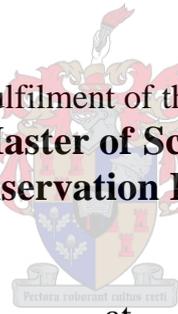


The importance of *heuweltjies* for arthropod biodiversity in the Succulent Karoo

by

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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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Summary

The Succulent Karoo biome of South Africa is home to unique patches of vegetation which are distinct from the surrounding homogenous matrix, locally known as *heuweltjies*. *Heuweltjies* are ubiquitous features of this landscape and support a variety of flora and fauna, however, whether and how they affect arthropod biodiversity in the landscape is poorly understood. Arthropods are vital for ecosystem functioning in resource limited environments. Therefore, understanding the importance of *heuweltjies* for arthropod biodiversity will allow us to better understand the role that *heuweltjies* play in conserving biodiversity and promoting landscape heterogeneity in this arid environment. The aims of this study were to determine whether *heuweltjies* promoted epigaeic (ground-dwelling) and foliage-dwelling arthropod abundance and diversity (measured as alpha- and beta-diversity) under drought conditions in the Prince Albert area, Western Cape, South Africa and how *heuweltjie* size, isolation and quality influenced this role.

Both epigaeic and foliage-dwelling arthropod species richness and abundance were greater on *heuweltjies* than the surrounding matrix. Additionally, both *heuweltjie* and matrix plots contained distinct arthropod communities even at a relatively small spatial scale, within sites (25 -50 m) and between sites (1 – 20 km). Epigaeic arthropod assemblage differences were driven by species turnover (replacement of species) between the matrix and *heuweltjie*, whereas foliage-dwelling arthropod communities were driven by turnover and the differences in species richness (nestedness) with higher species richness found on the *heuweltjies*. This suggests that the *heuweltjies* are promoting arthropod diversity locally, most likely through the provision of habitat heterogeneity and additional niches.

Both epigaeic and foliage-dwelling arthropods that were commonly associated with *heuweltjies*, responded to changes in *heuweltjie* size, isolation and quality. The best predictors of arthropod diversity on the *heuweltjies* were average distance to nearest *heuweltjies*, *heuweltjie* area, presence of termite frass, plant percentage cover and average plant height. This suggests that the presence of neighbouring *heuweltjies* and the size of patch are important landscape predictors, while having a living termite colony and good plant cover are important to retain local patch diversity.

The distinctive nature of *heuweltjies* within a homogenous landscape make them integral habitat features for arthropods, as they are for plants, as they provide suitable habitat conditions for oviposition and food as well as protection from predation and the harsh climatic conditions of the Succulent Karoo. In conclusion, *heuweltjies* are important for arthropod biodiversity in the Succulent Karoo during the ongoing drought gripping the region. Therefore, managing these areas in congruence with other land use practices such as livestock farming should be considered.

Additionally, considering the size, distance to neighbouring *heuweltjies* and vegetation cover may help in ensuring the conservation of arthropod communities of the Succulent Karoo.

Opsomming

Die Sukkulente Karoo-bloom van Suid-Afrika huisves unieke lappies plantegroei wat verskil van die omliggende homogene matriks, plaaslik bekend as *heuweltjies*. *Heuweltjies* is alomteenwoordige kenmerke van hierdie landskap en ondersteun 'n verskeidenheid flora en fauna, maar daar is 'n gebrek aan kennis oor hoe hulle die geledpotige biodiversiteit in die landskap beïnvloed. In omgewings met beperkte hulpbronne, is geledpotiges noodsaaklik vir ekosisteen funksionering. Kennis oor die belangrikheid van *heuweltjies* vir geledpotige biodiversiteit sal ons dus toelaat om die rol wat *heuweltjies* speel in die bewaring van biodiversiteit en die promosie van landskapsheterogeniteit in hierdie dorre omgewing beter te verstaan. Die doelwitte van hierdie studie was om vas te stel of *heuweltjies* epigaïese (grond-wonende) en blaar-wonende geledpotige hoeveelhede en diversiteit (gemeet as alfa- en beta-diversiteit) bevorder onder droogtetoestande in die Prins Albert-omgewing, Wes-Kaap, Suid-Afrika en hoe *heuweltjie*-grootte, isolasie en kwaliteit hierdie rol beïnvloed het.

Beide epigaïese en blaar-wonende geledpotiges specierikdom en hoeveelede was groter op *heuweltjies* as die omliggende matriks. *Heuweltjie*- en matriksplotte het ook afsonderlike gemeenskappe gehuisves, oor beide relatiewe klein (25 – 50 m) en groot (1 – 20 km) skale. Die verskille in epigaïese geledpotige gemeenskapsamestelling was aangedryf deur die omset van spesies (vervanging van spesies) tussen die matriks en *heuweltjies*. Die verskille in blaar-wonende geledpotige gemeenskapsamestelling was aangedryf deur die verskille in spesiesrykheid (nestigheid), met hoër spesiesrykdom op *heuweltjies*. Hierdie resultate dui daarop dat die *heuweltjies* plaaslik geledpotige-diversiteit bevorder, waarskynlik deur die voorsiening van habitat-heterogeniteit en bykomende nisse.

Beide epigaïese- en blaar-wonende geledpotiges wat baiekeer met *heuweltjies* geassosieer word was sensitief vir veranderinge in grootte, isolasie en kwaliteit van die *heuweltjie*. Die beste voorspellers van *heuweltjie*-geledpotigediversiteit was gemiddelde afstand na die naaste *heuweltjie*, *heuweltjie*-grootte, die teenwoordigheid van termiet frass, plantpersentasiebedekking en gemiddelde planthoogte. Hierdie dui daarop dat die teenwoordigheid van naburige *heuweltjies* en die grootte van die *heuweltjie* belangrike landskapsvoorspellers is, terwyl 'n lewende termietkolonie en goeie plantbedekking belangrik is om die plaaslike habitat-heterogeniteit te behou.

Die kenmerkende aard van *heuweltjies* binne 'n homogene landskap maak hulle integrale habitat-gelaatstrekke vir geledpotiges, net soos vir plante, aangesien hulle geskikte habitatsomstandighede bied vir oviposisie en voedsel, sowel as beskerming teen roofdiere en die strawwe klimaatstoestande van die Sukkulente Karoo. Ten slotte, *heuweltjies* is belangrik vir die geledpotige biodiversiteit van die Sukkulente Karoo tydens die voortslepende droogte wat die streek aangryp. Beter bestuur van

hierdie areas, met inagneming van die grootte, afstand tot naburige *heuweltjies* en plantegroei, kan dus help om bewaring van geledpotige gemeenskappe van die Sukkulente Karoo te verseker.

Dedication

This thesis is dedicated to

The greatest parents in the world.

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1. Chapter 1: General introduction and literature review

“If all insects on earth disappeared, within 50 years all life on earth would end.

If all human beings disappeared from the earth, within 50 years all forms of life would flourish” – Jonas Salk

1.1 The importance of habitat patches and diversity measurements

One of the quintessential aims of community and landscape ecology is to identify and understand patterns of diversity and composition at multiple spatial scales, ranging from a few meters to thousands of kilometres (Clark, 2010; Vasconcelos et al., 2010). Among the main factors that dictate these patterns is environmental heterogeneity (Stein et al., 2014). Environmental heterogeneity is ubiquitous in most natural systems and is vital in promoting biodiversity, ecosystem functioning and resilience (Tilman, 1982; Oliver et al., 2010; Dronova, 2017). Heterogeneous landscapes that are structurally complex offer a wider variety of habitats and greater access to resources, in the form of food and refuge, which should increase niche availability (Levin, 1974; Chesson, 2000). Thus allowing more species to coexist and persist during varying environmental conditions.

Landscapes can be defined as heterogeneous areas of land comprising of a mosaic of interacting ecosystems, habitat patches and/or landscape elements (Foreman and Godron, 1981, 1986). Habitat patches in particular, are small scale areas with distinct spatial properties that are used by species and have the ability to influence their communities, composition and structure (Levin and Paine, 1974). These patches can be found in a variety of systems, for example, caves (Simões et al., 2015); rock pools (Svennsson et al., 1999), tree canopies (Dean et al., 1999) and termite mounds (Holdo and McDowell, 2004). Therefore the identification of these potentially significant patches within a given landscape is important for understanding of the structure, function and dynamics of ecosystems.

Arid and semi-arid regions of the world are often perceived as homogenous landscapes with low diversity, when in fact they are highly dynamic environments (McNeely, 2003; Durant et al., 2012; IPCC, 2019). These areas often consist of heterogeneous landscapes coupled with high levels of functional diversity with many endemic species specially adapted to the harsh conditions (Cowling et al., 1998). A unique feature of the world’s drylands are their distinct patches of spatially patterned vegetation. The occurrences of natural earthen mounds are widespread throughout the world and have garnered much attention as a result of their enigmatic disposition. The peculiar nature surrounding non-anthropogenic earthen mounds and their various origins have attracted scientific attention such as the *campos de murudus* of Brazil (Silva et al., 2010), *hogwallow* and *mima- mounds* of North America (Arkly and Brown, 1954), *fairy circles* of Australia and Namibia (Getzin et al., 2016;

Juergens, 2013) and the *heuweltjies* of South Africa (Lovegrove and Siegfried, 1986). The presence of these patches in these nutrient poor landscapes are of particular importance due to their indirect ability to trap, modify and distribute nutrients (Seymour et al., 2014; McAuliffe et al., 2019) and ultimately alter plant and animal communities (Joseph et al., 2014; Liu et al., 2016).

Arthropod biodiversity in particular is an essential contributor to ecosystem services and functioning (Noriega et al., 2018; Vasconcellos et al., 2010). Especially in arid systems, where micro- and macroarthropod soil fauna assemblages are largely responsible for the spatial and temporal distribution of resources such as litter decomposition and nutrient cycling (Whitford, 1996; Janion-Scheepers et al., 2016). As a result, soil biota are equally as important as other biota in contributing to environmental heterogeneity. Therefore the interaction between arthropods and these patches is crucial for the heterogeneity in the landscape, but in order to correctly assess these interactions, the correct diversity measurements should be used.

The concept of biodiversity is multifaceted and can be applied to multiple scales which include, taxonomic (species), functional, genetic and phylogenetic components to name a few (Daly et al., 2018). Ecologists often use mathematical models commonly referred to as diversity indices to quantify biodiversity and compare it across spatial and temporal scales (Daly et al., 2018). Additionally, previous studies have focussed largely on quantifying local scale species richness (alpha-diversity), often overlooking the variation between community composition across multiple sites (Kim et al., 2018). Therefore, realistically measuring biodiversity should not only look at relative abundances of species but rather the difference between patterns of species richness (Leinster and Cobbold, 2012).

Whittaker (1960, 1972) was the first to propose the notion that species diversity should be partitioned into various spatial components. With this intention, scientists are fundamentally reliant on these components, alpha (α), beta (β) and gamma (γ) diversity, to adequately assess the condition of biodiversity in a given area at multiple spatial scales (Jost, 2007). Alpha-diversity refers to the diversity at a local scale, typically within an individual plot, site or habitat, whereas, gamma-diversity represents species diversity at a much larger scale, usually at a landscape, regional or global scale (Socolar et al., 2016). Beta-diversity provides a direct linkage between biodiversity at local and regional scales (Anderson et al., 2011) and can be broadly defined as the “variation or extent of change in species community composition” along a specific spatial, temporal or environmental gradient (Whittaker, 1960).

Initially there had been growing concern over the measurement of beta-diversity due to numerous studies developing different concepts and approaches (Anderson et al., 2011; Baselga and Orme, 2012; Legendre and De Cáceres, 2013). However, it was Baselga (2010) who brought forward the

concept of partitioning total beta-diversity (β_{total}) into two components of compositional dissimilarity: 1) turnover (β_{turnover}), which is the replacement of species between sites and 2) nestedness ($\beta_{\text{nestedness}}$), which refers to the loss or gain of species between sites (Figure 1.1). As a result, it has become the most commonly used approach towards effectively distinguishing patterns of spatial diversity (Soininen et al., 2018). Understanding these patterns in diversity remains a crucial task in the midst of extensive biodiversity loss.

Species extinctions are a natural process, however, the rate of global biodiversity loss has been increasing at an alarming rate because of anthropogenic activity (Dirzo et al., 2014). Constant human-induced change and its profound effect on the planet and its ecosystems has resulted in the present epoch being coined the “Anthropocene” (Lewis and Maslin, 2015). Large scale habitat loss caused by the continuous alteration and expansion of natural landscapes for urban and agricultural development, the introduction and spread of alien invasive species, pollution, overexploitation and the vagaries of climate change all pose major threats to global biodiversity (Wood et al., 2003; Pimm, 2008; Simberloff, 2013; Kehoe et al., 2017; Harvey et al., 2020). Ultimately, land use intensification and the creation of novel landscapes have led to capricious changes in species richness, community composition and diversity at multiple scales (Socolar et al., 2016). The world's drylands are complex and highly susceptible to a change in diversity and composition when faced with disturbances (Valone et al., 2002). These areas have undergone extensive transformation as a result of overgrazing, mining, poaching, and climate change (McNeely, 2003; Mucina et al., 2006; Arena et al., 2017). Although most of the world's drylands have distinct habitat patches within a homogenous matrix, the effect of habitat transformation may prove costly for the species that depend on these patches.

Habitat transformation includes changes into the size, shape and isolation of certain habitat patches (Fahrig, 2017). This was first proposed by MacArthur and Wilson (1963; 1967) in the form of Island biogeography theory which predicts that size, degree of isolation and quality of habitat patches are crucial in dictating species persistence. Immigrants and emigrants are more likely to encounter habitat patches that are larger, less isolated, and are of better environmental quality (Whittaker, 1960). Therefore, it is critical to understand to what extent does patch size, isolation and quality have on biodiversity in these regions especially in the midst of anthropogenic disturbances and climate change.

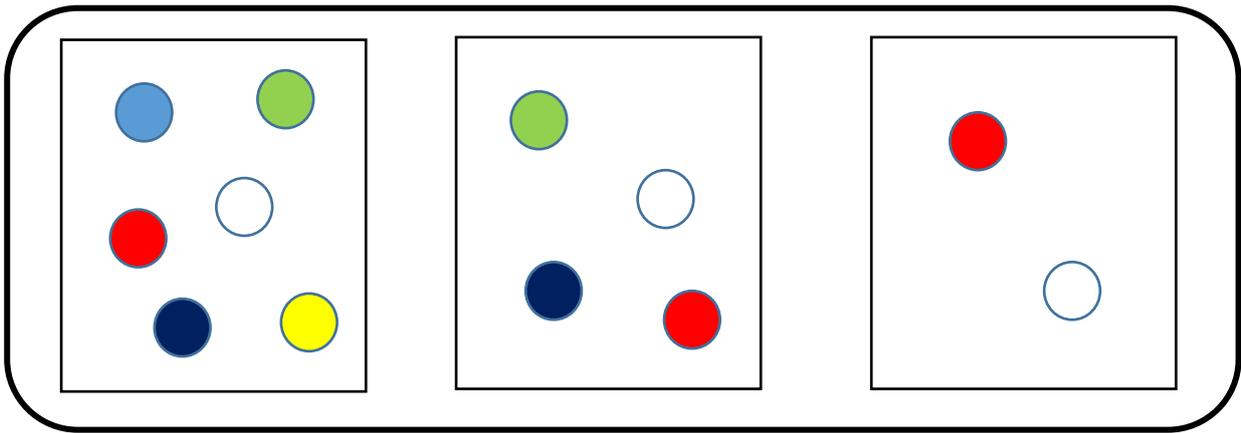
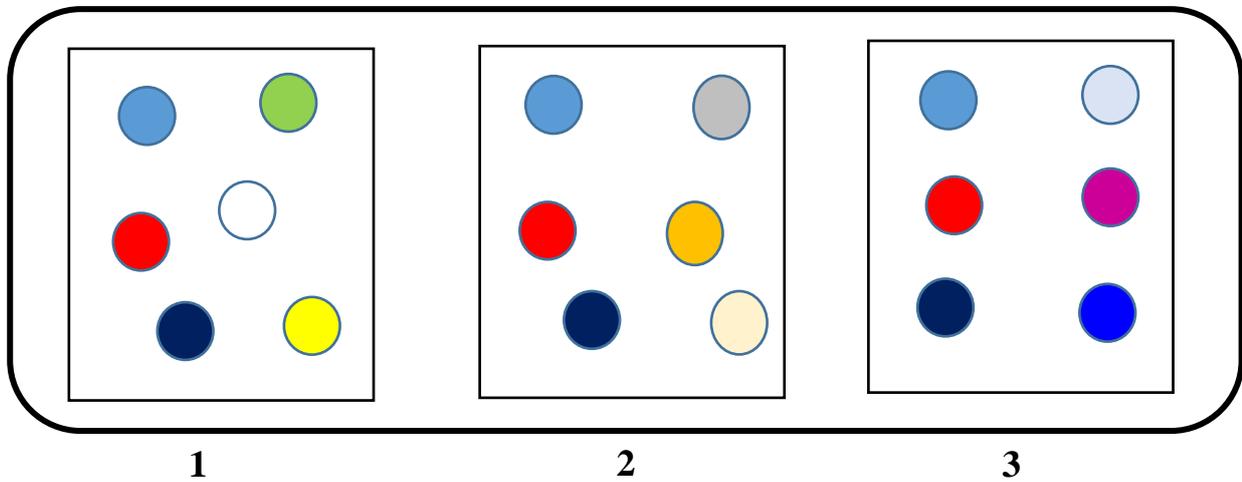
A - Nestedness**B – Turnover**

Figure 1.1: An example of nestedness, richness difference and turnover that has been adapted from Baselga et al (2010). Two separate localities (A-B), each with three sample sites (1-3) contain a variety of species. Each species is represented by a different colour. Sites A1-A3 have high nestedness as species present in A2 and A3 are poorer subsets of A1. The sites B1-B3 have high species turnover as they all have the same species richness (six), however, species present at one site are replaced by different species in a second site.

1.2 The Succulent Karoo biodiversity hotspot

1.2.1 Location and climate

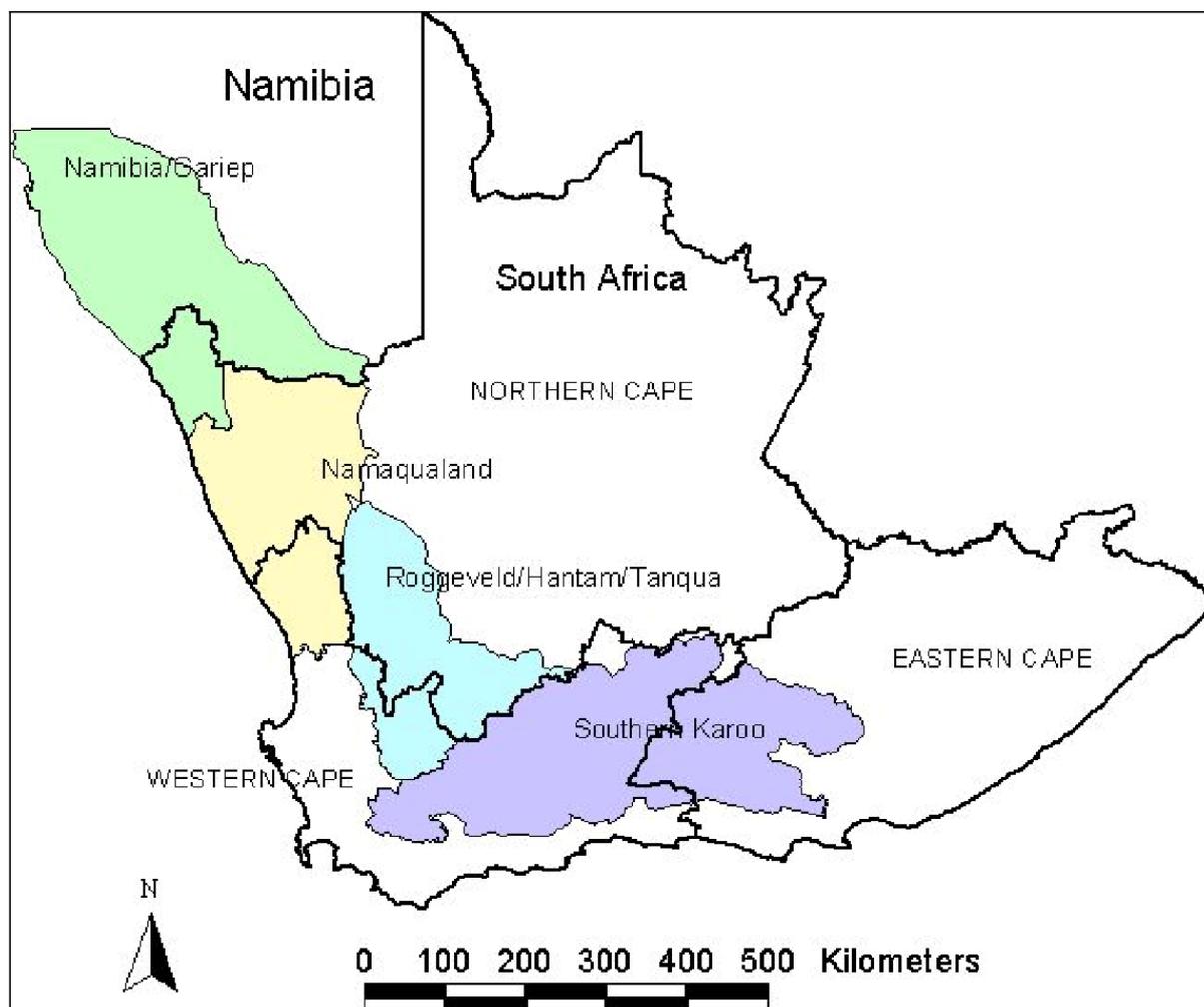


Figure 1.2: The Succulent Karoo biome of South Africa. Each colour shows each sub-region respectively (taken from Jonas, 2004). The Namaqualand and Namib sub-regions form part of the Namaqualand-Namib domain while the Tanqua and Southern Karoo form part of the Southern Karoo.

Biodiversity is not uniformly distributed across the Earth. The highest levels typically occur in the tropics, although some areas exhibit exceptional diversity and endemism despite being situated well outside these areas (Kerr, 2001). These high concentration areas of endemic plant and animal species are often referred to as ‘biodiversity hotspots’ and are threatened by anthropogenic activity (Myers et al., 2000). The hotspots make up 2.4% of the world's surface and are home to over 40% of all vascular plant species (Myers et al., 2000). The Succulent Karoo is regarded as one of the 35 biodiversity hotspots and holds significant importance as one of only two arid hotspots (Mittermeier et al., 2011; Noss et al., 2015).

The Succulent Karoo biome is located on the southern tip of Africa and found in between the Fynbos and Nama-Karoo biomes respectively (Figure 1.2). It stretches over 111 000 km² and occupies 5.35%

of South Africa's land surface, making it South Africa's fourth largest biome (Mucina et al., 2006). It spans from Lüderitz in southern Namibia towards the Cape Fold Mountains in the west. There are also patchy occurrences near the Baviaanskloof and Tsitsikamma mountains in the south (Myers et al., 2000; Mucina et al., 2006). The topography consists of hilly and broken veld upon flat undulating plains (Low and Rebelo, 1996). The elevation ranges from sea level up to 1500 m, but the majority of the area lies below 800 m (Mucina et al., 2006).

The climate of arid and semi-arid regions is characterized by extreme ranges in precipitation and temperature (Whitford, 2002). The Succulent Karoo is a semi-arid region with a relatively mild climate (Mucina et al., 2006). This biome is characterised by distinctive climatic conditions and can be split into two main domains, the Namaqualand-Namib region and Southern Karoo region (Jürgens et al., 1991) (Figure 1.1). Rainfall regimes in the Succulent Karoo remain fairly predictable with rare occurrences of prolonged droughts (Hoffman and Cowling, 1987; Desmet and Cowling, 1999).

The Namaqualand-Namib region has a strong maritime influence with unimodal winter rainfall. Here, dew and fog are significant contributors towards the mean annual rainfall, while the Southern Karoo displays either bimodal or all year round precipitation (Venter et al. 1986; Mucina et al., 2006). Arid environments are subjected to extreme variations in rainfall events and have a profound influence on vegetation structure and function, which is believed to have led to the floristic diversity of the Succulent Karoo (Desmet and Cowling, 1999). The mean annual precipitation (MAP) ranges from under 100 mm-300 mm, with a biome average of 170 mm (Mucina et al., 2006). Precipitation at higher elevations can, however, reach above 400 mm (Desmet, 2007). There are large fluctuations in excess of 20°C in daily and seasonal temperatures for most of the Karoo (Venter et al., 1986). The overall mean annual temperature is 16.8°C, however, there are some exceptions with lower averages around the elevated Roggeveld Karoo (Mucina et al., 2006).

1.2.2 Flora

The Succulent Karoo has 6 356 vascular plant species from 168 families, with 26% of them endemic and 14% near endemic species (Cowling and Hilton-Taylor, 1994; Driver et al., 2003; Mucina et al., 2006). The high levels of floral diversity are mainly driven by soil heterogeneity and climatic predictability (Cowling and Hilton-Taylor, 1994; Mucina et al., 2006). The majority of the Succulent Karoo is dominated by chamaephytes, particularly open dwarf succulents and shrubs largely belonging to the families, Aizoaceae, Asteraceae, Euphorbiaceae, Crassulaceae, Iridaceae, and Hyacinthaceae (Cowling and Hilton-Taylor, 1994). Perennial and geophytic growth forms contribute to the high floral diversity (Cowling et al., 1998). Annuals make up 8% of the flora and exhibit

colourful mass flowering displays in spring, while trees and grasses remain relatively uncommon (Cowling and Hilton-Taylor, 1994, Driver et al., 2003).

1.2.3 Arthropod fauna

Arthropods are by far the most diverse animal group on earth in terms of abundance and diversity (Samways, 2005). Of the 1.3 million species currently recorded on the planet, around 97% of them are invertebrates (Mora et al., 2011). This is no exception for the Succulent Karoo, with high levels of arthropod endemism (Janion-Scheepers et al., 2016). However, they remain under-sampled with limited knowledge as to their ecology and distributions (Vernon, 1999; Janion-Scheepers et al., 2016). Taxa such as Arachnida, Hymenoptera, and Blattodea (Isoptera), are dominant in the landscape (Vernon, 1999). The most commonly found Blattodea species is the harvester termite *Microhodotermes viator* (Latreille), while Hymenoptera is represented by a myriad of ant species (Formicidae). Arachnida is represented largely by families Ammoxinidae, Gnaphosidae, Scorpionidae and Salticidae (Dippenaar-Schoeman et al., 2005).

The inability to adequately identify species remains a challenge due to arthropods being a highly successful and speciose group (Vernon, 1999; Dippenaar-Schoeman et al., 2005; Janion-Scheepers et al., 2016). Other taxa have been extensively studied based on records from the Succulent Karoo, such as Diptera (bee flies, long-tongued flies), Hymenoptera (bees, masarid and vespid wasps), Coleoptera (monkey beetles) with their special relationship as a pollinator for host plants (Colville et al., 2002, Linder et al., 2010), and the recently discovered order, Mantophasmatodea (Picker et al., 2002).

Unfavourable conditions have excluded many taxa from the Succulent Karoo. Most lepidopteran species lack a readily available food resource during larval development (Whitehead et al., 1987). Apocrita, Chilopoda, Collembola, Dermaptera, Diptera, Gastropoda, Hemiptera, Mantodea, Mantophasmatodea, Orthoptera, Protura, Psocoptera, Thysanoptera and Thysanura have been recorded in the Succulent Karoo (Dean and Griffin, 1993; Seymour and Dean, 1999; Vernon, 1999, Picker et al., 2002), however, non-listed taxa will also occur here but have simply not been recorded due to a lack of biodiversity assessments, although records may be present in museum collection databases.

1.2.4 Land-use practices and threats

Recently, there has been an increase in the number of formally protected areas in the Succulent Karoo. However, around 8% of the Succulent Karoo is formally protected, which significantly under-represents its biodiversity (Hoffman et al., 2018). Therefore, a need to monitor the state of rangelands is crucial in providing early warning indicators of overuse (Winslow et al., 2011). By understanding

the factors that underpin biodiversity in the Succulent Karoo, key information can provide and improve conservation management decisions and strategies. Ultimately, without proper management, the threat of degradation and desertification may become a serious issue in the future. Rangeland expansion is inevitable, therefore, sustainable farming practices are needed to promote resilience against landscape degradation and is imperative in maintaining biodiversity in the face of an ever-expanding human population (Sala et al., 2000).

The biodiverse Succulent Karoo comprises a vast array of complex habitats ranging from coastal dunes, dwarf succulent shrublands and mountains (Mucina et al., 2006). This unique biodiversity hotspot is threatened by a host of land-use practices that threaten its biodiversity at local and regional scales. Currently the Succulent Karoo has undergone extensive habitat loss due to overgrazing from livestock farming, crop cultivation, mining expansion, invasive alien species, illegal collection of wild plants and animals as well as the effect of climate change (Mucina et al., 2006).

1.2.4.1 Livestock farming

The intensification of livestock farming in arid regions to meet the demand for meat and animal products has increased grazing pressure around the world (Thornton, 2010). Approximately 25% of the land's surface is used for agriculture or livestock farming with an estimated 73% regarded as degraded (Asner et al., 2004; Lund, 2007). Livestock grazing as a disturbance directly and indirectly alters ecosystem structure and function, with negative implications on plant, vertebrate and invertebrate communities (Seymour and Dean, 1999; Eccard et al., 2000; Neilly et al., 2016).

Although the impact on the landscape and its function is unknown, the adjustment towards livestock herding, coupled with the new farming practices brought on by the arrival of early European colonists, must have led to significant transformations to the Succulent Karoo. Arid system rangelands make up more than 35% of South Africa's land surface, yet is home to less than 2% of its population (Hill and Nel, 2018) and consists predominantly of livestock farming whereby natural vegetation is used as fodder (Allsopp, 1999; Arena et al., 2018). Currently, small scale and commercial livestock farming remain the dominant land use type throughout the Succulent Karoo, with many depending on it for an income (Jonas, 2004).

Rangelands can be defined as areas of primarily native vegetation that are grazed either by livestock or wild animals. Their low soil productivity and high climatic variability makes these areas highly susceptible to overgrazing (Schmiedel et al., 2016). Grazing has promoted changes in plant species abundance, structure, productivity and composition (Allsopp, 1999; Dean and Milton, 1995; Seymour et al., 2010). Perennial plant assemblage succession requires decades to recover from overgrazing

(Rahlao et al., 2008), thus creating a shift in plant composition from palatable perennial and dwarf leaf succulent plant species to unpalatable perennials (Todd and Hoffman, 1999).

Furthermore, grazing has an effect on both vertebrate and invertebrate assemblages. Rodent species in the Succulent Karoo were more abundant and speciose on ungrazed land compared to grazed areas (Eccard et al., 2000). Comparatively, heavy and moderate livestock grazing in an arid environment has led to a change in invertebrate species richness, abundance, and diversity, as well as a change in their assemblage composition (Seymour and Dean, 1999). Admittedly not all livestock grazing can be considered harmful to the environment if managed sustainably (Jakoby et al., 2015). It is rather the unsustainable livestock practices, which include overstocking, overgrazing, and trampling, that have significant effect on low-productivity arid environments such as the Succulent Karoo.

1.2.4.2 Crop farming

Early European settlers used alluvial terraces for the cultivation of crops, seeing as most of the Karoo's shallow soils do not receive sufficient rainfall (Dean and Milton, 1995), and the distance to an adequate water source remained unsuitable for crop farming (Ellis and Lambrecht, 1986). Intensive farming practices for crop farming have resulted in the removal of native vegetation and has become problematic because changes in vegetation in semi-arid regions such as the Succulent Karoo are notoriously slow processes (Dean and Milton, 1999). Similarly to overgrazing, perennial plant assemblages on previously cultivated land takes decades to re-establish even after being left fallow for over a decade (Dean and Milton, 1995; Allsopp, 1999). Consequently, due to unsustainable agricultural practices have left many areas deprived of biodiversity.

1.2.4.3 Climate change

Climate change is predicted to radically alter biome distribution in South Africa (Midgley et al., 2001). Since the pre-industrial era there has been a considerable rise in the observed mean land surface air temperature and atmospheric CO₂ (IPCC, 2019). Notably, temperatures across southern Africa have rapidly increased, at a rate twice as fast as the global average (Archer et al., 2018). Projected climate change scenarios for southern Africa indicate increases in aridity that may lead to high rainfall variability and prolonged dry periods (Archer et al., 2018). The Karoo is most likely to experience similar changes as the rest of southern Africa, with the onset of prolonged droughts caused by the variability in rainfall and increased surface temperatures, which could ultimately alter plant and animal communities (Mason et al. 1999).

Unfortunately it is clear that speciose regions are particularly vulnerable to climate change, thus putting the biodiverse Succulent Karoo under serious risk. Therefore, in order to understand its impact, greater knowledge is needed regarding species ecophysiology, distributions and phenology

(Bellard et al., 2012). Climate change presents a major threat to biodiversity especially when coupled with anthropogenic influences (e.g. habitat transformation) (Ehrlich and Pringle, 2008). These conditions may not only have disastrous effects on biodiversity but on the dominant land-use types as well which may affect crop yield, livestock production and human health (Archer et al., 2018).

South Africa is regarded as a semi-arid country with drought a typical feature of its climate (Rouault and Richard, 2003). The Karoo has been characterized by its limited sporadic rainfall events. There has been a steady decline in mean annual precipitation (MAP) since 2011 (Arena et al., 2018), subsequently much of the Succulent Karoo had been declared a disaster area due to the severe drought conditions which has gripped the region resulting in widespread losses for many farmers, their livestock and native biodiversity (Lephaila, 2020). Additionally, rainfall is the main driver of vegetation in the Succulent Karoo (Seymour et al., 2010) and although many plants exhibit tremendous drought resistance, these current drought conditions may have a significant effect on the biodiversity (Hoffman et al., 2009). Therefore, long term studies on how climate change may affect arid and semi-arid regions is crucial for land-use and water management decisions (Reynolds et al., 2007). What is equally important is the understanding of the response of biodiversity to these conditions to aid scientists and policy makers in developing strategies for climate-related conservation (Hannah et al., 2002).

1.3 Spatially patterned vegetation in arid systems

Vegetation in water-limited regions are commonly arranged in patches of high plant cover combined with low-cover matrix (Sala and Aguiar, 1996). These patches of spatially patterned vegetation are key features for community structure and dynamics (Maestre and Cortina, 2005) and are particularly important in nutrient poor environments as they provide spatial heterogeneity in the form of “fertile islands” that differ in terms of soil, plant and animal communities (Francis et al., 2013; Berg and Steinberger, 2008; Liu et al., 2016). For instance, shrub patches (Liu et al., 2016), vegetation tussocks (Carvalho et al., 2016), termite mounds (Seymour et al., 2014) and *heuweltjies* (Kunz et al., 2012) are examples of patches that promote heterogeneity in arid systems.

Dotted throughout the south-western region of South Africa are patches of over dispersed earthen mounds locally known as *heuweltjies* (Afrikaans for ‘little hills’; pronounced “heu-vil-keys”). *Heuweltjies* have been comprehensively studied over the past century, with much of the literature focusing on determining their age and origin (Lovegrove and Siegfried, 1989; Midgley, 2002; Cramer et al. 2012), soil nutrients and biogeochemical activity (Booi, 2011; Francis and Poch, 2019), plant composition (Midgley and Musil, 1990; Rahlao et al., 2007), plant response to grazing (Kunz et al.

2012), faunal activity (Louw et al., 2017). However, limited studies have dealt with the importance of *heuweltjies* for arthropod biodiversity (Cornell, 2014; Arena et al., 2020).

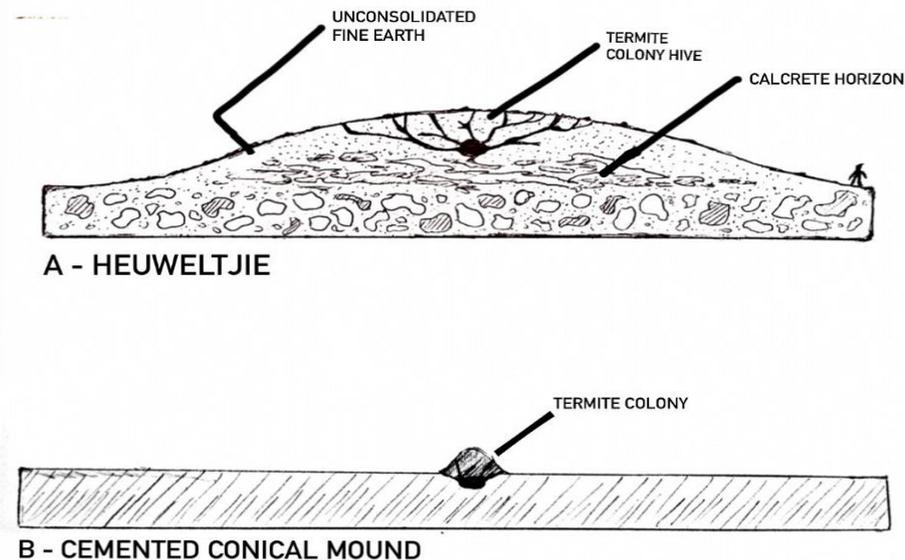


Figure 1.3: Difference between *heuweltjies* and *Macrotermes* termite mounds (Adapted from McAuliffe et al. 2019).

The origins and formations of these mounds are difficult to interpret due to a wide range of complex biotic and abiotic processes that produce similar mound patterns in different environments (Cramer and Barger, 2014). Hence, the various theories behind the origin of *heuweltjie* formations have remained a rather contentious topic despite being extensively studied. These theories can be categorized into two main schools of thought concerning “*heuweltjie*-genesis”; which have either been hypothesized to be biotic or abiotic (Lovegrove and Siegfried, 1989; Lovegrove, 1991; Moore and Picker, 1991; Midgley et al., 2002; Cramer et al., 2012; McAuliffe et al., 2014). The exact age of *heuweltjies* has also been debated, with estimates dating back around 4 500 to 30 000 years (Moore and Picker, 1991; Midgley et al., 2002; Potts et al., 2009). These ancient ubiquitous mounds are typically occupied by the southern harvester termite (*Microhodtermes viator*) which has led to the commonly accepted theory that the origin of the mound is termite related (Cox, 1987).

Although *heuweltjies* are often mistaken as termite mounds, they do share some commonalities and differences. Termite mounds are found throughout the world and are created by various species from the *Macrotermes* genus (subfamily: *Macrotermitinae*). The most noticeable difference between termite mounds and *heuweltjies* are the cemented above-ground conical structures produced by most *Macrotermes* termite species compared to the fine-earthen materials associated with *heuweltjies* (McAuliffe et al., 2018) (Figure 1.3). However, they are both important contributors to habitat

heterogeneity (Desmet, 2007; Okullo and Moe, 2012). Soils surrounding termite mounds are known to have increased mineral concentrations, pH, and moisture content (Seymour et al., 2014) which support distinct vegetation and animal communities (Holdo and McDowell, 2004), similar to that of *heuweltjies*.

1.3.1 Spatial patterns and distributions of *heuweltjies*

The vast majority of *heuweltjies* are found within the Succulent Karoo biome with patchy occurrences in the wetter parts of the Fynbos biome, particularly the Renosterveld (Lovegrove and Siegfried, 1986; Desmet, 2007; Picker et al., 2007) (Figure 1.4). These long standing features of the Succulent Karoo typically follow either a circular or lenticular shape and range from < 10 m to 30 m in diameter and in height from < 1 m - 2 m (McAuliffe et al., 2018). *Heuweltjies* occupy around 14 – 25% of the Succulent Karoo and are predominantly restricted to lower elevations near the west coast lowlands, inland flats and mountainous valleys (Lovegrove and Siegfried, 1986). *Heuweltjie* density depends on the geographical location, which ranges from 1.4 - 4 ha⁻¹ (Cramer and Midgley, 2015). *Heuweltjies* are distributed across a wide variety of vegetation types, rainfall, soil, elevation, geological as well as latitude and longitudinal gradients (Lovegrove and Siegfried, 1989; Picker et

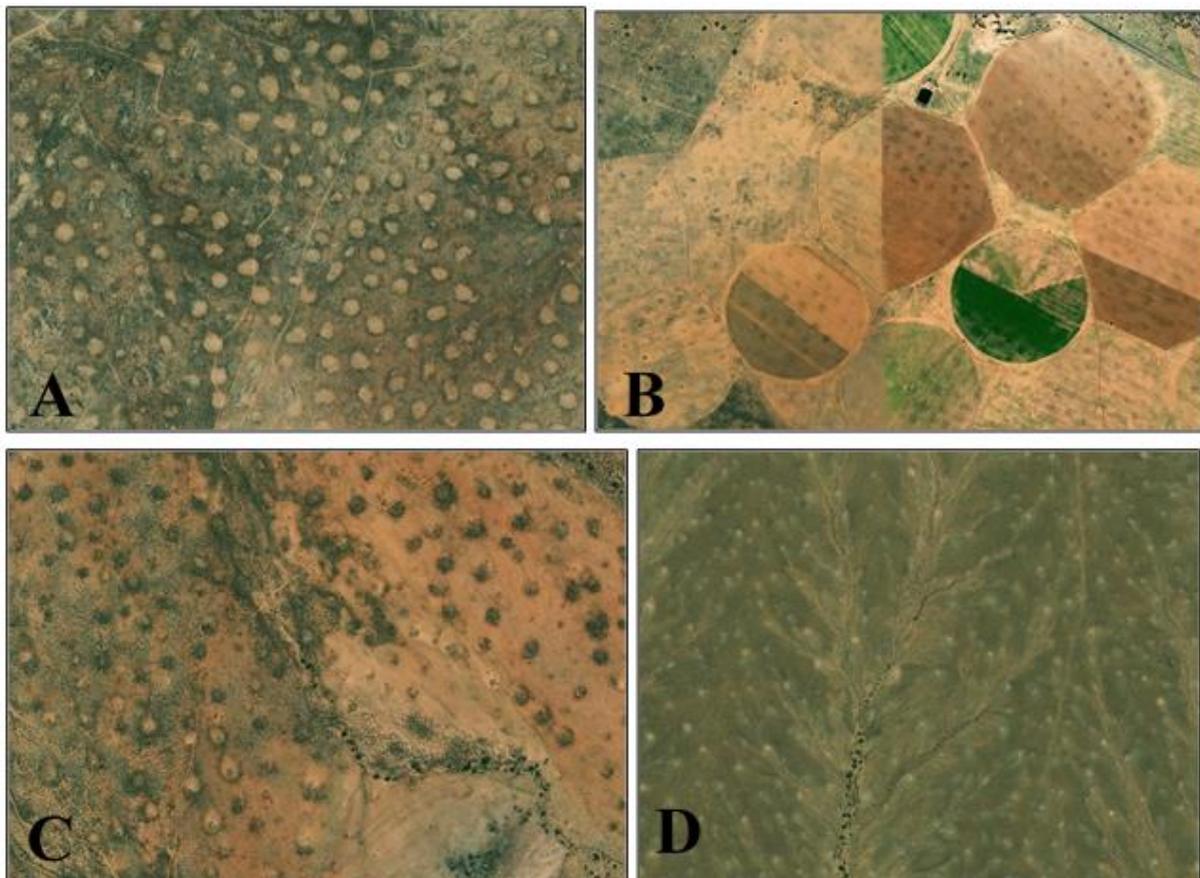


Figure 1.4: Variability within *heuweltjie* size, shape and density at four different locations in the Succulent Karoo. A = Garies (30°33'28"S 17°59'22"E), B = Lamberts Bay (32°04'60"S 18°18'00"), C = Touws River (33°44'12"S 21°10'55"E), D = Prince Albert (33°13'31"S 22°01'48"E).

al., 2007; McAuliffe et al., 2018), with their density being positively correlated with rainfall and high soil fertility gradients (Picker et al., 2007).

1.3.2 *Heuweltjie* soils and vegetation

Soils provide substrate for plant growth, facilitate in water and mineral retention, buffer against erosion and pollution and even allow a window into the past (Wurst et al., 2012; Retallack, 1998). Soils in arid areas support complex biota, which include bacteria, fungi, protozoans, nematodes, and arthropods (Wallwork, 1982). The soils of *heuweltjies* differ completely in composition to that of the ‘off-*heuweltjie*’ or matrix soil. They are easily identifiable by their distinct elevation and unconsolidated fine earthen material (McAuliffe et al., 2014). There are reported elevated levels in carbon, nitrogen, and phosphorus in comparison to the surrounding soils (Booi, 2011). Additionally, *heuweltjie* soils exhibited higher pH, electrical conductivity, silt content, and could retain more water, concluding that *heuweltjies* are ‘hotspots’ for nutrient and biogeochemical activity (Booi, 2011; Kunz et al., 2012). A cemented pedogenic calcium carbonate (calcrete) layer is often found underneath *heuweltjies* (Figure 1.3). Foraging behavior from termites allows excess mineral concentrations of Ca and Mg to leach down into the soil to form these calcrete hardpans (Potts et al., 2009).

The differences in soil structure and composition on *heuweltjies* allow the facilitation of different plant species composition and cover compared to the surrounding matrix (Rahlao et al., 2008; Booi, 2011). *Heuweltjie* vegetation is often dominated by annuals (Esler and Cowling, 1995), evergreen shrubs (Rahlao et al., 2008) and deciduous plants (Knight et al., 1989), however, this often differs depending on geographical location and disturbance regimes (Esler and Cowling, 1995).

1.4 Motivation behind the study

There is an estimated 5 - 9 million species on earth, all of which contribute towards functioning ecosystems in some way (Dirzo et al., 2014). Invertebrates are by far the most diverse animal group on Earth: Of the 1.3 million species currently described, around 97% of them are invertebrates (Mora et al., 2011). However, the arthropod diversity in the Succulent Karoo is poorly understood let alone its response to unique habitat patches such as *heuweltjies*. The majority of research surrounding the relationship between *heuweltjies* and arthropods has been limited to termites and ants (McAuliffe et al., 2018; Arena et al., 2020). This is a result of the unique association of the termite, *M. viator* with *heuweltjies*, and, ants are investigated given that they are good indicators of ecosystem health due to their ability to respond to the environment at small spatial scales (Andersen and Majer, 2004). Therefore conducting a multi-taxon approach with different diversity measures is needed to adequately assess the arthropod responses to *heuweltjies* at various scales especially in the midst of disturbances such as grazing and drought.

1.5 Thesis structure, objectives and research aims

This thesis consists of four chapters, chapters 2 and 3 are research chapters in which the findings of the research are presented. The results, discussion and general conclusions and recommendations are included in chapter 4. The main objective of this study was to ascertain the importance of *heuweltjies* for arthropod diversity in the rainshadow valley region of the Succulent Karoo. The arthropods associated on and off the *heuweltjies* were investigated.

Chapter 2 – Community responses of ground and foliage dwelling arthropods on and off of *heuweltjies* in the Succulent Karoo

Chapter 2 investigates the responses of epigaeic (ground dwelling) and foliage arthropod assemblages on and off of *heuweltjies* within three different land use types. The following research questions and objectives are addressed:

- Does arthropod species richness, abundance and community composition differ between biotopes (*heuweltjie* and matrix) and across sampling localities (Argentina, Tierberg LTER and Wolwekraal)?
- Are there differences between species richness and abundance between epigaeic and foilage arthropods associated with specific *heuweltjies* and matrix plots?
- Are there differences in beta-diversity (total beta-diversity, turnover and nestedness) within and between each biotope and sampling sites?

Chapter 3 – Assessing the influence of *heuweltjie* quality, size and isolation on arthropod biodiversity in the semi-arid Succulent Karoo.

Chapter three addresses the island biogeography and metapopulation theory to assess whether *heuweltjies* conform to it. The overall aim of this study was to investigate which patch and environmental variables might correlate with arthropod biodiversity in the Succulent Karoo. The following research questions were addressed:

- To identify and determine which environmental variables are correlated to observed arthropod patterns on and off *heuweltjies*.
- Determine how arthropod communities vary in relation to patch (*heuweltjie*) size, isolation (distance to nearest neighbor) and quality (plant percentage cover).
- Identify which indicator species occur on *heuweltjies* and how patch size, isolation and quality influence their species richness, abundance and composition.

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2. Chapter 2: Arthropod community responses to *heuweltjies* in the Succulent Karoo

Abstract

A notable feature of most dryland ecosystems is the patchy nature of the vegetation. *Heuweltjies* are naturally developed earthen mounds found throughout the Succulent Karoo. These mounds are significant contributors towards heterogeneity in the landscape and support distinct plant and animal communities. Arthropods in arid environments are responsible for key ecological functions, e.g., pollination and nutrient cycling. However, few studies have focused on the role that *heuweltjies* play in maintaining arthropod assemblages. This study investigates how arthropod abundance, species richness, beta-diversity and composition respond to *heuweltjies* at multiple spatial scales during drought conditions. Two sampling techniques (pitfall and vacuum sampling) were used to collect epigaeic and foliage dwelling arthropods between two biotope types, *heuweltjies* and matrix (natural vegetation present between the *heuweltjies*), at three different sites in the Southern Karoo during drought conditions. *Heuweltjies* had greater epigaeic and foliage alpha-diversity and abundance than the matrix. Additionally, epigaeic and foliage arthropod community composition were dissimilar at both the biotope and site level. At the biotope level, *heuweltjie* and matrix plots both showed high levels of beta-diversity, although epigaeic arthropods were mainly driven by species turnover whereas the foliage arthropods were driven by differences in species richness (i.e., by nestedness) and species turnover. At site level, high levels of beta-diversity across the three sites were driven by species turnover. This reinforces the hypothesis that *heuweltjies* are vital for a variety of organisms, including arthropods, particularly during adverse conditions created by drought with associated high plant mortality and lower foliage arthropod abundances. My results suggest that *heuweltjies* likely promote arthropod diversity and heterogeneity in the landscape. These patches and their distinct plant communities play a vital role as a refuge for many arthropod species.

2.1 Introduction

Environmental heterogeneity is crucial in dictating the processes that underpin biodiversity, community dynamics and ecosystem functioning at multiple spatial scales (Tilman, 1982; Stewart et al., 2000). MacArthur and MacArthur (1961) were the first to propose the “habitat heterogeneity hypothesis” (HHH) to assess the relationship between habitat heterogeneity and species diversity, suggesting that more heterogeneous habitats can support a wider variety of species through niche partitioning and greater resource availability. The HHH has been traditionally applied to local and regional scales (Field et al., 2009), however, multiple studies have observed spatial and temporal changes when assessing the relationship between habitat heterogeneity and diversity (Tews et al., 2004; González-Megías et al., 2011; MacFadyen et al., 2016). Beta-diversity and its components may be responsible for explaining these spatial changes between habitat heterogeneity and species diversity (Veech and Crist, 2007; Astorga et al., 2014; Soininen et al., 2018).

Beta-diversity is a useful measure for assessing the value of certain patches within a landscape by providing insight into which communities use them. Ever since the concept was first introduced by Whittaker (1960), there has been a vast array of definitions and approaches to analyse beta-diversity (Barton et al., 2013), although it can be simply defined as the variation in species composition (compositional dissimilarity) across sites (Anderson et al., 2011). Currently the most used approach divides beta-diversity into two components, turnover and species richness differences (nestedness), whereby the turnover refers to the replacement of species between sites, while the latter refers to the loss or gain of species between sites (Baselga, 2010). Furthermore, beta-diversity links local (alpha-) and regional (gamma-) diversity and can shed light on the spatial arrangement of communities, ecological interactions, habitat heterogeneity and productivity patterns (McKnight et al., 2007; Astorga et al., 2014; Soininen et al., 2018) in which can aid conservation management and spatial planning of protected areas.

Semi-arid and arid regions of the world are often perceived as areas with poor biodiversity because of their seemingly homogenous nature, low vegetation cover and extreme temperature and rainfall variability (McNeely, 2003). However, they represent highly dynamic environments with many specialized and endemic species (Durant et al., 2012). Often referred to as drylands, these regions cover approximately 41% of the earth’s surface (Feng et al., 2013). A typical feature of these environments are spatial patterns consisting of patches of vegetation surrounded by either nutrient poor soils or a homogenous vegetated matrix (Aguilar and Sala, 1999; Liu et al., 2016). These patches contribute substantially towards heterogeneity in the landscape (Levin and Paine, 1974) and are often created and maintained by “ecosystem engineers” - species that are readily able to modify the

availability and distribution of resources in the landscape (Jones et al., 1994), ultimately leading to the creation of patches that act as “fertile islands” or “hotspots” for a myriad of species (Berg and Steinberger, 2008; Jouquet et al., 2011), for example by concentrating nutrients into these patches. Plants and soil macroinvertebrates are prime examples of ecosystem engineers that can alter their surroundings, which in turn, have significant effects on soil processes, plant and animal communities and ecological functioning (Facelli and Brock, 2000; Joseph et al., 2011; Liu et al., 2016).

Along the south-western part of South Africa lies the semi-arid Succulent Karoo, one of only two arid biodiversity hotspots worldwide (Noss et al., 2015). A notable feature of the Succulent Karoo is the perplexing, near circular earthen mounds scattered throughout the biome (Lovegrove and Siegfried, 1986). These mounds, locally known as *heuweltjies* (*here-vil-keys*), reach up to 30 m in diameter and 2 m in height (McAuliffe et al., 2018). *Heuweltjies* occupy around 14 – 25% of the biome and are generally found at lower elevations and along gentle slopes (Lovegrove and Siegfried, 1989). As a result, their ubiquitous nature and specialized habitat conditions have interested many scientists. These unique features are significant contributors towards heterogeneity in the landscape because they differ in soil properties and vegetation structure from the surrounding matrix (Booi, 2011; Esler and Cowling, 1995). The enriched soils of *heuweltjies* support distinct plant assemblages compared to the off-mound plains or intervening matrix (Kunz et al., 2012; Rahlao et al., 2008), with the vegetation occurring on *heuweltjies* depending on geographical location, climatic condition and disturbance regime, which can either be denser or sparser than the surrounding matrix (Esler and Cowling, 1995; Kunz et al., 2012; Schmeidal et al., 2016). Generally, *heuweltjies* are considered areas of intense disturbance caused by livestock foraging of palatable plant species and burrowing activities of rodents and aardvarks (Armstrong and Siegfried, 1990; Esler and Cowling, 1995; Milton et al., 1992; Louw et al., 2017). Additionally, these mounds are often associated with southern harvester termite (*Microhodotermes viator*), which has led to extensive research on the termites role as ecosystem engineers (McAuliffe et al., 2019). Arthropods in the Succulent Karoo are especially important as they provide vital ecosystem services, such as pollination and nutrient cycling (Vernon, 1999, Colville et al., 2002; Mayer, 2006). Previous studies have found a greater diversity of spiders (Henschel and Lubin, 2018) and ants (Arena et al., 2020) on *heuweltjies*, however, their effects on other arthropod taxa are unknown. Therefore, a multi-taxon approach may provide a better indication of the surrounding underlying ecological mechanisms that *heuweltjies* have on the environment.

There has been ongoing debate around the impact climate and land use practices (e.g. livestock farming) have on the vegetation dynamics in the Succulent Karoo (Hoffman et al., 2018). Historical overgrazing from livestock farming coupled with high susceptibility to extreme weather events such as droughts associated with high rainfall variability has led to much uncertainty behind the root causes

of dryland degradation (Seymour et al., 2010; Hoffman et al. 2018). Nonetheless, future projections state that the Succulent Karoo biome could contract owing to increases in aridity (Engelbrecht and Engelbrecht, 2016). Although the Succulent Karoo is known for its slow plant succession and cyclic wet and dry periods, the current drought (2011 - present) that is gripping the region has visibly impacted species presence and activity in the short-term, however the region is adapted to these cyclical events and the ecosystem is expected to recover (Vetter, 2009).

This study investigates the importance of *heuweltjies* for arthropod biodiversity in the semi-arid Succulent Karoo. I assess epigaeic and foliage dwelling arthropod abundance, community composition, alpha-diversity (species richness) and beta-diversity within and between *heuweltjies* and the inter-*heuweltjie* vegetation (matrix), as well as across three sites. I hypothesize that they will support greater epigaeic arthropod alpha-diversity and abundances coupled with differentiating communities since some ground dwelling arthropods in arid regions prefer bare ground (Dean and Griffin, 1993). *Heuweltjies* are considered areas of intense disturbance, therefore, I hypothesize that greater plant percentage cover, whether it be associated with either the homogenous matrix or *heuweltjie*, would be more suitable for the foliage dwelling arthropods. Additionally, I hypothesize that there will be changes in arthropod beta-diversity within and between the habitat patches as well as beta-diversity across the different sites. Changes in arthropod communities may highlight the importance of these habitat patches. However, the severe drought and high plant mortality in the region may significantly impact these predictions owing to the current adverse conditions creating fewer suitable niches for arthropod communities to occupy. Therefore, understanding the effects that these patches have on arthropods may shed light on the dynamics of this system providing baseline data from the midst of a severe drought.

2.2 Methods

2.2.1 Study area

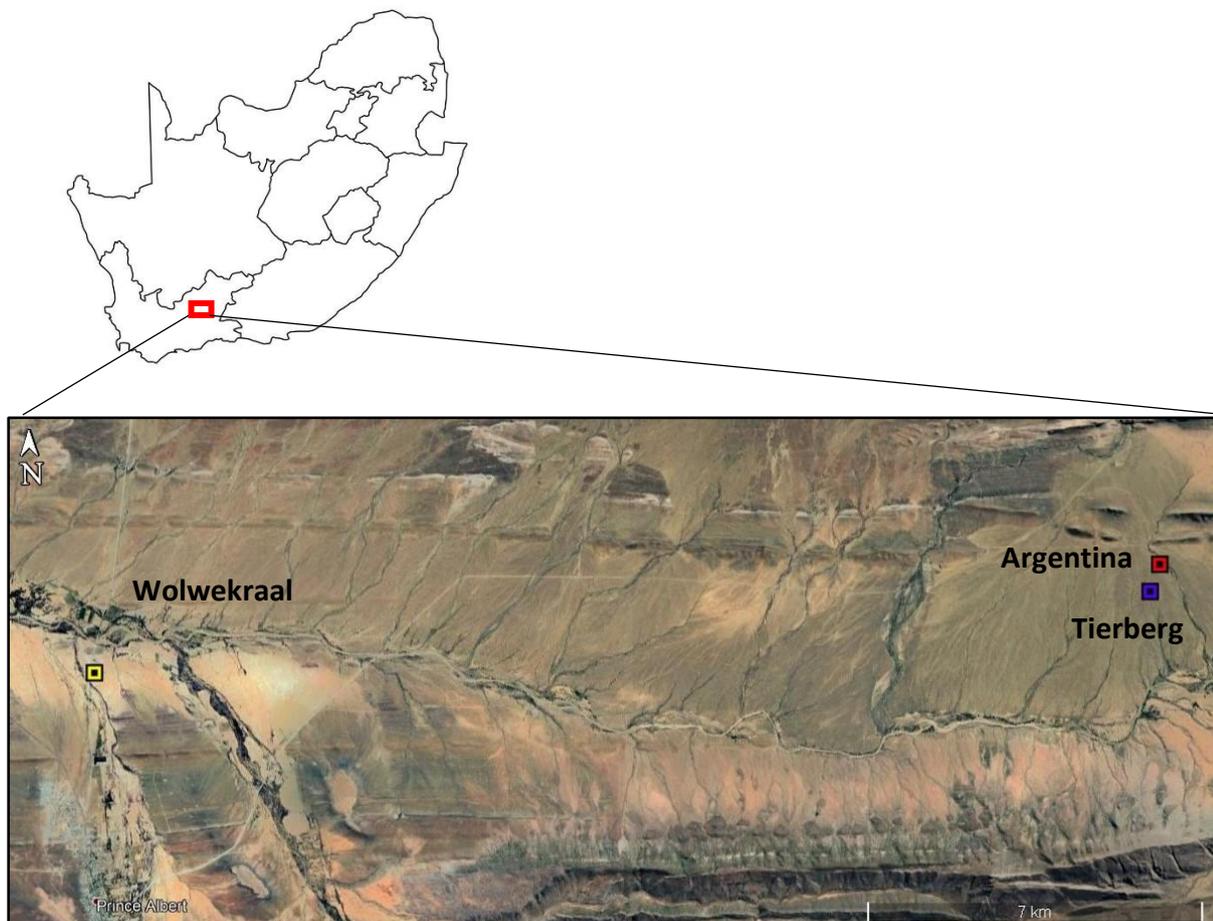


Figure 2.1: Sample sites are located around Prince Albert, Western Cape, South Africa ($33^{\circ}13'31''\text{S}$; $22^{\circ}01'48''\text{E}$). Yellow = Wolwekraal Nature Reserve, Blue = Tierberg LTER, Red = Argentina Wildlife Farm (Google Earth).

The study area is situated within the surrounds of the small farming town of Prince Albert in the southern Karoo ($33^{\circ}13'31''\text{S}$; $22^{\circ}01'48''\text{E}$, Figure 2.1). Prince Albert lies at the foot of the Swartberg Mountain range along the interface between the Succulent and Nama Karoo biomes. A great part of the area consists of livestock (usually Dorper and Merino sheep) farming. The natural vegetation in the area forms part of the rainshadow valley Karoo region and is populated with low cover leaf succulent mesembs and small-leaved shrubs (Milton et al., 1992). The landscape is relatively flat with stony ridges. Annual rainfall is low, but can occur all year round (165 mm, CV 38%), with peaks in autumn and spring (Mucina et al. 2006).

Sampling was conducted on three sites, Tierberg Long Term Ecological Research (LTER) station, Wolwekraal Nature Reserve and Argentina wildlife farm (Figure 2.2). Argentina is currently a 12 000 ha game and livestock farm. Argentina was grazed by goats, sheep and ostriches between 1913 and

1980, which led to overgrazing. Since then, it has been moderately grazed by cattle, sheep and various game species such as gemsbok, steenbok, ostriches and giraffe. Tierberg LTER, which has excluded livestock grazing since 1987, is an enclosed 100 ha area within Argentina. Tierberg LTER was established to understand the long-term patterns and processes governing Karoo ecosystem structure and function to address the issues surrounding overgrazing and poor land management (Arena et al., 2018). Wolwekraal Nature Reserve has been registered as a CapeNature protected area since 2013. The Dorpsrivier runs through the 123 ha reserve, comprised of natural Karoo shrubland. The site has excluded livestock grazing since the 1970s and is the only formally protected area of Prince Albert Succulent Karoo vegetation type. However, it is threatened by the development of housing, illegal firewood collection and effluent seepage from the neighbouring waste water treatment plant (Arena et al., 2018).

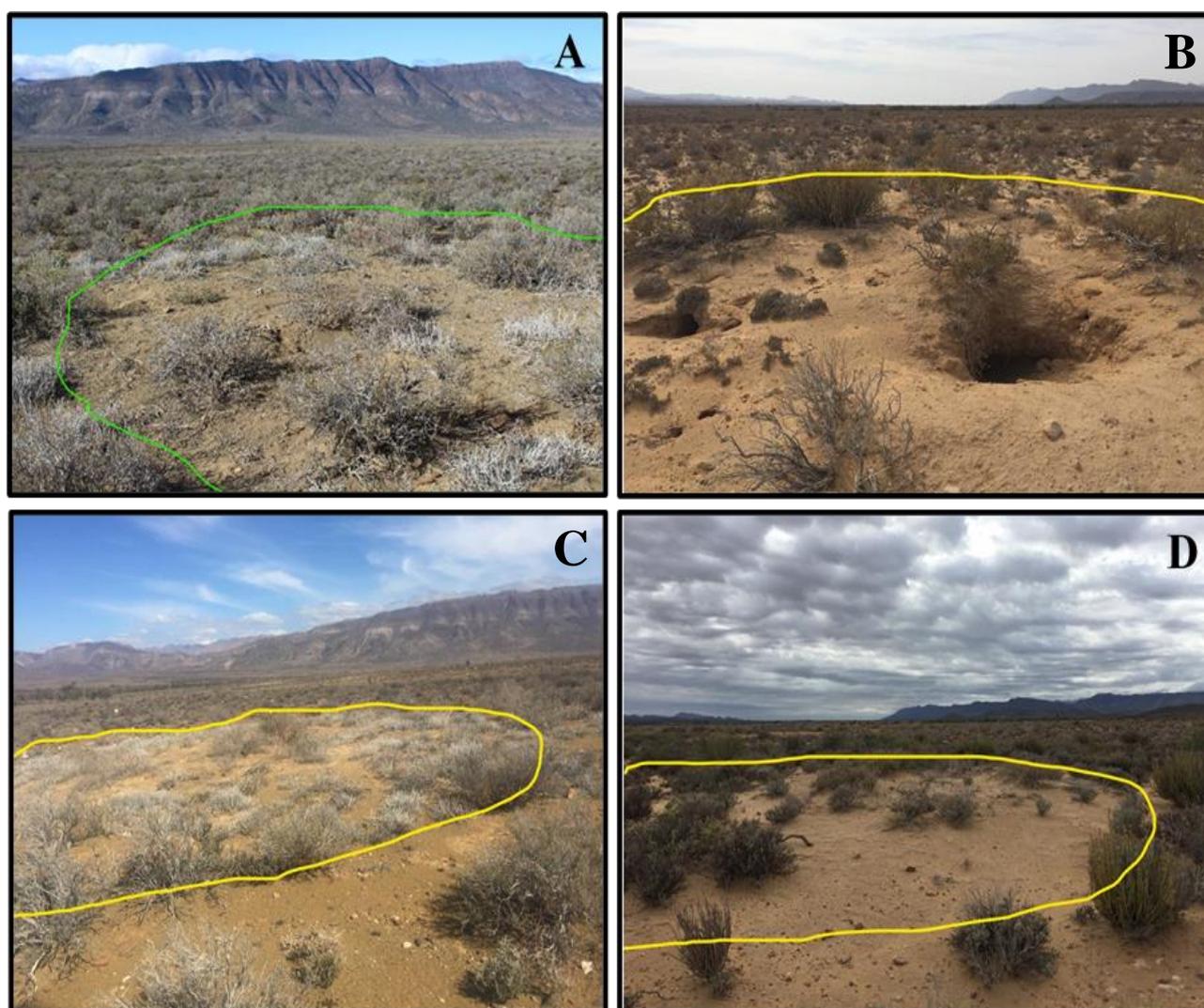


Figure 2.2: The difference between biotope types at different sampling localities. A-C) A typical heuweltjie and adjacent matrix (inter-heuweltjie vegetation) at Tierberg LTER (S33° 10.197', E22° 16.094') and Argentina wildlife farm (S33° 09.889', E22° 16.232'). D) A typical heuweltjie and adjacent matrix at Wolwekraal nature reserve (S33° 10.915', E22° 01.829'). The green and yellow lines separates the heuweltjie and the matrix.

The soil in the area is a relatively sandy loam and weakly structured derived from Ecca shales and Dwyka tillites (Ellis and Lambrecht, 1986, Milton and Dean, 1992). *Heuweltjies* are an important element of the Prince Albert Succulent Karoo vegetation type with a density of approximately 2 per hectare (Dean and Milton, 1999; Mucina et al., 2006). Vegetation cover is variable owing to different grazing pressure by livestock, ostriches as well as other game species in different areas (Booi, 2011). *Heuweltjies* are highly disturbed patches that are suitable for opportunistic pioneer species such as short-lived annuals and members of the Mesembryanthemaceae (Esler and Cowling, 1995). Mesembryanthemaceae have high seed retention (stored in the canopy) and high seed dormancy to help compensate for the high levels of disturbance caused by livestock (and presumably in the past, game) grazing while the matrix is dominated by long-lived perennial shrubs species that exhibit rapid germination rates to exploit the infrequent rainfall events (Esler and Cowling, 1995). Common taxa associated with *heuweltjies* in this area include *Brownanthus vaginatus* (Lam.) previously called *Brownanthus ciliatus* (Aiton), *Psilocaulon utile* (Bolus) and *Malephora lutea* (Haw), whereas the matrix is dominated by *Osteospermum sinuatum*, *Pteronia pallens*, *Hereroa latipetala* and *Ruschia spinosa*. (Milton et al., 1992). However, the *heuweltjie* species also occur within disturbed matrix sites (Esler and Cowling, 1995). Additionally, *heuweltjie* substrate in this area also contains higher silt, nitrogen, phosphorus, calcium, potassium, magnesium and sodium concentrations than the matrix (Milton et al., 1992).

2.2.2 Vegetation sampling

Vegetation surveys were conducted during the first sampling session (early spring) using the line-intercept method (Ellenberg and Mueller-Dombois, 1974). 5 transects (5 m long with 1 m spaced out between each transect) were placed in the centre of each *heuweltjie* and corresponding matrix plot (plot refers to all 5 transects) (Figure 2.3). Every plant (both dead and alive) that touched the transect was recorded along with their height and cover to the nearest cm. From the data collected, average plant height, total plant percentage cover and dead plant percentage cover was calculated. The presence or absence of termite frass was also recorded.

2.2.3 Arthropod sampling

Arthropods were sampled in early spring (September 2019) and late summer (February 2020), on *heuweltjies* and in the inter-*heuweltjie* plains (matrix). Eight *heuweltjies* were chosen at random at each of the three sites (Wolwekraal, Argentina and Tierberg). Each *heuweltjie* was paired with a matrix plot 25 m away in a random direction, but also not close to another *heuweltjie*. Pitfall traps are an effective sampling method for surveying ground dwelling arthropods in open areas (Harris et al.,

2003). Four pitfalls, 55 mm in diameter, were placed approximately 1 m apart in a square at the centre of each *heuweltjie* and matrix plot, giving 8 pitfalls per plot pair (Figure 2.3). Pitfall traps were half filled with a 1:1 solution of ethylene glycol and water, with a drop of dishwashing liquid to break the surface tension. Traps were left open for six days, and then replaced for a second round of sampling of six days. Once collected, all pitfall samples were placed into a 70% ethanol solution and stored until sorted. Sampling consisted of 384 pitfalls per season and 768 pitfalls in total.

Vacuum sampling, which is effective for sampling arthropods found either near the ground or in low vegetation (Cooper and Whitmore, 1990; Harper and Guynn, 1998), was conducted by walking along five transects of 5 m on each *heuweltjie* and matrix plot (25 m of vacuum sampling per plot) (Figure 2.3). Sampling was replicated twice, once in early spring and again in late summer. To standardize this, each site was sampled at the same time (09:00 – 14:00) on different days because insect activity fluctuates depending on the time of day. A fine mesh sock was attached to a STIHL 86 2-stroke petrol leaf blower to sample shrub-dwelling arthropods. Vacuum sampling differed depending on the size of the vegetation occurring along each transect. The vacuum sampler was inserted twice for three seconds over all smaller plants encountered, while larger vegetation received 3-6 insertions, each lasting one second. This was done to ensure all plants along the transect were “vacuumed” for 6 seconds to allow for comparative replication. Although there is a concern that sampling effort is not equal throughout the transects, the vegetation at each plot was thoroughly sampled (high counts of dead plants made it easier to sample) to ensure maximum sampling effectiveness.

All debris and arthropods caught were transferred to large resealable plastic bags and tightly sealed and placed into a freezer until sorted. Specimens were sorted into morphospecies and later identified to order and family level where possible using taxonomic resources (Dippenaar-Schoeman, 2014; Slingsby, 2017). Using morphospecies allows rapid sampling of specimens to be categorised according to morphological similarities instead of identifying them to species level (Oliver and Beattie, 1993).

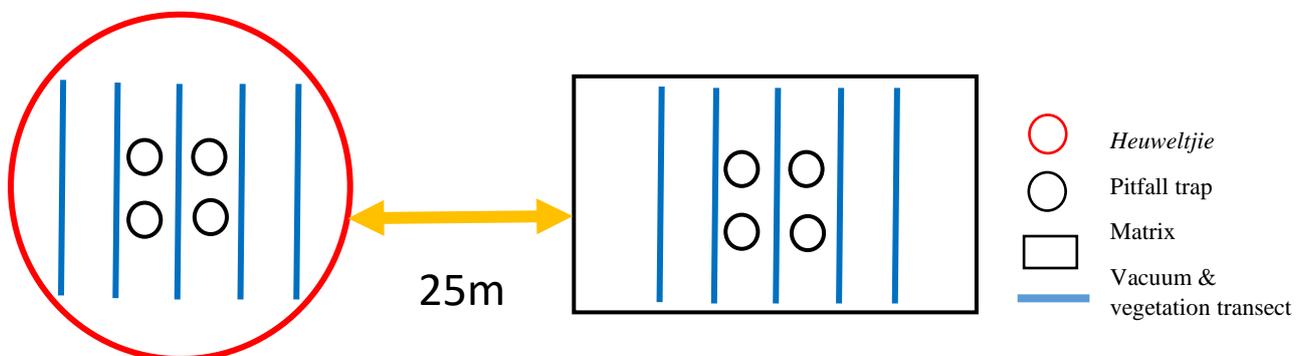


Figure 2.3: Sample design for pitfall, vacuum and vegetation sampling

2.2.4 Statistical analyses

To assess overall sampling effectiveness, a species accumulation curve was plotted along with species diversity estimates, based on Hill numbers, $q = 0$ (observed species richness), 1 (Shannon's entropy), 2 (Simpson diversity), across each biotope (*heuweltjie* and matrix) using the *vegan* and *iNEXT* packages (Chao, 1987; Hsieh et al., 2016) in R version 4.0.1 (R Core Team, 2020). Spatial autocorrelation was tested using the Mantel test from the *ade4* package (Dray and Dufour, 2007). There was spatial autocorrelation for both epigaeic (Mantel test = 0.44, $p = 0.032$) and foliage arthropods (Mantel test = 0.060, $p = 0.007$). Therefore, a random spatial variable in this case, "Site" which refers to each of the three farms (Argentina, Tierberg and Wolwekraal), was added to all models to account for any influence of spatial autocorrelation.

Local scale species richness (alpha-diversity) and abundance were tested for 1) overall (combined epigaeic and foliage arthropods), 2) epigaeic and 3) foliage arthropods and 4) epigaeic arthropods excluding ants on each biotope (*heuweltjie* and matrix) using generalized linear mixed effects models (GLMM) from the *lme4* package (Bates et al., 2007). Abundances of epigaeic arthropods, excluding ants, were calculated to account for the extremely high ant abundances. Species richness for overall and epigaeic (including and excluding ants) arthropods were fitted using a Poisson distribution while foliage arthropods were fitted with a negative binomial distribution. All abundance data were logged and fitted to a Gaussian distribution. All GLMMs were fitted with Laplace approximations. Additionally, the package *BAT* (Cardoso et al., 2015) was used for individual based rarefaction for observed overall, epigaeic and foliage arthropod species richness (alpha diversity) for *heuweltjie* and matrix plots at each of the three sites. This was done as there was a concern that the sampling effort for the vacuum sampling was not the same throughout despite extensively sampling both *heuweltjie* and matrix plots to achieve a more accurate depiction of species richness at different locations. The observed data were rarefied 100 times to calculate the alpha diversity of each biotope at each site.

I used two complementary approaches to assess variation in arthropod community composition among the two biotopes (*heuweltjie* and matrix) and three sites Argentina, Tierberg and Wolwekraal): 1) a multivariate extension of a GLM was run using the "manyglm" function from the *mvabund* package (Wang et al., 2012) and 2) latent variable modelling was used through the *boral* package (Hui et al., 2015). The "manyglm" function is designed for multivariate abundance data which fits individual generalised linear models for each species at each site to assess the effect between environmental data and community composition (Wang et al., 2012). The *boral* package on the other hand employs a set of underlying latent variables and/or explanatory variables in an attempt to explain community composition whereby the posterior median values of the latent variables are used as co-

ordinates on the ordination axes (Hui et al., 2015). Two models were fitted to epigaeic and foliage arthropod abundance data: 1) a pure latent variable model and 2) a latent variable biplot with environmental covariates. The second model was run using environmental covariates (total plant percentage cover, dead plant percentage cover and average plant height) to account for species biotic interactions (Hui et al., 2015). All multivariate models were fitted with a negative binomial distribution.

Beta-diversity was assessed between: 1) biotopes, 2) sites and 3) biotopes at each site, to determine whether community dissimilarity is driven by species replacement (turnover) or differences in species richness (nestedness). This was done using the *BAT* package (Cardoso et al., 2015) for all, epigaeic and foliage arthropods. The function ‘beta’ calculated beta diversity (β_{total} = total beta-diversity) as well as its two components, turnover (β_{repl} = beta-diversity through species replacement) and nestedness (β_{rich} = beta-diversity through species gain and loss) (Cardoso et al., 2015). Additionally, beta-diversity was assessed within each: 1) biotope, 2) site and 3) biotope at each site using the *betapart* package (Baselga et al., 2012). Similar to the “beta” function from the *BAT* package, the ‘beta.multi.abund’ function calculated total (beta.BRAY/ β_{total}) and partitioned beta-diversity (nestedness (beta.bray.GRA/ β_{rich}) and turnover (beta.bray.BAL/ β_{repl})) for overall, epigaeic and foliage arthropods. Abundance data were used to match the Sørensen beta-diversity and Bray-Curtis dissimilarity measures.

2.3 Results

2.3.1 *Heuweltjie* and matrix vegetation

The line-intercept transects revealed that average plant height on *heuweltjies* was significantly lower than that of the matrix, yet had greater total percentage cover (Table 2.1), although most of the total percentage cover consisted of dead plants in both biotopes. The dominant vegetation of Argentina consisted of *P. pallens* but also consisted of high counts of dead plants and leaf litter. Tierberg and Wolwekraal were dominated by dead plants and leaf litter (Table 2.1). *Heuweltjies* were largest at Wolwekraal, followed by Argentina and Tierberg (Table 2.1).

Table 2.1: Vegetation results from the line-intercept transects along each biotope and site. Additionally the mean area of the sampled *heuweltjies* and the dominate vegetation on each biotope.

Site	Biotope	<i>Heuweltjie</i> area (m ²)	Plant height (cm)	Percentage cover (%)	Dead percentage cover (%)	Dominant
Argentina	<i>Heu</i>	83.31 (±21.05)	12.97 (±7.88)	41.28 (±13.54)	14.88 (±10.29)	Dead, litter, <i>P. pallens</i> , <i>M. lutea</i> and <i>Lampranthus uniflorus</i>
	Matrix	-	16.36 (±5.50)	34.63 (±7.20)	5.97 (±2.81)	Dead, litter, <i>Ruschia spinosa</i> , <i>P. pallens</i> , <i>B. vaginatus</i> , <i>O. sinuatum</i> and <i>Zygophyllum retrofractum</i>
Tierberg	<i>Heu</i>	90.31 (±32.94)	17.26 (±4.85)	53.75 (±13.06)	31.45 (±14.55)	Dead, litter, <i>P. pallens</i> , <i>B. vaginatus</i> , <i>M. utile</i> and <i>Peersia</i> spp.
	Matrix	-	18.83 (±3.60)	39.31 (±9.60)	14.48 (±10.33)	Dead, litter, <i>P. pallens</i> , <i>R. spinosa</i> , <i>Crassula subaphylla</i> , <i>O. sinuatum</i> , <i>Hereroa latipetala</i> and <i>Z. retrofractum</i>
Wolwekraal	<i>Heu</i>	138.88 (±118.04)	14.02 (±13.54)	37.33 (±13.54)	11.63 (±13.54)	Dead, litter, <i>R. spinosa</i> , <i>Z. retrofractum</i> , <i>Fingeruthia africana</i> and <i>Ruschia approximata</i>
	Matrix	-	12.42 (±5.11)	26.11 (±12.16)	7.24 (±5.24)	Dead, litter, <i>R. approximata</i> , <i>R. spinosa</i> and <i>P. pallens</i>

2.3.2 Invertebrate species accumulation curves and diversity estimates

A total of 16 932 individuals belonging to 353 morphospecies were sampled during this study with 9802 specimens (275 morphospecies) collected on *heuweltjies* compared to 7130 (229 morphospecies) collected in the matrix. Epigaeic arthropods comprised of 14 631 individuals, with 8044 (133 morphospecies) collected on *heuweltjies* and 6587 (114 morphospecies) in the matrix. Foliage arthropods comprised of 2 301 individuals, 1758 (142 morphospecies) collected on *heuweltjies* and 543 (115 morphospecies) in the matrix. Formicidae were most abundant, 12 265 (72% of all individuals), although contributing to only 12% of all morphospecies identified. The high abundance can be attributed to pitfall traps being placed close to active nests of harvester ants (*Messor capensis*). The most speciose group was Coleoptera (74 morphospecies; 21%) followed by other Hymenoptera, bees and wasps, (56 morphospecies; 16%), Araneae (54 morphospecies; 15%), Hemiptera and Diptera (37 morphospecies; 10%). Other less abundant assemblages sampled consisted of Acari, Blattodea, Lepidoptera, Mantodea, Orthoptera, Scorpiones, Siphonaptera, Solifugae, Thysanura and Thysanoptera (Appendix R).

The species sample completeness curve (Hill number, $q=0$) reached an asymptote suggesting that overall sample completeness was achieved (Appendix A). The species accumulation curve for overall arthropod diversity on *heuweltjies* and matrix plots showed higher estimated species richness, and Shannon and Simpson diversity indices for *heuweltjies* (Appendix B). Chao1-estimated overall species richness was 540.1 (S.E \pm 44.3) (Appendix C). Extrapolated epigaeic arthropod species richness, Shannon and Simpson diversity indices was relatively similar for both *heuweltjie* and matrix plots ($q = 0, 1, 2$). However, Chao1 estimated higher epigaeic arthropod diversity on the *heuweltjies* compared to the matrix (Appendix C). Additionally, Shannon and Simpson diversity indices had higher estimated overall diversity on *heuweltjies* (Appendix C). While extrapolated foliage species richness, Shannon and Simpson diversity (Hill number; $q = 0, 1, 2$) showed matrix plots to have a greater diversity than that of *heuweltjies* (Appendix C).

2.3.3 Arthropod response to biotope type and sampling localities

Overall alpha-diversity and abundance were significantly greater on *heuweltjies* than the matrix ($\chi^2 = 28.26$, $p < 0.001$; $\chi^2 = 10.25$, $p < 0.01$) (Figure 2.4a; 2.4e, 2.7a). Additionally, *heuweltjies* had a significantly higher epigaeic alpha-diversity and abundance than the matrix ($\chi^2 = 13.97$, $p < 0.001$; $\chi^2 = 5.71$, $p < 0.05$) (Figure 2.4b; 2.4f, 2.7b). Moreover, foliage arthropods also showed significant differences, with higher alpha-diversity and abundances on the *heuweltjies* compared to the matrix ($\chi^2 = 9.31$, $p < 0.01$; $\chi^2 = 28.71$, $p < 0.001$) (Figure 2.4c; 2.4g, 2.9c). When ants were excluded to

correct for possible sampling near ant nests, similar patterns arose with epigaeic arthropod alpha-diversity and abundance significantly higher on the *heuweltjies* ($\chi^2 = 16.06$, $p < 0.001$; $\chi^2 = 9.71$, $p < 0.01$) (Figure 2.4d; 2.4h). Diptera ($\chi^2 = 25.766$, $p < 0.001$; $\chi^2 = 93.303$, $p < 0.001$) and Coleoptera ($\chi^2 = 13.29$, $p < 0.001$; $\chi^2 = 7.049$, $p < 0.01$) were the only orders with significantly high alpha diversity and abundance on the *heuweltjies* compared to the matrix (Figure 2.5b, c, f, g). Ant ($\chi^2 = 1.089$, $p > 0.05$; $\chi^2 = 2.535$, $p > 0.05$) and Araneae ($\chi^2 = 0.188$, $p > 0.05$; $\chi^2 = 0.045$, $p > 0.05$) showed no significant differences between the two biotopes (Figure 2.5a, d, e, h).

At site level, rarefied alpha-diversity differed significantly between the three sites (Figure 2.6a). Tierberg had the highest alpha-diversity followed by Wolwekraal and Argentina. When looking at arthropod alpha-diversity of each biotope within the three sites, the highest rarefied alpha-diversity amongst *heuweltjies* was observed at Wolwekraal followed by Tierberg and Argentina, whereas for the matrix sites, Argentina had the lowest rarefied alpha-diversity followed by Wolwekraal and Tierberg (Figure 2.6b). Argentina had similar alpha-diversity between the two biotopes, Tierberg showed higher alpha diversity in the matrix compared to the *heuweltjie* while Wolwekraal had the most noticeable differences between the two biotopes, with higher alpha-diversity on the *heuweltjies* (Figure 2.6b).

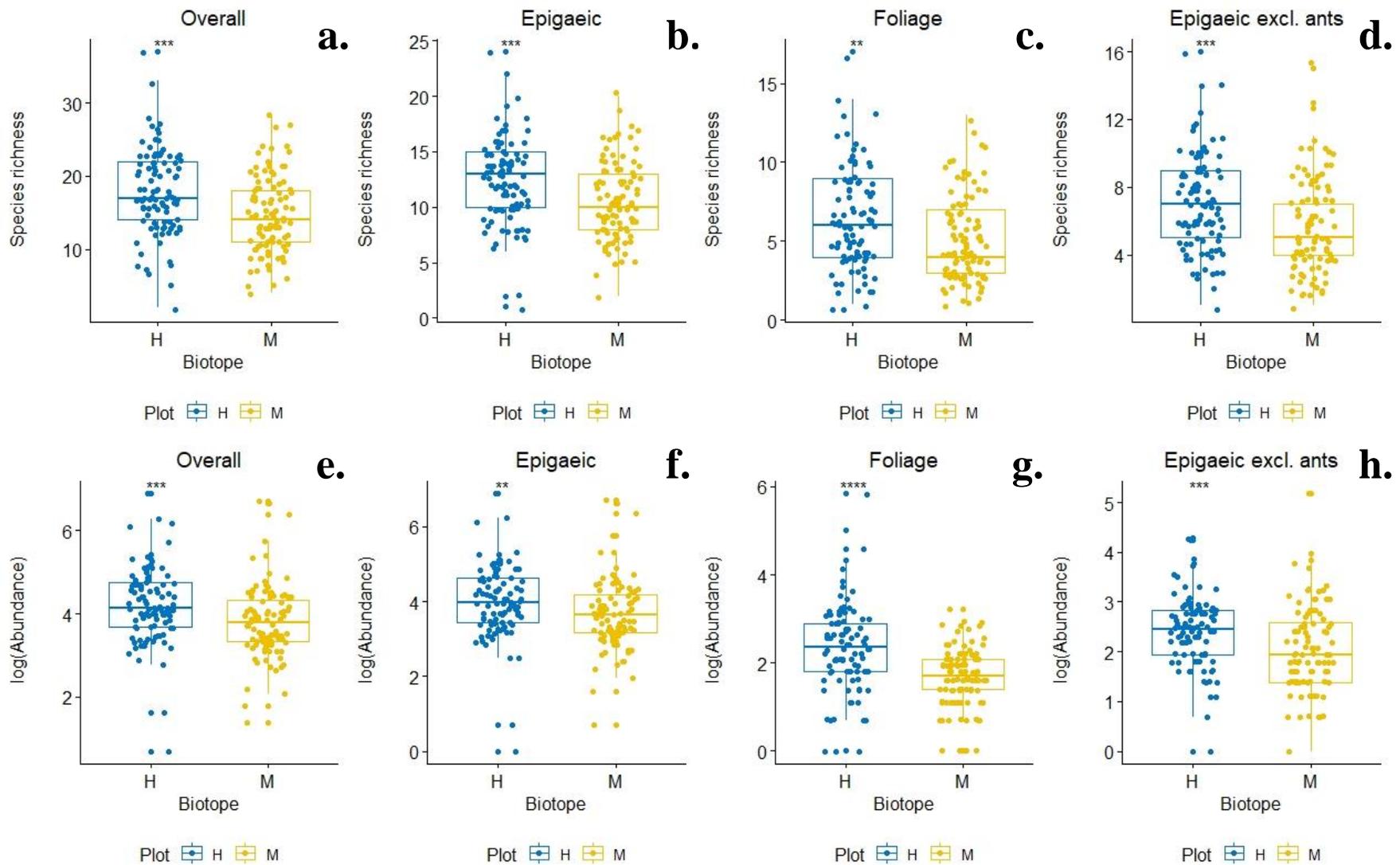


Figure 2.4: The relationship between biotope type (H = *heuweltjie*, M = matrix) and species richness (alpha-diversity) and abundance for A) Overall, B) Epigaeic, C) Foliage, D) epigaeic arthropods (excluding ants) All significant plots are marked with an *.

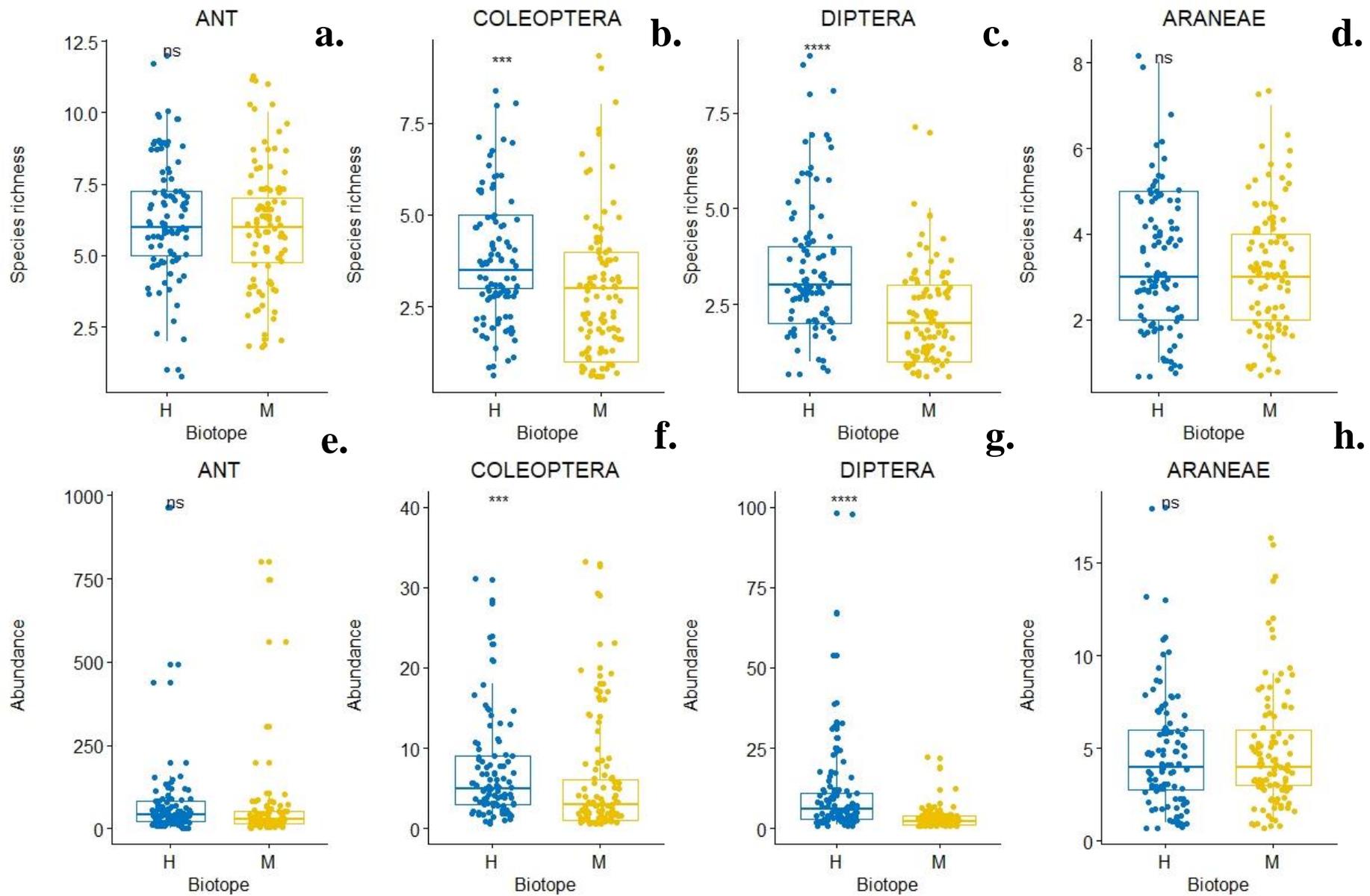


Figure 2.5: The relationship between biotope type (H = *heuweltjie*, M = matrix) and species richness (alpha-diversity) and abundance for Formicidae (Hymenoptera), Coleoptera, Diptera and Araneae. 40

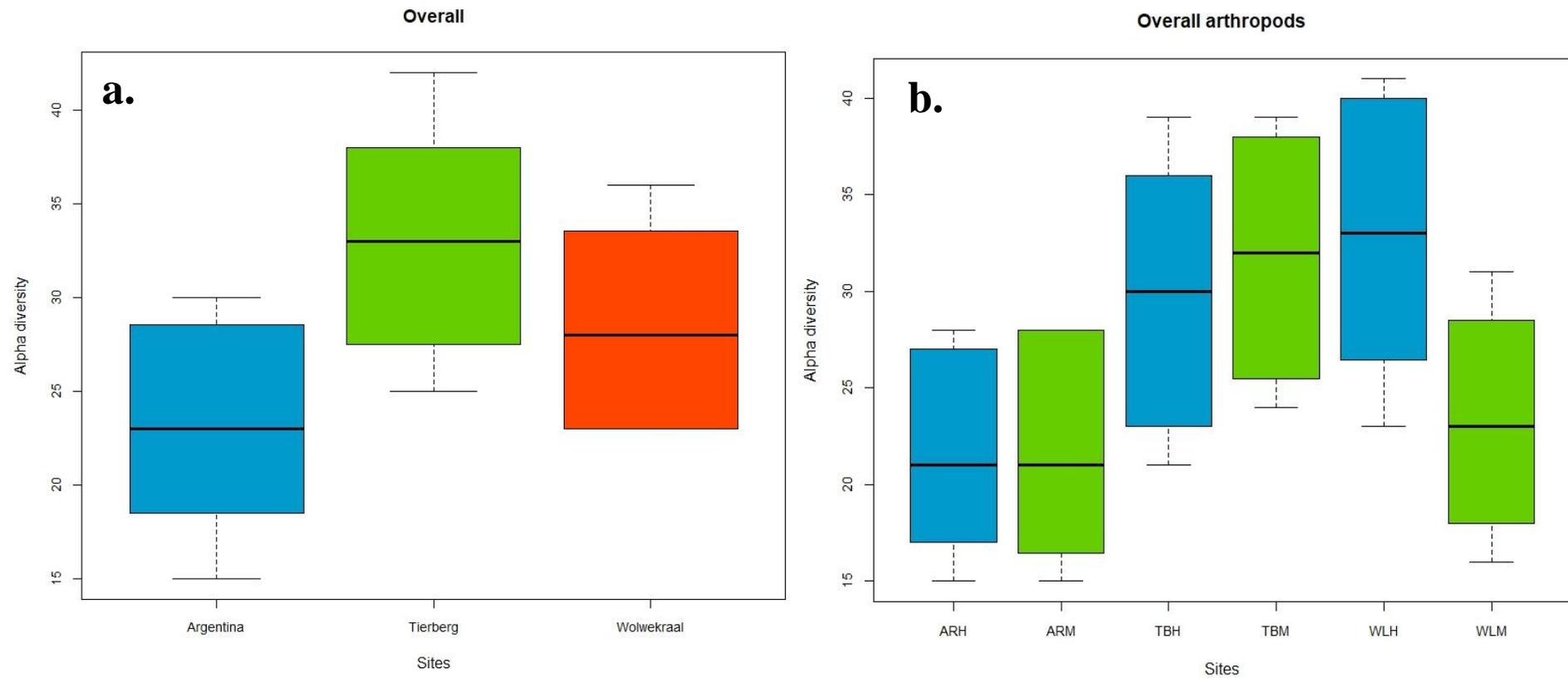


Figure 2.6: Rarefied alpha diversity for overall arthropods between A) all sampling localities (AR = Argentina, TB = Tierberg, WL = Wolwekraal), B) *heuweltjie* and matrix plots (H = *heuweltjie*, M = matrix) within the three sample sites.

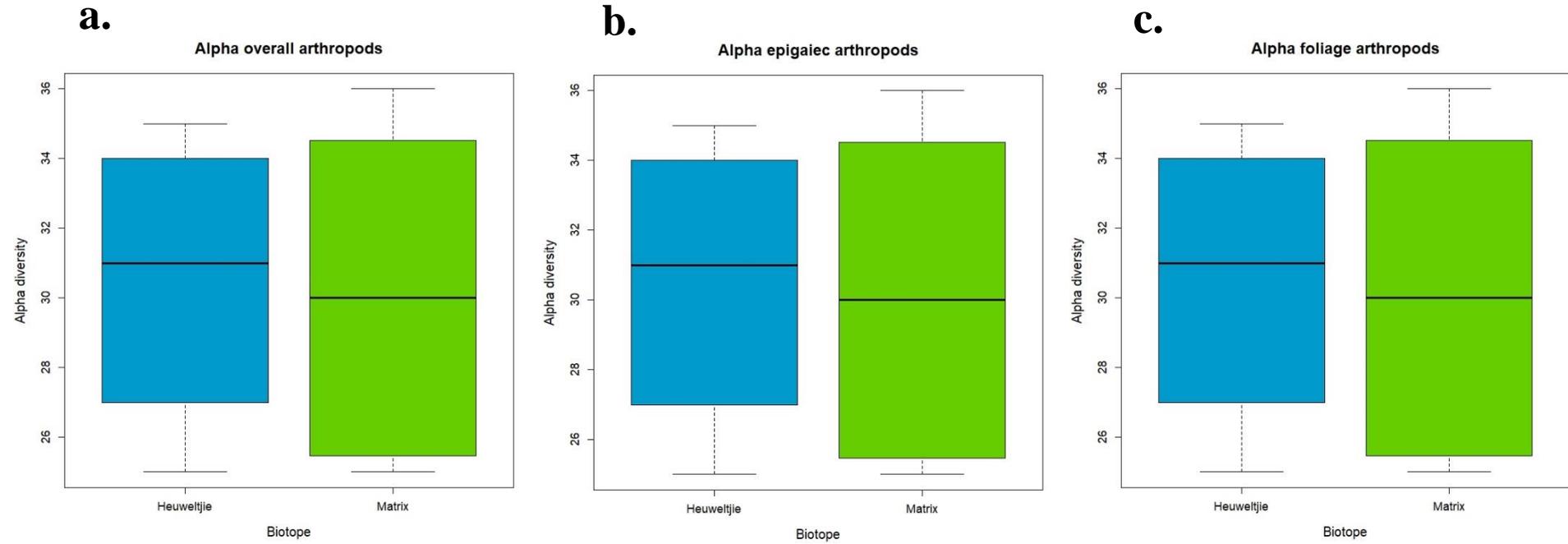


Figure 2.7: Rarefied alpha diversity for A) overall arthropods, B) epigeic arthropods and C) foliage arthropods at each biotope (*heuweltjie* and matrix).

2.3.4 Arthropod community composition

Arthropod species community composition differed markedly at the biotope and site level. Overall, epigaeic and foliage arthropods showed a clear difference in community composition between *heuweltjie* and matrix plots ($\chi^2 = 1007$, $p < 0.001$; $\chi^2 = 381.7$, $p < 0.001$; $\chi^2 = 377.6$, $p < 0.001$). The pure latent variable model showed clear grouping between *heuweltjie* and matrix plots for epigaeic arthropod community composition (Figure 2.8a). Furthermore, to account for biotic interaction, the residual biplot with environmental variables revealed a clear segregation between the *heuweltjie* and matrix with slight overlap (Figure 2.8b). The pure latent variable plot and residual biplot for foliage arthropods was less discernible yet still significantly different, with species composition on *heuweltjie* plots overlapping the matrix plots (Figure 2.11a-b). Clear epigaeic arthropod community composition was observed at site level for epigaeic and foliage arthropods (ANOVA: $\chi^2 = 618.9$, $p < 0.001$; $\chi^2 = 787.7$, $p < 0.001$; $\chi^2 = 446.2$, $p < 0.001$). The pure latent variable and residual model revealed slight overlap between Argentina and Tierberg indicating comparable epigaeic species composition (Figure 2.8c-d). Slight patterns were observed for the foliage arthropods between all sites for both the pure and residual plot (Figure 2.9c-d).

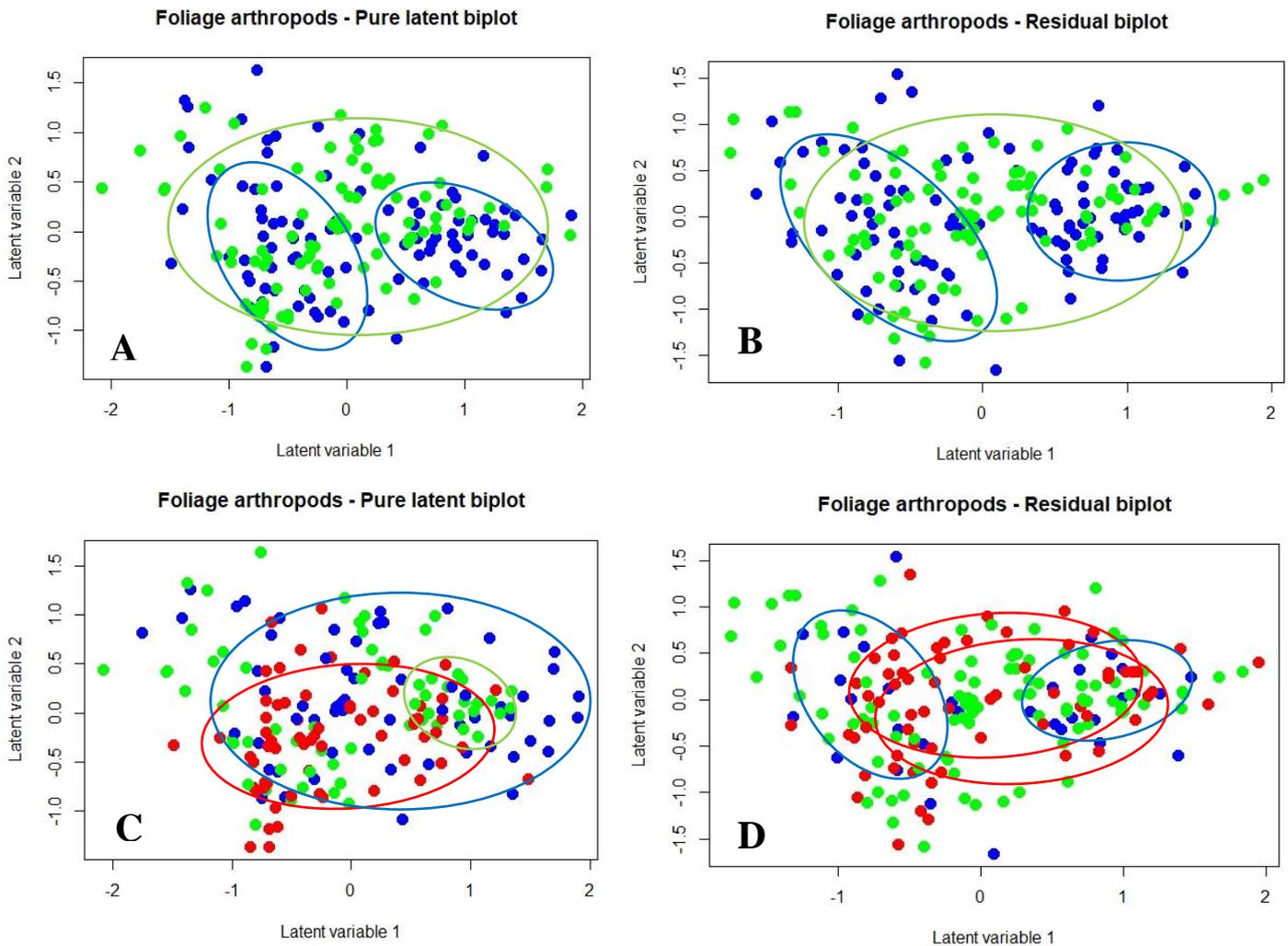


Figure 2.8: Latent variable models for epigeic arthropod species community composition at the biotope (A-B) and site (C-D) level. A species distribution plot showing the means of the latent variable model with negative binomial distribution. A & C = pure latent variable model B & D = residual biplot with environmental covariates. (A-B) Green = matrix and blue = *heuweltjie*. (C-D) Green = Argentina, Blue = Tierberg and Red = Wolwekraal. The ovals represent the different groupings of the biotopes and sites.

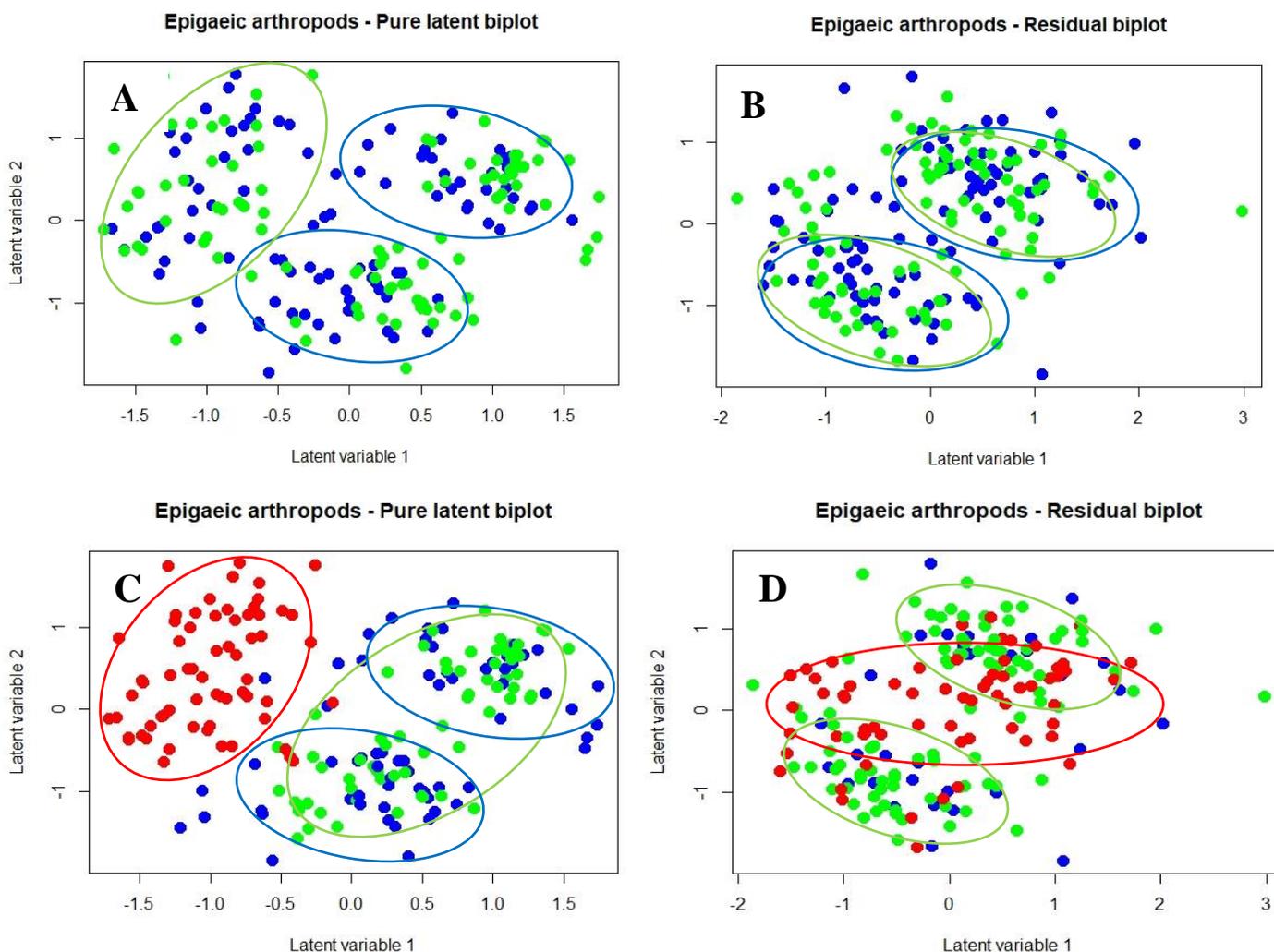


Figure 2.9: Latent variable models for foliage arthropod species community composition at the biotope (A-B) and site (C-D) level. A species distribution plot showing the means of the latent variable model with negative binomial distribution. A & C = pure latent variable model B & D = residual biplot with environmental covariates. (A-B) Green = matrix and blue = *heuweltjie*. (C-D) Green = Argentina, Blue = Tierberg and Red = Wolwekraal.

2.3.5 Beta diversity

A moderate total beta-diversity was found between *heuweltjie* and matrix plots for overall, epigaeic and foliage arthropod assemblages (Appendix D, Figure 2.10). Overall (combined epigaeic and foliage-dwelling arthropods) and epigaeic arthropods were mainly driven by species turnover while species richness differences were the main contributor for foliage arthropods (Appendix D). Additionally, at the site level, overall arthropod assemblages had high beta-diversity between Argentina – Wolwekraal and Tierberg – Wolwekraal that were mainly caused by species turnover whereas Argentina - Tierberg had a lower total beta-diversity driven mostly by differences in species richness (Appendix E, Figure 2.10a). Epigaeic arthropods followed a similar pattern, with moderate

total beta-diversity (Figure 2.10b). Foliage arthropod assemblages had moderate total beta-diversity between Argentina – Tierberg and Argentina – Wolwekraal that were largely driven by species richness differences while Tierberg – Wolwekraal had low beta-diversity (Figure 2.10c).

When assessing beta-diversity between *heuweltjie* and matrix plots across each site, both *heuweltjie* and matrix plots had moderate to low total beta-diversity for all arthropods (Appendix F - H). The beta-diversity between *heuweltjies* at each site were mainly driven by species turnover for the overall and epigaeic arthropods while the foliage arthropods were driven by species richness differences (Figure 2.10d-f). Additionally, most of the differences in matrix plots between each site were driven by species turnover (Figure 2.10g-i). Beta-diversity within each *heuweltjie* and matrix plot was extremely high for overall, epigaeic and foliage arthropod communities with species turnover being the biggest contributor (Appendix I). This was also the case when looking at the beta-diversity within each site and within the *heuweltjie* and matrix plots at each site (Appendix J).

Total beta-diversity and species turnover was significantly different between *heuweltjie* and matrix plots for overall ($F_{1:198} = 20.07$, $p < 0.001$; $F_{1:198} = 19.06$, $p < 0.001$) and epigaeic ($F_{1:198} = 4.24$, $p < 0.05$; $F_{1:198} = 6.20$, $p < 0.05$) arthropod assemblages (Figure 2.11a, c, d, f). There were significant differences in total beta-diversity and species richness between *heuweltjie* and matrix plots of the foliage arthropods ($F_{1:198} = 12.37$, $p < 0.001^{***}$; $F_{1:198} = 4.62$, $p < 0.05^*$) (Figure 2.11h – i). Overall, epigaeic and foliage arthropod assemblage composition differed significantly between each site as well as between *heuweltjies* and matrix plots at each site (Table 2.2).

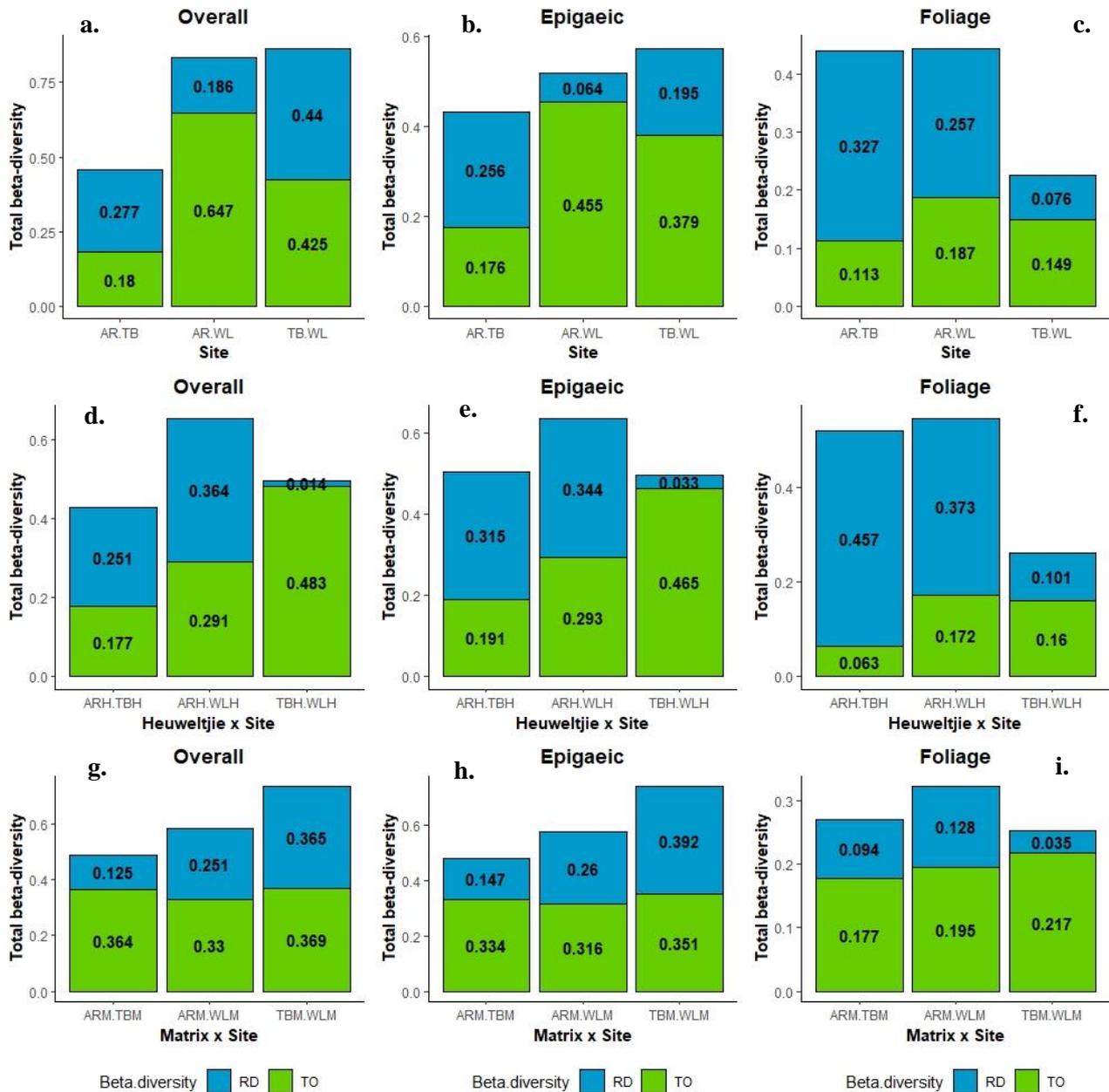


Figure 2.30: Two components of total beta-diversity (TO = Turnover, RD = Richness difference) for overall, epigeaic and foliage arthropods between each site (AR = Argentina, TB = Tierberg, WL = Wolwekraal) (A – C) and between each biotope at each site (H = *Heuweltjie* (D – F), M = Matrix (G– I)).

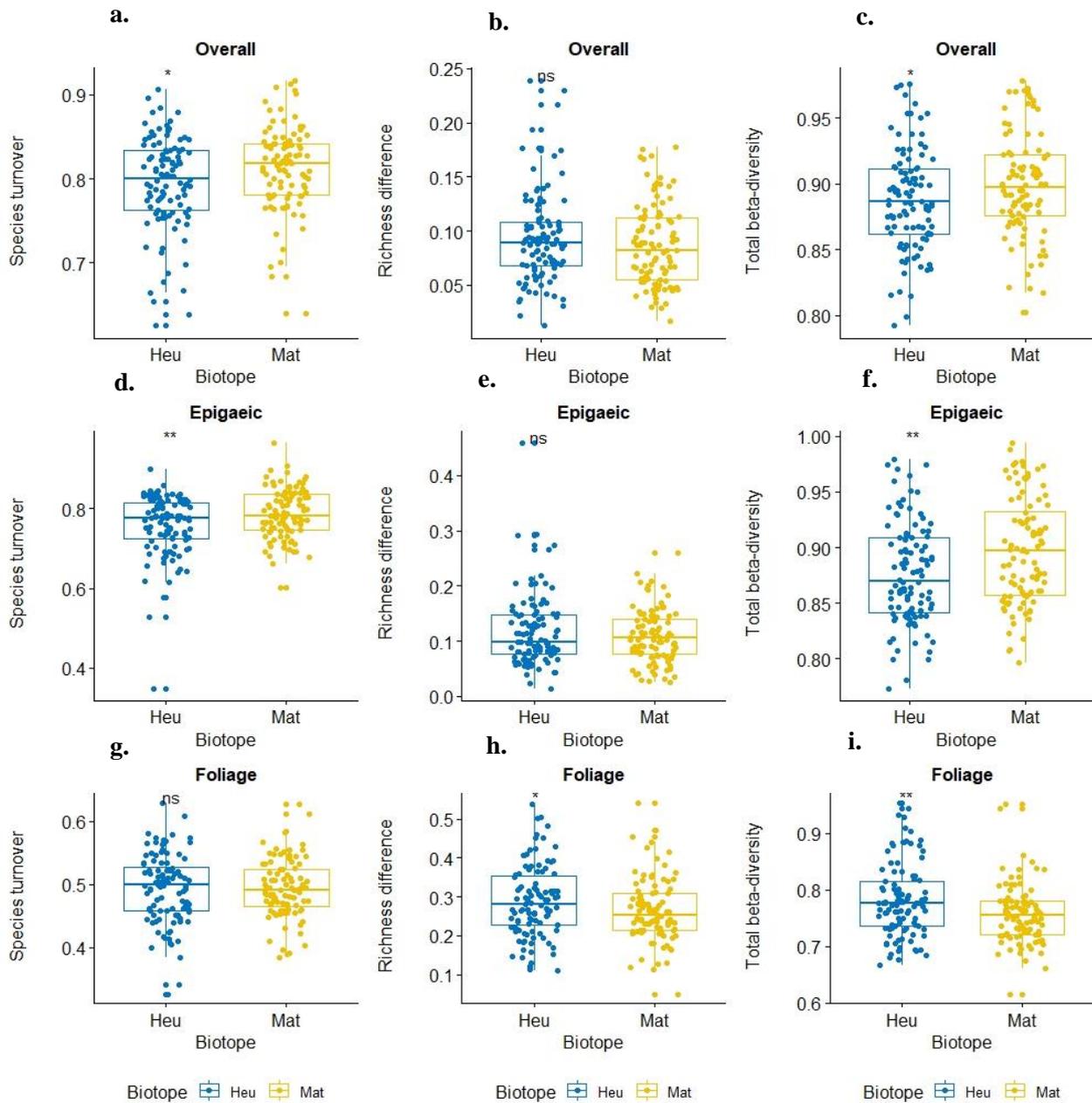


Figure 2.41: Boxplot showing the results from the one-way ANOVA comparing the differences in total beta-diversity, species turnover and richness differences between all *heuweltjie* and matrix plots for overall, epigaic and foliage arthropods. Heu = *Heuweltjie*, Mat = Matrix. (“n.s.” = non-significant, $p < 0.05^*$; $p < 0.01^{**}$, $p < 0.001^{***}$).

Table 2.2: Multiple comparisons procedure results for beta diversity for overall, epigaeic and foliage arthropod assemblages between each site, *heuweltjies* at each site and matrix plots at each site. Significant main test (F-test) results are indicated with (*). Pairwise test (Tukey posthoc) indicates differences between within the factors.

Group	Factor	Beta-diversity	Main test	Pairwise test
Overall	Site	β_{total}	7.672***	AR – WL
		B_{repl}	5.597***	AR – TB
		B_{rich}	7.864***	AR – WL; TB – WL
	<i>Heuweltjie</i> x site	β_{total}	29.02***	ARH – TBH; ARH – WLH
		B_{repl}	4.443*	ARH – WLH
		B_{rich}	4.502*	ARH – TBH
	Matrix x site	β_{total}	16.48***	ARM – TBM; ARM – WLM
		B_{repl}	1.73	
		B_{rich}	14.48***	ARM – TBM; ARM – WLM
Epigaeic	Site	β_{total}	5.39 ⁻⁶ ***	AR – WL
		B_{repl}	0.511	
		B_{rich}	3.724*	AR – WL
	<i>Heuweltjie</i> x site	β_{total}	40.38***	ARH – TBH; ARH – WLH
		B_{repl}	0.834	
		B_{rich}	11.12***	ARH – TBH; ARH – WLH
	Matrix x site	β_{total}	12.02***	ARM – TBM; ARM – WLM
		B_{repl}	0.004	
		B_{rich}	10.2***	ARM – TBM; ARM – WLM
Foliage	Site	β_{total}	40.19***	AR – WL; TB – WL
		B_{repl}	9.617***	AR – WL; TB – WL
		B_{rich}	8.357***	AR – WL; AR – TB
	<i>Heuweltjie</i> x site	β_{total}	40.19***	ARH – TBH; ARH – WLH
		B_{repl}	54.11***	ARH – TBH; ARH – WLH
		B_{rich}	32.27***	ARH – TBH; ARH – WLH
	Matrix x site	β_{total}	12.08***	ARM – TBM; ARM – WLM
		B_{repl}	0.355	
		B_{rich}	9.474***	ARM – WLM

($p < 0.05^*$; $p < 0.01^{**}$, $p < 0.001^{***}$).

2.4 Discussion

Although the Succulent Karoo is often perceived as relatively homogenous due to its semi-arid nature, it contains considerable heterogeneity provided by *heuweltjies*. In this study, I find that arthropod biodiversity differs significantly in species richness, abundance and composition between *heuweltjies* and their surrounding matrix. Arthropod ecology is understudied in the Succulent Karoo with most studies focussing on plant-pollinator relationships (Colville et al., 2002, Mayer et al., 2006), arthropod responses to grazing (Seymour and Dean, 1999; Nchai, 2008; Henshel and Lubin, 2018) and the role of the termite, *Microhodotermes viator* in the formation of *heuweltjies* (Cramer et al., 2017; Francis and Poch, 2019; McAuliife et al., 2019). However, few studies have used a multi-taxon approach to understand the role these unique patches have on arthropod biodiversity.

2.4.1 Species richness (alpha-diversity) and abundance

Alpha-diversity and abundance were significantly greater for overall and epigaeic arthropods on *heuweltjies* compared to the matrix. These findings were similar to those by Cornell (2014), who found greater invertebrate species richness and abundance on *heuweltjies* in the Karoo Desert Botanical Garden in Worcester, Western Cape, South Africa. Multiple pitfall traps were incidentally set near ant nests, so the analysis of epigaeic arthropods was repeated with ants excluded, because social insects like ants may skew results because of their high abundances. However, even when ants were excluded, epigaeic arthropod alpha-diversity and abundance remained greater on *heuweltjies*. Despite being unable to adequately sample the foliage arthropods due to high plant mortality and large gaps of bare ground within both *heuweltjie* and matrix plots which resulted in significantly lower abundances compared to the epigaeic arthropods, foliage arthropods still exhibited higher alpha-diversity and abundances on the *heuweltjies* than the matrix.

Conversely to the hypothesis that *heuweltjies* would have lower plant cover because of increased disturbance, *heuweltjies* exhibited higher percentage cover than that of the matrix although they were mostly dominated by dead plants and litter. This adds support that vegetation patches in arid systems are considered key for arthropod diversity (Liu et al., 2016). Additionally, higher species richness and abundances on *heuweltjies* may be attributed to their differences in soil characteristics and vegetation structure as they have the potential to provide greater resources for food and refuge (Booi, 2011; Rahlao et al., 2008). Although studies have shown that vegetation productivity (NDVI) in the Succulent Karoo has remained relatively unchanged from 1982 – 2015 (Hoffmann et al., 2018), the drought in the region, currently in its seventh year, has significantly affected the vegetation, with high levels of plant mortality. These negative effects on the vegetation have undoubtedly impacted

both epigaeic and foliage dwelling arthropods, especially phytophagous and web building taxa, which are heavily reliant on vegetation structure and cover (Benade et al., 2016; Henschel and Lubin, 2017).

Rarefied alpha-diversity across the three sites revealed Tierberg had the highest overall species richness followed by Wolwekraal and Argentina. The high levels of alpha-diversity at Tierberg could be attributed to its exclusion and subsequent partial recovery from livestock grazing and other forms of disturbances. Although all three sites have a history of overgrazing, Argentina is the only site that is still subjected to moderate grazing from livestock and various game species (Seymour et al., 2010). Additionally, Wolwekraal and Tierberg LTER have been protected from livestock grazing since the late 1970s and 80s (Arena et al., 2018). The southern border of Wolwekraal nature reserve is situated along Prince Albert's municipal dump where stray cats and dogs actively hunt, and people remove firewood: these disturbances could pose a threat to vegetation and arthropods at the site, as cats may prey on invertebrates (Seymour et al., 2020), and removal of vegetation and wood affects habitat availability at that site.

2.4.2 Community composition

As *heuweltjies* are considered areas of high disturbance, it is not surprising that community composition for *heuweltjie* and matrix plots differed considerably, with each biotope hosting distinct epigaeic and foliage arthropod communities. Again, these results coincide with the findings from Cornell (2014), who found distinct invertebrate communities on *heuweltjies*. Arid and semi-arid environments are often limited by water and nutrients, therefore patches, such as *heuweltjies*, which consist of differing soil textures, nutrients and water retention capabilities compared to the matrix, are significant contributors towards the heterogeneity in the landscape (Midgely and Musil, 1990). Burrowing activities are common for reptiles and invertebrates in arid areas as a means to escape from harsh temperature extremes (Lovegrove, 1999). The finer texture of *heuweltjie* soils may provide an easier substrate for arthropods to burrow into compared to harder soils of the matrix. Additionally, burrowing disturbances from mammals such as the aardvark, *Orycteropus afer*, and various rodent species are common occurrences on *heuweltjies*. The effect of these actions are key in increasing the heterogeneity in the landscape (Louw et al., 2017), which provides more niches for arthropods to occupy (Milton and Dean, 2015).

The unique arthropod communities in the matrix could be attributed to plant species such as *Ruschia spinosa* and *Hereroa latipetala*, which occur in the matrix, have developed rapid seed germination (Esler and Cowling, 1995). These rapid germination events produce many small seeds which may be

an important food source for various granivorous arthropod taxa, although this might need to be assessed further since many plants are not producing any seed because of the drought. Additionally, the unique arthropod communities in the matrix could be attributed to more generalist and opportunistic species as generalist ant species are known to be more commonly associated with the matrix (Arena et al., 2020). Furthermore, arthropods along old fields at Tierberg were proven to be positively correlated with plant cover and perennial plant species and are negatively correlated with annuals (Dean and Milton, 1995). Although perennial species are found on *heuweltjies*, the competitive release of some perennial plant species on *heuweltjies* may result in a shift towards annual species while the matrix is mostly occupied by long-lived perennial species.

Additionally, when comparing community composition at the site level, all sites displayed clear clustering. Argentina and Tierberg LTER were relatively similar in terms of community composition, while Wolwekraal was grouped independently. Geographical location is known to affect arthropod communities at small spatial scales (Seymour and Dean, 1999). Although Argentina and Tierberg LTER have undergone different historic grazing regimes, their proximity to one another might be able to explain the similarities in community composition. Furthermore, both Argentina and Tierberg LTER had similar plant communities. This is due to plant succession in the Succulent Karoo being a notoriously slow process (Rahlao et al. 2007; Seymour et al. 2010). Vegetation often takes decades to recover, which may explain why these plant communities resemble one another and, as a result, may allow for similar arthropod communities to occur. Additionally, Wolwekraal Nature Reserve exhibited different plant and arthropod communities compared to Tierberg and Argentina. Wolwekraal is located over 20 km away from the other sampling localities and differs significantly with regards to its habitat and environmental conditions compared to Argentina and Tierberg which have similar soils. The *heuweltjies* at Wolwekraal were much larger on average, had different soil texture and had significantly lower plant cover than the previous two sites.

2.4.3 Beta-diversity

Beta-diversity can be quantified in various ways, with these metrics often leading to differing results (Anderson et al., 2011). Partitioning beta-diversity into turnover (β_{repl}) and species richness differences (β_{rich}), provides a better understanding into the underlying causes of spatial organization of biotic communities (Baselga, 2010; Mori et al., 2018). Our results found that both beta-diversity components varied widely across the different biotopes and sites. The beta-diversity between *heuweltjie* and matrix plots were not as high as previously thought, with moderate beta diversity for both epigaeic and foliage arthropods, although species turnover, the replacement component, was

more responsive to the different biotopes for epigaeic arthropods than foliage arthropods, for which a combination of species turnover and differences in species richness were more influential.

In contrast, high levels of beta-diversity were found within *heuweltjie* and matrix plots for both epigaeic and foliage arthropods. Epigaeic arthropods on *heuweltjies* were driven by species turnover whereas the foliage arthropods had almost equal proportions of species turnover and species richness difference. Species turnover was responsible for the high beta-diversity in the matrix for both the epigaeic and foliage arthropods. In other words, changes in arthropod communities within each biotope arise because of species replacement rather than differences in species richness. Similarly, Cornell (2014) found that changes in arthropod communities can be attributed to *heuweltjies* contributing towards the beta-diversity and species turnover in the region. Intra-*heuweltjie* and – matrix plots were significantly different in species composition pointing to the value of both *heuweltjie* and matrix patches to epigaeic and foliage arthropod communities. These communities are generally well conserved as the replacement of species allows different species to occupy different niches. Conversely, the *heuweltjies* in Worcester have shown signs of biotic homogenization, as lower species turnover was observed within the *heuweltjie* patches (Cornell, 2014). It is possible that *heuweltjies* and matrix plots may be at different developmental stages, in terms of the age, termite activity or geographical location, which may explain changes in communities.

When considering beta-diversity of epigaeic arthropods between sites, species turnover explained most of the differences. Epigaeic arthropod communities showed greatest dissimilarity between Argentina – Wolwakraal and Tierberg – Wolwakraal. Unlike the ground dwelling arthropods, foliage arthropods exhibited beta-diversity driven largely by species richness differences with the greatest dissimilarity between Argentina – Tierberg and Argentina – Wolwakraal. Wolwakraal is located over 20 km away from Argentina and Tierberg and differs significantly with regards to its habitat and environmental conditions. The *heuweltjies* at Wolwakraal were much larger on average, had different soil texture and had significantly lower plant cover and plant height than the previous two sites. The three sites are not far from one another which add support that *heuweltjies* are key for arthropod communities at different spatial scales. These unique biotopes increase heterogeneity in the landscape and so increase regional biodiversity.

2.4.4 Conclusion

In conclusion, both *heuweltjies* and matrix plots are important biotopes for arthropod biodiversity in the Southern Karoo. Although multiple studies have shown that *heuweltjies* are highly disturbed

sites, it seems as if these patches provide suitable conditions for different arthropod communities regardless of the extent of the disturbance. Landscape heterogeneity depends on the structural complexity of habitats, as more complex habitats provide greater resources and niches for species to persist compared to less complex ones (MacArthur and MacArthur, 1961). Understanding how these patches affect alpha- and beta-diversity gives us insight into what processes *heuweltjies* provide and the role they play in maintaining arthropod diversity. Additionally, understanding which factors maintain ecological communities at various spatial scales may provide insights to how certain disturbances affect biodiversity (Dornelas et al., 2014). Only 8% of the Succulent Karoo is protected, which severely underrepresents the biodiversity in the biome (Hoffman et al., 2018). The change in arthropod communities within *heuweltjies* across a relatively small spatial scale, suggests that these communities are vital for ecological functioning as *heuweltjies* make up almost a quarter of the biome (Lovegrove and Siegfried, 1986) and should be adequately managed in congruence with other land use practices (e.g livestock farming) in a way that benefits both parties.

It is important to note that this study only focussed on the influence that different biotopes have on the diversity of arthropod taxa (morphospecies). Further research into other diversity types such as phylogenetic or functional diversity may possibly highlight other patterns of diversity (Cardoso et al., 2014). This study has set out a baseline of species occurrence on and off *heuweltjies* which can facilitate future assessments of change in arthropod communities over time, particularly under future scenarios of good and poor rainfall. Additionally, habitat preferences of species are needed to understand the effects that climate change will have in the Succulent Karoo as long-lived arthropod species such as the cicada, *Quintilla consepsa*, are highly dependent on *heuweltjie* soils and rainfall as a cue for oviposition, egg development and the juvenile survival (Milton and Dean 1992). Furthermore, short pulses of rain are proven to be crucial in buffering against species extinctions during drought conditions in arid regions (Maute et al., 2019), making extreme weather events crucial in dictating arthropod abundances and distributions.

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3. Chapter 3: Assessing the influence of *heuweltjie* quality, size and isolation on arthropod biodiversity in the semi-arid Succulent Karoo

Abstract

A characteristic feature of earth's drylands is the patchy nature of the vegetation, often referred to as a two-phase mosaic landscape, comprised of a homogenous matrix and distinctive vegetated patches. The latter are considered vital for ecosystem functioning as they provide refuge to biota from the harsh conditions. Both epigaeic and foliage arthropods contribute considerably to biodiversity patterns and processes, but little is known of how their richness, abundance and composition varies between patches and the matrix in these dryland systems. A unique feature found throughout the Succulent Karoo are distinct patches, locally referred to as *heuweltjies*. Despite their highly disturbed nature, these mounds are hotspots for both floral and faunal biodiversity. In this study I investigate the response of epigaeic and foliage-dwelling arthropod communities and how they respond to *heuweltjie* isolation (distance to nearest neighbour, average distance to nearest neighbour, density), size and quality (average plant height, dead plant percentage cover, termite frass). Additionally, I identified which species are significantly associated with these mounds and determine whether they are influenced by *heuweltjie* isolation, size and quality. Patch isolation and quality were the most significant in dictating arthropod richness, abundance and community composition. More specifically, average proximity of sampled *heuweltjies* to other neighbouring *heuweltjies*, termite frass and vegetation structure (percentage cover and height) were key determinants for epigaeic and foliage dwelling arthropods. The uniqueness of these mounds as landscape features providing suitable habitats for arthropods and emphasizing their importance in promoting landscape heterogeneity, highlight *heuweltjies* as key resources for arthropod biodiversity in the Succulent Karoo.

3.1 Introduction

Habitat patches are areas of vegetation that are distinct from their surroundings and often vary in terms of their size and spatial configuration (Forman, 1995). Through provision of resources, refuges and niches, habitat patches contribute significantly towards plant (Joseph et al., 2011), arthropod (Liu et al., 2016), bird (Dean et al., 1999), reptile (Michael et al., 2008) and mammal (Mapelli and Kittlein, 2009) diversity, ultimately affecting the spatial distribution of species. Although habitat patches are often talked about in fragmented landscapes in agriculture (Briggs et al., 2019) and urban areas (Johansson et al., 2019), there are many smaller naturally-occurring patches found throughout the world such as temperate forest canopies (Swart, 2020), termite mounds (Okullo and Moe, 2012), mud wallows (Beck et al., 2010), shrub patches (Liu et al., 2016) and non-anthropogenic earth mounds (mima mounds and nabkhas) (Dalquest and Scheffer, 1942; Nickling and Wolfe, 1993). Therefore, understanding why certain habitat structures or patches support different patterns of diversity remains valuable for conservation management purposes (Pryke et al., 2013; Seymour et al., 2016).

The semi-arid and arid regions of the world, often referred to as drylands, occupy approximately 41% of earth's terrestrial surface (Feng and Fu, 2013). Since water availability is limiting in these environments, soil heterogeneity can play an important role in modulating water storage, infiltrability, accessibility to plants and hydraulic conductivity (Mucina et al., 2006; Francis et al., 2007; Vásquez-Méndez et al., 2011), which offers heterogeneous settings for flora and fauna to inhabit (Liu et al., 2016; Meloni and Martinez, 2020). A unique feature of drylands and contributor to soil heterogeneity is spatially patterned vegetation typically found in patches, surrounded either by relatively homogenous vegetation or bare soil (Aguair and Sala, 1999). The spatial arrangement and quality of these natural patches for arthropod communities have received little attention and are not fully understood, however, especially in the drier regions of the world.

Arthropod communities are suitable for sampling in arid regions as they are often abundant and highly diverse (Pinero et al., 2011). Epigaeic arthropods refers to all arthropods that spend part of their lives on the soil or leaf litter surface. Epigaeic arthropods are essential components for ecosystem functioning in arid and semi-arid environments (Whitford, 1996). These organisms are directly or indirectly involved in modulating soil processes such as water infiltration, litter decomposition, nutrient and biogeochemical cycling (Whitford, 1996; Booij, 2011; Janion-Scheepers et al., 2016). Foliage dwelling arthropods are those directly dependent on vegetation as a food resource, nesting site or that spend majority of their lives on plants. Foliage dwelling arthropods of the Succulent Karoo are vital for the pollination of many plant species (Struck, 1994), with

specialized pollinator relationships being developed between the highly endemic monkey beetles (Scarabaeidae: Hopliini) and various Mesembryanthemaceae species (Colville et al., 2002; Mayer et al., 2006). Additionally, many leafhoppers and cicadas are dependent on a myriad of plant species, as their roots are an important food source during their larval stages (Milton and Dean, 1992). Therefore changes in epigeaic and foliage arthropod community structure may alter key ecosystem processes (Whitford, 1996). The Succulent Karoo invertebrate assemblage is dominated by species from Blattodea, Coleoptera, Diptera and Hymenoptera (Colville, 2002; Nchai 2008). Most of the work surrounding arthropods in the Succulent Karoo has been centred on the harvester termite *Microhodtermes viator* (Latrielle) and the role it plays in the formation of peculiar earthen mounds called “*heuweltjies*” (Lovegrove and Siegfried, 1989; McAuliffe et al., 2019). However, the other arthropod fauna of Succulent Karoo remain relatively unknown (Vernon, 1999; Janion-Scheepers et al., 2016).

Dotted throughout the semi-arid south-western region of southern Africa are soil mounds locally known as *heuweltjies* (Lovegrove and Siegfried, 1989, Picker et al., 2007). These ubiquitous circular mounds are regularly spaced and make up roughly a quarter of the biome (Lovegrove and Siegfried, 1986, 1989). Their sizes differ dependent on geographical location but reach up to 30 m in diameter and 2.5 m in height (Moore and Picker, 1991). The pattern of *heuweltjies* in the Succulent Karoo forms a mosaic network of localized soil and plant patches that are clearly distinguishable from the surrounding homogenous matrix due to their unique edaphic properties that differ in terms of texture, nutrients and water retention (Midgely and Musil, 1990; Booï, 2011; Kunz et al., 2012). Numerous studies have found consistent evidence that *heuweltjies* support distinct plant assemblages which differ in terms of composition and cover (Rahlao et al., 2008; Booï, 2011; Kunz et al., 2012) and attract a variety of animals (Louw et al., 2017; Arena et al., 2020). However, few studies have focussed on the influence of these patches on arthropod communities.

Island biogeography theory and metapopulation ecology predict that size, degree of isolation and quality of habitat patches are crucial in dictating species persistence (Hanski, 1999, MacArthur and Wilson, 2016). Immigrants and emigrants are more likely to encounter habitat patches that are less isolated, in this case *heuweltjies* spaced closely together within a homogenous matrix. Additionally patches that are larger should experience a higher probability of species persistence (Whittaker, 1960) owing to increased niche availability and microhabitats such as aardvark burrows. Larger patches are more likely to contain more burrows than smaller patches. Aardvark burrows are commonly found on *heuweltjies* and have lower thermal regimes compared to unborrowed *heuweltjies* and the matrix (Louw et al., 2017). These conditions may provide refuge for a host of arthropod species against unfavourable climatic conditions and predation. Therefore species richness

should be directly correlated with an increase in “island” size and a decrease with isolation. In theory, conserving large areas of land that exhibit high levels of connectedness should be a priority. However, given rates of habitat transformation and degradation, large natural patches often do not exist in drylands, instead these patches are rather small and fragmented throughout the landscape (Lovegrove and Siegfried, 1989). Multiple studies have indicated the significance behind the spatial distribution of natural habitat patches to ensure species are able to move to and from patches with better resources and less competition (Liu et al., 2016; Meloni et al., 2020). *Heuweltjies* are regularly dispersed (non-randomly dispersed) and debated to be caused by abiotic or biotic processes or a combination of the two (Moore and Picker, 1991; Cramer et al., 2012; McAuliffe et al., 2014). It is interesting, therefore, to consider how the spatial patterning of *heuweltjies* might affect arthropod communities.

Landscape degradation is an ever increasing problem facing the world’s drylands with the Succulent Karoo being no exception. Disturbances such as overgrazing and extreme climatic events (i.e., prolonged droughts) are known to decrease vegetation cover which in due course affects the spatial patterning of the vegetation (Kefi et al., 2007; Verwijmeren et al., 2014) as well as impacting arthropod communities (Seymour and Dean, 1999; Nchai, 2008). With only 8% of the Succulent Karoo protected (Hoffman et al., 2018), understanding the spatial arrangement of *heuweltjies* and its influence on arthropod biodiversity may provide further insight into the importance of these patches. *Heuweltjies* may act as refuges for a myriad of arthropod species because of their unique soil properties. If *heuweltjies* are associated with high numbers of arthropod species and abundance, some consideration towards appropriate management of the landscape should be taken into account since *heuweltjies* are embedded within the landscape.

Although not commonly applied in ecology, the mesofilter presents a unique way to assess certain landscape elements for conservation purposes. The mesofilter approach was first introduced by Hunter (2005); it identifies which landscape features (e.g., *heuweltjies*) are important for certain species in a specific area. This allows rapid assessment of an area since landscape features are much easier to examine compared to surveying multiple species (Crous et al., 2013). Using landscape features such as percentage rockiness (Crous et al., 2013), presence of logs (Barton et al. 2009) and aspect (Weiss et al. 2013) has proven important for various arthropod assemblages. Aridity has a significant effect on *heuweltjie* distribution over large spatial scales (Lovegrove and Siegfried, 1989), with *heuweltjie* size and distance to nearest neighbour decreasing from west-east while *heuweltjie* density increases from west-east (Lovegrove and Siegfried, 1989). Evaluating *heuweltjies* in terms of their size, isolation and quality at smaller spatial scales may provide a better way to rapidly assess which mounds are important for arthropod communities.

To encourage further discussions surrounding the importance of small habitat patches for arthropod biodiversity in arid and semi-arid regions, I present my findings regarding the influence that the spatial organization *heuweltjies* has on epigaeic and foliage arthropod species richness, abundance and composition. The spatial characteristics of the *heuweltjies* were split into three categories: 1) patch size, 2) patch isolation, which includes distance to nearest neighbour (DNN), average distance to nearest six neighbours (ADNN) and density of neighbours within a 100 m buffer zone and 3) patch quality, which comprises of vegetation percentage cover, dead vegetation percentage cover, average plant height, plant species richness and the presence of termite frass. Additionally, I identified

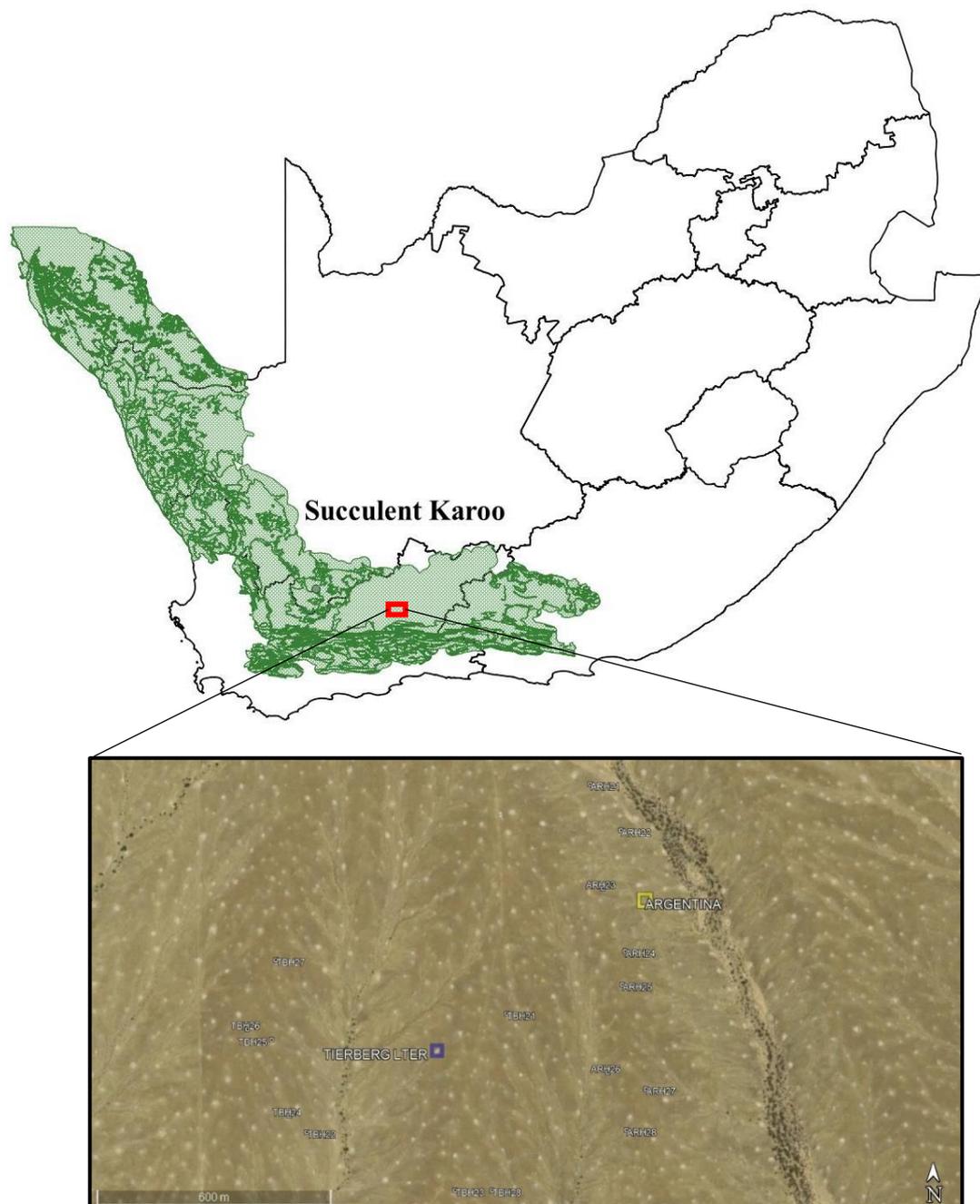


Figure 3.1: Sample sites are located around Prince Albert, Western Cape, South Africa ($33^{\circ}13'31''\text{S}$; $22^{\circ}01'48''\text{E}$). Yellow = Argentina Wildlife farm, Blue = Tierberg LTER. *Heuweltjies* (lightly coloured spots) can be clearly seen in the picture above.

indicator species for each biotope type (*heuweltjie* and matrix) and assess which patch variables are important for these indicator species. Following the island biogeography and metapopulation theories, I hypothesize that both epigaeic and foliage-dwelling arthropods will respond to patch size, isolation and quality. *Heuweltjies* that are larger in size, more closely situated and have higher quality (plant species richness, percentage cover and termite frass) compared to other *heuweltjies* will exhibit greater arthropod diversity. Additionally, *heuweltjies* will also contain more indicator species compared to the matrix and these *heuweltjie* indicator species also responding positively to *heuweltjie* size, decreased distance to nearest neighbour and better patch quality.

3.2 Methods

3.2.1 Study area

The study was conducted near Prince Albert, Western Cape, South Africa (33°13'31"S; 22°01'48"E) (Figure 3.1). Most of the area is dominated by either currently or previously grazed livestock farms. Two sites were chosen; Tierberg long-term ecological research station (LTER) and the adjacent wildlife and livestock farm, Argentina, which is found within the Sandrivier valley (fully described in Milton, 1992). The climate is semi-arid throughout this region and overlaps both summer and winter rainfall (Arena et al. 2018). However, rainfall is limited due to the rain shadow effect caused by the Swartberg mountain range (Mucina et al., 2006). The mean annual precipitation (MAP), over a 30 year period is 196 mm (CV 38%) with most falling in autumn (62 mm) (Mucina et al. 2006; Arena et al. 2018). Temperatures range from -5 °C to 43 °C, with a mean annual temperature (MAT) ranging from 16 °C - 17.5 °C (Mucina et al., 2006; Seymour et al., 2010). Elevation ranges from 480 – 1120 m above sea level (Mucina et al., 2006).

The study area falls under the Prince Albert Succulent Karoo vegetation type (SKv 13) which consists of flat plains and stony ridges that are colonized by leaf succulents and small-leaved karroid shrubs (Mucina et al., 2006). *Heuweltjies* are an important feature in this vegetation type, and have a density of $\sim 2.1^{-1}$ ha (Dean and Milton, 1999); they support distinct sets of succulent and salt-tolerant plants such as *Augea capensis*, *Psilocaulon utile* and *Salsola* species while *Pteronia pallens* and *Ruschia spinosa* are often found within the inter-*heuweltjie* plains (matrix) (Mucina et al., 2006; Arena et al., 2018). Since 2011 up until the time the study took place (2020), the Succulent Karoo has experienced severe drought conditions. The well below average rainfall has significantly affected both the flora and fauna in this region.

3.2.2 Arthropod sampling

Arthropods were sampled in early spring (September 2019) and late summer (February 2020), on two biotope types: *heuweltjies*, and in the inter-*heuweltjie* plains (matrix). Eight *heuweltjies* were randomly chosen at two sampling localities (Argentina and Tierberg). Two arthropod sampling methods were used: 1) pitfall traps and 2) vacuum sampling. Each *heuweltjie* was paired with a matrix plot placed 25 m away in a random direction. Four pitfalls, 55 mm in diameter, were placed approximately 1 m apart at the centre of each *heuweltjie* and matrix plot, resulting in 8 pitfalls per site (Figure 2.2). Pitfall traps were filled halfway with a 1:1 solution of ethylene glycol and water, with a drop dishwashing liquid to break the surface tension. Traps were positioned in a square and spaced 1 m apart. Traps were left open for 12 days and replaced every six days. Once collected, all pitfall samples were placed into a 70% ethanol solution and stored until sorted. Sampling consisted of 384 pitfalls per season with 768 pitfalls in total.

Vacuum sampling of foliage-associated invertebrates was conducted along 5 x 5 m transects at each sampled *heuweltjie*. Sampling took place in early spring and replicated again in late summer. To standardize this, each site was sampled at the same time (between 09:00 – 14:00) on different days because insect activity fluctuates depending on the time of day. A fine mesh sock was attached to a STIHL 86 2-stroke petrol leaf blower to sample shrub-dwelling arthropods. Vacuum sampling differed depending on the size of the vegetation occurring along each transect. This was done to avoid any catching bias towards the smaller plants. The vacuum sampler was inserted twice for three seconds over all smaller plants encountered, while larger vegetation received 3 – 6 insertions, each lasting one second. All debris and arthropods caught were transferred to large ziplock bags and tightly sealed and placed into a freezer until sorted. A total of 32 vacuum samples were taken.

Arthropod identification was done to the lowest taxonomic level possible using taxonomic resources (Dippenaar-Schoeman, 2014; Slingsby, 2017). However, due to time constraints and lack of available taxonomic resources to identify the targeted taxa, the “morphospecies” approach was used. The usage of morphospecies or recognizable taxonomic units (RTU) as a proxy for species level sorting allows for the rapid assessment of species based on morphological traits (Oliver and Beattie, 1993) and is proven to be reliable for arthropod communities (Derraik et al., 2002).

3.2.3 Environmental variables

The environmental variables selected were split into three metrics: 1) patch size, 2) patch isolation and 3) patch quality. *Patch size* (*heuweltjie* area) was calculated using the length and breadth measurements obtained in the field. *Heuweltjies* are circular in nature and therefore the area (patch

size) was calculated using the formula: $A = \pi r^2$. To assess the role of patch isolation, high resolution satellite images of the two sites (Argentina and Tierberg LTER) were analysed (Google Earth, 2020). In order to ensure that all visible *heuweltjies* were counted, separate satellite images from different years were analysed (Figure 3.3). The following measurements were calculated to assess *patch isolation*: 1) D_{NN} , *heuweltjie* distance to nearest neighbour, 2) D_{AN} , average distance between the sample *heuweltjie* and six nearest *heuweltjies* and 3) D_{DD} , the total number of *heuweltjies* (density) within a 50 m radius (100 m diameter) of the sampled *heuweltjie*. *Patch quality* was assessed using different environmental variables. Using the line-intercept method from Ellenberg and Mueller-Dombois (1974), vegetation cover, average plant height, dead plant percentage cover and plant species richness were recorded along 5 x 5 m transects on each sampled *heuweltjie*. Additionally the presence and absence of termite frass was noted. Site (Argentina and, Tierberg) was used as random variables.

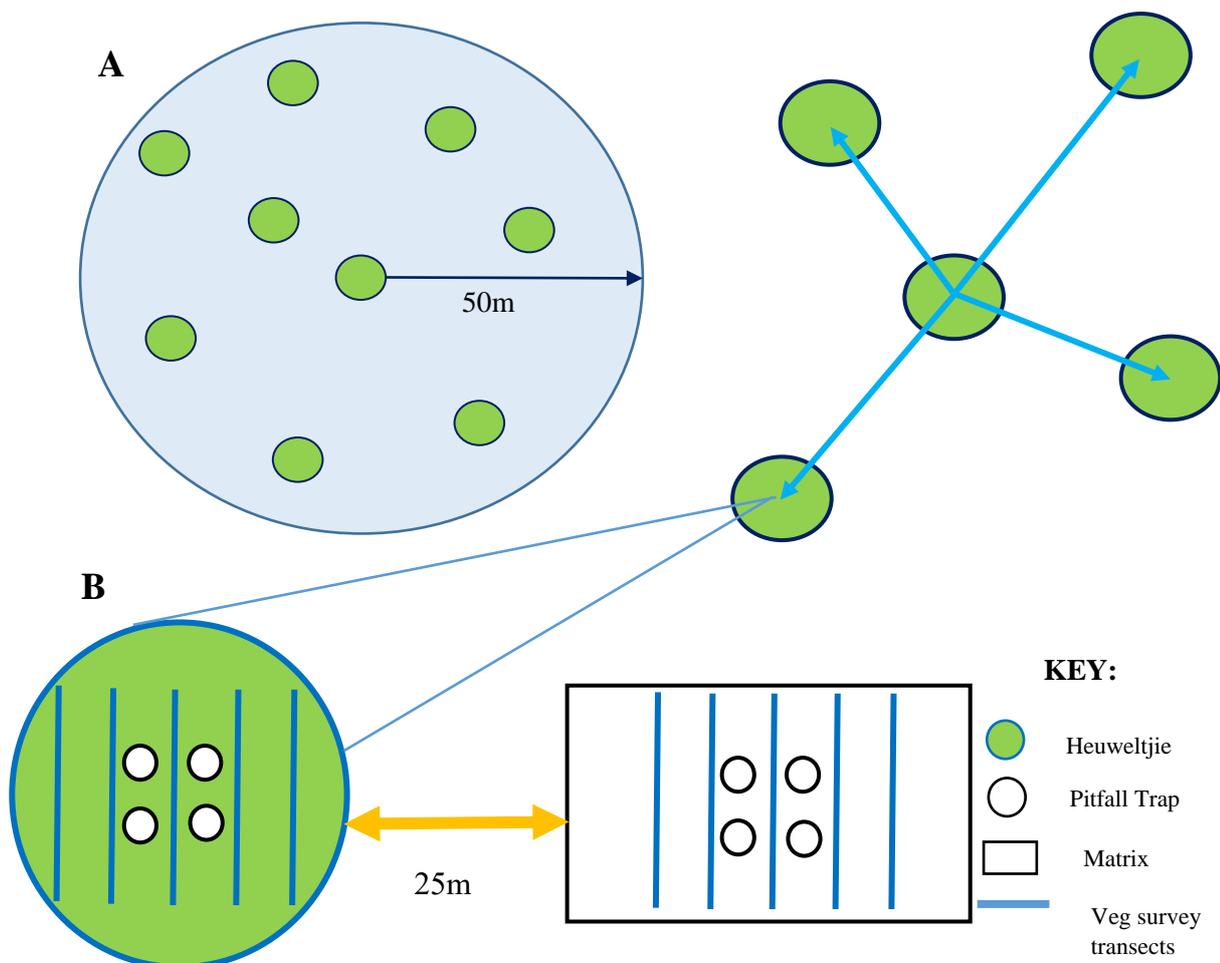


Figure 3.2: Sample design for measuring patch variables and arthropod sampling. A) Patch sampling contained measurements of *heuweltjie* size, distance to nearest neighbour, average distance to nearest six neighbours and the amount of *heuweltjies* within a 100 m buffer zone. B) Sample design for pitfall and vegetation surveys.

3.2.4 Statistical analyses

In order to assess which of the three patch metrics (isolation, size and quality) had an influence on epigaeic and foliage dwelling arthropod species richness and abundance, a model selection procedure was used (Barton, 2009). The procedure tests which environmental variables are responsible for the observed patterns on the *heuweltjies* at the two sites. Firstly, all environmental variables were scaled and then using the variance-inflation factor (VIF) function from the *car* package (Fox and Weisberg, 2019) to check for multiple collinearity and redundancy between predictor variables. Environmental variables with high VIF values were taken out until all variables had a $VIF < 3$, resulting in nine variables suitable for analysis. These nine variables were split into three categories, where applicable, according to the theory of island biogeography: 1) patch size – *heuweltjie* area (m^2), 2) patch isolation – distance to nearest neighbour (m), average distance to nearest six neighbours (m) and *heuweltjie* density within a 50m radius (100 m buffer zone) and 3) patch quality – plant species richness, total vegetation cover (%), total dead vegetation cover (%), presence of frass and average plant height (cm).

In the arthropod abundance data for both epigaeic and foliage dwelling species, Generalised Linear Mixed Models (GLMMs) were then constructed for species richness and abundance analyses with site as a random factor. Both epigaeic and foliage species richness and abundance were not normally distributed and were therefore fitted with a negative binomial and gamma distribution using the *glmmADMB* package (Bolker et al., 2012). The package *glmmADMB* is a generalized linear mixed model AD model builder for non-linear data. Models were constructed with all possible combinations of the nine explanatory variables using the “dredge” function from the *MuMIn* package (Bartón, 2015). The models were ranked using the corrected Akaike Information Criterion with a $\Delta AICc$ of ≤ 4 , to find the best possible combination of environmental variables. As a result, using the “model.avg” function, the top models (those with the lowest $\Delta AICc$ values within 4 units of that with the lowest AICc) conditional averages was reported to avoid the model shrinking to zero.

To gauge which of the nine patch variables had an effect on epigaeic and foliage species composition, the *mvabund* package (Wang et al., 2012) fitted with a negative binomial distribution was used. The “manyglm” function employs multiple individual GLMs on a combination on variables between the community and the environmental data to ascertain the effects on community composition (Wang et al. 2012). Test statistics were calculated using the “pit.trap” resampling method with 999 permutations combined with the “shrink” parameter (ridge regularization) which assumes that predictor responses are correlated.

A species indicator analysis was performed to assess the relationship between species abundance in a specific habitat (Dufrene and Legendre, 1997). I used the *indicspecies* package (De Caceres et al., 2016) to determine which species were significantly associated with either the *heuweltjie* or matrix for epigaeic and foliage dwelling arthropods. The “multipatt” function calculates a value ranging from 0-1 which is made up of two components of the Indicator Value Index (IndVal); specificity (A) and sensitivity (B). The first component (A), *specificity*, determines the probability that a particular species occurs at a specific site while the second component (B), *sensitivity*, is the probability that all sites include a specific species. P-values were estimated using 9999 random permutations to test the significance between a particular species and biotope. Additionally, model selection (Bartón, 2015) and mvabund (Wang et al., 2012) procedures as mentioned above were run again using only the indicators species identified on the *heuweltjies*. This was done for species richness, abundance and composition to evaluate whether these species respond to any of the three patch variables stated above. The multivariate abundance data for indicator species composition were additionally analysed using the *boral* package (Hui et al., 2016). *Boral* is a model-based analysis that generates an unconstrained ordination using Bayesian Markov Chain Monte Carlo (MCMC) methods by

employing a set of latent variable models to visually assess the effect of environmental variables at the community level (Hui et al., 2016).

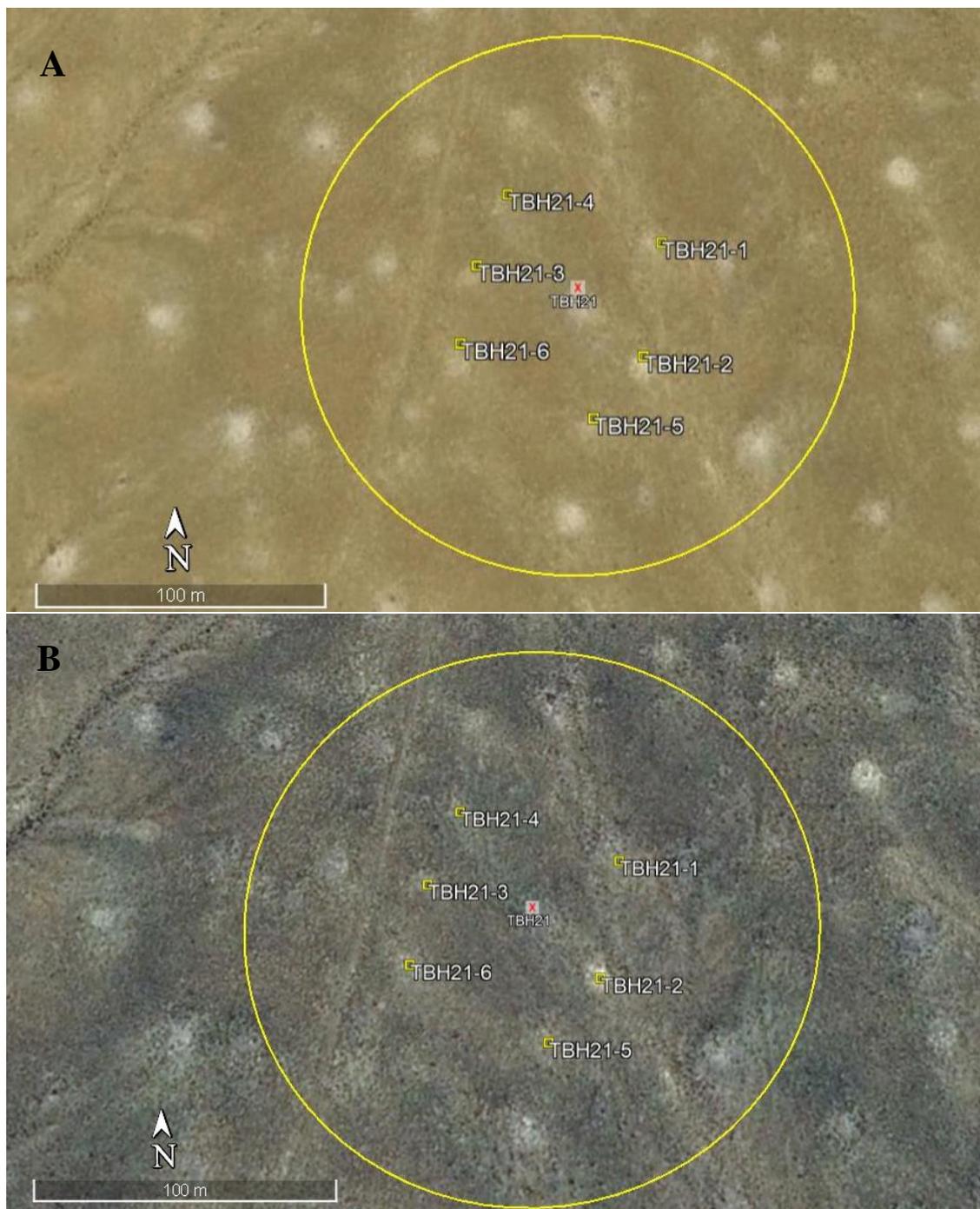


Figure 3.3: Two high resolution satellite images from Google Earth Pro. A) Image from Tierberg LTER date 12/2020. B) Image from Tierberg LTER dated 11/2018. The red circle, 50m radius, outlines the zone in which all *heuweltjies* were counted. The centrally positioned TBH21 represents the sampled *heuweltjie*. The yellow points represent the nearest six *heuweltjies* in relation to the sampled *heuweltjie*.

3.3 Results

3.3.1 Arthropod and environmental variables

Table 3.1 gives a summary of the environmental variables associated with the two sites, Argentina and Tierberg. The nearest neighbour (closest *heuweltjie* from the sampled *heuweltjie*) distances ranged from 26.18 m - 56.1 m at Argentina and between 23.73 m - 53.76 m at Tierberg (Appendix K). Average distance to the nearest six neighbours ranged from 47.97 m – 79.95 m at Argentina and between 44.13 m – 81.28 m (Appendix K). *Heuweltjies* also varied in size at the two sites with an average of 83.31 m² at Argentina and 90.31 m² at Tierberg (Table 3.1).

Table 3.1: Results showing from the environmental variables (average plant height, total plant percentage cover (PC), dead plant percentage cover (DPC)), distance to nearest neighbour (DNN), average distance to nearest neighbours (ADNN), *heuweltjie* density (Dens) and *heuweltjie* size (area) at Argentina and Tierberg. Additionally the dominate vegetation associated with the mounds and matrix. Significant variables are marked with *.

<i>Site</i>	<i>Argentina</i>		<i>Tierberg</i>	
<i>Biotope</i>	<i>Heu</i>	Mat	<i>Heu</i>	Mat
<i>Area (m²)</i>	83.31 (±21.05)	-	90.31 (±32.94)	-
<i>Height (cm)</i>	12.97 (±7.88)	16.36 (±5.50)	17.26 (±4.85)	18.83 (±3.60)
<i>PC (%)</i>	41.28 (±13.54)*	34.63 (±7.20)*	53.75 (±13.06)*	39.31 (±9.60)*
<i>DPC (%)</i>	14.88 (±10.29)*	5.97 (±2.81)*	31.45 (±14.55)*	14.48 (±10.33)*
<i>DNN</i>	40.99 (±10.62)	-	36.62 (±9.97)	-
<i>ADNN</i>	64.34 (±12.12)	-	54.80 (±11.66)	-
<i>Dens</i>	15.25 (±3.85)*	-	19.62 (±3.74)*	-
<i>Dominate</i>	Dead, litter, <i>P. pallens</i> , <i>M. lutea</i> and <i>L. uniflorus</i>	Dead, litter, <i>R. spinosa</i> , <i>P. pallens</i> , <i>B. vaginatus</i> , <i>O. sinuatum</i> and <i>Z. retrofactum</i>	Dead, litter, <i>P. pallens</i> , <i>B. vaginatus</i> . <i>M. utile</i> and <i>Peersia</i> spp.	Dead, litter, <i>P. pallens</i> , <i>R. spinosa</i> , <i>C. subaphylla</i> , <i>O. sinuatum</i> , <i>H. latipetala</i> and <i>Z. retrofactum</i>

Plant percentage cover, both total and dead, was higher on *heuweltjies* than in the matrix at both sites. The *heuweltjies* at Tierberg had a higher total and dead plant percentage cover compared to Argentina (Table 3.2). *Heuweltjies* at Tierberg had a higher average plant height than Argentina however, they were both less than the average plant height within the matrix (Table 3.1). Out of the 16 *heuweltjies* sampled, termite frass was present on 10, 6 in Argentina and 4 in Tierberg. Pairwise comparisons show that *heuweltjie* density was the only significant variable between the *heuweltjies* at Argentina and Tierberg ($p = 0.021$) while total and dead plant percentage cover was significant between the *heuweltjie* and matrix ($p < 0.001$; $p = 0.005$) (Table 3.1). Arthropod assemblages found in the traps consisted of Acari, Aranea, Blattodea, Coleoptera, Diptera, Hymenoptera, Lepidoptera, Mantodea, Orthoptera, Scorpiones, Siphonaptera, Solifugae, Thysanura and Thysanoptera. Within the 100 m buffer zone from each sampled *heuweltjie*, density ranged from 11 – 20 at Argentina and 14 – 25 at Tierberg (Appendix K).

3.3.2 Which patch variables drive arthropod diversity on *heuweltjies*

Total percentage cover and plant species richness had the highest generalised variance-inflation (collinearity) values as they were found to be correlated with dead plant percentage cover and *heuweltjie* area and were therefore excluded from all the generalised- and linear mixed models. Distance to nearest neighbour (DNN), average distance to nearest neighbours (ADNN), *heuweltjie* density, dead plant percentage cover, average plant height, presence/absence of termite frass and *heuweltjie* size were all included in the model selection procedure. Five out of the nine variables were significant for epigeic and foliage arthropod species richness, abundance and composition. Significant explanatory variables were average distance to nearest neighbour, distance to nearest neighbour, average plant height, dead plant percentage cover and the presence of frass.

The best model for epigeic species richness selected termite frass and average distance to nearest neighbour whereas distance to nearest neighbour, *heuweltjie* density, *heuweltjie* size, average plant height and dead plant percentage cover had no significant effects on epigeic species richness (Appendix L). Species richness decreased when average distance to nearest neighbours increased and increased when termite frass was present on *heuweltjies* (Appendix L, Figure 3.4a-b). The model selection procedure for epigeic abundance included average distance to nearest neighbour, *heuweltjie* density, and distance to nearest neighbour and termite frass as strong predictors for epigeic species abundance (Appendix L). Distance to nearest neighbour (DNN) and *heuweltjie* size (area) were significantly correlated with epigeic abundance with higher abundances found as distance to nearest neighbour increased and as *heuweltjie* size decreased (Appendix M, Figure 3.4c-d).

The environmental patch variables significantly affecting epigaeic species community composition included distance to nearest neighbour, average distance to nearest neighbour, average plant height, dead plant percentage cover and the presence of frass (Table 3.2).

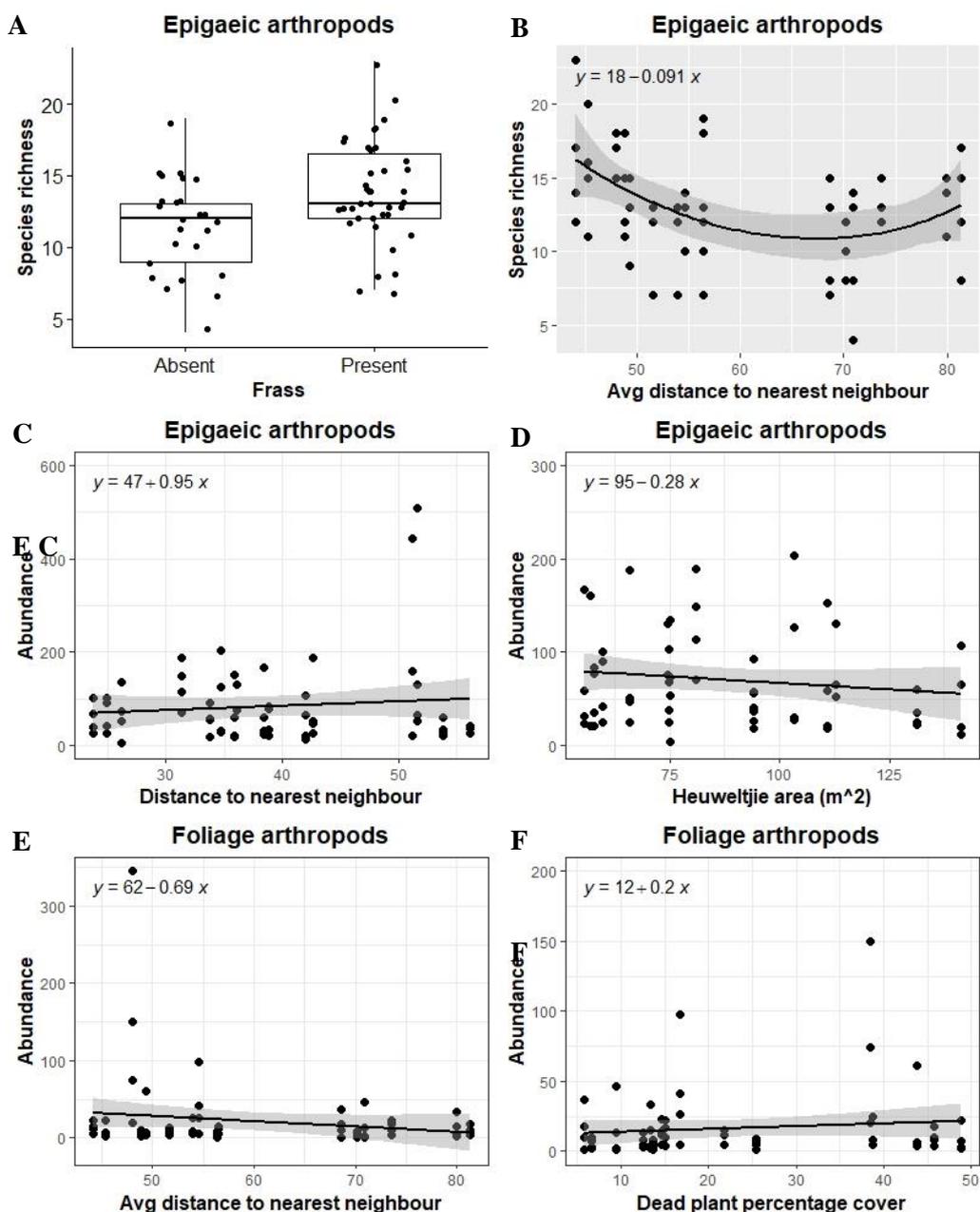


Figure 3.4: Graphs showing the relationship between a) epigaeic species richness and termite frass, b) epigaeic species richness and average distance to nearest neighbours, c) epigaeic abundance and distance to nearest neighbours and d) epigaeic abundance and *heuweltjie* size, e) foliage arthropod abundance and average distance to nearest neighbour and f) foliage arthropod abundance and dead plant percentage cover.

As for the foliage arthropod species richness, termite frass was the only patch variable included in the model selection procedure (Appendix L), however, it had no significant impact on species richness. Foliage arthropod abundance included average distance to nearest neighbour, termite frass and *heuweltjie* size as the best model (Appendix L). Only average distance to nearest neighbour and dead plant percentage cover exhibited a significant difference with foliage arthropod abundance

(Appendix M, Figure 3.4e-f). The quality and isolation categories proved to be important for foliage community composition with significant differences found between average distance to nearest neighbour and average plant height (Table 3.2).

Table 3.2: Results from the manyGLM analyses exploring the effect of each patch variable - distance to nearest neighbour (DNN), average distance to nearest neighbours (ADNN), *heuweltjie* density (Dens), *heuweltjie* area (HArea), dead plant percentage cover (DeadPC), average plant height and termite frass on epigaeic and foliage arthropod assemblage composition. Significant differences are marked in bold.

<i>Epigaeic arthropod composition</i>	<i>Patch var</i>	χ^2	<i>p-</i>	<i>Df</i>	<i>Foliage arthropod composition</i>	<i>Patch var</i>	χ^2	<i>p-</i>	<i>Df</i>
	DNN	11.373	0.006	62		DNN	6.852	0.493	62
ADNN	10.304	0.026	61	ADNN	7.266	0.092	61		
Dens	9.696	0.086	60	Dens	6.020	0.192	60		
HArea	7.733	0.181	59	HArea	6.415	0.009	59		
DeadPC	8.348	0.044	58	DeadPC	5.068	0.107	58		
Height	7.923	0.022	57	Height	5.758	0.008	57		
Frass	10.098	0.032	56	Frass	4.453	0.563	56		

3.3.3 Indicator species

Of the 353 morphospecies identified, 14 were recognizable as “indicators” for the *heuweltjie* and matrix plots. There were eleven morphospecies indicators identified amongst epigaeic arthropods with 7 associated with the *heuweltjie* and 4 with the matrix. The *heuweltjie* indicators were 5 coleopteran, 1 isopteran (Blattodea) and 1 Pseudoscorpiones species while the matrix indicators consisted of 3 ant (Formicidae) species (Appendix N, Figure 3.5). For the foliage dwelling arthropods only 4 morphospecies were associated with *heuweltjies*. Three belonged to Diptera with one hymenopteran (wasp) (Appendix N, Figure 3.5). High specificity values (component A) were found for all the species, both epigaeic and foliage dwelling arthropods, indicating that they are significantly associated with a specific biotope type. However, sensitivity values (component B) were considerably lower except for one dipteran species (Fly8) which had the highest probability of being found on *heuweltjies* (Appendix N).

As for which patch metrics significantly affected indicator species richness, abundance and composition, the presence of termite frass was the only patch variable included in the model selection procedure (Appendix L). Indicator species richness was significantly greater on *heuweltjies* with termite frass (Appendix O, Figure 3.6a). The best model for indicator abundance included average distance to nearest neighbour, dead plant percentage cover, *heuweltjie* size and termite frass (Appendix O). All patch variables were significantly different with the presence of termite frass, dead plant percentage cover and *heuweltjie* size showing positive relationships between indicator

abundance (Figure 3.6b-c), while average distance to nearest neighbour exhibited a negative relationship (Figure 3.6d). Indicator composition was significantly affected by termite frass and average plant height (Appendix P, Figure 3.7).

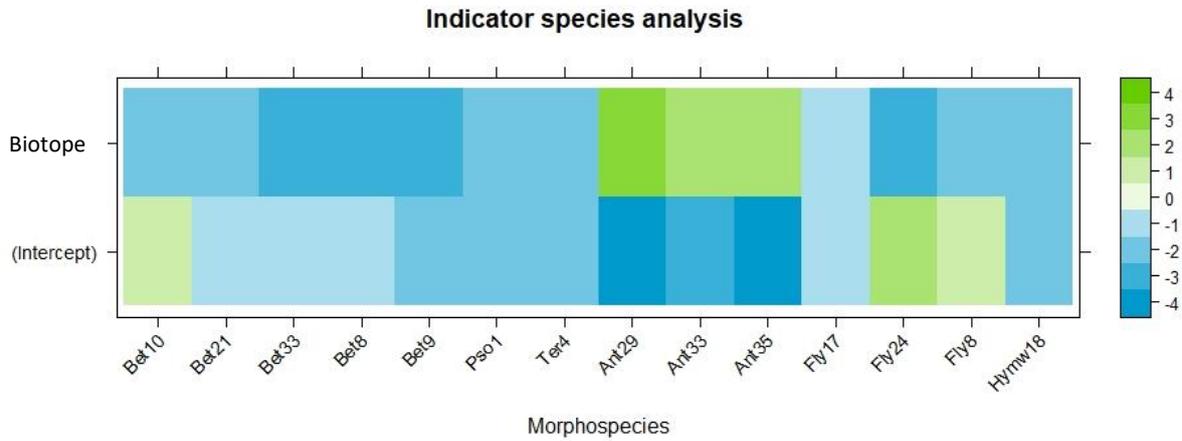


Figure 3.5: Coefficients of arthropod species that are most likely to occur on *heuweltjies* or matrix plots. Blue represents *heuweltjies* while the green represents the matrix. The darker the colour, the more likely a species occurs on that biotope

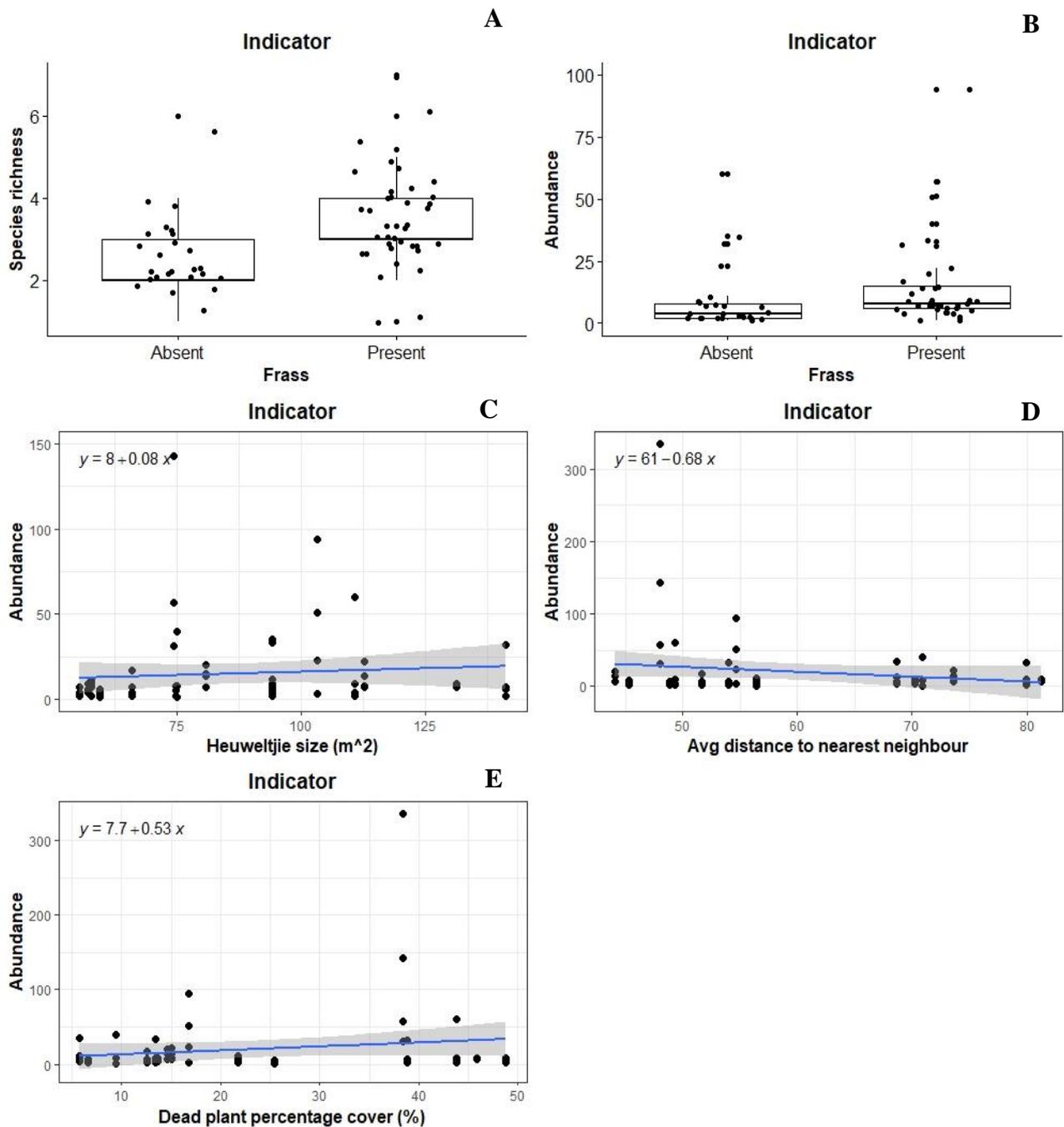


Figure 3.6: Graphs showing the relationship between a) indicator species richness and termite frass, b) indicator abundance and termite frass, c) indicator abundance and *heuweltjie* size and d) indicator abundance and average distance to nearest neighbour and e) indicator abundance and dead plant percentage cover.

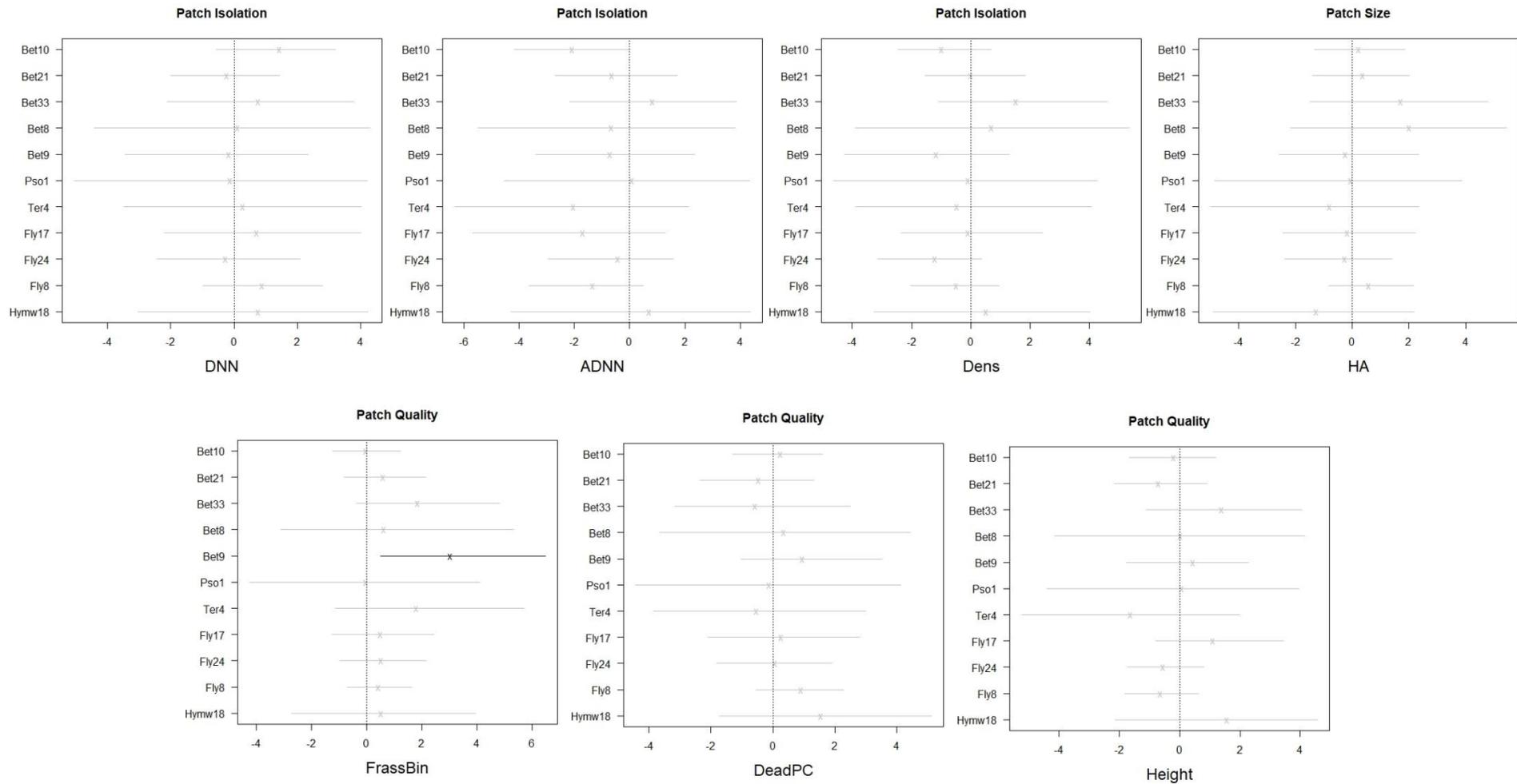


Figure 3.7: Indicator species influence on patch isolation (DNN- distance to nearest neighbour, ADNN- average distance to nearest neighbours, Dens – density) size (HArea – *heuweltjie* area) and quality (FrassBin – termite frass, DeadPC – dead plant percentage cover, Height – average plant height). Significant associations are shown in black and non-significant associations are shown in grey.

3.4 Discussion

This study showed that the quality and spatial organization of *heuweltjies* in the Succulent Karoo strongly influenced epigaic and foliage dwelling arthropod species richness, abundance and composition. My findings support the hypotheses that arthropods respond to patch closeness, size and quality. Epigaic (ground dwelling) arthropod communities exhibited a strong response towards distance to nearest neighbour (DNN), average distance to nearest neighbour (ADNN), *heuweltjie* area, presence of termite frass, dead plant percentage cover and average plant height whereas average distance to nearest neighbour, *heuweltjie* area, dead plant percentage cover and average plant height were the major determinants for the foliage arthropod communities.

There is a benefit of having a network of good quality patches that are closer together which enables the effective movement and dispersal of species because, alone, small isolated patches are not viable for species persistence (Zuidema et al., 1996). However, the factors that affect arthropod distributions are often multi-faceted and complex and are often influenced by the condition of the patch (Meloni et al., 2020), resource availability (Coatan and Cheasby, 1974), inter- and intraspecific competition (Lee and Wood, 1971; Cloudsley-Thompson, 2012), predation risks (Groner and Ayal, 2001) and dispersal behaviour (Grez and González, 1995).

3.4.1 Epigaic and foliage arthropod responses to isolation, size and quality of *heuweltjies*

Out of all three patch variables that encompassed patch isolation, distance to nearest neighbour and average distance to nearest neighbours proved to be the predominant variables affecting epigaic species richness, abundance and composition. While average distance to nearest neighbours only affected foliage arthropod abundance. The distance between habitat patches is proven to be significant for a variety of arthropod communities, with a decrease in species richness as patch distance increases (Liu et al., 2016, Meloni et al., 2020). Patches that are closer together enhances the connectivity and allows easier movement between patches of better quality, resulting in a higher probability of finding food while minimizing their time spent in the matrix.

Interestingly, epigaic arthropod abundance increased as distance to nearest neighbour increased. This could be indicative of arthropod dispersal behaviour as well as inter- and intra-specific competition since competition between species is often more prevalent in resource

limited environments (Lu et al., 2021). Additionally, arthropods differ in their dispersal behaviour ultimately affecting their immigration and emigration to and from different *heuweltjies*. Arthropods with higher dispersal capabilities have a higher probability of reaching other patches compared to arthropods with low dispersal abilities, who are more reliant on the quality of the patch. Additionally some arthropods vary in their dispersal with Coatan and Sheasby (1974) finding that *M. viator* tends to move further distances in search of food when plant cover is low.

Despite the historical exposure of the two localities to different grazing impacts, vegetation species richness was similar within Tierberg and Argentina. Due to multiple dead and unidentifiable plant species, caused by the current drought, only the most conspicuous species were accounted for. Both Argentina and Tierberg *heuweltjies* had a greater percentage cover and a lower average height than the matrix despite being considered areas of concentrated disturbance (Esler and Cowling, 1995; Louw et al., 2017). The vegetation on *heuweltjies* at Argentina and Tierberg consisted of generalist perennial species such as *Pteronia pallens*, *Brownanthus vaginatus* and *Malephora lutea*. Nonetheless, it is widely accepted that vegetation structure is a key factor for arthropod communities (Shelef and Groner, 2011). The results add further support for the importance of vegetation structure for epigeaic and foliage arthropod composition. More specifically, the two patch quality variables, dead plant cover and average plant height significantly affected arthropod species composition. Although dead plant cover was used since it was correlated with total plant cover, as it had a lower variance-inflation value, the branches and roots of dead plants often remain intact and contribute towards to vegetation structure.

Semi-arid regions such as the Succulent Karoo are characterized by their extreme environmental conditions in the form of high temperatures, radiation and aridity (Mucina et al., 2006). Additionally, these environments are often resource limited with availability of food and suitable refuges regulating species richness and abundances of many arthropod species. Plant communities provide refuge from predation, act as a food source and are potential mating and egg-laying sites (Dean and Milton, 1991). Although many species are adapted to these conditions, through the provision of increased percentage cover and plant height, these patches provide a unique microhabitat that ameliorates the harsh conditions. Termite mounds provide unique microclimates that are much cooler than their surroundings (Joseph et al., 2018).

Additionally, some beetle species in arid regions are known to use vegetation structure for thermoregulation purposes and a refuge against predation (Groner and Ayal, 2001; Shelef and Groner, 2011). *Pteronia pallens* occurs on both *heuweltjies* and matrix tends to grow taller on *heuweltjies* compared to the matrix (Louw et al., 2017), which may provide unique microclimates for some arthropods. However, it must be noted that due to the current drought in the Succulent Karoo most plants sampled were either long- to medium-lived perennials or dead and unidentifiable because no leaves or flowers were present. This could affect arthropods that rely on the vegetation as a drought refuge and food source, thus masking the true effect vegetation has on arthropod communities. It would be highly beneficial to conduct a follow-up comparative study during wetter conditions.

Heuweltjies are distributed across a variety of soil and vegetation types as well as rainfall and altitudinal gradients (Lovegrove and Siegfried, 1986; Picker et al., 2007). Mound density is correlated with rainfall and vegetation productivity (Picker et al., 2007). According to island biogeography theory, one would expect that larger *heuweltjies* to support greater diversity. However, this was not the case with only epigeic abundance influenced by patch size, with decreasing abundance as patch size increases. *Heuweltjie* density showing no significant effects on both epigeic and foliage arthropod richness, abundance and composition. The *heuweltjies* at Tierberg and Argentina are spread out at around $\sim 2.1 \text{ ha}^{-1}$ and have little variability in their size (Dean and Milton, 1999). Patch size is not always important for arthropods (Grez and Gonzalez, 1995). Due to the low variability in *heuweltjie* size and close proximity to other mounds, size may not play a significant role as initially thought as there are many other patches to choose from.

Despite the unresolved nature surrounding *heuweltjie* formation, there is substantial evidence indicating association of southern harvester termites, *Microrhodotermes viator*, with these mounds (Moore and Picker, 1991, Picker et al., 2007). A study from McAuliffe et al. (2019) proposed that ecosystem-engineering from *M. viator* coupled with abiotic factors such as precipitation and aeolian deposition results in positive feedback loops that aid in the *heuweltjie* formation and preservation. Social insects, such as termites, are renowned for their ecosystem engineering capabilities (Jones et al., 1994). They play a vital role in modifying both the chemical and physical properties of soils which benefit a myriad of plant and animal species. An additional benefit of *M. viator's* occupancy on *heuweltjies*, is their production of faecal pellets known as frass.

The results show that the presence of these faecal pellets was a major determinant for epigaeic species richness, abundance and composition. Foliage arthropods were not affected by termite frass as they are less likely to encounter the frass since they spend majority of their lives within the foliage. Termite frass is rarely found in large quantities in the homogenous matrix as well as unoccupied *heuweltjies*. *Heuweltjies* that contained no termite frass had significantly less arthropod diversity compared to when the frass was present which reiterates the importance of *M. viator* as a keystone species. Frass is used as a food source for a host of beetle and fly species occurring on *heuweltjies* across three locations in the Succulent Karoo (Cornell, 2014). Furthermore social insects are an abundant source of food for many arthropod species. The ant, *Ophthalmopone hottentota* (Ponerinae: *Ophthalmopone*), various daesiid solifugaes (Daesiidae: *Hemiblossia*) and *Ammoxenus* spiders (Araneae: *Ammoxinidae*) are known to exclusively prey on *M. viator* (Wharton, 1981, Dean, 1988, Dean, 1989). Another reason could be that ecosystem variables (such as habitat conditions and food sources) that are suitable for the termites may also be suitable for the various other arthropod species.

3.4.2 Indicator species

My findings indicate that more arthropods are significantly associated with *heuweltjies* than the matrix. There were fourteen indicator species identified, three belonging to the matrix and eleven on *heuweltjies*, which further suggests the value of these patches. As for the indicator species found on the *heuweltjies*, they comprised seven epigaeic and four foliage arthropod species which consisted of flies, termites, beetles and pseudoscorpions. More epigaeic indicator species (7 species) were found than foliage indicator species (4 species), therefore indicator species could follow similar trends as the epigaeic species mentioned in the previous section.

The indicator species responded strongly towards *heuweltjie* isolation with average distance to nearest neighbour experiencing a negative correlation with indicator abundance. Termite frass and average plant height were the significant variables that affected patch quality. Termite frass had a significant effect on indicator species richness, abundance and composition while plant height had a significant effect on indicator abundance. The *heuweltjie* indicator arthropod abundance was significantly associated with *heuweltjie* size, unlike the overall (combined epigaeic and foliage-dwelling arthropods), epigaeic and foliage-dwelling arthropod abundances, which suggest size of the *heuweltjies* does matter for these more specialised species.

Social insects like termites and ants are ubiquitous throughout arid and semi-arid regions. They make up most of the biomass in the region and are regarded as ecosystem engineers due to their abilities to modulate a variety of soil processes. Despite many theories surrounding the origin and formation of *heuweltjies*, there is extensive evidence proving termites such as *Microhodotermes viator* are associated with these mounds (Coaton and Sheasby, 1974; Lovegrove and Siegfried, 1989; Moore and Picker, 1991). Therefore it is possibly unsurprising that termites are associated with *heuweltjies*. One pseudoscorpion species was significantly associated with *heuweltjies*. Although South African pseudoscorpions are not well studied in terms of their morphology and ecology, these small invertebrates tend to live in cryptic environments such as leaf litter, under rocks and within tree bark (Harvey, 1986; Janion-Scheepers et al., 2016). Pseudoscorpions have received their name because of their resemblance to scorpions, however they lack a telson (tail) and sting. They prey on a variety of small invertebrates such as ants, springtails, beetles and termites (Harvey, 1986; Dippenaar-Schoeman and Harvey, 2000; Tizo-Pedroso and Del-Claro, 2014). However, the leaf litter sampling methods of Winkler bags or Tullgren funnels are regarded as more appropriate for sampling pseudoscorpions and their true association with *heuweltjies* (Janion-Scheepers et al., 2016). Nonetheless, the fact that pseudoscorpions have high specificity values (high probability of occurring on a *heuweltjie*) suggests that these mounds provide a suitable leaf litter to survive as there is an abundant food resource provided by termite activity.

Tenebrionid beetles are a highly diverse and important group in arid and semi-arid areas (Koch, 1962). They are important detritivores and granivores and are a key food source for a host of invertebrates, reptiles and small mammals (Polis et al., 1998). The ridged seed beetle (*Stips dohrni*) and mouldy beetle (*Eurychora* sp) were two of the beetles significantly associated with *heuweltjies*. The soil texture of *heuweltjies* are much sandier than the surrounding matrix which may explain their association with these mounds. The ridged seed beetle prefers sandier habitats (Picker et al., 2004) whereas the mouldy beetle gets its name from the waxy hairs on its body that help trap dirt and sand in an attempt to camouflage itself. The soil texture of *heuweltjies* are much sandier than the matrix which may make it easier to camouflage themselves. Additionally, beetles are known to use plant cover for thermoregulation and a refuge against predation (Groner and Ayal, 2001).

3.4.3 Using arthropods as bioindicators for rangeland monitoring

Heuweltjies have been proposed as “indicator patches” for monitoring rangeland condition as their seasonal changes in vegetation are more evident than that of the matrix (Stokes et al., 2009). Since *heuweltjies* are such an enigmatic feature in the Succulent Karoo, arthropod species that use them exclusively could be used as an alternative bioindicator. Arthropods are good indicators for rangeland monitoring due to their short life spans, which make them highly susceptible to disturbances and subtle changes in the environment at small spatial scales (Rainio and Niemelä, 1999; Andersen et al., 2002). Arthropods are good indicators of disturbance as they have immediate responses, as opposed to vegetation, which is notoriously slow, especially in the Succulent Karoo. Although this study only highlights which species exclusively use these mounds, further studies can provide additional insight. In order to be considered suitable as a bioindicator species, there should be: 1) extensive knowledge surrounding a species taxonomy and ecology; 2) the species needs to be widely distributed; 3) be cost-effective in their sampling; 4) able to exhibit a certain degree of habitat specialization; and 5) provide evidence of change (Noss 1990). Alternatively, using *heuweltjies* that are closer together, have an active termite colony present (the presence of termite frass) and have good quality vegetation (plant height) are factors deemed appropriate for *heuweltjies* to be used as a mesofilter for conservation planning. This could be useful for conservation in the region as, presently, the biodiverse Succulent Karoo is highly under conserved, with only 8% formally protected (Hoffman et al., 2018).

As mentioned, drylands are characterized by their high temperature and rainfall variability, limited water availability and high frequency of drought conditions (D’Odorico and Bhattachan, 2012). Over time habitat transformation, overgrazing, climate change and other anthropogenically induced disturbances are the most likely impacts to alter the structure and function of *heuweltjies*. Drylands are highly sensitive to changes in climate (Maestre et al., 2012). Rainfall is important for animal species in general and even more so in moisture limited environments such as the Succulent Karoo. Currently, prolonged dry spells have resulted in the extensive loss in plant cover, abundance and diversity in the region. Modifications of local and regional climates through increasing temperatures and reduction in rainfall events may have cascading effects of soil fertility and vegetation cover and ultimately affecting the biodiversity (Maestre et al., 2006). Short-term rainfall events are crucial for buffering some arthropod species (Collembolla and Araneae) against decline during prolonged drought conditions in arid

environments (Maute et al., 2019). Although arthropods in the area are well adapted to dry conditions, this could be important for arthropod species in the Succulent Karoo as the current drought has significantly affected the biodiversity in the region.

3.4.4 Conclusion

In conclusion, this study demonstrates the importance of spatial organization and quality of *heuweltjies* for the distribution of epigaeic and foliage arthropods. Epigaeic arthropods prefer to inhabit *heuweltjies* that are closer together coupled with better vegetation structure and termite frass. Foliage arthropods exhibit the same pattern, however, they are not reliant on termite frass. *Heuweltjies* are significant landscape features for habitat heterogeneity in the Succulent Karoo and may act as landscape modulators that provide the necessary driving forces behind arthropod spatial distributions. Patches such as *heuweltjies* often go unnoticed due to their ubiquity but their ability to support a variety of arthropod species make them crucial for maintaining diversity and ecological functioning.

These findings add further support to the role small habitat patches play for arthropod biodiversity in dryland ecosystems (Lozano-Fondon et al., 2020; Meloni et al., 2020). The true biodiversity value of *heuweltjies* comes from these patches existing as an interconnected network that facilitates better movement of species instead of being considered as isolated. It seems as if *heuweltjies* act as a refuge against the unfavourable conditions caused by the drought. *Heuweltjies* that are closer together with greater quality vegetation and termite frass may provide better protection against and ameliorate the effects of the drought. Although, these patterns might not be as evident during wetter periods. Furthermore, *heuweltjies* are widely distributed in the Succulent Karoo and occupy around a quarter of the biome (Lovegrove and Siegfried, 1989), although, the study takes place in one location the wide distribution of *heuweltjies* may suggest their importance for a variety of arthropod species throughout the Succulent Karoo. Future research using multiple sample locations may confirm or refute these findings.

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4. Chapter 4: General discussion and conclusion

4.1 General discussion

Arid and semi-arid landscapes are often characterized by patches of vegetation that differ from their surroundings (Aguilar and Sala, 1999). Since these environments are resource limited, these patches are vital for biodiversity and ecological functioning. *Heuweltjies* are an excellent example of such patches and are integral landscape features in the Succulent Karoo biome of South Africa. Although there has been a considerable amount of research surrounding *heuweltjies* (Lovegrove and Siegfried, 1989; Esler and Cowling, 1995; Kunz et al., 2012; McAuliffe et al., 2019), the arthropods that occupy these patches remain relatively understudied. Furthermore, since *heuweltjies* are so widely distributed and regarded as an important landscape feature in the Succulent Karoo, investigating their importance for arthropod diversity provides insight into the significance of *heuweltjies* for biodiversity and provides baseline data for contributing towards conservation and management efforts. This thesis aimed to ascertain how important *heuweltjies* are for epigaeic and foliage dwelling arthropod species in the Succulent Karoo.

Chapter two assessed changes in overall, epigaeic and foliage dwelling arthropod alpha-diversity, abundance, community composition and beta-diversity between and within *heuweltjies* and the homogenous matrix at local scale, as well as across three more spatially distributed areas. I found that arthropods were more abundant and speciose on *heuweltjies* during my study, which took place during a prolonged drought. *Heuweltjies* were associated with greater overall, epigaeic and foliage arthropod alpha-diversity and abundance compared to the matrix. Although *heuweltjies* are considered sites of continuous disturbance as a result of preferential grazing from livestock and mammals like the aardvark and various rodent species (Kunz et al., 2012; Louw et al., 2017), they provide suitable habitat for both epigaeic and foliage dwelling arthropods. This adds further support that patches surrounded by homogenous vegetation are important for arthropod diversity (Liu et al., 2016, Meloni and Martinez, 2021). With regards to the different sites, Tierberg contained the highest total arthropod alpha diversity followed by Wolwekraal and Argentina. Tierberg is the only site that with no livestock grazing, stray animals or illegal firewood collection, which may explain its higher level of alpha-diversity compared to the other two sites.

Both epigaeic and foliage dwelling arthropod assemblages differed between the *heuweltjie* and matrix suggesting that different communities are present within the two biotopes. This study builds on existing evidence that *heuweltjies* and matrix plots are home to different arthropod communities (Cornell, 2014). This was also the case at the site level with arthropod communities differing between Argentina and Wolwekraal and Tierberg and Wolwekraal while the composition between Argentina and Tierberg was relatively similar. Despite Argentina and Tierberg's exposure to different grazing regimes, they abut each other, whilst Wolwekraal is 20km away. This proximity may explain the similarities in their communities and is indicative that arthropod communities vary over a matter of kilometres. Since *heuweltjies* are ubiquitous in the Succulent Karoo (Lovegrove and Siegfried, 1989), arthropod communities are expected to experience even greater differences at larger spatial scales caused by changes in climate and vegetation types.

Beta-diversity measures the factors that structure ecological communities (Whittaker, 1960; Socolar et al., 2016). It plays a crucial role in determining the spatial organization of biodiversity and their consequences on landscape heterogeneity and ecological functioning (Mori et al., 2018). Partitioning beta-diversity into species turnover (species replacement) and richness differences (nestedness) allows us to assess the variation in arthropod communities within and between each biotope, providing a better understanding of arthropod biotic homogenization.

Overall (combined epigaeic and foliage-dwelling arthropods) and epigaeic arthropod communities between the two biotopes (*heuweltjie* and matrix) consisted of moderate total beta-diversity, mostly driven by species turnover whereas the foliage dwelling arthropods had a moderate total beta-diversity driven by differences in species richness (nestedness). Even though beta-diversity was not high, it suggests that different epigaeic arthropods communities occupy the two biotopes, whereas the high nestedness of foliage dwelling arthropod communities suggests that many species are shared between the two biotopes, most likely in response to vegetation cover mostly as a result of their better dispersal capabilities (e.g. flying).

For the epigaeic arthropod communities between each of the three sites, Wolwekraal – Argentina and Wolwekraal – Tierberg had a high total beta-diversity driven by turnover (replacement) while Argentina – Tierberg had a moderate total beta-diversity driven by species richness differences (nestedness). Contrastingly, foliage arthropods exhibited beta-diversity driven largely by species richness differences with the greatest dissimilarity between Argentina – Tierberg and Argentina – Wolwekraal. This suggests that arthropod communities on each

heuweltjie and matrix plot support distinct species and showed little sign of biotic homogenization as previously reported (Cornell, 2014). This adds further support that communities differ over small spatial scales and hence increase regional diversity.

Differing arthropod communities within each biotope revealed that arthropod communities are extremely diverse across a small spatial scale. However, changes in species assemblages are complex and are influenced by a multitude of factors such as landscape heterogeneity, natural or anthropogenic disturbance (i.e., drought and grazing) and niche availability (Mori et al., 2018). Future studies could focus on the role beta-diversity plays in biotic communities especially in the Succulent Karoo as this biome is currently undergoing, and is predicted to undergo, large scale disturbances and environmental changes. Climate change forecasts suggest drylands such as the Succulent Karoo will increase in both size and aridity (Schlaepfer et al., 2017) coupled with large scale mining and fracking interventions (Todd et al., 2016) that will pose a significant threat to the flora and fauna in the region.

Since *heuweltjies* are distributed as isolated patches within a homogenous matrix, approximately 2 per hectare (Milton et al., 2010), the basic principles of island biogeography theory and metapopulation ecology (MacArthur and Wilson, 1967; Levins, 1969) could be applied to this study to assess the spatial characteristics of *heuweltjies* on arthropod species richness and composition. Thus, to further hone in on the importance of these patches, the focus of the third chapter, was to determine which patch variables, patch isolation, size and quality, influenced epigaeic, foliage and indicator (arthropods significantly associated with *heuweltjies*) arthropod species richness, abundance and community composition. Patch isolation comprised distance to nearest neighbour, average distance to nearest six neighbours, and *heuweltjie* density. Patch size comprised *heuweltjie* area while patch quality consisted of vegetation percentage cover, dead vegetation percentage cover, average plant height, plant species richness and the presence of termite frass.

Patch size, isolation and quality influenced both epigaeic and foliage dwelling arthropods. Average distance to nearest neighbour and *heuweltjie* area showed a negative correlation for epigaeic species richness and abundance while the presence of frass and distance to nearest neighbour exhibited a positive response towards epigaeic species richness and abundance. Foliage dwelling arthropod species richness showed no significant relationship between any of the three patch metrics, while foliage dwelling arthropod abundance was positive correlated with dead plant percentage cover and negatively correlated with average distance to nearest

neighbours. Epigaeic composition was significantly influenced by the average distance to nearest neighbours, distance to nearest neighbour, *heuweltjie* area, presence of termite frass, percentage dead plant cover and average plant height. Foliage dwelling arthropod community composition was influenced by *heuweltjie* area and average plant height.

Arthropod species richness is known to decrease as the distance between habitat patches increase (Liu et al., 2016). Well connected habitat patches allow for easier access to patches and reduces the time taken to travel between them, particularly in harsh environments. As for species richness decreasing as *heuweltjie* area increased, the closeness of patches could possibly supersede the need for bigger patches. *Heuweltjies* in the vicinity of the study area are distributed at around $\sim 2.1 \text{ ha}^{-1}$ and arthropods would be able to move freely between patches. The presence of frass assumes that there is an active termite colony on the *heuweltjie* which is a main food source for a variety of ants, daesiid solifugae and *Ammoxenus* spiders (Wharton, 1981; Dean, 1988; Dean, 1989), which all occurred on *heuweltjies*. Although this could also be because termites increase productivity of patches through their activities (more frass suggests more detritus is available) making it suitable for other arthropods, or that conditions favourable to termites are also favourable to other epigaeic arthropods.

Heuweltjies had greater percentage cover and lower average plant height than the matrix. Dead plant percentage cover was correlated with total percentage cover and proved to be a better predictor variable. Despite being dead, these plants still contribute to the vegetation structure in the landscape as their branches and roots remain intact. Together the vegetation structure, dead plant percentage cover and average plant height, provide protection from harsh conditions and predation (Dean and Milton, 1991). Elsewhere, termite mounds are associated with vegetation that creates unique microclimates that are much cooler than their surroundings (Joseph et al., 2018), and this could be investigated for *heuweltjies* and their resident termite species and vegetation. These results are consistent with island biogeography principles that patches that are closer together and contain better quality (plant percentage cover and termite frass) support greater arthropod species richness as well as different communities.

A total of fourteen indicator species were identified, eleven associated with the *heuweltjies* and three with the matrix. The indicator species associated with the *heuweltjies*, seven were epigaeic and four were foliage dwelling and contained beetles, flies, pseudoscorpions, termites and wasps. These indicator species were also affected by all three patch metrics, with species richness and abundance positively correlated with the presence of termite frass, *heuweltjie* size

and dead plant percentage cover. Indicator abundance was negatively correlated with average distance to nearest neighbour. *Heuweltjies* have been proposed as “indicator patches” for monitoring rangeland condition as their changes in vegetation are more distinguishable than that of the matrix (Stokes et al., 2009). These indicator species could be monitored as indicators of rangeland health, since arthropods are good indicators, because of their short life cycles and susceptibility to environmental changes at small spatial scales (Andersen et al., 2002). Further research into how the abundances of these species change with grazing and climatic variation might contribute to a method for monitoring rangelands at a level beyond just cover, but also by taking ecological function or process into account.

Arid and semi-arid regions are complex and highly dynamic environments that are crucial for sustaining life on earth (Maestre et al., 2016). The drylands of the world are home to 38% of the world’s population and are significant contributors in carbon sequestration, meat production and biodiversity (Huang et al., 2017; Foley et al., 2005). Although drylands are vital for biodiversity and livelihoods, they are unfortunately highly susceptible to environmental changes, ironically, through increased human-induced pressures such as the increase in human inhabitants, livestock farming, mining, poaching and the vagaries of climate change. The pressures can cause drastic changes in these environments, which may ultimately lead to large scale degradation and desertification.

A major problem currently facing the Succulent Karoo is the onset of drought conditions, decline in MAP (mean annual precipitation), since 2011 that has severely impacted the biodiversity and its inhabitants. This study took place during these conditions where a significant loss in plant abundance and percentage cover was observed and recorded. Drylands like the Succulent Karoo are highly sensitive to rapid changes in climate (Mucina et al., 2006; Maestre et al., 2012), increasing temperatures coupled with a reduction in mean annual rainfall may result in knock-on effects on soils and vegetation. Although an uncertain future lies ahead for arthropods, given the increasing decline in insect biomass regardless of habitat type, weather and land use types (Hallman et al., 2017), it seems as if arthropods are using *heuweltjies* as a refuge against the drought. This could be relevant to the arthropods of the Succulent Karoo given the current drought state the biome is in.

On the other hand, the Succulent Karoo has always experienced cyclical periods of dry and wet conditions. Most species in drylands are adapted to harsh conditions, the duration and intensity of extreme weather events may exceed the abilities of many organisms to persist. However, the arthropods of this region have evolved and adapted to these conditions (periods of drought and

recovery) (Hesse, 1938) and should be able to bounce back once the rainfall returns to normal. There has also been a general decline in crop and livestock farming through the Succulent Karoo (Hoffman et al., 2018). Hopefully, once drought conditions subside and there is a return to disturbance regimes that promote biodiversity, the Succulent Karoo may see greater arthropod diversity in and around *heuweltjies* once again.

4.2 Study limitations and future work

The impact of the COVID-19 pandemic prevented the use of more sophisticated methods for analysing the spatial configurations of *heuweltjies*. Unmanned aerial systems (UAS) or drones are a useful tool in measuring habitat features over multiple spatial scales. They collect reasonably high-resolution data at a finer scale in order to model habitat features across a landscape (Olsoy et al., 2018). By flying a drone over the sites, with the help of a trained professional, or using high resolution satellite imagery to accurately map the distance between, and the vegetation quality (plant height and percentage cover) of *heuweltjies* would have provided a better insight into the spatial configuration and quality of the mounds. Despite this imagery from Google Earth worked remarkably well as I was able to identify *heuweltjies* remotely. Although *heuweltjies* are known to be over-dispersed (non-randomly distributed) this method can open up newer ways in determining the importance of spatial configuration for both plants and arthropods at a relatively low cost.

A constraint of the study was the unsuitability of vacuum sampling for the foliage dwelling arthropods. I found vacuum sampling to not be suitable for sampling invertebrates on karroid vegetation. Often, the vegetation would ultimately rip the fine mesh sock used to catch any foliage dwelling arthropods. Furthermore, the number of foliage arthropod specimens caught was significantly less than the pitfall sampling despite adequately sampling each of the transects (assessed using species accumulation curves). However, this could also be caused by the drought which has left numerous dead plants that are unsuitable for foliage arthropods.

Future research on the influence *heuweltjies* have on arthropod diversity could cover various aspects. Firstly, seasonality is known to affect species richness and abundance of both epigaeic and foliage dwelling arthropods in the Succulent Karoo (Nchai, 2008; Stander, 2016). Sampling during different seasons (i.e. winter – summer, autumn – spring) should be considered especially since assemblages vary considerably across seasons and short –term climatic oscillations (Cardoso and Leather, 2019). Secondly, this study was conducted during severe drought conditions which has significantly affected the Succulent Karoo’s biodiversity

and its inhabitants. Although this allowed us to assess the impact during a drought, future work can be conducted during normal rainfall and “wetter” years to get a better picture of the role *heuweltjies* play for arthropod biodiversity.

Recognition of different models of, and perspectives on, landscapes is critically important because what humans define as a patch may differ significantly from the pattern perceived by another species. Previous work has been done on how vegetation is affected by grazing across different zones on *heuweltjies* (i.e. buffer, periphery and centre) (Schmiedel et al., 2016). This could be applied to arthropods to better assess immigration and emigration events of various arthropod metapopulations. Additionally, since this study highlights which species exclusively associated with *heuweltjies*, future studies can assess the suitability of these indicator species for rangeland monitoring or identify taxa that are crucial for ecosystem processes such as pollination or nutrient cycling.

There has been mounting interest into the dynamics of drylands, however, a comprehensive synthesis regarding the key organisms and the ecosystem processes that shape these environments is severely lacking, especially in the Succulent Karoo (Maestre et al., 2021; Vernon, 1999). This study has created a baseline dataset of arthropod species occurrences in the area which may facilitate further research assessing changes in arthropod communities in the Succulent Karoo. However, the arid regions (Succulent and Nama-Karoo) are under sampled and therefore we know relatively little about the arthropods that inhabit these unique landscapes (Vernon, 1999; Jainon-Scheepers et al., 2016). Studies on *heuweltjies* are mostly centred on vegetation, grazing, geological processes and the role *M. viator* plays in the formation of these mounds (Schmiedel et al., 2016; Cramer et al., 2017). However, this dissertation provides the first arthropod multi-taxon approach assessing their general response to certain landscape features, since single species studies often require significant taxonomic and ecological information (Kotze and Samways, 1999), something which the Succulent Karoo is severely lacking. Additionally, the fact that communities vary over relatively short distance suggests that arthropods are quite diverse in the Succulent Karoo.

To conclude, *heuweltjies* are important contributors towards the heterogeneity in the landscape and are home to higher epigaeic and foliage arthropod species, abundances as well as unique communities. Therefore, understanding the role arthropods play not only in the formation of *heuweltjies*, but also in their distributions can provide a better understanding surrounding the ecological processes of *heuweltjies*. *Heuweltjies* are vital for both epigaeic and foliage

arthropods and further and more detailed work on relevant arthropod taxa is needed but especially surrounding habitat features like *heuweltjies* since they are such ubiquitous features in the landscape.

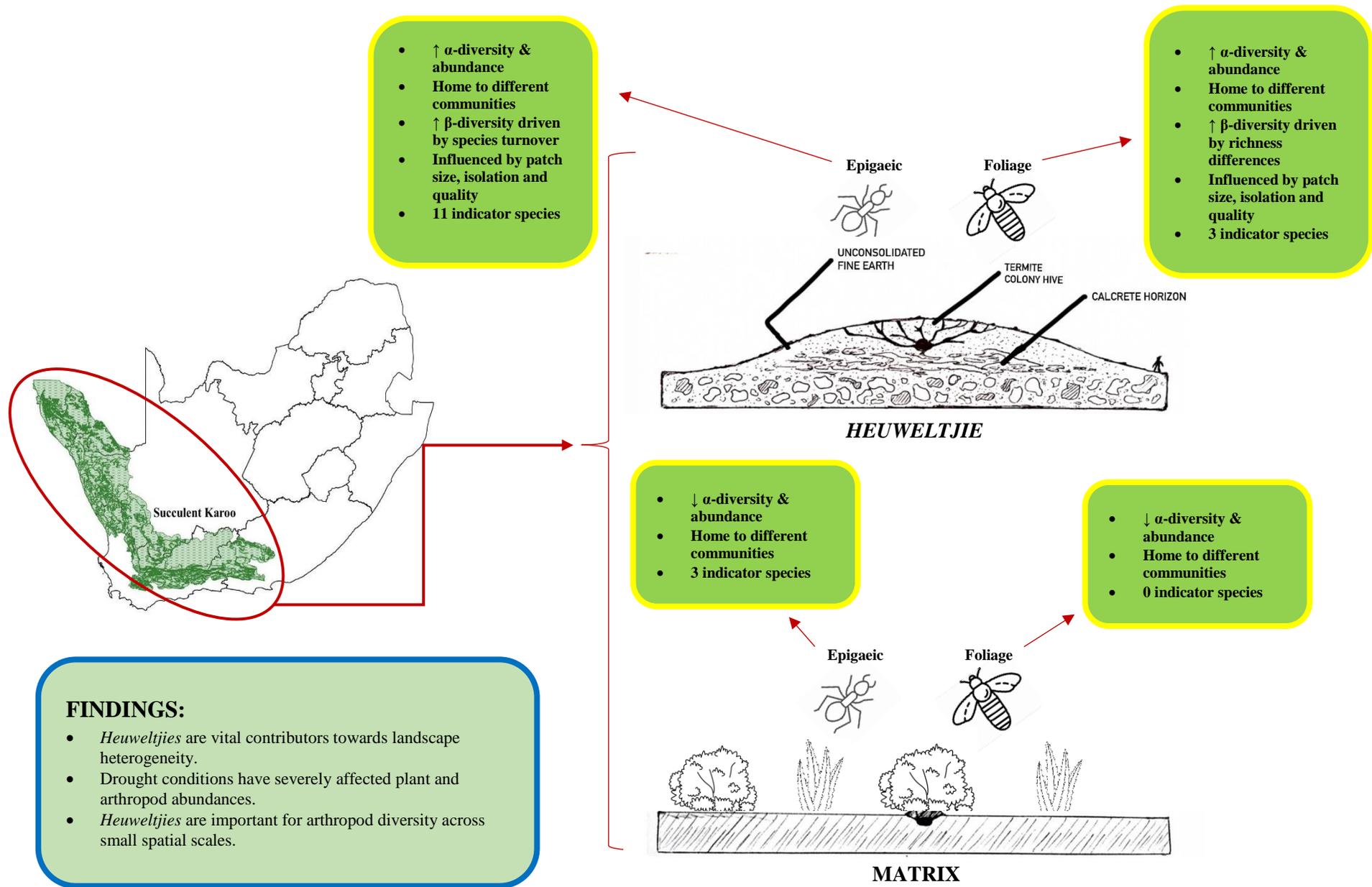


Figure 4.1: A brief summary of the study.

4.3 References

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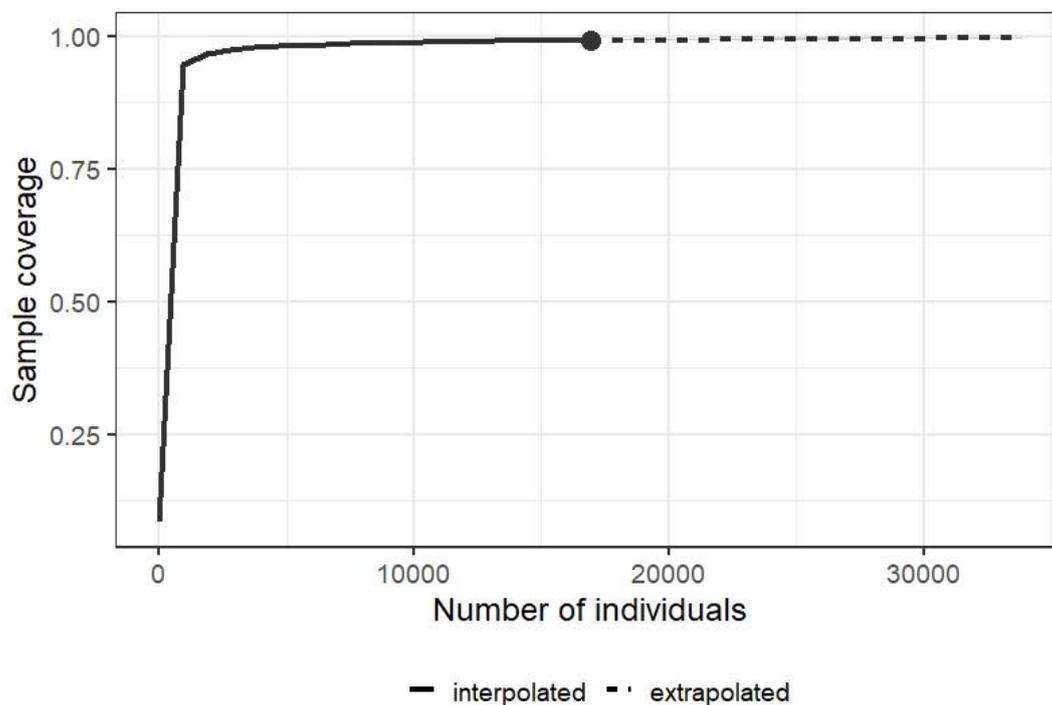
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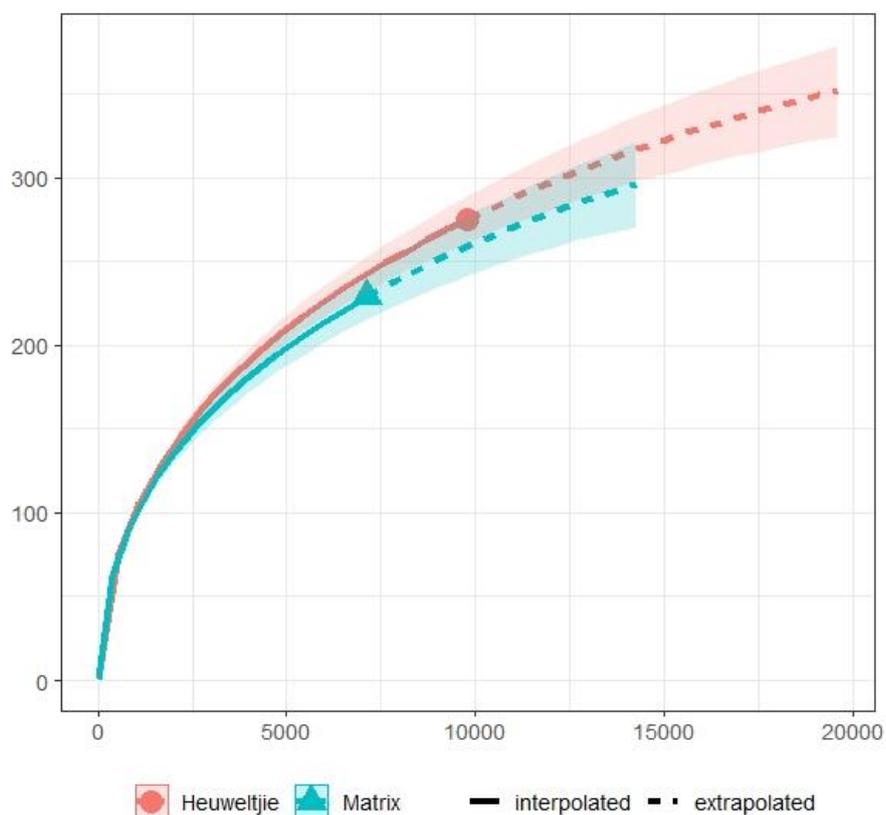
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5. Appendices



Appendix A: Species accumulation curves using Hill numbers ($q = 0$). 0 = species richness for *heuweltjie* (circle) and matrix plots (triangle).



Appendix B: Species accumulation curve for overall arthropod species.

Appendix C: Chao1, Shannon and Simpson diversity estimates for epigaeic and foliage arthropods occurring on *heuweltjie* and matrix plots. Shown below are diversity estimates with standard errors.

	Biotope type	Observed	Chao1	Shannon Diversity	Simpson Diversity
	<i>H + M</i>	353	540.1 (S.E ± 44.3)	27.4 (S.E ± 0.4)	11.7 (S.E ± 0.2)
Overall	<i>Heuweltjie</i>	275	425.6 (S.E ± 39.9)	23.5 (S.E ± 0.5)	9.1 (S.E ± 0.2)
	Matrix	229	367 (S.E ± 40.1)	21.2 (S.E ± 0.5)	7.5 (S.E ± 0.2)
Epigaeic	<i>Heuweltjie</i>	133	193 (S.E ± 25.9)	14.6 (S.E ± 0.3)	6.5 (S.E ± 0.1)
	Matrix	112	146 (S.E ± 14.7)	14.4 (S.E ± 0.3)	6.4 (S.E ± 0.1)
Foliage	<i>Heuweltjie</i>	144	232.7 (S.E ± 30.5)	15.3 (S.E ± 0.8)	5 (S.E ± 0.2)
	Matrix	117	244.2 (S.E ± 50.6)	65.8 (S.E ± 4.3)	32.83 (S.E ± 2.3)

Appendix D: The beta-diversity between biotope types (*heuweltjie* and matrix plots). Shown below is the total beta-diversity (β_{total}), turnover β_{repl} and species richness differences β_{rich} .

	Overall	Epigaeic	Foliage
β_{total}	0.540	0.521	0.515
β_{repl}	0.382	0.422	0.053
β_{rich}	0.158	0.099	0.462

Appendix E: Beta-diversity between the three sites, Argentina, Tierberg and Wolwekraal. Shown below is the total beta-diversity (β_{total}), turnover β_{repl} and nestedness β_{rich} .

Overall						
	Turnover (β_{repl})		Species loss/gain (β_{rich})		Total beta-diversity (β_{total})	
	Argentina	Tierberg	Argentina	Tierberg	Argentina	Tierberg
Tierberg	0.180		0.277		0.457	
Wolwekraal	0.647	0.425	0.186	0.440	0.834	0.865
Epigeaic						
	Turnover (β_{repl})		Species loss/gain (β_{rich})		Total beta-diversity (β_{total})	
	Argentina	Tierberg	Argentina	Tierberg	Argentina	Tierberg
Tierberg	0.176		0.256		0.431	
Wolwekraal	0.455	0.379	0.064	0.195	0.518	0.574
Foliage						
	Turnover (β_{repl})		Species loss/gain (β_{rich})		Total beta-diversity (β_{total})	
	Argentina	Tierberg	Argentina	Tierberg	Argentina	Tierberg
Tierberg	0.113		0.327		0.440	
Wolwekraal	0.187	0.149	0.257	0.076	0.444	0.225

Appendix F: Beta diversity between the biotopes occurring on different sampling localities (sites) for overall arthropods. Shown below is the total beta-diversity (β_{total}), species turnover (β_{repl}) and species richness difference (β_{rich}). AR = Argentina, TB = Tierberg, WL = Wolwekraal. H = *Heuweltjie* and M = Matrix plot.

Total beta-diversity (β_{total})						Turnover (β_{repl})					Species loss/gain (β_{rich})						
	ARH	ARM	TBH	TBM	WLH		ARH	ARM	TBH	TBM	WLH		ARH	ARM	TBH	TBM	WLH
ARM	0.715	-	-	-	-	ARM	0.297	-	-	-	-	ARM	0.418	-	-	-	-
TBH	0.529	0.640	-	-	-	TBH	0.177	0.562	-	-	-	TBH	0.251	0.078	-	-	-
TBM	0.685	0.489	0.520	-	-	TBM	0.168	0.364	0.319	-	-	TBM	0.516	0.125	0.201	-	-
WLH	0.655	0.773	0.497	0.657	-	WLH	0.291	0.710	0.483	0.470	-	WLH	0.364	0.064	0.014	0.187	-
WLM	0.736	0.582	0.667	0.735	0.501	WLM	0.550	0.330	0.490	0.369	0.310	WLM	0.186	0.251	0.177	0.365	0.191

Appendix G: Beta diversity between the biotopes occurring on different sampling localities (sites) for epigaeic arthropods. Shown below is the total beta-diversity (β_{total}), species turnover (β_{repl}) and species richness difference (β_{rich}). AR = Argentina, TB = Tierberg, WL = Wolwekraal. H = *Heuweltjie* and M = Matrix plot.

	Total beta-diversity (β_{total})					Turnover (β_{repl})					Species loss/gain (β_{rich})						
	ARH	ARM	TBH	TBM	WLH		ARH	ARM	TBH	TBM	WLH		ARH	ARM	TBH	TBM	WLH
ARM	0.695	-	-	-	-	ARM	0.341	-	-	-	-	ARM	0.354	-	-	-	-
TBH	0.506	0.648	-	-	-	TBH	0.191	0.604	-	-	-	TBH	0.315	0.044	-	-	-
TBM	0.643	0.480	0.502	-	-	TBM	0.167	0.334	0.313	-	-	TBM	0.476	0.147	0.189	-	-
WLH	0.637	0.775	0.498	0.644	-	WLH	0.293	0.765	0.465	0.487	-	WLH	0.344	0.011	0.033	0.157	-
WLM	0.723	0.576	0.673	0.743	0.502	WLM	0.620	0.316	0.455	0.351	0.252	WLM	0.103	0.260	0.219	0.392	0.250

Appendix H: Beta diversity between the biotopes occurring on different sampling localities (sites) for foliage arthropods. Shown below is the total beta-diversity (β_{total}), species turnover (β_{repl}) and species richness difference (β_{rich}). AR = Argentina, TB = Tierberg, WL = Wolwekraal. H = *Heuweltjie* and M = Matrix plot.

	Total beta-diversity (β_{total})					Turnover (β_{repl})					Species loss/gain (β_{rich})						
	ARH	ARM	TBH	TBM	WLH		ARH	ARM	TBH	TBM	WLH		ARH	ARM	TBH	TBM	WLH
ARM	0.712	-	-	-	-	ARM	0.034	-	-	-	-	ARM	0.678	-	-	-	-
TBH	0.520	0.405	-	-	-	TBH	0.063	0.085	-	-	-	TBH	0.457	0.320	-	-	-
TBM	0.902	0.271	0.372	-	-	TBM	0.079	0.177	0.139	-	-	TBM	0.623	0.094	0.233	-	-
WLH	0.545	0.533	0.260	0.468	-	WLH	0.172	0.126	0.160	0.142	-	WLH	0.373	0.407	0.101	0.326	-
WLM	0.665	0.324	0.337	0.252	0.359	WLM	0.063	0.195	0.137	0.217	0.064	WLM	0.602	0.128	0.200	0.035	0.294

Appendix I: Beta-diversity within the all *heuweltjie* and matrix plots for overall, epigaeic and foliage arthropods.

		Turnover (β_{repl})	Species loss/gain (β_{rich})	Total beta-diversity (β_{total})
Overall	<i>Heuweltjie</i>	0.794	0.095	0.889
	Matrix	0.813	0.086	0.899
Epigaeic	<i>Heuweltjie</i>	0.756	0.114	0.871
	Matrix	0.767	0.120	0.888
Foliage	<i>Heuweltjie</i>	0.431	0.388	0.818
	Matrix	0.501	0.224	0.724

Appendix J: Beta diversity within the three sites, AR = Argentina, TB = Tierberg and WL = Wolwekraal, for overall arthropods. Additionally, beta-diversity within the *heuweltjie* and matrix plots occurring across the three sites.

Site	Biotope		β_{repl}	β_{rich}	β_{total}		β_{repl}	β_{rich}	β_{total}		β_{repl}	β_{rich}	β_{total}
AR	Heu x Mat	Overall	0.781	0.130	0.911	Epigeaic	0.756	0.137	0.894	Foliage	0.449	0.389	0.837
	Heu		0.779	0.126	0.906		0.779	0.126	0.906		0.779	0.126	0.906
	Mat		0.790	0.108	0.898		0.790	0.108	0.898		0.790	0.108	0.898
TB	Heu x Mat		0.738	0.114	0.852		0.712	0.128	0.840		0.505	0.242	0.747
	Heu		0.703	0.129	0.832		0.703	0.129	0.832		0.703	0.129	0.832
	Mat		0.732	0.105	0.836		0.732	0.105	0.836		0.732	0.105	0.836
WL	Heu x Mat		0.775	0.095	0.870		0.755	0.119	0.874		0.472	0.255	0.727
	Heu		0.765	0.083	0.848		0.765	0.083	0.848		0.765	0.083	0.848
	Mat		0.753	0.129	0.882		0.753	0.129	0.882		0.753	0.129	0.882

Appendix K: Patch isolation variables (distance to nearest neighbour, average distance to nearest 6 neighbours and density) across the 16 sampled *heuweltjies* at Argentina and Tierberg.

Plot	DNN	ADNN	Dens
AR1	34.65	54.6	12
AR2	36.06	47.97	20
AR3	26.18	70.91	19
AR4	51.21	70.22	12
AR5	51.63	73.6	15
AR6	38.36	48.86	20
AR7	56.1	79.95	13
AR8	33.74	68.6	11
TB1	31.28	44.13	20
TB2	24.92	56.38	16
TB3	23.72	45.3	19
TB4	38.85	56.44	18
TB5	42	53.97	21
TB6	42.58	51.63	24
TB7	35.84	49.29	25
TB8	53.76	81.28	14

Appendix L: The best models for epigaeic and foliage species richness and abundance.

Best model	Df	AICc	Weight
<i>Epigaeic species richness</i>			
<i>ADNN + Frass</i>	5	343.01	0.29
<i>Epigaeic abundance</i>			
<i>DNNS + HArea</i>	5	711.56	0.11
<i>Foliage species richness</i>			
<i>ADNN</i>	4	295.95	0.07
<i>Foliage abundance</i>			
<i>ADNN + DeadPC + Frass</i>	6	493.56	0.20
<i>Indicator species richness</i>			
<i>Frass</i>	4	224.05	0.15
<i>Indicator abundance</i>			
<i>ADNN + HArea + Frass</i>	6	203.03	0.19

Appendix M: Model selection procedure for epigaeic and foliage species richness, abundance. All significant variables are highlighted in bold.

	<i>Variables</i>	<i>Patch category</i>	<i>Estimate</i>	<i>Std Error</i>	<i>Z value</i>	<i>Confidence Interval</i>	<i>Response</i>
<i>Epigaeic arthropod species richness</i>	DNN	Isolation	0.015	0.047	0.310	[-0.102;0.110]	Neutral
	ADNN	Isolation	-0.099	0.042	2.293*	[-0.197;-0.010]	Negative
	Dens	Isolation	-0.011	0.012	0.895	[-0.034;0.017]	Neutral
	HArea	Size	-0.005	0.042	0.116	[-0.103;0.079]	Neutral
	DeadPC	Quality	0.038	0.038	0.992	[-0.034;0.125]	Neutral
	Height	Quality	-0.019	0.037	0.497	[-0.091;0.058]	Neutral
	Frass	Quality	0.204	0.074	2.682**	[0.052;0.351]	Positive
<i>Epigaeic arthropod abundance</i>	DNN	Isolation	0.310	0.138	2.210*	[0.014;0.589]	Positive
	ADNN	Isolation	-0.209	0.192	1.069	[-0.608;0.203]	Neutral
	Dens	Isolation	-0.042	0.033	1.239	[-0.115;0.023]	Neutral
	HArea	Size	-0.267	0.123	2.130*	[-0.508;-0.002]	Negative
	DeadPC	Quality	-0.172	0.44	1.175	[-0.467;0.113]	Neutral
	Height	Quality	-0.135	0.123	1.053	[-0.380;0.103]	Neutral
	Frass	Quality	0.311	0.225	1.350	[-0.204;0.742]	Neutral
<i>Foliage arthropod species richness</i>	DNN	Isolation	-0.052	0.047	0.691	[-0.201;0.105]	Neutral
	ADNN	Isolation	-0.124	0.078	1.566	[-0.283;0.036]	Neutral
	Dens	Isolation	-0.016	0.021	0.764	[-0.057;0.028]	Neutral
	HArea	Size	-0.000	0.068	0.005	[-0.142;0.136]	Neutral
	DeadPC	Quality	0.053	0.062	0.848	[-0.073;0.181]	Neutral
	Height	Quality	-0.011	0.062	0.176	[-0.136;0.111]	Neutral
	Frass	Quality	0.182	0.124	1.431	[-0.068;0.427]	Neutral
<i>Foliage arthropod abundance</i>	DNN	Isolation	-0.023	0.173	0.129	[-0.477;0.311]	Neutral
	ADNN	Isolation	-0.411	0.149	2.691**	[-0.742;-0.101]	Negative
	Dens	Isolation	-0.001	0.041	0.034	[-0.082;0.095]	Neutral
	HArea	Size	0.201	0.164	1.199	[-0.138;0.574]	Neutral
	DeadPC	Quality	0.457	0.153	2.940**	[0.154;0.773]	Positive
	Height	Quality	-0.039	0.124	0.311	[-0.298;0.210]	Neutral
	Frass	Quality	0.448	0.254	1.725	[-0.059;0.980]	Neutral

Appendix N: Results from the IndVal analysis showing the indicator species for epigaeic and foliage species occurring on *heuweltjie* and matrix plots. Specificity (A) – the probability of this species occurring probability occurs at a specific site. Sensitivity (B) - the probability that all sites include a specific species.

Morpho	Group	Order	Biotope	Specificity (A)	Sensitivity (B)	Stat	P
Fly24	Foliage	Diptera	<i>Heuweltjie</i>	0.953	0.281	0.518	0.001
Bet 33	Epigaeic	Coleoptera	<i>Heuweltjie</i>	0.941	0.188	0.420	0.001
Bet8	Epigaeic	Coleoptera	<i>Heuweltjie</i>	0.938	0.104	0.312	0.008
Ant29	Epigaeic	Hymenoptera	Matrix	0.938	0.125	0.342	0.001
Bet9	Epigaeic	Coleoptera	<i>Heuweltjie</i>	0.933	0.135	0.356	0.001
Ant35	Epigaeic	Hymenoptera	Matrix	0.917	0.094	0.293	0.020
Pso1	Epigaeic	Pseudoscorpiones	<i>Heuweltjie</i>	0.910	0.073	0.275	0.042
Fly8	Foliage	Diptera	<i>Heuweltjie</i>	0.898	0.583	0.724	0.001
Ter4	Epigaeic	Blattodea (Isoptera)	<i>Heuweltjie</i>	0.889	0.094	0.289	0.031
Bet21	Epigaeic	Coleoptera	<i>Heuweltjie</i>	0.875	0.188	0.405	0.001
Ant33	Epigaeic	Hymenoptera	Matrix	0.862	0.104	0.300	0.043
Bet10	Epigaeic	Coleoptera	<i>Heuweltjie</i>	0.856	0.375	0.567	0.001
Fly17	Foliage	Diptera	<i>Heuweltjie</i>	0.776	0.177	0.371	0.023

Appendix O: Results from the model selection procedure for indicator species richness and abundance. All significant variables are highlighted in bold.

	<i>Variables</i>	<i>Patch category</i>	<i>Estimate</i>	<i>Std Error</i>	<i>Z value</i>	<i>Confidence Interval</i>	<i>Response</i>
Indicator arthropod species richness	DNN	Isolation	0.084	0.102	0.811	[-0.121;0.287]	Neutral
	ADNN	Isolation	-0.104	0.091	1.131	[-0.311;0.085]	Negative
	Dens	Isolation	0.012	0.019	0.620	[-0.033;0.051]	Neutral
	HArea	Size	0.034	0.074	0.455	[-0.128;0.183]	Neutral
	DeadPC	Quality	0.059	0.072	0.800	[-0.091;0.206]	Neutral
	Height	Quality	-0.025	0.074	0.455	[-0.176;0.123]	Neutral
	Frass	Quality	0.312	0.151	2.015*	[0.008;0.615]	Positive
Indicator arthropod abundance	DNN	Isolation	0.087	0.174	0.489	[-0.271;0.433]	Neutral
	ADNN	Isolation	-0.584	0.177	3.241**	[-0.947;-0.225]	Negative
	Dens	Isolation	0.018	0.044	0.412	[-0.070;0.105]	Neutral
	HArea	Size	0.380	0.172	2.167*	[0.035;0.730]	Positive
	DeadPC	Quality	0.354	0.172	2.208*	[0.012;0.698]	Positive
	Height	Quality	-0.126	0.135	0.917	[-0.390;0.158]	Neutral
	Frass	Quality	0.626	0.264	2.321*	[0.099;1.158]	Positive

Appendix P: Results from the manyGLM analyses exploring the effect of each patch variable - distance to nearest neighbour average distance o nearest neighbour, *heuweltjie* density, *heuweltjie* area, dead plant percentage cover, average plant height and termite frass on indicator arthropod assemblage composition. Significant differences are marked in bold.

	<i>Patch variable</i>	χ^2	<i>P value</i>	<i>Df</i>
Indicator composition	DNN	9.710	0.571	62
	ADNN	18.585	0.134	61
	Dens	16.554	0.109	60
	HArea	16.058	0.163	59
	DeadPC	8.472	0.627	58
	Height	26.415	0.016	57
	Frass	27.644	0.015	56

Appendix Q: Plant species sampled combined with their life form and survival duration.

<i>Species</i>	<i>Lifeform</i>	<i>Duration</i>
<i>Pteronia pallens</i>	Shrub	Long
<i>Augea capensis</i>	Succulent	Medium
<i>Brownanthus vaginatus</i>	Succulent	Medium
<i>Malephore lutea</i>	Succulent	Short
<i>Psilocaulon lutea</i>	Succulent	Long
<i>Peersia spp</i>	Succulent	Long
<i>Osteospermum sinuatum</i>	Forb	Long
<i>Ruchia spinosa</i>	Succulent	Long
<i>Ruschia approximata</i>	Succulent	Long
<i>Salsola spp</i>	Forb	Long
<i>Euphorbia spp</i>	Succulent	Medium
<i>Crassula subaphylla</i>	Succulent	Medium
<i>Asparagus sp.</i>	Shrub	Long
<i>Hereroa latipetala</i>	Succulent	Medium
<i>Mesembryanthemum utile</i>	Succulent	Medium
<i>Zygophyllum retrofactim</i>	Shrub	Medium

Appendix R: Orders sampled in alphabetical order.

Order	Morphospecies
Acari	
	Sp. 1
	Sp. 2
	Sp. 3
	Sp. 4
	Sp. 5
Araneae	
	Sp. 1
	Sp. 2
	Sp. 3
	Sp. 4
	Sp. 5
	Sp. 6
	Sp. 7
	Sp. 8
	Sp. 9
	Sp. 10
	Sp. 11
	Sp. 12
	Sp. 13
	Sp. 14
	Sp. 15
	Sp. 16

Sp. 17

Sp. 18

Sp. 19

Sp. 20

Sp. 21

Sp. 22

Sp. 23

Sp. 24

Sp. 25

Sp. 26

Sp. 27

Sp. 28

Sp. 29

Sp. 30

Sp. 31

Sp. 32

Sp. 33

Sp. 34

Sp. 35

Sp. 36

Sp. 37

Sp. 38

Sp. 39

Sp. 40

Sp. 41

Sp. 42

Sp. 43

Sp. 44

Sp. 45

Sp. 46

Blattodea

Sp. 1

Sp. 2

Sp. 3

Sp. 4

Sp. 5

Sp. 6

Coleoptera

Sp. 1

Sp. 2

Sp. 3

Sp. 4

Sp. 5

Sp. 6

Sp. 7

Sp. 8

Sp. 9

Sp. 10

Sp. 11

Sp. 12

Sp. 13

Sp. 14

Sp. 15

Sp. 16

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Sp. 36

Sp. 37

Sp. 38

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Sp. 40

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Sp. 60

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Sp. 62

Sp. 63

Sp. 64

Sp. 65

Sp. 66

Sp. 67

Sp. 68

Sp. 69

Sp. 70

Sp. 71

Sp. 72

Sp. 73

Sp. 74

Diptera

Sp. 1

Sp. 2

Sp. 3

Sp. 4

Sp. 5

Sp. 6

Sp. 7

Sp. 8

Sp. 9

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Sp. 11

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Sp. 27

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Sp. 30

Sp. 31

Sp. 32

Sp. 33

Sp. 34

Sp. 35

Sp. 36

Sp. 37

Hemiptera

Sp. 1

Sp. 2

Sp. 3

Sp. 4

Sp. 5

Sp. 6

Sp. 7

Sp. 8

Sp. 9

Sp. 10

Sp. 11

Sp. 12

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Sp. 29

Sp. 30

Sp. 31

Sp. 32

Sp. 33

Sp. 34

Sp. 35

Sp. 36

Sp. 37

Hymenoptera

Sp. 1

Sp. 2

Sp. 3

Sp. 4

Sp. 5

Sp. 6

Sp. 7

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Sp.89

Sp.90

Sp.91

Sp.92

Sp.93

Sp.94

Sp.95

Sp.96

Sp.97

Sp.98

Sp.99

Isopoda

Sp. 1

Lepidoptera

Sp.1

Sp.2

Sp.3

Sp.4

Mantodea

Sp. 1

Sp. 2

Sp. 3

Sp. 4

Sp. 5

Orthoptera

Sp. 1

Sp. 2

Sp. 3

Sp. 4

Sp. 5

Sp. 6

Sp. 7

Sp. 8

Sp. 9

Sp. 10

Sp. 11

Sp. 12

Sp. 13

Sp. 14

Sp. 15

Sp. 16

Sp. 17

Sp. 18

Sp. 19

Sp. 20

Sp. 21

Sp. 22

Sp. 23

Scopriones

Sp. 1

Sp. 2

Sp. 3

Sp. 4

Sp. 5

Pseudoscorpions

Sp. 1

Sp. 2

Sp. 3

Siphonaptera

Sp. 1

Thysanoptera

Sp. 1

Sp.2

Thysanura

Sp. 1

Unidentified

Sp. 1

Sp. 2

Sp. 3

Sp. 4

