beetle *Xiphoscelis shuckardi* (Scarabaeidae: Cetoniini) is another termitophilous species that was observed living in the frass of the termites (Holm & Marais 1992). The increased numbers of detritivores and other invertebrates (e.g. flea beetle (Coleoptera: Chrysomelidae: Alticinae) emerging from the frass and *heuweltjie* soils may also explain the higher greater abundance of spider predators trapped on *heuweltjies.*

Trophic cascades induced by heuweltjies

A noteworthy way in which *heuweltjies* influenced community composition and species turnover is through trophic cascades. Although herbivores were not separately analysed in this study, it has been well documented that phytophagous and fluid-feeding insects occur in greater numbers on fertilized plants as a direct response to enriched foliage (Lightfoot and Whitford, 1990; Mattson, 1980). What was observed in this study, however, was the response of predators, with greater numbers of spiders (Arachinda: Araneae) recorded on *heuweltjies (*25.8±7.0) than in the matrix (11.8±5.2) This process has been observed on the mounds of the termite *Odontotermes,* with vertebrate and invertebrate predators responding directly to increased abundance of on-mound prey items (Pringle *et al.* 2010). In this way, the increased foliar nutrient concentration and altered plant communities on *heuweltjies* (Midgley & Musil 1990) appear to induce a trophic cascade. It should be noted that this cascade is likely present in other predator guilds but it is more easily seen in spiders due to their high site fidelity, including the more mobile jumping spiders (Araneae: Salticidae) (Hoefler and Jakob 2006).

One invertebrate family that did not show any response to *heuweltjies* is the ants (Hymenoptera: Formicidae). The most abundant species recorded was *Anoplolepis custodiens* - an active, wide-foraging omnivore (Chong and Lee, 2009; Lach, 2012). It is therefore likely that the lack of response to *heuweltjies* is because its range of foraging is greater than that of the scale of spatial heterogeneity created by the *heuweltjies*.

The most numerous non-ant invertebrate recorded was the flea beetle (Coleoptera: Chrysomelidae: Alticinae). These beetles are clearly emerging preferentially from the soil of *heuweltjies*, as the large numbers were not reflected in the pitfall traps or in the matrix. This could be for a number of reasons. The larvae may be feeding preferentially on the enriched foliage above ground and then pupating in the soil (Lockett and Palmer 1997). Alternatively, the roots of the plants growing on the *heuweltjies* may also represent an enriched resource if the larvae are root-feeders (Simelane 2010). Increased *heuweltjie* clay content (Kunz et al., 2012; Midgley & Musil, 1990; Moore and Picker, 1990), enhanced organic matter input and the reduced compaction of *heuweltjie* soils due to continuous fossorial activity (Kunz *et al.* 2012) may also make the soils a more favourable environment for larval habitation or adult refuge (Del Bene and Conti 2009). *Heuweltjies* are therefore changing the local species composition and enhancing β-diversity through facilitation, a trophic cascade or some combination of both.

Homogenization of heuweltjie communities

Because the mean species turnover value between *heuweltjies* and the matrix is not greater than species turnover among matrix sites, the presence of *heuweltjies* does not increase species turnover compared to that among matrix sites. However, the relative decrease of turnover among *heuweltjies* (57.1 for the emergence and pitfalls combined) when compared to among matrix sites (65.7 for the emergence and pitfalls combined) means that *heuweltjie* invertebrate communities are more similar to one another than those communities in the matrix. This indicates that there is some aspect of *heuweltjies* that has a homogenising effect on these invertebrate communities. One likely explanation is a reduction in the variety of niches available to invertebrates, as inter-*heuweltjie* nutrient and organic matter enrichment was observed to be more uniform and consistent than across matrix sites. Hence, the biotic community is also more uniform on *heuweltjies.* This niche reduction has previously been observed on *heuweltjies* by Kunz *et al.* (2012), where on-mound homogenisation of the plant community was attributed to habitat simplification.

These homogenised invertebrate communities on *heuweltjies* are characterised by increased abundance of fewer dominant species. This hypothesis is supported by significantly lower J' evenness values on *heuweltjies* and higher diversity values in the matrix, all indicating dominance in the community by a few common species. The SIMPER analysis further supports this, with the species that contributed most to intra-*heuweltjie* similarity having a greater percentage contribution than those that contributed most to intra-matrix similarity. These species may be well adapted to exploit the distinct environmental niches on *heuweltjies,* with the enhanced productivity of the matrix allowing them to dominate numerically.

On the origin of *heuweltjies* by means of termite selection

The nutrient profile of the *heuweltjies* is more similar to the frass than to the matrix soils (Fig. 2), clearly showing that the presence of *M. viator* contributes to the *heuweltjie* enrichment. The foraging actions of the termite concentrate plant material at regularly spaced loci (on the *heuweltjies*), where it is consumed and expelled as frass. The termites are thus both concentrating nutrients and aiding in decomposition, in much the same way as *Macrotermes michaelensi* (Dangerfield *et al.* 1988). Francis *et al.* (2013) attributed the concentration of Ca (204 mmol.kg^{-1} on mound and 85 mmol.kg^{-1} off-mound) and Mg (239 mmol.kg^{-1} on-mound and 41 mmol.kg^{-1} off-mound) in the centre of termite-occupied *heuweltjies* to the foraging actions of *M. viator,* showing that this species too demonstrates this mechanism.

At the core of the *heuweltjie*-origin debate is not whether the actions of termites enrich the mounds but whether termites created the mounds or not. The elevated nutrient profile of heuweltjies cannot be attributed solely to frass input, as the plants on *heuweltjies* exhibit enhanced foliar nutrient content (Midgley & Musil 1990). Measuring the relative contributions of termites and plants to this enrichment is difficult, however, as very few previous studies have compared *heuweltjie* and matrix foliar content, and none have produced an elemental profile of *M. viator* frass. Instead, one can investigate whether bushclumps that concentrate nutrients in the matrix (the mechanism of *heuweltjie* formation proposed by Cramer *et al.* (2012)) could possibly enrich *heuweltjies* to the degree that is actually observed. When this is done, it is clear that termites elevate the soil nutrient content to a much higher degree than would be expected from the accumulation of resources by plants (see Table 6). While this may not appear supported by the on:off mound soil N ratio of *heuweltjies* in other studies, the termites at the Soebatsfontein site (Kunz *et al.* 2012) and the Worcester site of Midgley & Musil (1990) may have been packing their frass into subterranean galleries (Moore & Picker 1991), thereby concentrating the nutrients observed at the surface in this study below ground. This further illustrates that the degree of N enrichment seen in this study is due to the termite frass being present in the top layer of the soil.

The Ca enrichment seen in this study is much higher than could be attributed to bushclumps (Table 6). The on:off Ca ratio in the two *heuweltjie* studies at Worcester is very close, and greatly elevated relative to that observed in bushclumps. The on:off ratio for the Ca foliar concentration (1.26, 1.41 and 1.17) is much lower than the on:off ratio for the soil (13.13) (Midgley & Musil 1990). Additionally, termites have been shown elevate Ca concentrations – the on:off ratio in a study on *Macrotermes* mounds was 9.43 (Holdo 2004).

Table 6: Comparison of the ratios of bushclump soils:matrix soils and *heuweltjie* soils:matrix soils from this and other studies. ND means not determined in that study.

		On:off ratio	
Author	**Site type**	**N**	**Ca**
Jarvel & O'Connor	South-east African Savanna	1.7699	3.178469
Abanda et al. 2011	Semi-Arid South African Shrubland	2.5	ND
Escudero 2004	High Mountain Mediterranean shrubland	1.3	ND
Schlesinger et al 1996	Mojave - Coxcomb shrubland	2.25	0.98
	Sevilleta - Shrubland	2.93	0.9
	Jornuda - Shrubland	1.71	0.87
Midgely and Musil 1990	Worcester heuweltjie	1.37	13.13
Kunz *et al*. 2012	Soebatsfontein heuwltjie	2.2	ND
This study	Worcester heuweltjie	6.16	13.49

It has been shown in this study that termites and their frass greatly enrich the nutrient profile of the soils. Thus, when imposed on a uniform landscape they would, over time, create areas of local enrichment. This would facilitate denser plant growth and increased trapping of aeolian sediments (see McAuliffe *et al.* 2014). When the mound building activities of termites are also taken into account, it is highly plausible that termites facilitated the creation of these mounds. This is supported in various ways. Firstly by the range overlap of the *heuweltjies* and *M. viator* and the high level of occupancy by the termites (Lovegrove and Siegfried 1986; Moore and Picker 1991). Secondly, the overdispersion of the mounds is consistent with a biological agent, often attributed to termites (Laurie 2002; Picker *et al.* 2007). Thirdly, other species of termite have been shown to create mounds of similar sizes to *heuweltjies,* such as the lenticular mounds of *Odontotermes* (Darlington 1985) which subsequently act as nuclei for tree growth in a grassland matrix (Burtt 1942 and Troll 1936 in Darlington 1985). Hence, it is hypothesised that the *M. viator* facilitate the formation of bushclumps, and not the other way around

Ecosystem engineers

Microhodotermes viator are ecosystem engineers, through both direct impacts and their potential impacts as the likely founders of *heuweltjies*. By concentrating nutrients, altering the soil properties and producing frass mounds, these termites alter the plant and animal composition of the local landscape. The nutrients concentrated on *heuweltjies* mean that they not only contribute to spatial heterogeneity, but also to local productivity (Picker *et al.* 2007) and nutrient cycling. This impact is similar to other species of termite, which change local species composition (Griffioen & O'Connor 1990) contribute to habitat heterogeneity (Moe *et al.* 2009), thus acting as ecosystem engineers (Dangerfield *et al.* 1998).

Conclusions

Though much work has been done on *heuweltjies,* it is little understood how they impact animal diversity. This study has shown that the edaphic changes on *heuweltjies* that are reflected in the floral assemblage are also reflected in the invertebrate community. In this way, *heuweltjies* contribute to β-diversity and species turnover through a combination of facilitative and trophic processes. The nutrient-rich frass of *M. viator* is likely a strong driver of these processes, strengthening the case for a termite-origin of these earth mounds. Much like the mounds of many African termites, *heuweltjies* contribute spatial heterogeneity, and may be vital for ecosystem functioning and productivity.

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Appendices

Appendix 1: The mean height, diameter and density of heuweltjies measured at various sites in South Africa. Results are displayed as mean ± standard deviation or as a mean (smallest value – largest value), depending on the format of data in the source paper.

Site	Mean height (m)	Mean diameter (m)	*Heuweltjie* density (per km^2)
Cramer et al (2012)			
Clanwilliam dam (mean ± s.d)	0.86 ± 0.29	24.5 ± 4.08	340
Moore and Picker (1991)			
Clanwilliam dam (mean ± s.d)	1.42 ± 0.45	16.88 ± 4.83	360
McAuliffe et al (2014)			
Soebatsfontein (range)	1.46 (0.2-2.2)	27.8 (11-36)	450 (400-600)
Namaqua (range)	0.87 (0.4-1.45)	33.1 (24-42)	500 (400-600)
Inverdoorn (range)	0.44 (0.2-1.05)	16.2 (9-26)	440 (200-600)
Laingsberg (range)	0.5 (max.)	11 (8-15)	380 (300-500)

Appendix 2a: Abundance of morphospecies caught by sieving 100 L of frass on 10 *heuweltjies* at Malmesbury. # indicates family, not order. * indicates larval stage was found.

Order	Highest level of classification	Abundance
Coleoptera		
	Coleoptera*	7
	Tenebrionidae*	1
	Curculionoidea*	1
	Histeridae	1
	Scarabaeidae*	160
Diplopoda		
	Diplopoda	645
Diptera		
	Diptera*	13
	Asilidae*	1
Scolopendromorpha#		
	Scolopendromorpha	4
Isopoda		
	Isopoda	2

Appendix 2b: Abundance of morphospecies caught by sieving 100 L of frass on 10 *heuweltjies* at Vanrhynsdorp. # indicates family, not order. * indicates larval stage was found.

Order	Highest level of classification	Abundance
Coleoptera		
	Coleoptera*	7
	Tenebrionidae*	4
	Histeridae	5
	Scarabaeidae*	8
Diptera		
	Diptera*	4
Scolopendromorpha#		
	Scolopendromorpha	4
Isopoda		
	Isopoda	1
Thysanura		
	Lepismatidae	4

Appendix 2c: Abundance of morphospecies caught by sieving 100 L of frass on 10 *heuweltjies* at Worcester. # indicates family, not order. * indicates larval stage was found.

Order	Highest level of classification	Abundance
Coleoptera		
	Scarabaeidae*	23
	Histeridae	6
	Tenebrionidae*	2
Diptera		
	Diptera*	8
	Asilidae*	1
Scolopendromorpha#		
	Scolopendromorpha	3

Appendix 3: Morphospecies recorded at Worcester in this study, showing the highest classification possible. This includes individuals observed in the frass during random sieving, but not those caught during the one-off sieving survey at Worcester. # indicates class and not order. * indicates larval stage was caught in random sieving.

Order	Highest level of classification	No. species observed
Coleoptera		
	Coleoptera	7
	Staphylinidae	3
	Pselaphidae	1
	Scarabaidae	5
	Hopliini	2
	Ptinidae	1
	Carabidae	4
	Dynastinae*	1
	*Xiphoscelis shuckardi**	1
	Carabidae: Graphipterus	1
	Carabidae: Thermophilum	1
	Elateridae	3
	Histeridae	2
	Rhysodidae	1
	Coccinellidae	1
	Chrysomelidae	4
	Chrysomelidae: Alticinae	1
	Anthicidae	2
	Nitulidae	3
	Meloidae	2
	Throscidae	1
	Anobiidae	1
	Phalacridae	1
	Mordellidae	1
	Melyridae	1
	Tenebrionidae	2
	Tenebrionidae: *Psammodes striatus*	1
	Tenebrionidae: *Zophosis spp.*	1
	Dermestidae	1
	Buprestidae	1
	Curculionoidea	15
Pseudoscorpionida		
	Pseudoscorpionida	1
Hemiptera		
	Hemiptera	18
Diptera		
	Diptera	21
	Zaprionus	1
	Therevidae	1
	Tephritidae	1
	Asilidae	1
	Bombylidae	1
	Phoridae	1

Appendix 3 (cont.): Morphospecies recorded at Worcester in this study, showing the highest classification possible. This includes individuals observed in the frass during random sieving, but not those caught during the one-off sieving survey at Worcester. $^{\#}$ indicates class and not order.

Order	Highest level of classification	No. species observed
Hymenoptera		
	Chalcidoidae	8
	Bethylidae	1
	Pompiliidae	1
	Thynnidae	1
	Apoidae	1
	Apidae	1
	Chrysididae	1
	Mutillidae	2
	Megachilidae	1
	Thynnidae	2
	Anoplolepis custodiens	1
	Camponotus spp.	1
	Leptothorax spp.	3
	Tetramorium spp.	1
	Ocymyrmex spp.	1
	Messor spp.	1
	Pheidole spp.	1
Orthoptera		
	Gryllaceridiidae	1
	Gryllidae	1
	Acrididae	2
Neuroptera		
	Ascalaphidae	1
	Crysopidae	1
Scolopendromorpha$^{\#}$		
	Scolopendromorpha	2
Isopoda		
	Isopoda	1
Dermaptera		
	Dermaptera	2
Mollusca		
	Mollusca	1
Blattodea		
	Blattellidae	1
	Blattidae	1
Thysanura		
	Lepismatidae	1
Archaeognatha		
	Archaeognatha	1
Acarina		
	Acarina	16
Araneae		
	Araneae	36
	Ctenizidae	1
	Ammoxenidae	2
	Solifugidae	2