Conservation of ant (Formicidae) and springtail (Collembola) diversity in South African timber production landscapes

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 owner of the copyright thereof (unless to the extent explicitly otherwise stated), and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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SUMMARY

Soil invertebrates are excellent indicators of soil health and play significant roles in soil ecosystem processes. Globally, information on their distribution and response to environmental factors remain limited. Commercial forestry in South Africa aims for sustainable production, continuously adapting ecological principles to reduce its footprint on natural ecosystems and to ensure continued productivity for future tree growth. In this thesis, I examine the diversity and distribution of soil biodiversity within South African forestry landscapes, comprising mosaics of planted areas interspersed with interconnected natural habitat, known as ecological networks.

This dissertation highlights the importance of ecological networks for preserving high levels of irreplaceable soil biodiversity within plantation landscapes. Remnant grassland and indigenous forest among timber plantation block contributes greatly to higher taxonomic and functional soil biodiversity, and soil biological activity in the overall plantation landscape. Soil- and site-scale variables had a greater effect than landscape-scale variables on soil arthropods. In addition, I found varied responses between arthropod taxa to environmental variables, emphasizing the importance of not only conserving landscape-scale heterogeneity, but also conserving small-scale heterogeneity and localized soil quality within a timber-plantation landscape to maximally benefit a wide range of species with different functional traits.

Furthermore, I show that plantations can have similar levels of soil arthropod taxonomic diversity compared to natural systems. Beta-diversity within plantations were as high as in natural systems, which was mainly driven by high species replacement. This may have been caused by high environmental variation between plantation sites or spillover from natural areas. Additionally, exotic *Eucalyptus* tree compartments had equally high functional diversity as indigenous forests and grasslands, indicating seemingly high levels of ecosystem stability and functioning. Despite a high percentage of species shared between plantations and natural systems, there were significant shifts in soil arthropod species traits between the biotope types, with plantation assemblages having a prevalence of traits that may enable species to persist within plantations. This highlights the importance of sustainable management practices within plantations to limit the loss of functionally important soil fauna.

Harvest residue management is important within commercial plantations as a nutrient management tool and to reduce fire risk. In the short-term, there was limited response of arthropod taxonomic and functional diversity, as well as assemblage composition and below-ground feeding activity, to different residue management treatments, despite highly varied conditions among treatments. However, this may have been due to the well-buffered clay soils on which the experiment took place. Therefore, assessment over a longer term and across different soil types are required to determine the best residue management practice which allows the greatest recovery of soil arthropods.

This dissertation provides guidelines for soil arthropod conservation in plantation landscapes, highlighting the importance of remnant natural areas, high environmental heterogeneity, and sustainable management of soils within timber production areas to ensure their continued functioning for future generations. It also highlights the great diversity, responsiveness to environmental variation and adaptations to novel conditions of these functionally important taxa.

OPSOMMING

Grond ongewerweldes is uitstekende aanwysers van grondgesondheid en speel 'n belangrike rol in die ekosisteemprosesse van die grond. Wêreldwyd bly inligting oor die verspreiding daarvan en reaksie op omgewingsfaktore beperk. Kommersiële bosbou in Suid-Afrika streef na volhoubare produksie, deurlopend die ekologiese beginsels aan te pas om sy voetspoor op natuurlike ekosisteme te verminder en om voortgesette produktiwiteit vir toekomstige boomgroei te verseker. In hierdie proefskrif ondersoek ek die diversiteit en verspreiding van grondbiodiversiteit in Suid-Afrikaanse bosboulandskappe, bestaande uit mosaïek van aangeplante gebiede afgewissel met onderling verbonde natuurlike habitat, bekend as ekologiese netwerke.

Hierdie proefskrif beklemtoon die belangrikheid van ekologiese netwerke vir die behoud van hoë vlakke van onvervangbare biodiversiteit in plantlandskappe. Oorblywende grasveld en inheemse bos tussen houtplantasieblokke dra grootliks by tot 'n hoër taksonomiese en funksionele grondbiodiversiteit, en grondbiologiese aktiwiteit in die algehele plantasie-landskap. Grond- en terreinskaalveranderlikes het 'n groter uitwerking as veranderlikes op landskapskaal op grond geleedpotiges. Daarbenewens het ek uiteenlopende reaksies gevind tussen geleedpotige taksa op omgewingsveranderlikes, en beklemtoon die belangrikheid daarvan om nie net die heterogeniteit van landskapskaal te bewaar nie, maar ook om kleinskaalse heterogeniteit en gelokaliseerde grondkwaliteit binne 'n houtplantasie-landskap te bewaar om 'n groot verskeidenheid spesies met verskillende funksionele eienskappe te baat.

Verder toon ek aan dat plantasies soortgelyke vlakke van taksonomiese diversiteit in die grond geleedpotiges kan hê in vergelyking met natuurlike stelsels. Betadiversiteit in plantasies was so hoog soos in natuurlike stelsels, wat hoofsaaklik gedryf is deur hoë spesievervanging. Dit is moontlik veroorsaak deur groot omgewingsvariasie tussen plantasies of oorstromings uit natuurlike gebiede. Boonop het eksotiese *Eucalyptus*-boomkompartemente ewe hoë funksionele diversiteit as inheemse woude en grasvelde, wat op oënskynlik hoë vlakke van stabiliteit en funksionering van die ekosisteem dui. Ten spyte van 'n hoë persentasie spesies wat tussen plantasies en natuurlike stelsels gedeel word, was daar 'n beduidende verskuiwing in die eienskappe van grond geleedpotiges tussen die biotope tipes, met plantasie samestellings wat 'n voorkoms van eienskappe het wat spesies in staat sou stel om binne plantasies te oorleef. Dit beklemtoon die belangrikheid van volhoubare bestuurspraktyke binne plantasies om die verlies aan funksioneel belangrike grondfauna te beperk.

Die bestuur van oesreste is belangrik in kommersiële aanplantings as 'n hulpmiddel vir die bestuur van voedingstowwe en om die brandrisiko te verminder. Op kort termyn, was die taksonomiese en funksionele diversiteit van geleedpotige reaksies beperk, sowel as die samestellingstruktuur en voedingsaktiwiteite onder die grond, ondanks die baie uiteenlopende toestande tussen behandelings. Dit kan egter te wyte wees aan die goed gebufferde kleigrond waarop die eksperiment plaasgevind het. Daarom is assessering oor 'n langer termyn en oor verskillende grondsoorte nodig om die beste bestuurspraktyk te bepaal wat die grootste herstel van geleedpotiges moontlik maak.

Hierdie proefskrif bied riglyne vir die bewaring van grond-geleedpotiges in plantasie-landskappe, wat die belangrikheid van oorblywende natuurgebiede, hoë omgewingsheterogeniteit en volhoubare bestuur van gronde in houtproduksiegebiede beklemtoon om die voortgesette funksionering daarvan vir toekomstige geslagte te verseker. Dit beklemtoon ook die groot diversiteit, reaksie op omgewingsvariasie en aanpassings by nuwe toestande van hierdie funksioneel belangrike taksa.

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"A nation that destroys its soil destroys itself. Forests are the lungs of our land, purifying the air and giving fresh strength to our people." ~ *F.D. Roosevelt*

DEDICATION

In loving memory of my grandparents:
Mr. G.B. Eckert (2003), Mr. A.W. Rossouw (2017) and Mrs. H.M. Rossouw (2018)

To my family:
For all the love and support they have given throughout this dissertation

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CHAPTER 1

General introduction

1.1. Soil ecology: A brief history

Soil biodiversity was rarely considered during the development of important biodiversity theories, as we know them today (Wardle 2006; Barot et al. 2007). Charles Darwin was the one of the first ecologists to recognize the importance of soil fauna, i.e., earthworms, regarding important soil ecosystem function (Darwin 1881). Others built on Darwin's work, demonstrating that the loss or addition of key taxa in the soil can alter litter decomposition (Butcher et al. 1971). Swift et al. (1979) divided soil biodiversity into their respective size classes, expressing the role each played in the soil. Soil biodiversity therefore gained increased recognition for its importance in the functioning of the soil (Setala and Huhta 1991). Stork and Eggleton (1992) describing the functional role of various soil invertebrates and illustrating how they can be useful indicators of soil quality. Others have shown how disturbances such as agriculture can affect soil species diversity and composition and the detrimental effects on ecosystem processes (Moore and de Ruiter 1991, Freckman and Ettema 1993). In 1996, Giller et al. was one of the first to highlight the biodiversity of soil communities. They emphasized that even though the diversity of soils can be high, we need to improve our understanding of soil communities (Giller et al. 1996) and implement sustainable management practices, i.e. practices which allow a level of diversity or functioning to be maintained, to avoid the possible irreversible damage to our soils and their functioning (Shaw et al. 1991; Lal 1997; Lal and Singh 1998).

Since then, soil ecology has become a growing research interest both globally (Nielsen et al. 2015; Birkhofer et al. 2016; Cameron et al. 2018) and in South Africa (Janion-Scheepers et al. 2016a; Yekwayo et al. 2018; Eckert et al. 2019). However, our understanding of belowground communities is limited compared to aboveground communities (Decaëns et al. 2010; Bardgett and van der Putten 2014), and even though our knowledge of belowground communities has increased, and continues to evolve, more research is still required (Nielsen et al. 2015; Janion-Scheepers et al. 2016b). Reviews by Decaëns et al. (2010) and Cameron et al. (2019) highlight that above- and belowground biodiversity responds in contrasting ways to environmental gradients, and therefore, that conservation practices for aboveground biodiversity would not necessarily be effective in conserving belowground biodiversity. More than ever, now is the time to gain a better understanding of soil biodiversity and their ecology to make applied soil studies effective to ensure the sustainable management of soils and ensure soil health for future generations (Janion-Scheepers et al. 2016a).

1.2. Soil health, ecosystem services, and biodiversity

As soils are the foundation of primary production in terrestrial ecosystems, with the global economy and human well-being depending on the sustainability of soils, they are at the center of addressing various major issues relating to biodiversity, health, food and water security, climate change, and land management (Keestra et al. 2016). This has led to a growing interest in the *value* of soil, especially its biodiversity and the ecosystem services it provides (Brussaard 2012; Pascual et al. 2015). This is not surprising as it is now known that the soil is one of the most biologically diverse systems on Earth (Bender et al. 2016) and a natural capital asset (Pascual et al. 2015). Due to its heterogeneous spatial structure, both vertically and horizontally, the soil is also one of the most complex ecosystems (Briones 2018), from which a variety of important ecosystem services are produced (Kareiva et al. 2011).

Regulating services provided by soils include climate and gas regulation, biological control of diseases and pests, water retention, detoxification of waste and the filtering of nutrients and contaminants (Jónsson and Davíðsdóttir 2016). Supporting services include nutrient cycling, water cycling, and acting as a biodiversity pool (Jónsson and Davíðsdóttir 2016). Provisioning services include biomass production and raw materials, clean water provisioning, and the physical environment for biodiversity and anthropogenic activities (Jónsson and Davíðsdóttir 2016). Soils may also provide cultural services by means of recreational (e.g., ecotourism), cognitive (e.g., aesthetic, spiritual and educational) and heritage (e.g., as an archaeological, ecological, and geological archive) services (Decaens et al. 2006; Jónsson and Davíðsdóttir 2016). However, the functioning of the soil and the services it provides, is highly dependent on the biological diversity within the soil (Baveye et al. 2016).

Soils contain more than 25% of terrestrial biodiversity (Bach et al. 2020) by providing habitat to a wide range of organisms ranging from micro- (e.g., nematodes), meso- (e.g., springtails and mites) to macrofauna (e.g., earthworms, ants, termites, woodlice, centipedes, and millipedes) (Orgiazzi et al. 2016a) that are involved in fundamental ecosystem functions (Kumssa et al. 2004; Barrios 2007; Orgiazzi et al. 2016a). Larger, burrowing mammals utilizing the soil environment are classified as megafauna (Orgiazzi et al. 2016a). The presence of soil biota is a critical component of the soil system, which contributes largely to the quality and health of the soil (Yan et al. 2012). Soil health can be defined, in the simplest terms, as “the capacity of the soil to function” (Doran 2002; Paz-Ferreiro and Fu 2016). Soil health is best described as the biological integrity of the soil community, i.e., the balance among organisms within the soil and between soil organisms and their environment (Curell et al. 2012). Healthy soils maintain a diverse community of soil organisms which recycle essential plant nutrients, improve soil structure with positive repercussions for soil water and nutrient holding capacity and ultimately improve primary production. Soil biota, such as arthropods, fungi and microbes, are the basis of terrestrial ecosystem functioning (Kumssa et al. 2004) as they play important roles in soil processes and functions, as well as important ecosystem services such as decomposition and nutrient cycling (Yan et al. 2012).

However, soil biodiversity is declining due to the immense pressure on our soils (Wall et al. 2015; Orgiazzi et al. 2016a,b; Tibbett et al. 2020). Major threats include agricultural activities (Geisen et al. 2019; Pilling et al. 2020), urbanization (Li et al. 2017; Ge et al. 2019), and climate change (Ripple et al. 2017; Mammola et al. 2018). Strong baseline information on how to conserve soil biodiversity is crucial to ensure continued productivity for future generations (Tahat et al. 2020). This lack of comprehensive information on soil biodiversity limits our ability to adequately manage and conserve them. This includes taxonomic information (Wilson et al. 2014; Janion-Scheepers et al. 2016b; Cameron et al. 2018), information on their spatial and temporal distributions (Guerra et al. 2020; Thakur et al. 2020), and vulnerability of soil organisms to different environmental stressors (Coyle et al. 2017; Bastida et al. 2020). These gaps mainly exist due to the historical research focus on aboveground biodiversity, while belowground biodiversity remains understudied (Geisen et al. 2019; Thakur et al. 2020). For this reason, soil biodiversity remains neglected in global biodiversity assessments and environmental policies (Cameron et al. 2018, 2019; Mammola et al. 2019; Bach et al. 2020), of great concern considering the urgency for conservation actions to mitigate biodiversity declines (Samways et al. 2020). It is also becoming increasingly evident that conservation strategies for aboveground diversity may not be applicable for limiting threats to belowground diversity (Cameron et al. 2019; Geisen et al. 2019; Thakur et al. 2020). Recent work demonstrates convincingly that global biodiversity patterns (Cameron et al. 2019) and responses to land-use (Le Provost et al. 2021) vary between above- and belowground biota. Thus, we need to consider them as two distinct components of biodiversity if we are to manage and conserve whole-ecosystem biodiversity more efficiently (Cameron et al. 2019; Le Provost et al. 2021).

1.3. Mitigation measures for agricultural impacts on biodiversity

Human activities such as intensive agriculture and forestry, degrade soil quality, directly affecting productivity (Titshall 2015). Historically, plantation forests were often established as continuous, even-aged monocultures, with no regard for topography or other landscape elements, and were intensively managed throughout the landscape to meet wood production demands (Evans 1997; Samways and Pryke 2016). Today, both globally and in South Africa, there is growing awareness that we need to shift away from large-scale, intensive monoculture production systems as they are no longer considered to be socially, economically, and ecologically viable. This is because they impose a great ecological footprint, are inefficient in terms of resource use, and are making soils more vulnerable to climate change (Nicholls et al. 2016). One of the greatest threats to biodiversity is habitat degradation and loss, as well as landscape fragmentation (Habel et al. 2019).

Habitat loss and fragmentation are often complementary, which can lead to reduced connectivity throughout the landscape (Fischer and Lindenmayer 2007; Fletcher Jr. et al. 2018). Plantation forestry contributes to this, as the extensive planting of exotic monocultures can lead to habitat loss and possibly reduced connectivity throughout the landscape for certain species (Liu et al. 2017; Vasconcelos et al. 2019; Sweaney et al. 2021). This in turn, can have adverse effects on insect survival within highly transformed, fragmented landscapes (Cardoso et al. 2020). In addition, commercial plantation stands are typically characterized by reduced levels of biodiversity compared to mixed stands and natural habitats, which in turn, makes them less capable to provide biodiversity-linked ecosystem services (Brockerhoff et al. 2008; Thompson et al. 2009). This means that to preserve the functional integrity of the ecosystem and to mitigate further loss of biodiversity throughout these timber production landscapes, alternative landscape management practices need to be adopted.

Two unique and contrasting management approaches have been proposed as a solution to reconcile trade-offs between biodiversity and agricultural production: land sharing and land sparing (Waggoner 1996; Green et al. 2005; Phalan et al. 2011). These approaches are at two ends of a continuum, each with its own set of unique advantages and disadvantages (Green et al. 2005; Fischer et al. 2008; Balmford et al. 2019). With these approaches, biodiversity is either integrated (i.e., land sharing) or separated (i.e., land sparing) in a production landscape (Phalan et al. 2011; Fischer et al. 2014). The land sharing approach is most beneficial for species adapted to move across an agricultural matrix, whereas the land sparing approach is crucial for the conservation of species which are incompatible with agricultural (Phalan et al. 2011; Grass et al. 2019). Although studies suggest the contrast between agricultural land and natural vegetation is stronger with the land sparing approach compared to the land sparing approach (Fischer et al. 2008), some studies support the use of the land sparing approach as it is beneficial for maintaining or conserving a variety of fauna and flora within a production landscape (Phalan et al. 2011; Dotta et al. 2016; Williams et al. 2017). However, within a timber plantation landscape context, use of the land sparing approach is supported as a means of biodiversity conservation in a timber harvesting system where the canopies of trees close, shading the soil, and the logistics and economics of tree felling and removal have to be considered. In this system, land sparing can be in the form of large scale remnant grasslands and forests across this landscape mosaic, while providing few opportunities for land sharing (Samways 2007; Pryke and Samways 2012).

1.4. Ecological networks (ENs) and plantation forestry

South Africa has a long history of commercial plantation forestry (Zahn and Neethling 1929; Van der Zel 1995; Dye 2013) to cope with insufficient natural wood resources in the country (Samways et al. 2010a). Most recent estimates indicate that plantation forests account for 1.2% of the total surface area of the country (Xulu et al. 2019; FSA 2020). These plantations are primarily located in the eastern parts of the country, within the Mpumalanga and KwaZulu-Natal provinces (Tewari 2001), occurring within the threatened grassland biome (Samways et al. 2010a). However, the South African timber industry is making significant efforts to mitigate the ecological impact of timber production (Kirkman and Pott 2002). Even though plantation forestry is intensive at the compartment scale (Brockerhoff et al. 2008), its impacts are being alleviated through the implementation of the large-scale land sparing approach, i.e., conservation of wildland such as natural grassland interspersed with production land, in the form of ecological networks (ENs) of conservation corridors. This is done to comply with sustainable management guidelines such as those of the South African National Biodiversity Strategy and Action Plan (DEA 2015), the Global Aichi Biodiversity Targets (CBD 2018) and the Forest Stewardship Council (FSC) (FSC 2020). These interconnected corridors and nodes of unplanted, remnant areas within the plantation landscape form the EN (Jongman 1995; Samways et al. 2010a) and consist mainly of natural grasslands (Samways et al. 2010a; Joubert et al. 2016) but may also include indigenous forests and wetlands (Joubert et al. 2014), which can occur extensively across the plantation mosaic (Samways and Pryke 2016).

Ecological networks are implemented to offset the negative effects of plantation forestry on local biodiversity (Kirkman and Pott 2002; Samways 2007), such as habitat fragmentation and transformation (Fischer et al. 2006; Joubert et al. 2016) and aim to enhance the structural and functional connectivity between remnant natural areas of high conservation value within the production landscape (Samways and Pryke 2016). Ecological networks can also act as extensions of protected areas (Pryke and Samways 2012b) and are highly effective at conserving biodiversity of a wide range of taxa, such as plants (Joubert et al. 2016), dragonflies (Kietzka et al. 2015), grasshoppers (Bazelet and Samways 2011) and small mammals, butterflies and birds (Haddad et al. 2003), contributing to increased regional biodiversity. Research in ENs have increased our understanding of species diversity and their distribution in production landscapes, while also informing local EN design and management. However, the soil biota is a less-studied group of organisms yet has a great functional importance within ecosystems (Warren and Zou 2002; Barrios 2007).

In South Africa, few studies have focused on these soil organisms, including within timber production landscapes (Yekwayo et al. 2016; Nadel et al. 2007; Eckert 2017). Initial work on soil biota in local

ENs show that there are high levels of assemblage segregation between different natural biotopes in the landscape mosaic, contributing to high landscape-scale soil biodiversity (Yekwayo et al. 2016; Eckert 2017). We have, however, not yet fully explored the contribution of these diverse natural habitats to regional biodiversity and how soil organisms are influenced by landscape and habitat heterogeneity. We also have limited knowledge of factors that may lead to local hotspots of soil biodiversity. Many factors influence the local abundance and distribution of species (Pryke and Samways 2010; Samways et al. 2010a; Bazelet and Samways 2011), some of which include natural environmental gradients, current and historical management effects, and EN design variables. We therefore expect corresponding benefits of landscape complexity to soil fauna, as different guilds may respond differently to environmental drivers. A better understanding of the responses of soil biodiversity to natural landscape heterogeneity is critical for effective conservation planning and prioritization within these landscapes.

Moreover, there is high contrast between the different landscape elements within plantation landscapes (Yekwayo et al. 2017; van Schalkwyk et al. 2021). The landscapes comprise open-structured, low-growing grasslands that contrast with closed-canopy indigenous forests, both of which are compositionally diverse in terms of its plant diversity. Furthermore, commercial timber stands are highly homogenous in terms of its structure and composition. However, little is known of the response of soil biodiversity to these differences within these landscapes. This indicates that we need to understand how soil biodiversity patterns (e.g. alpha, beta, and functional diversity) changes from more heterogeneous, natural conditions to more homogenous, transformed conditions. Studies of soil alpha and beta-diversity is still limited (Bishop et al. 2015; Kuznetsova and Saraeva 2018; Kim et al. 2018), and therefore we need a better understanding how soil alpha and beta diversity changes to protect soil biodiversity efficiently and successfully within these production landscapes.

Intensive management practices within plantation blocks can also have detrimental effects. Management practices such as timber harvesting operations, mechanical site preparation, prescribed fires, and fertilizer and biocide applications have a significant effect on the soil environment (Ballard 2000). Venanzi et al. (2016), for example, demonstrated that harvesting operations can significantly impact the biological, physical, and chemical properties of the soil, which in turn, can influence soil processes. Harvesting practices may also lead to changes in the soil microclimate, soil structure, leaf litter quality and quantity and nutrient availability (Edlund et al. 2013), which in turn, can affect soil biodiversity. In addition, harvest residue management is an important issue in plantation forests both from an operational viewpoint and for maintenance of soil fertility for future rotations (Mendham et al. 2003; de Moraes Goncalves et al. 2004; Laclau et al. 2010). The effects of harvest residue management on the soil's chemical and physical properties have received much attention in South Africa (du Toit et al. 2000; Smith and du Toit 2005; du Toit 2008), while the biological component remains poorly investigated (Gill et al. 2011; Nadel et al. 2007; Puga et al. 2017).

Today, fire is often used as a silvicultural management tool for harvest residue (Arno 1996; Grigal 2000). Historical studies on the effects of fire on the soil ecosystem, was mainly focused on the soil's physical or chemical properties (Kutiel and Naveh 1987; Ulery and Graham 1993), as it can alter a site's productivity (Grigal 2000). However, of all the soil components, the biological component (i.e., soil biota) is one of the first to respond to fire (Bezkorovainaya et al. 2007). In recent years, post-fire ecology of soil organisms was limited and not well understood (Ahlgren 1974; Staddon et al. 1996; Beaudry et al. 1997). More recently, the response of soil arthropods to fire is known to vary among arthropod taxa and functional guilds (Vasconcelos et al. 2009; Kwon et al. 2013). This was also found within the Cape Floristic Region in South Africa (Yekwayo et al. 2018), along with a variation in response to fire between species of the same taxa (Janion-Scheepers et al. 2016a). Some arthropods may be more protected from the effects of fire by their location during a fire, life history traits, and mobility. Surface-dwelling arthropods are suggested to be more at risk than soil-dwelling arthropods (Bezkorovainaya et al. 2007) and arthropods with high mobility are less at risk than arthropods with lower mobility (Certini 2005).

As most soil organisms are depended on the soil for survival, biodiversity monitoring is therefore crucial to support sustainable management decisions (Venanzi et al. 2016), especially in terms of soil biodiversity, being inherently linked to the functioning of the soil (Barrios 2007; Kibblewhite et al. 2008). Although limited, studies suggest aboveground taxa are more vulnerable to disturbances than belowground taxa (Zaitsev et al. 2014; Gongalsky et al. 2012; Korobushkin et al. 2017). We therefore need a better understanding the extent to which soil biodiversity is impacted by management practices as it is essential for determining the most sustainable practices to maintain long-term soil productivity (Fox 2000; Hou et al. 2020).

1.5. Focal taxa for this dissertation

Arthropods were selected for this study as they are excellent environmental and ecological bio-indicators, based on their small size and mobility (Gerlach et al. 2013; Samways 2005). They have short generation times (Samways et al. 2010b), are hyper-diverse and can be sampled in large numbers (Pryke and Samways 2015). They are also known to be sensitive to disturbances associated with agriculture (Ponge et al. 2013), such as the simplification of ground cover (Loranger-Merciris et al. 2006), soil compaction (Heisler and Kaiser 1995), fertilizer application (Cole et al. 2005; van der Wal et al. 2009), and pesticide treatment (Rebecchi et al. 2000, Cortet et al. 2002).

Soil and litter arthropods are especially efficient indicators of land use impacts on soil properties (McIntyre 2000; Venuste et al. 2018). Thus, throughout this thesis, I focus on two arthropod taxa, namely Collembola (springtails) and Formicidae (ants). Springtails are one of the most important, abundant taxa within the soil (Buşmachiu et al. 2017; Chang et al. 2017) contributing to soil ecosystem functioning through litter decomposition and soil microstructure formation (Hopkin 1997; Rusek 1998), which is greatly influenced by their abundance (Milcu et al. 2008). They are highly responsive to management practices such as fire (Malmström 2012; Janion-Scheepers et al. 2016a) and environmental gradients, such as elevation (Wang et al. 2009), vegetation, and soil conditions (Ponge et al. 2003). Springtails are thus excellent bioindicators due to their sensitivity and significant responses to environmental changes and disturbances. Ants, on the other hand, are important components of the soil ecosystem as they constitute a great part of the soil animal biomass (Folgarait 1998: Graham et al. 2009) are identified as one of the most important soil ecosystem engineers (Folgarait 1998; Jouquet et al. 2006) and indicators of soil quality (Venuste et al. 2018). They participate in soil mixing and aeration, improving soil porosity and texture (Fatima et al. 2008) as well as contributing to nutrient transport among the different soil horizons (Bagyaraj et al. 2016).

Not only do these two taxa differ from each other morphologically, but also ecologically. For example, ants are generally highly mobile (Heil et al. 2001), whereas springtails are less mobile (Rantalainen et al. 2008; Lessel et al. 2011). Regarding habitat specificity, springtails are moisture- and acidity-sensitive arthropods (Tsiafouli et al. 2005; Auclerc et al. 2009), whereas ants generally prefer more open-structured habitats with higher temperatures (Lassau and Hochuli 2004; Gollan et al. 2011). The dietary requirements of ants are species-dependent, which can be either herbivorous, predaceous, omnivorous, or opportunistic feeding (Hölldobler and Wilson 1994). In contrast, most springtails feed on either algae, fungi, bacteria, or plant material, although some species are predacious (Larink et al. 1997; Hopkin 1997; Malcicka et al. 2017), although this is species-dependent. In addition, both ants and springtails are sensitive to habitat changes and disturbances (Andersen et al. 2002; Maunsell et al. 2013). Therefore, as these two taxa differ in dietary requirements and mobility, and show a strong response to habitat change, it will allow me to assess a broad range of potential responses to different environmental factors and disturbances.

In addition, functional diversity of soil arthropods and how species traits differ across landscapes remain poorly researched (Ulrich and Fiera 2009, 2010; Bishop 2017). By examining functional diversity and species trait differences, and how they respond to different land-uses, we can understand how species are adapting within the transformed landscapes and how they are able to persist under different environmental conditions (Bishop et al. 2015). By understanding how soil biodiversity (i.e., alpha, beta, and functional diversity) responds to various environmental factors and how these drive their patterns, knowledge gaps can be filled and ensure appropriate management practices can be implemented to maintain local soil biodiversity and ensure the long-term success of ENs within timber production landscapes (Pryke and Samways 2012a, 2015).

1.6. Dissertation outline and aims

The overall purpose of this study is to gain an in-depth understanding of two important soil arthropod taxa, namely ants (Formicidae) and springtails (Collembola), regarding their diversity, distribution and responses to land-use and management practices, within South African forestry landscapes which comprise mosaics of remnant natural habitat along with timber production areas. Previous work has indicated that different taxonomic and functional groups show contrasting responses to landscape composition (Birkhofer et al. 2017; de Graff et al. 2019; Schoeman et al. 2019) and that there is a mismatch of biodiversity hotspots and drivers between above- and belowground biodiversity (Cameron et al. 2019; Le Provost et al. 2021). I therefore expect that my focal arthropod taxa would be less sensitive to landscape factors and more responsive to immediate habitat conditions and soil related variables (Boeraeve et al. 2019; Le Provost et al. 2021), and the responses by these soil arthropod taxa to environmental conditions to be different (Geisen et al. 2019; George et al. 2019).

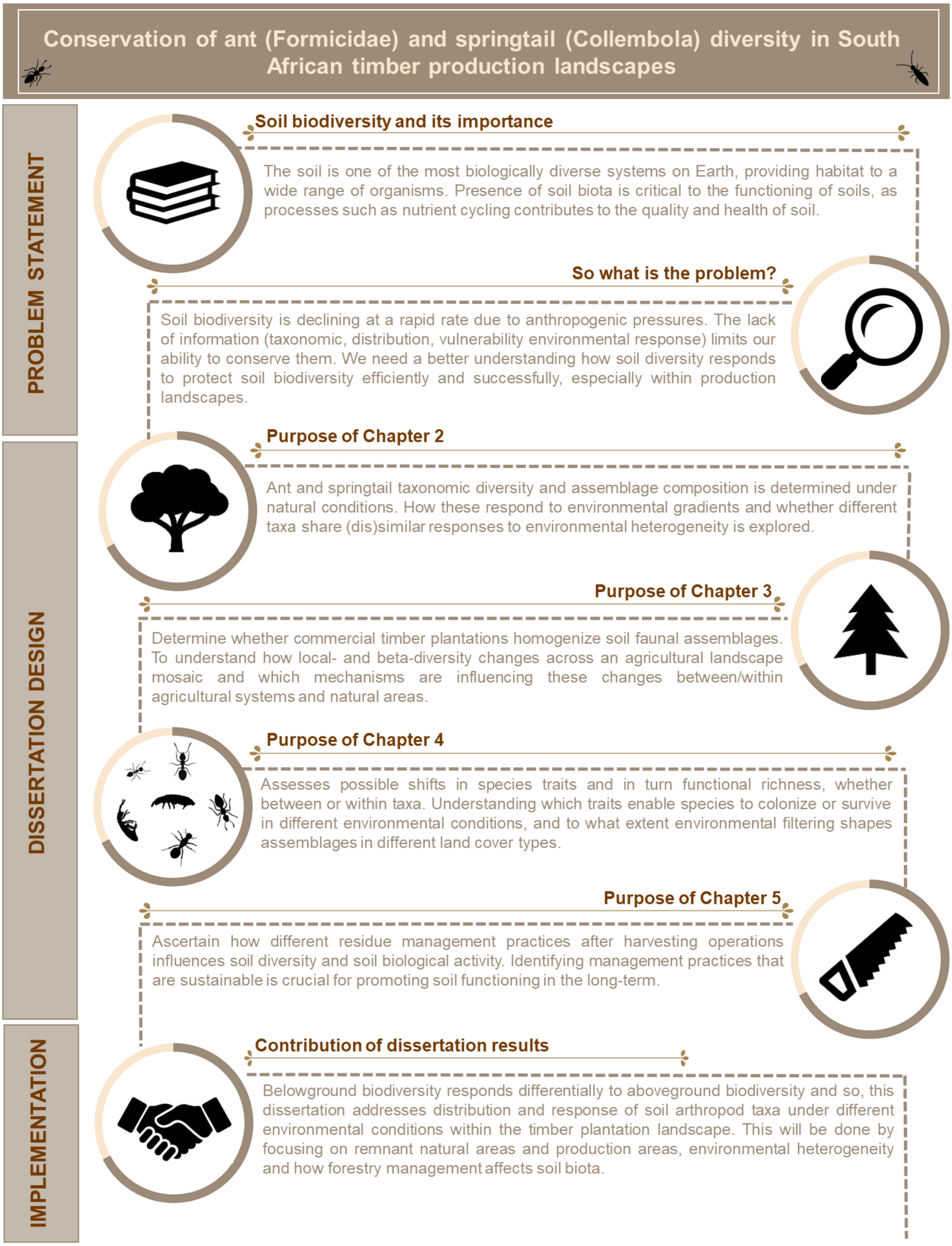
The aim of the first research chapter (chapter 2) is to determine how environmental variation in untransformed, natural habitats influence ant and springtail biodiversity. This study is conducted at the sub-regional scale, across several plantation estates representing highly varied soil and environmental conditions. I focus on two dominant natural biotopes, grasslands, and indigenous forest, and assess the influence of a wide range of environmental variables at the local-, patch- and landscape-scale on various response variables, including soil biological activity as well as the abundance, species richness and assemblage composition of the ants and springtails. Here (and for the chapters to follow), “assemblage composition” refers to a group of different species that collectively occur in a given space and/or time (Gaston and Blackburn 2000; Stroud et al. 2015). This provides detailed baseline information on their assemblage composition and taxonomic diversity under natural conditions and assesses whether different taxa share similar responses to environmental heterogeneity. This information informs local conservation planning and management, while contributing to our understanding of soil biotic response to multi-scale heterogeneity.

In the third chapter I assess whether commercial timber plantations homogenize soil faunal assemblages. This will be done by examining the change in alpha- and beta-diversity, as well assemblage composition, of ants and springtails between natural biotopes (grassland and indigenous forest) and plantations (pine and eucalypt) within several EN-plantation landscape mosaics across different regions. Understanding how local- and beta-diversity of soil biodiversity changes across large-scale, transformed landscapes clarifies the impact of plantation forestry on soil biota at different spatial scales. I also assess whether responses of soil biota in these systems correspond to global findings of land-use intensification leading to biotic homogenization.

The aim of the fourth chapter is to ascertain differences in ant and springtail functional diversity, and differences in species traits between natural (grassland and indigenous forests) and transformed (*Pinus* and *Eucalyptus* compartments) biotopes. Functional diversity helps to understand the link between communities and their potential effects on ecosystem functioning. This study provides important information on the potential impact of forestry on soil ecosystem resilience. Furthermore, it provides a better understanding of which traits enable species to colonize or survive in different environmental conditions, and to what extent environmental filtering shapes assemblages in different land cover types.

The aim of the fifth chapter is to determine how different residue management practices after harvesting operations influences soil diversity and soil biological activity within commercial timber production blocks. Four different management practices are examined, namely 1) retention of residue, 2) high-intensity burning of residue, 3) complete removal of residue, and 4) low-intensity burning of residue after harvesting. To determine the relative and short- to medium-term impact of the management treatments, sampling occurs prior to the implementation of management practices, as well as 1 month and 12 months thereafter. Determining the best residue management practice would be valuable for land managers for promoting soil function through the sustainable management of the soil for the long-term.

In my sixth and final chapter, I synthesize the results obtained throughout the dissertation, focusing on emergent themes. Here, I will highlight the most important findings and make recommendations for the best conservation management strategies to maintain and conserve soil biodiversity within commercial plantation landscapes. By ensuring sustainable plantation forestry, soil biodiversity can be maintained and conserved, promoting the biological functioning of the soil, thereby safeguarding soil health and quality into the future.



Conservation of ant (Formicidae) and springtail (Collembola) diversity in South African timber production landscapes

PROBLEM STATEMENT

Soil biodiversity and its importance

The soil is one of the most biologically diverse systems on Earth, providing habitat to a wide range of organisms. Presence of soil biota is critical to the functioning of soils, as processes such as nutrient cycling contributes to the quality and health of soil.

So what is the problem?

Soil biodiversity is declining at a rapid rate due to anthropogenic pressures. The lack of information (taxonomic, distribution, vulnerability environmental response) limits our ability to conserve them. We need a better understanding how soil diversity responds to protect soil biodiversity efficiently and successfully, especially within production landscapes.

DISSERTATION DESIGN

Purpose of Chapter 2

Ant and springtail taxonomic diversity and assemblage composition is determined under natural conditions. How these respond to environmental gradients and whether different taxa share (dis)similar responses to environmental heterogeneity is explored.

Purpose of Chapter 3

Determine whether commercial timber plantations homogenize soil faunal assemblages. To understand how local- and beta-diversity changes across an agricultural landscape mosaic and which mechanisms are influencing these changes between/within agricultural systems and natural areas.

Purpose of Chapter 4

Assesses possible shifts in species traits and in turn functional richness, whether between or within taxa. Understanding which traits enable species to colonize or survive in different environmental conditions, and to what extent environmental filtering shapes assemblages in different land cover types.

Purpose of Chapter 5

Ascertain how different residue management practices after harvesting operations influences soil diversity and soil biological activity. Identifying management practices that are sustainable is crucial for promoting soil functioning in the long-term.

IMPLEMENTATION

Contribution of dissertation results

Belowground biodiversity responds differentially to aboveground biodiversity and so, this dissertation addresses distribution and response of soil arthropod taxa under different environmental conditions within the timber plantation landscape. This will be done by focusing on remnant natural areas and production areas, environmental heterogeneity and how forestry management affects soil biota.

Figure 1.1 Infographic describing the problem statement, chapter layout and possible implementation recommendations of results found throughout the dissertation.

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CHAPTER 2

Environmental drivers of soil arthropod diversity are highly context- and taxon-specific in conservation timber plantation mosaics in different geographical areas

ABSTRACT

Humanity relies on soil for important ecosystem services. Soils must therefore be managed sustainably to ensure their long-term function. However, knowledge on soil biodiversity is limited globally, and the effect of environmental drivers on soil faunal distributions is poorly understood. I focus here on environmental drivers at different spatial scales on ant and springtail diversity, and soil biological activity, within remnant natural forests and grasslands making up conservation corridors among plantation mosaics in two contrasting geographical regions (the Midlands and Zululand) in South Africa. The inland Midlands sites, with their complex topography and nutrient-rich and deep soils, generally had higher soil arthropod diversity and biological activity than the coastal, shallow Zululand soils. However, diversity patterns between biotopes differed depending on taxon and region. Environmental drivers differentially influenced the two focal taxa and biological activity. Soil biological activity was driven by soil-related variables regardless of biotope type and region. Ants and springtail diversity and assemblage composition showed varied responses to environmental drivers, showing more diverse and pronounced responses in the Midlands compared to Zululand. Site-related variables (e.g. plant diversity, leaf litter, and herbaceous cover) were most influential on springtail diversity, whereas soil variables (e.g. soil carbon and nitrogen content) were most influential on ant diversity in the Midlands. Presence of remnant natural vegetation contributes to the persistence of soil biodiversity within these production landscapes. Lower estimates of soil biodiversity and activity in Zululand compared to the Midlands emphasize the importance of limiting further homogenizing threats to soil fauna (e.g. presence of alien vegetation, excessive grazing, and intensive fire management regimes). Furthermore, soil- and site-scale variables had a greater effect than landscape-scale variables, showing the importance of conserving the localized quality of the soil at the fine scale. Varied responses to environmental variables highlighted the importance of managing and conserving small-scale heterogeneity to maximally benefit a wide range of organisms.

Key words: Ants, Collembola, Forest, Formicidae, Grassland, Springtails

2.1. Introduction

Within agricultural and forestry landscapes, the presence of undisturbed, remnant natural areas are of major importance, especially for disturbance-sensitive species (Samways et al. 2020). Their proportion and position within the landscape relative to cultivated areas play an important role as population source pools and refuges (Pfiffner et al. 2000). Landscape elements, such as natural grasslands and indigenous forest fragments, are crucial for the maintenance and conservation of biodiversity, particularly in agricultural landscapes (Jeanneret et al. 2003). This is especially important for South Africa's timber production landscapes, which comprise a mosaic of commercial timber blocks interspersed with ecological networks (ENs) of natural vegetation (Samways and Pryke 2016), as the survival of arthropods depends greatly on the presence of suitable habitats (Jeanneret et al. 2003).

In South Africa, the ENs within commercial plantations aim to structurally and functionally connect remnants of high value natural habitats (consisting of grasslands and indigenous forests) to conserve various taxa, and to mitigate the effects of timber production (Samways and Pryke 2016). Even though indigenous forest is the smallest biome in the country (Eeley et al. 2001), it is considered a high conservation priority for arthropod biodiversity containing relatively high proportions of terrestrial biodiversity (Brockerhoff et al. 2008; Yekwayo et al. 2016a). Grasslands within these plantation landscapes are also important for arthropod biodiversity (Yekwayo et al. 2016a). Various studies have been conducted within South African EN-timber compartments landscape mosaics in KwaZulu-Natal, showing the importance of natural heterogeneity (Pryke and Samways 2015; Joubert-van der Merwe et al. 2019). This has significantly contributed to the development and improvement of management strategies within these ENs. However, few studies within this landscape context have focused on soil arthropods (Eckert et al. 2019), although ants as important soil ecosystem engineers show distinct responses across this landscape (van Schalkwyk et al. 2017; Yekwayo et al. 2017). Given the importance of soil biodiversity within agricultural landscapes, guidelines are needed which aim to maintain and enhance soil biodiversity. Investigating the distributions and responses of soil arthropods to environmental gradients is important, as soil arthropods might show different distribution patterns and responses to environmental gradients compared to above-ground arthropods or vegetation due to differences in mobility and resource requirements. Therefore, the conservation approaches for soil biodiversity might not be the same as for aboveground biodiversity (Cameron et al. 2019).

Understanding patterns of biodiversity is a global challenge (Joern and Laws 2013). In ecology, a major goal is to understand the relationship between spatial heterogeneity and biodiversity, more specifically, the environmental drivers of the distribution of species within agricultural landscapes (Tscharntke et al. 2005; Le Roux et al. 2008). A fundamental concept in ecology is that heterogeneity is one of the most important factors which influences biodiversity (Fuller et al. 2004; Fahrig et al. 2011). Spatial heterogeneity affects ecological systems by influencing the interactions (Polis et al. 2004), movement (Fahrig 2007) and persistence (Fraterrigo et al. 2009) of species, but also ecosystem functioning (Lovett et al. 2005). However, soil ecosystems are rarely considered in biodiversity surveys, even though they are one of the most complex and biologically diverse terrestrial ecosystems (Briones 2018). Although soil arthropods make up a large and functionally important component of total terrestrial biodiversity (Decaëns et al. 2006), even basic knowledge of them is lacking or far from complete (Janion-Scheepers et al. 2016b). In addition, research on the response of soil biodiversity to environmental factors is limited (Barrios 2007; Birkhofer et al. 2016). Even with their important functional roles, soil arthropods are rarely included in conservation or land-use planning decisions (Janion-Scheepers et al. 2016b). Therefore, a better understanding of soil biodiversity is needed for their conservation (Menta 2012).

Most studies investigating environmental drivers of soil fauna have been confined to small spatial scales. Therefore, the relationship between abiotic and biotic drivers at larger spatial scales remain largely unexplored (Vanbergen et al. 2007; Birkhofer et al. 2011). In addition, very few studies have considered multiple spatial scales within the same study in determining the key drivers of soil biodiversity (Eggleton et al. 2005; Vanbergen et al. 2007). Therefore, it remains unclear which components of landscape heterogeneity has the greatest influence on soil biodiversity. Furthermore, as the influence of factors (whether biotic or abiotic) may vary between taxonomic groups (Schoeman et al. 2019), it is also important to identify environmental influences which are taxon-specific (Seibold et al. 2016). In cases where generalities in response to environmental factors (i.e. groups of factors or factors at a specific spatial scale) are found among taxa, the results can be used as a conservation management tool by identifying areas with high value for soil biodiversity. In contrast, if no generalities in responses to environmental factors are found among taxa, these results would also be important, as it would indicate that conservation strategies need to be tailored to different situations and locations.

Globally, soil biology research has been limited, especially compared to research on soil physical or chemical characteristics (Wilson et al. 2014). One of the main reasons for this is the taxonomic challenge associated with using invertebrates as bio-indicators (Orgiazzi et al. 2016). However, the laborious counting and identification of numerous soil arthropods can be avoided (or supplemented) by using proxies of soil faunal diversity (Klimek and Niklińska 2020). As stated by Rożen et al. (2010), the assessment of soil feeding (i.e. biological) activity can also be used as a sufficient indicator of ecological and biological processes. This is one of the first and most basic factors likely to change due to fluctuations in abiotic and biotic conditions (Gongalsky et al. 2004). The bait-lamina test developed by Von Törne (1990) is used for assessing the biological activity of soil fauna (Birkhofer et al. 2011). It has the advantage of being a simplistic, low-cost method (Kratz 1998) which can detect changes in soil biological activity in a short time, and with little labour (Klimek and Niklińska 2020). In addition, these measurements are highly dependent on arthropods such as earthworms and enchytraeids, and to a lesser extent, arthropods such as springtails, mites and microorganisms (Gongalsky et al. 2008; Birkhofer et al. 2011). This method has been applied in various contexts under different environmental conditions to examine the response of soil biological activity to soil pollution (Filzek et al. 2004; André et al. 2009), soil properties (Gongalsky et al. 2008), vegetation characteristics (Hamel et al. 2007; Rożen et al. 2010), agricultural practices (Jacometti et al. 2007;

Reinecke et al. 2008) and land-use type (Hamel et al. 2007; Riutta et al. 2016). Examining soil biological activity and determining key environmental factors which drive soil biological activity, may contribute to a better understanding of soil ecosystem functioning, as it is a functional indicator of the influence of the soil decomposer community on important processes (e.g. nutrient cycling) through their feeding activity (André et al. 2009; Römbke 2014).

Invertebrates are excellent candidates as ecological indicators, as they are highly sensitive to variations in resource availability (Ilieva-Makulec et al. 2004), habitat structure (Santorufo et al. 2012), vegetation and soil conditions (Nahmani and Lavelle 2002), microclimate (Harte et al. 1996), habitat complexity and even landscape diversity (Vanbergen et al. 2007). For example, landscape factors, such as elevation (Wang et al. 2009), slope and/or aspect (Jouquet et al. 2012; Seppey et al. 2020), and land-use type (Sousa et al. 2006; Milano et al. 2017) can be important drivers of soil arthropod biodiversity. In other cases, vegetation characteristics, such as cover (Sylvain and Wall 2011), diversity (Wardle et al. 2006; Liu et al. 2008), composition, or type (Barrow et al. 2007; Li et al. 2007), have been identified as important drivers. Other factors relating to vegetation characteristics such as canopy cover (Vanbergen et al. 2007; Henneron et al. 2017) and leaf litter quality and quantity (Mueller et al. 2015; Milano et al. 2017) can also be important drivers of soil biodiversity. Some studies also found soil biodiversity to be significantly influenced by soil properties mostly relating to moisture and pH (Eggleton et al. 2005), temperature (Sylvain and Wall 2011) or soil chemical elements (Mueller et al. 2015; Milano et al. 2017).

This study aims to determine the similarity of environmental drivers on ant and springtail biodiversity within remnant natural vegetation types across much of the EN-plantation landscape in South Africa. This was addressed by examining two geographical regions that vary in their topographical and environmental complexity, soil types, and management histories (Midlands and Zululand), focusing on two structurally distinct natural ecosystem types (grassland and indigenous forest), and two ecologically distinct soil arthropod taxa (ants and springtails), as well as soil biological activity. By examining these distinct regions, biotopes, and biodiversity responses, it was possible to assess whether there are common ecological drivers of soil biodiversity, or whether species response to environmental variables vary between contexts and taxa. In addition, this would provide detailed, baseline information on the biodiversity and assemblage compositions of soil arthropods under natural conditions. In view of the issues given above, the objectives here are 1) to determine the effect of biotope type, geographical region, and their interactions with soil biological activity in terms of ant and springtail abundance and species richness and assemblage composition, 2) to determine which environmental variables (landscape, habitat, or soil) contribute significantly to ant and springtail biodiversity patterns within each biotope type and region, and 3) to determine the extent of environmental effects on ant and springtail biodiversity when comparing the two regions and biotopes (natural areas within the ENs). Firstly, I hypothesize that my response variables would be significantly different between regions, as they are topographically and climatically different. Secondly, that there would be significant differences in the response variables between biotope types within the same region, as species may be adapted to persist under quite different environmental conditions. Thirdly, as my focal arthropod taxa are dependent on the soil environment for their survival, I would expect that small-scale factors, i.e. variations in soil and habitat properties, would play a greater role than landscape-scale factors. Lastly, I also expect large differences in the comparative response of ants and springtails to environmental variables, regardless of biotope and region, as they require different habitat conditions and resources for their survival. Gaining an in-depth understanding of how these arthropods respond to environmental gradients, and whether or not these responses are similar in different contexts, would be beneficial to land-managers, as it would aid conservation practices in identifying areas of high biodiversity and landscape management practices to ensure the living soils' continued functionally important roles within the soil ecosystem.

2.2. Materials and methods

2.2.1. Study area and design

In South Africa, the KwaZulu-Natal (KZN) province is an important timber production area, characterized by a subtropical climate with warm, wet summers and cool, dry winters (Fairbanks and Benn 2000). This study was carried out in two different geographical regions: the Midlands (Fig. 2.1A) and Zululand (Fig. 2.1B) in KZN. These two regions differ in their overall elevation, with Midlands occurring at higher elevations compared to Zululand (details below). The Midlands is dominated by the threatened Mistbelt Grassland and Drakensberg Foothill Moist Grassland, whereas Zululand is dominated by the Maputaland Wooded Grassland (Mucina and Rutherford 2006). These vegetation types naturally occur as a grassland matrix, with small and naturally isolated remnant patches of indigenous forests embedded within them. These areas have natural vegetation types that are fragmented by commercial timber blocks. In addition, the complex landscape topography of the Midlands contrasts with the less complex landscape topography of Zululand (Bazelet and Samways 2012). The Midlands are also dominated by deep, humic soils with rocky outcrops, whereas Zululand is dominated by shallow, sandy soils, and so were selected to ensure a wide range of environmental variables.

Fieldwork was conducted on ten spatially separate plantation estates (five in each region), to maximize on landscape variation. The plantation estates selected in the Midlands included Batche-

Figure 2.1 The focal plantation estates in a) the Midlands and b) Zululand, KwaZulu-Natal, South Africa. Illustrated is the study area containing sites within the indigenous forest or grassland biotopes. Plantation blocks (grey) and non-plantation areas (white), as well as plantation estate names also indicated.

lors (30°09'12.77"S, 29°47'53.37"E), Cottingham (30°07'23.7"S, 29°47'14.49"E), Fabershill (29°40'13.3"S, 29°55'59.5"E), Maybole (30°13'53.64"S, 29°44'8.95"E) and Mount Shannon (29°41'11.8"S, 29°58'43.0"E) (Fig. 2.1A). For Zululand, plantation estates included Canewood (32°05'42.84"S, 28°37'56.52"E), Mcilrath (31°58'38.14"S, 28°42' 53.61"E), Montigny (32°11' 9.12"S, 28°35'41.9"E), Port Dunford (31°50'16.7"S, 28°53'30.92"E) and SQF Kwambonambi (32°10'27.06"S, 28°39'26.68"E) (Fig. 2.1B). In each region, 18 indigenous forest sites and 18 grassland sites were selected, totaling to 72 sites for the whole study. Midlands sites occurred either within the Mooi Rivier Highland Grassland, Midlands Mistbelt Grassland and Southern Mistbelt Forest vegetation types, while Zululand sites occurred either within the Maputaland Coastal Belt, Mapulaland Wooded Grassland, Northern Coastal Forest, Swamp Forest vegetation types and Subtropical Alluvial Vegetation (Mucina and Rutherford 2006; SANBI 2012). Sites within the same biotope type were >250 m apart. Sites occurred within the elevation range of 1061-1496 m a.s.l. in the Midlands, and 26-71 m a.s.l. in Zululand. Sampling was conducted in the summer months (which is a high activity period for arthropods in these regions) of January-February 2018 for Midlands, and November-December 2018 for Zululand.

2.2.2. Arthropod sampling

The first arthropod sampling method used was the pitfall trapping method (Prasifka et al. 2007). This method is a simple and efficient technique by which to collect surface-active arthropods (Samways et al. 2010). Pitfall trapping was conducted using four 300 ml plastic cups (9.5 cm diameter and 8 cm deep) which were placed in a 2 m^2 grid at each site, with the rim of the trap level with the soil surface. Traps were filled with 50 ml of 60% ethylene glycol with two drops of detergent to break the surface tension. Pitfall traps were left open for seven days. To complement pitfall trapping, direct sampling through hand-collecting arthropods (Zanetti et al. 2016) was included, as it is a technique which focuses on leaf- and topsoil-inhabiting arthropods which are not as easily captured by pitfall trapping (Mesibov et al. 1995). A 1 m^2 quadrat was placed at random within each site. Litter within the quadrat was turned over and the top 2 cm of the soil was disturbed to collect any arthropods within these layers. This was done by two people for 10 min within the quadrat at each site. In addition, arthropods were extracted from soil core samples using a modified Tullgren-Berlese extraction technique (Bird et al. 2004). Within each site, multiple small samples (i.e. 10 x 100 g each) were taken and combined to form 1 L of soil. Soil samples were placed on top of a mesh (0.5 mm aperture size) and placed within a funnel. Soil was left for seven days, allowing the soil to dry out, causing the arthropods to move downwards and fall into a 130 ml plastic jar containing 75% ethanol which was attached to the bottom of the funnel.

2.2.3. Focal arthropod taxa and identification

For this study, focal arthropod taxa included springtails (Collembola) and ants (Formicidae). These taxa were selected as they are among the most functionally important and highly abundant groups within the soil ecosystem (Graham et al. 2009; Chang et al. 2017). These two taxa differ in mobility, habitat specificity, sensitivity to disturbance, and diet, allowing me to determine whether different soil arthropods respond in the same way to different environmental factors.

Ants are highly mobile (Heil et al. 2001), consisting of a range of feeding groups (Hölldobler and Wilson 1994), and are generally associated with open-structured habitats with higher temperatures (Lassau and Hochuli 2004; Gollan et al. 2011). In contrast, springtails are a less mobile arthropod taxon (Rantalainen et al. 2008; Lessel et al. 2011), and moisture- and acidity-sensitive (Tsiafouli et al. 2005; Auclerc et al. 2009), and polyphagous (feeding mostly on fungi, algae and detritus) (Scheu and Folger 2004). Both focal taxa are also sensitive to ground alterations and disturbances (Andersen et al. 2002; Maunsell et al. 2013). All springtail and ant individuals were sorted into morphospecies (from here on referred to as 'species') and counted. Ant species were identified to genus using relevant literature (Hölldobler and Wilson 1990; Bolton 1994; Picker 2012; Fisher and Bolton 2016; Slingsby 2017). Springtail specimens were identified by a taxonomic expert. Ant reference specimens are maintained in Stellenbosch University's entomology museum. Springtail reference specimens are maintained at the Iziko South African museum.

2.2.4. Biological activity using bait-laminae

To assess the feeding activity (from here on referred to as 'biological activity') within the indigenous forests and grasslands of each region, the bait-laminae method (Von Törne 1990) was used. For this study, modified plastic bait-lamina strips (150 mm long, 18 mm wide and 2 mm thick) were used, consisting of 25 perforated holes (1.5 mm diameter and 5 mm apart) (similar perforation sizes as Birkhofer et al. 2011). The bait-material consisted of cellulose powder, active charcoal and flavored powdered jelly (70:5:25), made into a paste by adding a small amount of water. Jelly (with the manufacturer and flavor kept constant across all sites) was used as a component of the bait-material as its properties allowed the bait to securely remain within the perforated holes of the bait-laminae (unlike agar-agar in a preliminary test to select bait-material). The bait-laminae were filled two days before they were placed into the soil, to allow the bait to air-dry and be refilled if necessary. At each site, four bait-laminae strips were arranged 10 cm apart, inserted vertically into the soil. Exposure time (i.e. the amount of days the bait-laminae are left in the field) can vary from as little as 5 days to >14 days (Filzek et al. 2004; André et al. 2009) depending on soil moisture (Von Törne 1990; Kratz 1998), temperature, and bait type (Gongalsky et al. 2004). Therefore, an exposure period of 7 days was chosen, given that the sites occurred in a subtropical climate region (see Hamel et al. 2007; Römbke 2014). Following the collection of the bait-laminae, biological activity was recorded by categorizing the holes as fully empty (i.e. 'eaten') or intact. As the number of empty holes is an indication of biological activity, it was expressed as an overall percentage for each site.

2.2.5. Biotic and abiotic environmental variables

Various vegetation and soil characteristics were recorded within each site. A 1 m^2 quadrat was placed at random three times within the site. Within the quadrat, a soil moisture and pH meter (Kelway, Inc.) and a soil penetrometer (Lang Penetrometer, Inc.) were used to measure soil moisture, pH and soil compaction. Various vegetation and leaf litter characteristics were also recorded within the quadrat. These variables were: vegetation height (m), vegetation cover (%), number of plant species, leaf litter cover (%), leaf litter depth (cm), herbaceous cover (%), shrub cover (%), grass cover (%) and bare ground cover (%). All recorded data from the three quadrats were combined and an average of each parameter was used in the analysis. Additionally, in a 5 m radius surrounding the quadrat (an area of 80 m^2), amount of shade (%), dead wood cover (%), rock cover (%) and tree coverage (%) (i.e. the percentage of trees occurring within 80 m^2), was also determined. For this study, plant or litter identity was not considered for this study as 1) as Swart et al. (2020) found no effect of overhead tree species on the decomposition of leaf litter, and 2) these indigenous forests and grasslands have high plant diversity (Mucina and Rutherford 2006), which would have made it nearly impossible to identify specific plant or litter species for further analysis in this study.

Landscape-scale environmental variables were calculated in QGIS (version 2.18.0) (QGIS Development Team 2009). These landscape variables included elevation, amount of focal biotope in the surrounding landscape (estimated as the percentage of the sampled biotope type in a 1 km radius around each site) and percentage transformed landscape (estimated as the percentage of plantation within a 1 km radius of each site). A Digital Elevation Model (DEM) of 1 m resolution (provided by the Mondi Group) was used to calculate the slope, aspect, terrain ruggedness index (TRI) and terrain roughness (TR) of each site.

2.2.6. Soil collection and chemical analysis

Within each site, ten soil samples (100 g each) were collected from all 72 sites at random and combined to form 1 L of soil (which served as one sampling unit per site), to account for small-scale variation in soil parameters. From the sampling unit, a sub-sample of 500 g was then taken and used as a representative sample of the site. The representative sample was kept at room temperature and sent to a soil analytical laboratory for elemental analysis. Estimates for the following were extracted:

carbon (C), nitrogen (N), sulphur (S), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na). C, N and S were analyzed using the Dumas combustion approach using a Leco Trumac CNS analyzer (Leco, USA). P was analyzed using the Bray II phosphorus method (Bray and Kurtz 1945). Ca, Mg, K and Na were analyzed by adding 25 ml 1M Ammonium Acetate to 5 g of air-dried soil, then shaken on a reciprocating shaker and filtered through Whatman no. 42 filter paper (Merck, Germany). The sample was then analyzed on an Agilent 4100 Microwave Plasma Atomic Emission Spectrometer (MP-AES) (Agilent, USA). Analysis was conducted by the Institute for Commercial Forestry Research (ICFR).

2.2.7. Data analysis

All analyses were performed separately for springtails and ants using pooled data from all sampling methods. To determine whether arthropod sampling was sufficient within each biotope type (Gotelli and Colwell 2001), species accumulation curves were created separately for each arthropod taxon in R (version 3.6.3) (R Core Team 2016) using the *iNEXT* package (Hsieh et al. 2019) (Appendix A). Non-parametric species richness estimators Chao2 and Jackknife2 were calculated using the *fossil* package in R (Vavrek 2012). For highly diverse communities, these estimators are suitable for estimating species diversity (Colwell and Coddington 1994).

2.2.7.1. Objective 1: Determining response of ants and springtails to biotope and region

2.2.7.1.1. Univariate analyses

All data were pooled to test for the overall effect of biotope, region, and their interaction on the univariate response variables. Thereafter, the effect of biotope type on all response variables was tested separately per region. Response variables included biological activity, as well as activity density (from here on referred to as ‘abundance’) and morpho-species richness (from here on referred to as ‘species richness’). For both overall effects across regions, as well as biotope effect for each region, data showed a non-normal distribution (ants) or normal distribution (springtails) based on Shapiro-Wilk tests conducted using the *nortest* package in R (Gross and Gross 2009). Spatial independence of all datasets were examined using the Mantel test of the *ade4* package in R (Dray and Dufour 2007). To test the effects, generalized linear mixed models (GLMMs), linear models (LMs) or linear mixed models (LMMs) using the *lme4* package (Bates et al. 2014) in R were performed. Models to test overall effects were performed with region, biotope type and their interaction as fixed parameters, and where applicable plantation estate was included as random parameter (Fig. 2.1). Models testing the effect of biotope type within each region were performed with biotope type as fixed parameter and where applicable plantation estate as a random parameter (to account for the unequal spatial distribution of sites) (Fig. 2.1). Within the GLMMs, family was specified as negative binomial for abundance, Poisson (with specified log-link function) for species richness and gamma (with specified log-link function) for biological activity data. Family distribution was determined using the *car* and *mass* packages in R (Fox et al. 2012; Ripley et al. 2013). Post hoc tests were conducted using the *multcomp* package in R (Bretz et al. 2008). Boxplots using pooled biotope type data per region were constructed for all response variables using the *ggpubr* package (Kassambara 2017) in R.

2.2.7.1.2. Multivariate analyses

All data were pooled to test for the overall effect of biotope, region, and their interaction on the ant and springtail assemblages. Thereafter, the effect of biotope type on ant and springtail assemblages was tested separately per region. To test these effects, multiple generalized linear models (GLMs) were performed for ants and springtails using negative binomial distribution of abundance data with the *mvabund* package (Wang et al. 2012) and the *manyglm* function in R. For overall effects models, GLMs were performed with region, biotope type and their interaction as fixed parameters. GLMs testing the effect of biotope type within each region were performed with biotope type as a fixed parameter. For unconstrained ordination and visualizing differences in assemblage composition using pooled biotope data per region, latent variable models (LVMs) were made using the *Boral* package (Hui 2016) in R. These biplots show ordinations without (pure biplot) and with (residual biplot) the influence of environmental variables (Hui 2016). For these ordinatations, I used biotope type as my environmental variable.

2.2.7.2. Objectives 2 and 3: Determining response of ants and springtails to environmental variables and the (dis)similarity of responses

2.2.7.2.1. Univariate analyses

An information-theoretic approach was used to determine the effect of environmental variables on biodiversity responses (Burnham and Anderson 2002). A total of 31 environmental variables were recorded, ranging from landscape-scale to soil chemical elements. To determine the effect of environmental variables, they were first categorized into one of three groups: landscape, site and soil variables. To assess auto-correlation and multi-collinearity among variables, two tests were performed (following de Sá et al. 2019). First, Spearman Rank order correlations were conducted to assess auto-correlation between variables and reduce the number of variables. Where variables showed strong correlations (>0.60 or <-0.60), one variable was selected, and the other discarded. Selected landscape variables were slope, aspect, elevation, TRI, percentage focal and transformed biotope. Selected site variables were percentage rock, dead wood, shade, leaf litter, herbaceous, shrub, grass and bare ground cover, number of plant species, and vegetation height. Selected soil variables were soil moisture, pH, compaction and nitrogen, carbon, phosphorus, and sulphur content. Secondly, multi-collinearity of the remaining variables in each category were assessed by calculating the variance inflation factor (VIF) scores for each model using the *usdm* package (Naimi 2015) in R with a VIF threshold of < 3 specified (Zuur et al. 2009). Following VIF, 6 landscape, 10 site and 7 soil variables remained and were used in further analysis (see Appendix B).

Models were conducted separately per biotope and region. As not all variables were relevant for both grassland and forest biotopes, there were slight differences in the variables included for the different models, but with the core variables the same to aid interpretation and comparison between models. Environmental variables selected for each model are given in Appendix B. To determine the effect of environmental variables on response variables within each biotope type per region, model selection and averaging using the *MumIn* package (Barton 2018) was then performed in R. GLMMs, LMMs and LMs were performed (with plantation estate included as a random parameter within the GLMMs and LMMs). Prior to analysis, all variables were standardized to mean of 0 and SD of 0.5, to enable direct comparison of effect sizes. Second-order Akaike's Information Criterion (AICc) was used as a selection criterion to rank candidate models using the *dredge* function. Thereafter, the criteria of Δ AICc of ≤ 2 was used to create a subset of best models for model averaging (Burnham and Anderson 2002). Full model averaging of the best model subset was then performed using the *mod.avg* function (Barton 2018) in the *MumIn* package in R. Unconditional estimates and 95% confidence intervals were obtained and reported, with a parameter having a significant effect when the confidence interval does not include 0 (Grueber et al. 2011).

Lastly, the variation in environmental variables was assessed by calculating the standard deviation for each variable per biotope, for each region (Appendix H for the Midlands, and Appendix I for Zululand). Additionally, the coefficient of variation (CV) was calculated for each environmental variable (standard deviation divided by the mean) (Reed et al. 2002). As a rule of thumb, a CV value of > 1 indicates high variation, whereas CV < 1 indicates low variation (Appendix H, I).

2.2.7.2.2. Multivariate analyses

GLMs using the *mvabund* package and the *manyglm* function in R were also created to test for the effects of environmental variables on assemblage composition within biotope types per region, using the same selected environmental variables used in univariate modelling according to category (i.e. landscape, site and soil variables) (see Appendix B). A forward-selection procedure (i.e. each parameter individually added) was followed and permutated 999 times to determine their importance within each model. To visualize the effect of environmental variables on springtail and ant assemblage composition, a redundancy analysis (RDA) model was built using the *Vegan* package (Oksanen et al. 2013) and the biplot using the *ggord* package (Marcus 2017). For each taxon, all regional data containing all biotopes were pooled, and analyzed separately for each environmental category, i.e. landscape-, site- or soil-related.

2.3. Results

For both arthropod taxa, observed species richness were similar to Chao2 and Jacknife2 species estimates, nearly reaching asymptotes in both regions (Table 2.1, Appendix A). Midlands samples consisted of 14 757 ant individuals, in 50 morphospecies belonging to 19 genera in 4 sub-families. Zululand samples consisted of 8 464 ant individuals, consisting of 51 morphospecies belonging to 25 genera in 6 sub-families. For springtails, Midlands samples consisted of 61 437 individuals, in 67 morphospecies belonging to 10 sub-families and 17 genera. Zululand's samples consisted of 2 522 springtail individuals, in 45 morphospecies belonging to 11 sub-families and 18 genera. Species collected in the Midlands and Zululand can be seen in Appendix C (ants) and Appendix D (springtails).

Table 2.1 Number of collected species (N) and species estimators Chao 2 and Jacknife 2 for springtails (Collembola) and ants (Formicidae) within the indingeous forest and grassland biotopes, for Midlands and Zululand.

	Collembola			**Formicidae**		
	N	**Chao2**	**Jacknife2**	**N**	**Chao2**	**Jacknife2**
Midlands						
Indigenous forest	45	51.05	52.00	20	33.00	27.99
Grassland	53	58.00	67.00	47	92.05	91.00
Zululand						
Indigenous forest	24	36.50	27.00	49	66.90	64.00
Grassland	34	46.10	45.98	25	34.90	31.00

2.3.1. Objective 1: Determining response of ants and springtails to biotope and region

2.3.1.1. Effect of region and biotope type abundance, species richness and biological activity

A significant interaction between region and biotope type was found for overall springtail abundance (χ^2 = 20.33, P < 0.001, df = 3). Overall, mean abundance of springtails did not differ between indigenous forests and grasslands (χ^2 = 0.34, P = 0.561, df = 1), but was significantly higher in the Midlands compared to Zululand (χ^2 = 18.76, P < 0.001, df = 1) (Appendix E). In addition, when comparing biotope types within each region, springtail abundance did not differ between indigenous forest and grassland in the Midlands (χ^2 = 2.23, P = 0.136, df = 1) or Zululand (χ^2 = 0.92, P = 0.336, df = 1) (Fig. 2.2A). Furthermore, a significant interaction between region and biotope type was found for overall ant abundance (χ^2 = 46.87, P < 0.001, df = 3). Overall, mean abundance of ants was significantly higher in the Midlands compared to Zululand (χ^2 = 4.92, P = 0.027, df = 1), and was significantly higher within the grassland compared to indigenous forest (χ^2 = 24.63, P < 0.001, df = 1) (Appendix F). Furthermore, ant abundance was significantly higher in grassland than indigenous fores in the Midlands (χ^2 = 41.88, P < 0.001, df = 1), but did not differ between biotopes in Zululand (χ^2 = 0.07, P = 0.786, df = 1) (Fig. 2.2B).

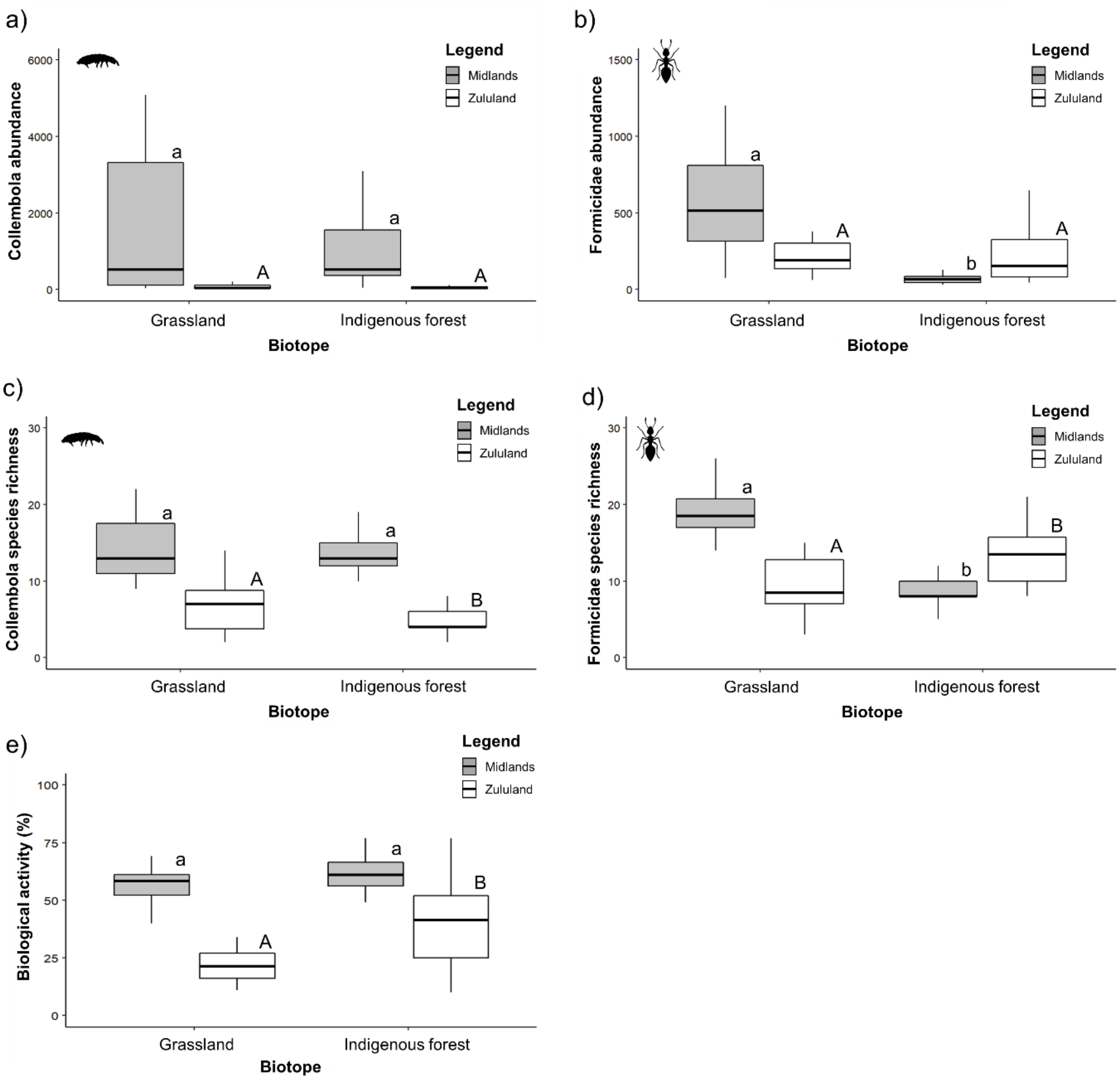

Figure 2.2 Boxplots with central horizontal line indicating the median value, the boxes indicating the interquartile range and the whiskers indicating standard deviation within each biotope. Boxplots show a) Collembola and b) Formicidae abundance; c) Collembola and d) Formicidae species richness and e) biological activity between indigenous forest and grassland biotope types, within each region. Means with small letters (Midlands dataset only) and capital letters (Zululand dataset only) in common between biotopes, are not significantly different at P < 0.05.

A significant interaction between region and biotope type was found for overall springtail species richness (χ^2 = 21.54, P < 0.001, df = 3). Overall, mean springtail species richness did not differ significantly between indigenous forest and grassland (χ^2 = 1.96, P = 0.126, df = 1), but was significantly higher in the Midlands compared to Zululand (χ^2 = 25.07, P < 0.001, df = 1) (Appendix E). Springtail species richness was significantly higher in grassland than in indigenous forest in

Zululand ($\chi^2 = 3.97$, $P = 0.046$, df = 1), but did not differ between biotopes in the Midlands ($\chi^2 = 0.15$, $P = 0.700$, df = 1) (Fig. 2.2C). In addition, a significant interaction between region and biotope type was found for overall ant species richness ($\chi^2 = 80.33$, $P < 0.001$, df = 3). Overall, mean ant species richness did not differ between Midlands and Zululand ($\chi^2 = 2.23$, $P = 0.135$, df = 1), but was significantly higher within the grassland compared to indigenous forests ($\chi^2 = 12.49$, $P < 0.001$, df = 1) (Appendix F). Ant species richness was significantly higher in grassland than indigenous forest in the Midlands ($\chi^2 = 67.71$, $P < 0.001$, df = 1), but significantly higher in indigenous forest than grassland in Zululand ($\chi^2 = 10.81$, $P = 0.001$, df = 1) (Fig. 2.2D).

Lastly, a significant interaction between biotope type and region was found for overall biological activity ($\chi^2 = 29.68$, $P < 0.001$, df = 3). Overall, mean biological activity was significantly higher within the Midlands compared to Zululand ($\chi^2 = 10.74$, $P = 0.001$, df = 1), and was also significantly higher within the indigenous forest compared to grassland ($\chi^2 = 11.34$, $P < 0.001$, df = 1) (Appendix G). Furthermore, biological activity was significant higher in indigenous forest than grassland in Zululand ($\chi^2 = 9.99$, $P = 0.001$, df = 1), but did not differ between biotopes in Midlands ($\chi^2 = 2.21$, $P = 0.137$, df = 1) (Fig. 2.2G).

2.3.1.2. Effect of region and biotope type on assemblage composition

A significant interaction between biotope type and region was found for springtail assemblages (Wald $\chi^2 = 8.59$, $P < 0.001$, df = 68) (Fig. 2.3A) and ant assemblages (Wald $\chi^2 = 5.83$, $P = 0.004$, df = 68) (Fig. 2.3B). Overall, springtail assemblages differed significantly between Midlands and Zululand (Wald $\chi^2 = 14.86$, $P < 0.001$, df = 70), but also between indigenous forest and grassland (Wald $\chi^2 = 13.44$, $P < 0.001$, df = 69) (Fig. 2.3A). In addition, overall ant assemblages also differed significantly between Midlands and Zululand (Wald $\chi^2 = 14.07$, $P < 0.001$, df = 70), but also between indigenous forest and grassland (Wald $\chi^2 = 14.60$, $P < 0.001$, df = 69) (Fig. 2.3B). Furthermore, assemblage composition of both arthropod taxa showed similar responses to biotope type within both study regions. Springtail (Wald $\chi^2 = 13.91$, $P < 0.001$, df = 34) (Fig. 2.3A) and ant (Wald $\chi^2 = 30.76$, $P < 0.001$, df = 34) (Fig. 2.3B) assemblages differed between the indigenous forest and grassland in the Midlands. No significant difference in springtail assemblage composition was found between indigenous forest and grassland (Wald $\chi^2 = 5.21$, $P = 0.174$, df = 34) (Fig. 2.3A) in Zululand, however, ant assemblage was significantly different (Wald $\chi^2 = 7.53$, $P = 0.013$, df = 34) (Fig. 2.3B). The distinction between springtail and ant assemblages in both grassland and indigenous forest appears to be more pronounced for the Midlands than for Zululand.

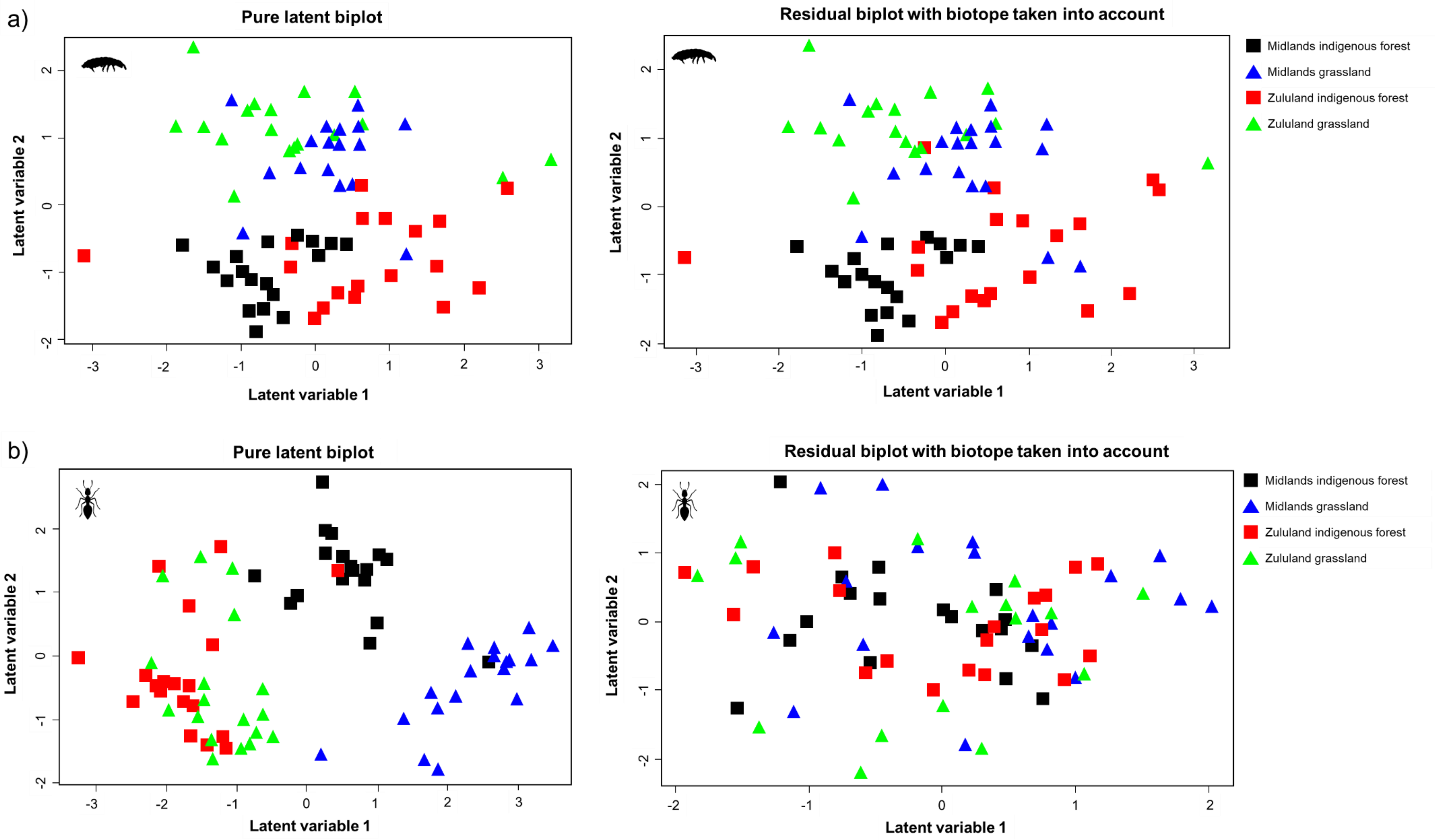

Figure 2.3 Model-based pure (left) and residual (right) ordination for a) springtail and b) ant assemblages in the Midlands and Zululand, between indigenous forests and grasslands. Pure biplots are without the influence of biotope type, whereas the residual bioplot included the influence of biotope type.

2.3.2. Objective 2 and 3: Determining response of ants and springtails to environmental variables and the (dis)similarity of responses

2.3.2.1. Significant environmental variables on univariate responses in indigenous forests

Springtail abundance in the Midlands was negatively associated to the percentage focal biotope in the landscape, and percentage dead wood and shade cover at the site scale (Table 2.2). Springtail species richness was negatively associated with site elevation, but positively associated with percentage of transformed biotope in the landscape and soil pH (Table 2.2). Springtail species richness in the indigenous forests of Zululand was positively associated with soil moisture and pH (Table 2.2). Additionally, springtail species richness within the indigenous forests of Zululand showed a positive association with site aspect, with south-facing sites having the greatest species richness (Table 2.2). Biological activity responded to various environmental variables in both Midlands and Zululand, but the variables differed between the regions. Biological activity showed a strong association to soil variables in Zululand, being positively associated with soil nitrogen, carbon and sulphur content, but also negatively associated to soil pH and bare ground cover (Table 2.2). However, in the Midlands, biological activity was associated to a combination of soil variables (Table 2.2). Here, biological activity was negatively associated to shrub cover and soil nitrogen content, but positively associated with number of plant species, soil moisture, and soil phosphorus content. Biological activity was also associated with site aspect, with south-facing slopes having the highest biological activity. Within indigenous forests, no environmental variables were significant drivers of ant abundance and species richness (Table 2.2). In Zululand indigenous forests, no environmental variables were significant drivers of springtail abundance, or ant abundance and species richness (Table 2.2). The means and standard error of environmental variables for indigenous forests in Midlands and Zululand are given in Appendix G and H.

2.3.2.2. Significant environmental variables on univariate responses in grassland

In grassland, there was a far greater number of environmental variables influencing faunal univariate responses in the Midlands than in Zululand, similar to the patterns observed in indigenous forest. Within grassland, springtail abundance was more associated with soil variables in the Midlands than in Zululand, being positively associated to soil nitrogen content, but also negatively to sulphur content in the Midlands, while no response to soil variables were found in Zululand (Table 2.2). In Zululand, springtail abundance was negatively associated to bare ground cover, and positively associated with soil moisture (Table 2.2). Springtail species richness was positively associated with vegetation height, but negatively associated with the number of plant species in the grassland of Zululand (Table 2.2). Ant abundance only responded to environmental drivers related to the soil in the Midlands, being positively associated to soil carbon content, but negatively to nitrogen content (Table 2.2). Biological

Table 2.2 Model-averaged estimates of environmental variables predicting biological activity, or the abundance and species richness of ants and springtails per biotope type in the Midlands and Zululand. Only variables with significant effects on the response variables are reported. Landscape, site and soil variables were performed separately.

Indigenous forest	**Midlands**					**Zululand**				
	95% CI	**EST**	**SE**	**RI**	**NCM**	**95% CI**	**EST**	**SE**	**RI**	**NCM**
Biological activity (%)										
Site aspect	0.08; 0.20	0.04	0.07	0.30	1					
Shrub cover (%)	-0.15; -0.02	-0.08	0.03	1.00	4					
Number of plant species	0.09; 0.21	0.15	0.03	1.00	4					
Bare ground (%)						-0.55; -0.10	-0.33	0.11	1.00	3
Soil moisture (%)	0.03; 0.24	0.11	0.07	0.83	3					
Soil pH						-0.93; -0.06	-0.06	0.18	0.13	1
Nitrogen (mg/kg)	-0.24; -0.02	-0.06	0.07	0.44	1	0.11; 1.15	0.33	0.36	0.53	2
Phosphorus (mg/kg)	0.01; 0.22	0.02	0.05	0.17	1					
Sulphur (mg/kg)						0.07; 1.22	0.12	0.28	0.19	1
Carbon (mg/kg)						-0.03; -0.06	-0.06	0.18	0.13	1
Collembola abundance										
% Focal biotope	-2.38; -0.26	-1.32	0.49	1.00	6					
Dead wood cover (%)	-2.98; -0.25	-1.03	0.93	0.64	2					
Shade cover (%)	-2.03; -0.14	-0.86	0.59	0.79	2					
Collembola species richness										
Site aspect						0.33; 4.91	2.62	1.08	1.00	2
Site elevation (m)	-8.65; -2.41	-5.53	1.47	1.00	3					
% Transformed biotope	0.92; 7.17	4.04	1.47	1.00	3					
Soil pH	1.65; 6.92	4.28	1.24	1.00	4					
Soil moisture (%)						0.10; 3.99	2.05	0.91	1.00	2
Phosphorus (mg/kg)						0.71; 4.88	2.79	0.98	1.00	2

Grassland	**Midlands**					**Zululand**				
	95% CI	**EST**	**SE**	**RI**	**NCM**	**95% CI**	**EST**	**SE**	**RI**	**NCM**
Biological activity (%)										
Bare ground (%)	-0.26; -0.02	-0.11	0.08	0.78	2					
Soil moisture (%)						-1.03; -0.18	-0.28	0.33	0.46	6
Soil compaction (psi)						-0.91; -0.11	-0.22	0.28	0.44	6
Soil pH						-0.89; -0.03	-0.09	0.20	0.20	2
Sulphur (mg/kg)						-1.28; -0.01	-0.34	0.39	0.53	6
Phosphorus (mg/kg)						-0.74; -0.09	-0.17	0.22	0.40	5
Collembola abundance										
Bare ground (%)						-1.97; -0.04	-0.25	0.49	0.25	1
Soil moisture (%)						0.53; 0.80	0.66	0.06	0.19	1
Nitrogen (mg/kg)	2.69; 9.09	5.31	2.25	0.90	3					
Sulphur (mg/kg)	-10.24; -4.74	-6.76	2.53	0.90	3					
Collembola species richness										
Vegetation height (m)						0.34; 6.56	3.45	1.44	1.00	2
Number plant species						-7.29; -1.98	-4.64	1.24	1.00	2
Formicidae abundance										
Carbon (mg/kg)	0.58; 7.76	1.07	2.01	0.26	1					
Nitrogen (mg/kg)	-8.18; -0.50	-1.12	2.10	0.26	1					

CI = Confidence intervals, EST = Estimate, SE = Standard error, RI = Relative importance, NCM = Number of containing models

activity also showed a strong association with soil variables in Zululand, being negatively associated with soil moisture, compaction, pH, sulphur and phosphorus content (Table 2.2). In contrast, biological activity in the Midlands was only negatively associated to bare ground cover (Table 2.2). Within grasslands, no environmental variables were found to be significant drivers of ant and springtail species richness in the Midlands (Table 2.2). Within the grassland of Zululand, no environmental drivers were found for ant abundance and species richness (Table 2.2). The means and standard errors of environmental variables for grassland in Midlands and Zululand are given in Appendix G and H.

2.3.2.3. Effect of environmental variables on assemblage composition

Assemblages within indigenous forest and grassland, per region, showed varied responses to environmental variables (Table 2.3). In the Midlands, ant assemblages within indigenous forest were influenced by leaf litter cover and soil pH, whereas within the grassland they were influenced by soil compaction, pH, carbon, nitrogen and sulphur content (Table 2.3). Springtail assemblages in the Midlands were influenced by shade cover, vegetation height and number of plant species, as well as by soil pH, carbon and nitrogen soil content within indigenous forest, while only being influenced by leaf litter cover in the grassland (Table 2.3). Within the indigenous forest in the Midlands, springtail and ant assemblages showed no response to any landscape variables (Table 2.3). Within the grassland of the Midlands, ant assemblage showed no response to any landscape or site variables, while springtail assemblage showed no response to any landscape or soil variables (Table 2.3).

Table 2.3 Significant effects of forward-selection of environmental variables on ant (For) and springtail (Col) assemblages within each biotope, within the Midlands and Zululand. Likelihood Ratio Test values (LRT) are reported, with significant variables indicated in bold and * showing significance strength.

	Indigenous forest				**Grassland**			
	Midlands		**Zululand**		**Midlands**		**Zululand**	
	For	***Col***	***For***	***Col***	***For***	***Col***	***For***	***Col***
Site slope (°)	12.21	74.33	90.11	21.78	86.94	81.14	29.02	31.34
Site aspect	22.30	70.94	63.39	33.49	108.00	88.48	33.41	35.28
TRI	23.12	64.04			80.82	92.64	35.88	36.93
Site elevation (m)	16.74	68.16	86.60	**52.63***	106.80	76.82	39.79	**65.84***
% Focal biotope	24.63	65.34	**107.10***	32.75	100.30	68.37	35.37	66.75
% Transformed biotope	29.36	45.71						
Rock cover (%)	31.00	84.20			121.00	89.17		
Dead wood cover (%)	39.66	36.95						
Shade cover (%)	36.94	**91.29***	83.17	23.60				
Vegetation height (m)	40.03	**95.02***	67.26	37.12	100.70	86.03	58.63	54.16
Number plant species	30.98	**92.08***	80.09	31.45	85.44	74.90	41.77	46.96
Leaf litter cover (%)	**55.25***	62.50	**111.10***	18.57	97.55	**120.60***	**69.56***	30.20
Herbaceous cover (%)					89.21	75.21	**62.90***	**90.43***
Shrub cover (%)	15.28	64.15	71.52	29.04	76.99	47.03		
Grass cover (%)	24.22	58.09	69.86	39.54				
Bare ground (%)			41.49	9.31	94.91	76.26	54.81	45.65
Soil moisture (%)	44.41	63.07	99.13	33.67	98.08	54.17	53.48	**71.10***
Soil compaction (psi)	40.79	83.27	88.12	25.71	**116.50***	66.10	28.64	52.18
Soil pH	**67.53****	**104.90***	107.50	41.67	**130.00****	67.60	24.24	47.24
Phosphorus (mg/kg)	25.47	52.47	57.94	31.80	106.20	56.67	48.65	50.89
Carbon (mg/kg)	28.20	**85.12***	80.13	30.55	**132.50***	82.96	27.70	20.97
Nitrogen (mg/kg)	24.01	**80.55***	80.33	26.68	**141.40***	89.41	28.21	24.50
Sulphur (mg/kg)			**95.48***	29.61	**129.60***	97.42	15.61	97.42

Significance codes: *p < 0.05, **p < 0.01, ***p < 0.001

In Zululand, ant assemblages within indigenous forest were influenced by percentage of focal biotope, leaf litter cover and soil sulphur content, whereas within the grasslands they were influenced by leaf litter and herbaceous cover (Table 2.3). Springtail assemblages in Zululand were influenced by elevation, whereas within the grassland they were influenced by elevation, herbaceous cover, and soil moisture (Table 2.3). Within the indigenous forest in Zululand, the springtail assemblage showed no response to any site or soil variables (Table 2.3). Within the grassland of Zululand, ant assemblages showed no response to any landscape or soil variables (Table 2.3).

Redundancy analysis (RDA) biplots showing the effects of environmental variables (landscape-, site- and soil-related) on springtail and ant assemblages in the Midlands and Zululand, between indingeous forest and grassland, can be seen Appendix J. For springtails, the variation in assemblage composition between biotopes and regions were explained by the landscape- (45.26%), site- (35.42%) and soil- (50.64%) (Appendix J) variables, separately. For ants, the variation in assemblage structure between biotopes and regions were explained by the landscape- (55.90%), site- (41.36%) and soil- (48.77%) (Appendix J) variables, separately.

2.4. Discussion

2.4.1. Effect of region and biotope type on ant and springtail assemblage measurements

The regional effects on measured biological parameters of this study could be explained by differences in climate between these two regions (Zululand having a sub-tropical climate and Midlands a temperate climate) and differences in topographical complexity (Zululand less complex than the Midlands). The higher topographical complexity in the Midlands could offer greater environmental heterogeneity with a wider range of microclimate conditions, which is beneficial for biodiversity (Kallimanis et al. 2010; Fjeldså et al. 2012), compared to the less complex, topographically simple landscape of Zululand. In addition, the Midlands experiences heavy and frequent mist, which contributes to additional moisture (Mucina and Rutherford 2006) and has differing vegetation types (Mucina and Rutherford 2006) and fire regimes (Bazelet and Samways 2012). Most importantly, the structure of the soil also differs significantly between these two regions, with Zululand dominated by nutrient poor, shallow sandy soils, and the Midlands by high nutrient, deep clay soils.

In this study, the overall effect of biotope type (i.e. indigenous forest and grassland) across regions was more pronounced for ants, showing variations in overall abundance and species richness between the biotope types. This pronounced response may be attributed to ants being particularly sensitive to changes in environmental conditions (Wiezik et al. 2015). In addition, overall ant assemblages also differed significantly between indigenous forests and grasslands across the regions, as well as between biotope types within each region. This concurs with other studies showing ants to be more speciose and abundant within grasslands compared to indigenous forests, and that ant assemblages can be significantly different between these two biotope types (Lassau and Hochuli 2004; Frainer and Duarte 2009; Wiezik et al. 2015). Interestingly, only overall springtail species richness, and not abundance, differed between biotope types across the regions. These results were not expected as springtail diversity responds to land cover changes (Frainer and Duarte 2009; Kutcherov et al. 2019), more specifically due to the structural and microclimatic contrast between open and closed habitat types (Ponge et al. 2003). However, here, overall springtail assemblage composition differed significantly between indigenous forests and grasslands only in the Midlands, also observed by Winck et al. (2017). However, interestingly, there was no difference in springtail assemblage composition between indigenous forest and grassland in Zululand.

Within each of the regions, ants and springtails responded differently to biotope type. In the Midlands, for example, ant abundance and species richness were always higher within the grassland compared to indigenous. These patterns correspond to other studies within this Afromontane grassland systems, showing higher ant diversity within the grassland compared to indigenous forest in the Midlands (Yekwayo et al. 2016a, 2017). This may have occurred due to species being either heat- or cold-tolerant (Andersen 1995, 1997). Here, grasslands may have been favoured by to open-habitat species which prefer hot environments, whereas some cold-tolerant species may have preferred the closed-canopy, cooler environments. However, the high ant species richness within the indigenous forest compared to grassland in Zululand was unexpected, as ants are generally associated with habitats with an open structure and increased solar radiation exposure (Lassau and Hochuli 2004; Gollan et al. 2011). In this case, the higher ant species richness in Zululand indigenous forest compared to grassland could be explained by the structural differences between indigenous forests between the regions. For example, Zululand indigenous forests have greater open canopy structure compared to the dense indigenous forest canopies in the Midlands. This open canopy structure of indigenous forests in Zululand could have been beneficial to ants which prefer a warmer, more open-habitat environment, as it allowed more solar radiation to penetrate the soil surface. However, significant shifts in assemblage composition for ants between indigenous forest and grassland was still observed in Zululand. As there can be strong habitat preferences related to habitat openness for ants (Andersen 2019), grasslands and indigenous forests may have offered different suitable conditions, causing significant shifts in their richness and assemblage composition. However, it is unclear how ants are adapted (i.e morphological or physiological characteristics and dietary requirements) to persist within these different environments, and therefore requires further examination to explain shifts in assemblages between landuse covers with different environmental conditions.

What was interesting, was that springtail species richness was significantly higher within the grassland compared to indigenous forest in Zululand. In addition, no differences between indigenous forest and grassland were found for either springtail abundance and species richness in the Midlands. In general, environmental factors such as low soil moisture and high temperatures can be limiting factors for arthropods, such as springtails (Tessaro et al. 2011; Twardowski et al. 2016). Therefore, the high springtail numbers in grassland in both regions were not expected, given that from an ecological perspective, environmental conditions should have been more favourable to springtails within indigenous forest compared to grassland, as grassland have lower leaf litter quantity and quality (Christopher and Cameron 2012) and experience higher solar radiation (affecting soil moisture and temperature) (Groffman et al. 2009). In addition, these grasslands undergo prescribed burns in the ENs to simulate these conditions (Cadman et al. 2013), with burning regimes being very different in the Midlands compared to in Zululand. There is limited information on springtail responses to fire, but their high diversity and abundance in these grassland systems suggest that they may be well-adapted to fire impacts, as in other fire-prone systems (Janion-Scheepers et al. 2016a).

When Yin et al. (2019) examined the effects of landuse change on springtail eco-morphological life forms of Collembola (i.e. epedaphic, hemiedaphic, and euedaphic species), they found that grassland supported the most abundant assemblages with high specie richness. However, this was in terms of overall estimates. Further examination showed that the effect of landuse type depends on springtail life forms, as they can respond differently. This may therefore be a possible explanation for my findings, as the majority of springtails collected belonged to Entomobryomorpha and Symphypleona, with the minority belonging to Poduromorpha (Appendix D). Species of Poduromorpha are mainly soil-dwelling, whereas species belonging to Entomobryomorpha and Symphypleona are more litter- or vegetation-dwelling (Orgiazzi et al. 2016). Springtails that are larger in size and are adapted for above-soil living have higher dissication-tolerance compared to soil-living species (Vannier 1983; Winck et al. 2017). This may explain why the grasslands harboured similar or even higher estimates of richness to the indigenous forests. However, I still found that springtail assemblages were different between indigenous forest and grassland biotopes. As this was not examined within this study, further examination into species traits could be valuable in explaining the shifts in assemblage compositions, as one would assume different species would occur under different conditions based on species-specific adaptations (Winck et al. 2017; Yin et al. 2020).

The soil biological activity measured here most likely represents the activity of a wide range of taxa rather than just that of ants and springtails. In this study, biological activity was more responsive to biotope type in Zululand, with indigenous forest showing higher values compared to grassland. This corresponds with studies by Rożen et al. (2010) and Siebert et al. (2019), showing soil biological activity can vary under different environmental contexts (i.e. landscapes consisting of different land cover types). In contrast, although soil biological activity was high in both biotope types, no difference was found between indigenous forest and grassland in the Midlands, which corresponds with Diekötter et al. (2010) showing biological activity does not differ with landscape context. However, finding no significant differences in soil biological activity between indigenous forest and grassland is surprising, as increased temperatures and drier conditions can result in reduced levels of feeding activity (Thakur et al. 2018). However, as these biotopes are expected to have different species that are adapted to those specific environmental conditions, it would not necessarily mean that changes in overall assemblage composition would lead to reduced feeding activity. This would, however, require further examination.

Broadly speaking, the differences in the biological parameters measured here between biotope types, across and within each region, can be explained by these biotopes differing in structural and compositional vegetation characteristics (with indigenous forest having a greater diversity of plants, canopy cover, and greater quantity and quality of leaf litter compared to grassland) (Yekwayo et al. 2016a). Furthermore, management regimes and disturbances are also different between the biotopes (grassland frequently experiences grazing pressure, grass cutting and fires, whereas indigenous forest is unmanaged and protected from the effects of plantation forestry and timber harvesting) (Bazelet and Samways 2012; Yekwayo et al. 2016a,b). This means that the boundaries between indigenous forest and grassland are characteristically sharp (Mucina and Rutherford 2006). However, in the Midlands, the contrast between indigenous forest and grassland is more distinct, with grassland showing no presence of trees and dominated by grass species (Mucina and Rutherford 2006). Furthermore, the forests within these two regions also have very different histories. Indigenous forests within Zululand are secondary compared to the primary, ancient forests in the Midlands (Mucina and Rutherford 2006). In the past, forests were highly disturbed due to agricultural activities and logging, whereas the location of forests within the Midlands (either in valleys or high up in gorges) gave them the advantage of not undergoing the same anthropogenic pressures as in Zululand (Feely 1980, 1987). This could therefore also be attributable to higher segregation and contrast differences between indigenous forests and grasslands in the Midlands, compared to the comparison between indigenous forests and grasslands in Zululand.

2.4.2. Environmental drivers of diversity and assemblage composition within regions and biotope types

Major differences in environmental drivers were found for springtails and ants between biotopes and regions. Here, landscape variables appear to play a less important role in driving soil biodiversity patterns than soil- and site-scale variables. Surprisingly within the biotopes of each region, no environmental drivers were found to be significant drivers of ant species richness within either the biotopes in each region, whereas springtail species richness did show some response. The main finding here was that, even within the same biotope type and within the same region, ants and springtails responded differently to environmental drivers.

Within the indigenous forests, springtails in the Midlands responded more to site-variables (e.g. plant diversity), whereas a lack of response to environmental drivers occurred in Zululand. This was surprising, as soil characteristics and vegetation characters play a role in driving springtail biological patterns (Salamon et al. 2008; Errington et al. 2018). Errington et al. (2018) even suggested that soil characteristics play a greater role in driving springtail biological patterns than vegetation characteristics. In addition, as temperature is one of the main stress factors for springtails (Ellers et al. 2018), the negative effects from other factors here (e.g. vegetation height, shade, and rock cover) on springtails could be related to the thermal tolerance of springtails (see Raschmanová et al. 2015, 2018), as they contribute to lower temperatures (i.e. more shade) which might be disadvantageous to springtail diversity. In the case of ants, there was also a lack of response to environmental conditions within the indigenous forests in both the Midlands and Zululand, which is surprising as studies often report ants to respond to factors relating to the soil (e.g. texture or moisture content), vegetation (e.g. structure or diversity) or landscape (e.g. habitat type or elevation) (Lassau and Hochuli 2004; Boulton et al. 2005; Sabu et al. 2008). Here, the negative association of leaf litter cover on ants in Zululand may be due to their general positive association with increased bare ground cover (i.e. habitat openness) (Radtke et al. 2014).

Within the grassland, ants and springtails were influenced by contradicting soil-related conditions. Increased nitrogen content within the grassland soils of the Midlands were beneficial to springtails, but were associated with reduced ant diversity. In contrast, increased soil carbon content within the grasslands of the Midlands were most beneficial to ant diversity patterns. As the soil's biological, chemical and physical properties are correlated to the amount and structure of nutrients (such as soil nitrogen and carbon pools) (Meyer et al. 2013; Wu et al. 2013), this may explain why these properties play an important role on ant assemblages and activity, as ants predominantly nest, forage and feed at/within the soil layer. However, the effect of soil chemical elements on springtails can be direct by altering pH balance of the soil (Cassagne et al. 2003; Nielsen et al. 2015) or indirect by affecting plant communities (Bokhorst et al. 2017), which in turn, influence springtail assemblages through their effect on leaf litter quality and quantity (Das and Joy 2009; Milcu et al. 2006). However, within the grasslands of Zululand, both ants and springtail diversity patterns showed a lack of response to environmental drivers. The amount of bare ground and herbaceous cover were found to be detrimental to both springtail and ant diversity, respectively. However, increased soil moisture did benefit springtail abundance within the grasslands of Zululand. Vegetation structure and cover play an important role in the amount of moisture that reaches the soil surface (Greenslade et al. 2011). This implies that high plant diversity and cover would be beneficial, as springtails are moisture-sensitive arthropods (Tsiafouli et al. 2005; Auclerc et al. 2009), which could explain why increased bare ground cover negatively affected springtails. However, here, I also found high plant diversity negatively affected springtail species richness in the grasslands of Zululand. Furthermore, ants generally prefer more open-structured habitats with higher temperatures (Lassau and Hochuli 2004; Gollan et al. 2011), which would explain why increased vegetation cover negatively affected ants.

The differences in species compositions between indigenous forest and grassland assemblages for both ants and springtails, highlight that these taxa respond differentially to environmental factors, under similar conditions. These findings may be attributable due to their differences in mobility (Heil et al. 2001; Lessel et al. 2011) and dietary requirements (Hölldobler and Wilson 1994; Hopkin 1997; Malcicka et al. 2017). This may also have explained shifts in assemblage compositions within each taxon between the biotope types, as the effects of these factors can be species-specific. However, species traits were not examined within this study, and therefore requires further examination to determine how different species are adapted to persist within land covers under different environmental conditions. Furthermore, the need to identify environmental factors which drive trait convergence or divergence is crucial, especially for landscape and conservation planning, in order to ensure greater diversity within, and enhanced functioning of, our soils.

When examining soil biological activity, environmental drivers also varied between the biotope types and regions. Within indigenous forest, soil biological activity was driven by soil-related factors, and to a lesser extent site- or landscape-related factors, in both Midlands and Zululand. Within the grasslands, soil biological activity was greatly influenced by site-related and soil-related variables in the Midlands and Zululand, respectively. These results are in line with other studies showing strong effect of soil-related variables (e.g. soil moisture, pH, sulfur and phosphorus content) on soil biological activity (Gongalsky et al. 2008; Andre et al. 2009; Rożen et al. 2010). In addition, the strong effect of soil-related variables (more specifically related to nutrients) in the grasslands and indigenous forests of Zululand may be due to this area having soils with little organic matter content and nutrient-poor soils (Dovey et al. 2014; Scheepers and du Toit 2017), and as a result, even small changes in nutrients may have cascading effects. Lastly, the effect of nutrients on soil biological activity may also be more indirect (Rożen et al. 2010), by altering the pH of the soil (Gotte and Gajbhiye 2018; Siwik-Ziomek et al. 2018). These changes in soil pH (i.e. higher acidity levels), affects most soil organisms (Cao et al. 2016; Errington et al. 2018) as well as soil biological activity (Eggleton et al. 2009).

2.5. Conservation implications

Presence of both indigenous forest and grassland, in both regions here, are beneficial for soil biodiversity, showing high levels of uniqueness and complementarity, and contributing to soil biodiversity within these plantation landscape systems. In addition, the lower estimate of soil biodiversity and activity in Zululand compared to the Midlands, emphasizes the importance of minimalizing further homogenizing threats to soil fauna (Qian and Guo 2010; Park and Razafindratsima 2019). In this context, threats include invasive alien vegetation and excessive grazing and fire management regimes. Furthermore, sandy soils generally have low clay and organic matter content, and hence low fertility (Noble et al. 2005). In turn, litter and nutrient management are more important for sandy soils, as their nutrient pools are already low, and further nutrient losses can have significant detrimental effects on nutrient dynamics. As Zululand's soils are sensitive to management practices (du Toit et al. 2001; du Toit and Oscroft 2003) and have a high risk of degradation (i.e. their ability to buffer disturbances and changes to either its biological, chemical or physical properties are limited) (Dovey et al. 2014), conservation and management practices within Zululand need to be ecologically sustainable and context-specific.

Additionally, to promote and improve conservation planning within EN-plantation landscape mosaics, elements that are improving, or are detrimental to, biodiversity need to be identified to inform land managers on what conditions (landscape, site, or soil) to focus on in conservation and management practices to gain the most benefit regarding soil biodiversity. Here, site- and soil-scale environmental drivers were most important for promoting springtail and ant biodiversity. For springtails, areas which show high soil moisture content, plant diversity and cover are areas which favour springtail diversity, which should be an important management consideration for springtail diversity conservation within these landscapes. In contrast, ants are more responsive to soil-related variables, favouring areas with high soil carbon content. This emphasizes the importance of areas with high soil organic matter for ant diversity, which also are an important management consideration for ant diversity conservation within these landscapes.

As these two arthropod taxa respond differently to the same environmental gradients within the same habitat, the conservation and management of small-scale habitat heterogeneity is crucial. If common environmental drivers were found, these results could have been used as indicators for biodiversity hotspots. Here however, I show environmental factors that are beneficial for one group of arthropods are not necessarily beneficial for another, and vice versa. As these taxa respond differentially under the same environmental conditions, even simple conservation management recommendations cannot be made, beyond the land sparing approach of mitigating the effects of plantation forestry using networks of conservation corridors. However, my results nevertheless highlight the importance of managing and conserving small-scale heterogeneity to maximally benefit a wide range of organisms. This is in line with other studies showing that a small-scale, mosaic management practice and microhabitat heterogeneity is important for conserving arthropod diversity (Bazelet and Samways 2011; Joubert et al. 2016), but more importantly soil biodiversity (Burton and Eggleton 2016; García-Tejero and Taboada 2016).

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CHAPTER 3

Do commercial timber plantations homogenize soil faunal assemblages in an ecological network-plantation landscape mosaic?

ABSTRACT

Landscape transformation for agriculture is one of many drivers affecting global biodiversity through simplification of ecosystems. The aim of this study was to determine whether large-scale commercial timber plantations (*Pinus* and *Eucalyptus*) contribute to the biotic homogenization of soil biodiversity relative to natural systems (indigenous forests and grasslands) within timber production landscape mosaics. This was done by examining ant and springtail alpha- and beta-diversity, and assemblage composition between the biotopes in two regions, the Midlands and Zululand, in KwaZulu-Natal, South Africa. The alpha diversity of ants in the plantations was similar to the natural biotopes, except in the Midlands where ant species richness was highest within the grasslands, but significantly lower in the pine compartments. Additionally, plantations and natural systems supported equally high springtail species richness in both regions. Contrary to expectations, ant and springtail beta-diversity was as high in plantations as in the natural biotopes, and in all biotopes this diversity was driven mainly by high turnover, i.e. species replacement as opposed to nestedness. A potential mechanism for the high alpha- and beta-diversity in plantations includes the high environmental variation among plantation sites, as some species may persist or be excluded under certain conditions based on habitat requirements. Furthermore, colonization from natural areas may contribute to high diversity in the plantations, as a high percentage of species were shared between the plantations and natural systems, and few species with high biotope fidelity and specificity were recorded. While the overall local- and landscape-scale taxonomic diversity was relatively high in the plantations, there was still clear segregation of assemblages between all biotope types, indicating shifts in assemblage composition.

Key words: Beta-diversity; Collembola, Forest, Formicidae; Grassland, Landscape transformation; Plantation forestry

3.1. Introduction

Anthropogenic activities modified and simplified many ecosystems (Steffen et al. 2015). Land use change, such as landscape transformation for agriculture or urbanization, is one of the major current drivers affecting global biodiversity change (Sala et al. 2000; Foley et al. 2005; Miranda et al. 2015). Land use change can lead to local species extinctions, species range or distribution shifts, and can lead to exotic species introductions (Solar et al. 2015). Additionally, increasing agricultural intensity can lead to further declines in local biodiversity (Kleijn et al. 2009). Species that are rare, specialized or range-restricted are generally most vulnerable to land use change, and are often replaced by widespread, generalist species (Solar et al. 2015) or by invasive species that are better adapted to the novel conditions (Olden 2006; Olden and Rooney 2006). These processes lead to communities becoming more similar in terms of their species composition across the landscape (Dornelas et al. 2014; Newbold et al. 2015). Biotic homogenization occurs when taxonomic and functional assemblages become more similar (Olden and Rooney 2006). This is of great conservation concern, as the simplification of taxonomic and functional diversity may lead to the loss of important ecosystem services and functions (Olden and Rooney 2006; Mitchell et al. 2015), a decline in ecosystem resilience (Olden 2006; Norden et al. 2009), and a loss of unique, locally-adapted species and their interactions (Cardoso et al. 2020).

In addition to measures of alpha diversity (i.e., within-habitat diversity), the change in assemblage composition (i.e. groups of species occurring within a given space and/or time) (Gaston and Blackburn 2000; Stroud et al. 2015) between sites (i.e. among-habitat diversity) is also an important factor for determining regional diversity (i.e. total within-landscape diversity) (Whittaker 1977; Gianuca et al. 2017). The level of dissimilarity between sites is defined as "beta-diversity" (Anderson et al. 2011) and is often used to determine the level of assemblage homogenization, i.e. how biologically similar communities are, with a high beta-diversity estimate indicating high dissimilarity (Whittaker 1960; Knop 2016; Socolar et al. 2016). This change is driven by two simultaneous processes, replacement of species (i.e. turnover) and gain/loss of species (i.e. nestedness) among sites (Knop 2016). It is crucial to understand the contribution of each of these components of beta-divesrity, as each would imply different conservation strategies. For example, where the nestedness component is dominant, it implies conservation strategies need to prioritize sites with high alpha diversity given the low complementarity among sites (Gianuca et al. 2017). In contrast, the dominance of the turnover component implies the conservation of multiple sites to maintain local biodiversity (Gianuca et al. 2017). To enhance conservation practices, we therefore need a better understanding of local biodiversity (alpha-diversity) and how assemblage (dis)simmilaity (beta-diversity) drives regional diversity (Socolar et al. 2016), especially across different spatial scales (Gering et al. 2003; Anderson et al. 2011).

High assemblage dissimilarity across space is expected in heterogeneous landscapes as environmental heterogeneity is one of many factors that govern changes in species diversity and composition structure (Stein et al. 2014). A more heterogenous environment supports more species through greater resource availability and partitioned niche space (Price et al. 2014; Weisberg et al. 2014; Schindler et al. 2015). Additionally, some species may require specific conditions for their survival. Some species may be adapted to persist under certain environmental conditions, whereas others might be excluded (Wong et al. 2019), which may also result in high assemblage dissimilarity between sites. As such, beta-diversity is expected to be higher in natural systems compared to managed systems, due to differences in environmental complexity, with natural systems generally having higher heterogeneity whereas managed systems are more homogenous (Fayle et al. 2010; Wang and Foster

2015). This is of particular interest in timber plantation landscapes. Timber plantations are essential to meet the increasing demand for timber products (FAO 2010, 2016). However, these are large-scale, monocultural compartments that are often non-native trees which generally have negative impacts on local biodiversity through lower habitat diversity and complexity (Brockerhoff et al. 2008). Commercial plantation forestry is often practiced at large spatial scales, with potential to affect large-scale biodiversity patterns. Additionally, plantations of exotic trees are often structurally and compositionally different from native vegetation. Thus, recolonization from natural vegetation into the plantation compartments is often limited due to the high contrast between them, specifically in the case of above-ground arthropod taxa (Pryke and Samways 2001; Pryke and Samways 2012). Nonetheless, research has shown that plantation compartments can harbor moderate levels of diversity and support some native species, by providing additional habitat (Brockerhoff et al. 2008, 2013; Irwin et al. 2014). Although plantations can even include threatened or rare species (Brockerhoff et al. 2008), generally, specialist diversity is lower within the plantations compared to natural systems, while the opposite is found for generalist species or actively dispersing taxa (Brockerhoff et al. 2008). To date, biotic homogenization has been studied more intensively for birds and plants, whereas arthropods have received less attention (Knop 2016). Therefore, the question remains to what degree timber plantations contribute to the biotic homogenization of the soil arthropod assemblage.

The soil ecosystem is one of the most species-rich terrestrial ecosystems (Bender et al. 2016). However, the patterns of below-ground species diversity and composition changes are less well-known compared to above-ground species (Wardle 2006). Furthermore, they might not respond to the same environmental gradients as above-ground taxa (Cameron et al. 2019). For example, active soil species spend most of their life cycle in or at the soil surface. Therefore, soil fauna may be less responsive to changes in vegetation characteristics and more responsive to changes in soil characteristics caused by land-use transformation (Errington et al. 2018), whereas the opposite may be true for above-ground taxa (Pryke and Samways 2001; Pryke and Samways 2012). As soil organisms have an important functional role within the soil (Yan et al. 2012) and are the basis of ecosystem functioning (Kumssa et al. 2004), it is essential to understand the mechanisms driving their diversity and compositional changes (Widenfalk et al. 2016). This will also enable predictions of future changes in soil communities due to climate and land-use changes (Bardgett et al. 2005). However, research focusing on beta-diversity is still gaining momentum in soil ecology (Kuznetsova et al. 2018), and drivers of alpha diversity are better understood compared to drivers of beta-diversity (Paknia and Pfeiffer 2014). Therefore, research examining the change in alpha and beta-diversity of soil arthropods within a timber plantation landscape, and how timber plantations contribute to the biotic homogenization of soil arthropod assemblages, remain poorly understood (Santoandré et al. 2019; Li et al. 2020).

This study aims to determine whether the presence of timber plantations within the landscape is contributing to the biotic homogenization of soil biodiversity within an ecological network-plantation landscape mosaic in South Africa. Ecological networks (ENs) of conservation corridors are remnant natural vegetation elements, such as grasslands and indigenous forests, interspersed within the plantation landscape, which aim to mitigate the negative effects that timber plantations may have on local biodiversity (Joubert and Samways 2014; Joubert et al. 2016). Ants and springtails were selected as focal soil arthropods for this study, due to their high abundance within the soil and their functionally important roles within the soil ecosystem (Rusek 1998; Graham et al. 2009; Chang et al. 2017). They contrast in habitat specificity, mobility and diet, and together will give a broad understanding as to how they are affected by the large-scale, simplistic environmental conditions of the timber plantations compared to the more complex environmental conditions within natural habitats.

To determine whether biotic homogenization occurs due to the presence of timber plantations, patterns of alpha- and beta-diversity were examined within and between natural biotopes (grasslands and indigenous forests) and plantations (pines and eucalypts) within EN-plantation landscape mosaics. Understanding how alpha- and beta-diversity of soil biodiversity changes across large-scale, transformed landscapes will aid land managers in conservation planning and management (Socolar et al. 2016), which will ensure their continued presence and important functional roles within the soil ecosystem. To address this issue, my first objective is to determine how ant and springtail species richness (i.e. alpha-diversity) is affected by the presence of timber plantations relative to the natural areas. I expect timber plantations to have lower levels of species richness relative to the natural biotopes, due to their homogenous nature regarding their structural complexity and leaf litter composition, as found by other studies (Fayle et al. 2010; Wang and Foster 2015).

The second objective is to examine the change in ant and springtail species assemblages (i.e. beta-diversity) between sites of the same biotope type (i.e. within-biotope beta-diversity). It is expected that overall beta-diversity would be lower between sites of the plantations relative to the natural areas. Furthermore, I expect nestedness (i.e. dissimilarity attributed due to the loss of species) to play a greater role within the plantations due to loss of species between sites, in contrast to the natural areas where species turnover (i.e. dissimilarity attributed due to the replacement of species) is expected to play a greater role. These results are expected, as previous studies found environmental heterogeneity can drive beta-diversity (Van Schalkwyk et al. 2019), and plantations are considered to be environmentally less complex compared to natural areas (Fayle et al. 2010; Wang and Foster 2015). I will therefore also assess the level of environmental variation between sites as a possible mechanism for driving beta-diversity (Van Schalkwyk et al. 2019). Studies have shown within-site environmental variation needs to be considered for biodiversity assessments (Lessard et al. 2011; Hansen et al. 2016a,b). However, as my study was conducted within a highly complex landscape consisting of different biotopes at a landscape-scale, emphasis was given more to habitat-level variation (i.e. between-site variation) rather than site-level variation (i.e. within-site variation), to gain baseline information regarding possible drivers of diversity within each biotope.

The third objective is to determine potential colonization from natural areas into the plantations. To achieve this, I assess between-biotope beta-diversity. In addition, overall assemblage composition is compared between biotopes, and the number of shared species between biotopes and species associated with a particular biotope type is also examined. First, I expect overall beta-diversity (i.e. dissimilarity between assemblages) would be highest between grassland and plantations, compared to indigenous forest and plantations, due to higher contrast differences between these biotopes (Yekwayo et al. 2017). Secondly, as studies have found litter arthropods to be shared between natural areas and plantations (Yekwayo et al. 2016, 2017; Basset et al. 2017), I expect a small subset of my focal taxa will also be shared between the natural areas and the plantations. In turn, I would therefore expect turnover, rather than nestedness, to have the greatest contribution to assemblage dissimilarity between the natural areas and the plantations, as high nestedness between biotopes is an indication of reduced recolonization (Inclán et al. 2015).

3.2. Materials and methods

3.2.1. Study area and design

This study was conducted in KwaZulu-Natal (KZN), South Africa, a province is highly suitable for timber production (Neke and du Plessis 2004). The study was conducted in two different geographical areas: Midlands and Zululand (from here on referred to as regions) (Fig. 3.1). Their contrasting environmental differences in elevation ranges, soil type, dominant vegetation types, and topographical complexity provided a wide range of conditions under which to address the study objectives. Study sites were distributed across several separate plantation estates within each region (Fig. 3.1), and were situated within four different biotopes (landscape elements): indigenous forest, grassland, pine tree compartments (*Pinus* spp.), and eucalypt compartments (*Eucalyptus* spp.). However, as Zululand is dominated by eucalypt, no pine sites were available within this region, and only eucalypt compartments were included. The plantation estates selected in the Midlands included

Figure 3.1 The focal plantation estates in a) the Midlands and b) Zululand, KwaZulu-Natal, South Africa. Illustrated are the study sites within indigenous forests, grasslands, pine and eucalypt compartments. Plantation compartments (grey), non-plantation areas (white) and estate names indicated.

Batchelors (30°09’12.77”S, 29°47’53.37”E), Cottingham (30°07’23.7”S, 29°47’14.49”E), Fabershill (29°40’13.3”S, 29°55’59.5”E), Harcourt (29°51’00.2”S, 30°10’36.1”E), Maybole (30°13’53.64”S, 29°44’8.95”E), Mkhuzane (29°49’33.9”, 30°18’10.8”E) and Mount Shannon (29°41’11.8”S, 29°58’43.0”E) (Fig. 3.1). For Zululand, plantation estates included Canewood (32°05’42.84”S, 28°37’56.52”E), Mcilrath (31°58’38.14”S, 28°42’ 53.61”E), Montigny (32°11’ 9.12”S, 28°35’41.9”E), Port Dunford (31°50’16.7”S, 28°53’30.92”E) and SQF Kwambonambi (32°10’27.06”S, 28°39’26.68”E) (Fig. 3.1). All selected plantation compartments were in a mature growth stage, i.e. > 6 years old. For each region, 18 sites were selected for each biotope type to maximize on landscape variation, totaling 126 sites (Fig. 3.1). Sites within the same biotope type were > 250 m apart. Also, sites were selected within each region to occur within the same spatial extent for each biotope type. Sites were selected at 60 m from the boundary, to focus on the interior of the biotope and to avoid any possible edge effects (Pryke and Samways 2012). Sites were present within the elevation range of 917-1528 m a.s.l. in the Midlands, and 26-131 m a.s.l. in Zululand. Average, minimum and maximum distances between sites of the same biotope type, for both regions, can be seen in Appendix K. As insects are highly active within the summer months of these regions, sampling was conducted in January-February 2018 for Midlands and November-December 2018 for Zululand.

3.2.2. Arthropod sampling and identification

Arthropods were collected using various sampling methods. Pitfall trapping (Prasifka et al. 2007) was conducted by placing four 300 ml plastic cups (9.5 cm diameter and 8 cm deep) in a 2 m^2 grid at each site, with the rim of the trap level with the soil surface. All traps were filled with 50 ml of 60% ethylene glycol with a small amount of detergent to break the surface tension. Pitfall traps were left in the field for seven days, after which they were collected. Hand-collecting (i.e. direct sampling) (Zanetti et al. 2016) of arthropods was also conducted at each site. This method was included to collect arthropods not easily captured by the pitfall trapping method (Mesibov et al. 1995). This was conducted by searching for 10 min within a randomly placed 1 m^2 quadrat at each site. The top 2 cm of the litter and soil within the quadrat was disturbed (turned over) to collect any arthropods within these layers, using an aspirator or tweezers. Lastly, 10 x 100 g subsamples were randomly collected and combined to form 1 L of soil, from which arthropods were extracted from using a modified Tullgren-Berlese extraction technique (Bird et al. 2004). The soil sample was placed on top of a mesh (0.5 mm aperture size) and placed within a funnel. The soil could dry out over seven days, causing the arthropods to move downwards into the attached 130 ml plastic jar of 75% ethanol at the bottom of the funnel. All collected specimens were sorted into morphospecies (from here on referred to as ‘species’) and counted. Springtail specimens were identified by a taxonomic expert, while ants were identified to genus level using Hölldobler and Wilson (1990), Bolton (1994), Picker (2012), Fisher and Bolton (2016) and Slingsby (2017). Collected species in both regions are given in Appendix C for ants, and Appendix D for springtails.

3.2.3. Biotic and abiotic environmental variables

A 1 m^2 quadrat was randomly placed three times within each of the study sites, in which various soil and vegetation characteristics were recorded. Vegetation characteristics were recorded including vegetation height (m), vegetation cover (%), number of plant species and compositional characteristics, including herbaceous, shrub and grass cover (%). Bare ground cover, (%) leaf litter cover (%), and leaf litter depth (cm) were also recorded. An area of 80 m^2 (i.e. a 5 m radius) surrounding the quadrat was used to record additional environmental variables including amount of shade (%), deadwood cover (%), rock cover (%), and tree coverage (%) (i.e. the percentage of trees occurring within 80 m^2). Soil variables including soil moisture, pH, and soil compaction were measured using a soil moisture and pH meter (Kelway, Inc.) and a soil penetrometer (Lang Penetrometer, Inc.) within the quadrat. Recordings from all three quadrats were averaged as an estimate for the site. QGIS (version 2.18.0) (QGIS Development Team 2009) was used to calculate additional landscape-scale environmental variables. These included site elevation (m), site slope (^{o}), site aspect (North or South-facing), terrain roughness (TR), terrain ruggedness index (TRI), amount of focal biotope (estimated as the percentage of the sampled biotope type in a 1 km radius around each site), and percentage transformed landscape (estimated as the percentage of plantation within a 1 km radius of each site). A Digital Elevation Model (DEM) of 1 m resolution (provided by the Mondi Group) was used to calculate slope, aspect, TR and TRI of each site. Means (with standard deviations) of all recorded variables are given in Appendix H for the Midlands, and Appendix I for Zululand.

At each site, ten 100 g soil subsamples were collected randomly. These were then combined into a 1 L soil sample per site. This accounted for small-scale variations in soil parameters within the site. A 500 g sub-sample was taken from the sampling unit, which served as a representative sample, and kept at room temperature. The representative sample was then sent to a soil analytical laboratory for element analysis, of which the following information was extracted: carbon I, calcium (Ca), magnesium (Mg), nitrogen (N), phosphorus (P), potassium (K), sodium (Na) and sulphur (S). The Dumas combustion approach using a Leco Trumac CNS analyzer (Leco, USA) was used to analyze C, N and S, while the Bray II Phosphorus method (Bray and Kurtz 1945) was used to analyze P. Ca, K, Na and Mg was analyzed using an Agilent 4100 Microwave Plasma Atomic Emission Spectrometer (MP-AES) (Agilent, USA). Means (with standard deviations) of these soil elements are given in Appendix H for the Midlands, and Appendix I for Zululand. Analysis was conducted by the Institute for Commercial Forestry Research (ICFR).

The variation in environmental variables was assessed by calculating the standard deviation for each recorded variable per biotope, for each region (Appendix H for the Midlands, and Appendix I for

Zululand). Additionally, the coefficient of variation (CV) was calculated for each environmental variable (standard deviation divided by the mean) (Reed et al. 2002). As a rule of thumb, a CV value of > 1 indicates high variation, whereas CV < 1 indicates low variation (Appendix H, I).

3.2.4. Data analyses

Data analyses were performed separately for springtails and ants of each region, using pooled data from all sampling methods. Species accumulation curves, of all species collected, were created for each arthropod taxon, separately per biotope and region, using the *iNEXT* package (Hsieh et al. 2019) (Appendix A) in R (version 3.6.3) (R Core Team 2016), to determine whether sampling was sufficient (Gotelli and Colwell 2001).

First, the number of singletons and doubletons were evaluated across the entire assemblage for each arthropod taxon (i.e. regardless of biotope type). For ants, singletons and doubletons consisted of 8 species in the Midlands (21.62% of the total number of species) and 13 species in Zululand (22.41% of the total number of species). For springtails, singletons and doubletons consisted of 28 species in the Midlands (29.47% of the total number of species) and 20 species in Zululand (42.55% of the total number of species). However, when removing the singletons and doubletons from assemblages, the error rate decreased and accuracy increased (Allen et al. 2016). Therefore, due to the high occurrence of singletons and doubletons within each of the assemblages, they were removed from the entire assemblages, and the remaining assemblage was used in all further analyses of this study.

3.2.4.1. Objective 1: Examination of ant and springtail alpha diversity amongst natural areas and plantations

Local species richness was estimated for each site using morpho-species richness (from here on referred to as 'species richness'). Data showed normal distribution (Midlands springtails and Zululand ants) and non-normal distribution (Midlands ants and Zululand springtails) according to Shapiro-Wilk tests using the *nortest* package in R (Gross and Gross 2009). All response variables were spatially autocorrelated, based on Mantel tests using the *ade4* package in R (Dray and Dufour 2007). Therefore, to test for the effect of biotope type, linear mixed models (LMMs) for normally distributed data and generalized linear mixed models (GLMMs) for non-normally distributed data were made using the *lme4* package (Bates et al. 2014) in R. Biotope type was included as a fixed parameter and plantation estate as a random parameter (Fig. 3.1). After examining the distribution fit of the data with the *car* and *mass* packages in R (Fox et al. 2012; Ripley et al. 2013), the distribution family was specified as Poisson with specified log-link function within the GLMMs. Post-hoc tests were conducted using the *multcomp* package in R (Bretz et al. 2008). Boxplots were constructed using the *ggpubr* package (Kassambara 2017) in R.

3.2.4.2. Objective 2: Examination of ant and springtail assemblage dissimilarity between sites of the same biotope type

Total within-biotope beta-diversity was assessed for each biotope, as well as the species turnover and nestedness components (Baselga 2010), which together drive changes in beta-diversity (Cardoso et al. 2015). For this study, abundance-based, rather than presence-absence data, were used, as it is more robust to minor changes in community/assemblage composition and sampling effects (Tucker et al. 2016; Kim et al. 2018). First, beta-diversity and partitioned beta-diversity within each biotope type, for each arthropod taxon and region were examined, using the *betapart* package (Baselga et al. 2017) in R. Analysis was conducted using abundance-based data, with the index family specified as Bray-Curtis. The *beta.sample.abund* function was used to compute three dissimilarity measures, i.e. total beta-diversity ($\text{Beta}_{\text{Bray}}$), nestedness ($\text{Beta}_{\text{Grad}}$) and turnover ($\text{Beta}_{\text{Bal}}$), within each biotope type for the Midlands and Zululand, respecitively. Within this function, six sites were selected at random to calculate the three dissimilarity measures. The randomly selected sites were then resampled, i.e. permutated 100 times, to obtain an average estimate and standard deviation for the three dissimilarity measures within each biotope type. To determine the effect of biotope type on these components, linear models (LMs) were conducted with the *lme4* package with each of the components of beta-diversity (total, nestedness, or turnover) as the response variable, and biotope type as the fixed parameter. Where significant effects occurred, post-hoc tests were conducted using the *multcomp* package in R.

3.2.4.3. Objective 3: Examination of ant and springtail assemblage dissimilarity between paired biotopes

Secondly, beta-diversity and partitioned beta-diversity between pairs of biotope types for each arthropod taxon and region was examined to assess assemblage dissimilarity between different biotopes using the *BAT* package (Cardoso et al. 2015) in R. Analysis was conducted using abundance-based data with the Soerensen beta-diversity measure, which computed the total beta-diversity (B_{total}), nestedness (B_{rich}) and turnover (B_{repl}) between biotopes. Boxplots were also constructed using the *ggpubr* package in R. To test for the effect of biotope type on ant and springtail assemblage composition within each region, generalized linear models (GLMs) with a negative binomial distribution of abundance data was conducted using the *mvabund* package (Wang et al. 2012) and the *manyglm* function in R. Biotope type was included as a fixed parameter within the GLM. For unconstrained ordination and visualizing differences in assemblage composition between the biotope types, latent variable models (LVMs) were made using the *Boral* package (Hui 2016) in R. These biplots show ordinations without (pure biplot) and with (residual biplot) the influence of environmental variables (Hui 2016). For these ordinations, I used biotope type as my environmental variable. In addition, significant indicator species within each biotope were determined using the *multipatt* function of the *indicspecies* package (De Cáceres and Legendre 2009; De Cáceres et al. 2010) in R.

3.3. Results

Species accumulation nearly reached the asymptotes in both regions (Appendix A), indicating that sufficient sampling was done. Midlands samples consisted of 15 969 ant individuals, in 37 morphospecies belonging to 15 genera in 3 sub-families. Zululand samples consisted of 9 808 ant individuals, consisting of 29 morphospecies belonging to 18 genera in 4 sub-families. *Camponotus* (5 spp.), *Tetramorium* (5 spp.), *Crematogaster* (4 spp.) and *Pheidole* (4 spp.) were the most speciose genera in the Midlands, while *Tetramorium* (4 spp.) and *Nesomyrmex* (3 spp.), *Pheidole* (3 spp.) and *Plagiolepis* (3 spp.) were the most speciose genera in Zululand. For springtails, Midlands samples consisted of 77 012 individuals, in 61 morphospecies belonging to 13 genera and 10 sub-families. Zululand's samples consisted of 4 856 springtail individuals, in 27 morphospecies belonging to 8 sub-families and 6 genera. *Seira* (28 spp.) and *Hypogastrura* (3 spp.) were the most speciose genera in the Midlands. *Seira* (14 spp.) and *Hypogastrura* (2 spp.) were also the most speciose genera in Zululand.

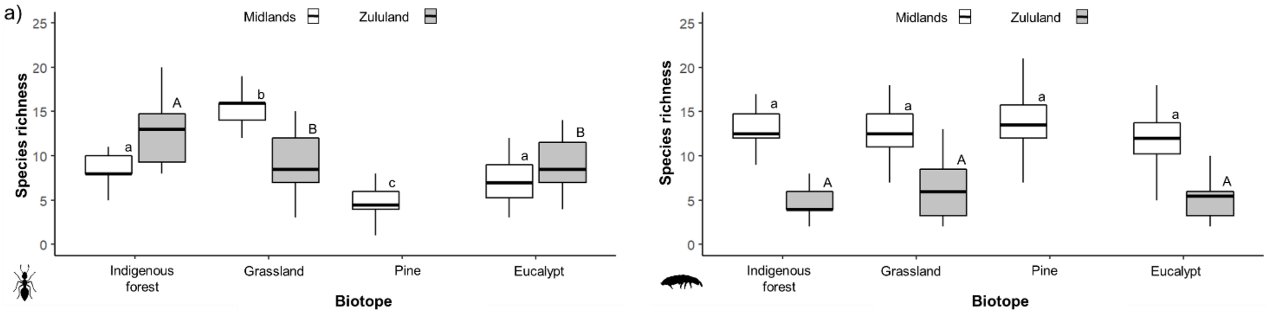

Figure 3.2 Boxplots with central horizontal line indicating the median value, boxes indicating the interquartile range, and the whiskers indicating standard deviation within each biotope. Boxplots show a) ant and b) springtail species richness in the Midlands and Zululand. Means with small letters (Midlands) and capital letters (Zululand) in common between the biotopes, are not significantly different at $P < 0.05$.

3.3.1. Objective 1: Alpha diversity amongst natural areas and plantations

Ant species richness differed significantly between biotope types in the Midlands ($\chi^2 = 89.56$, $P < 0.001$, $df = 3$) (Fig. 3.2A), with grasslands containing the highest number of ant species, followed by indigenous forests, eucalypt compartments and pine compartments. However, ant species richness between indigenous forests and eucalypt compartments did not differ significantly. In Zululand, ant species richness also differed significantly between biotope types ($\chi^2 = 14.54$, P = 0.047, df = 2) (Fig. 3.2A), with indigenous forests having the highest number of ant species, followed by grasslands and eucalypt compartments. Ant species richness of eucalypt compartments did not differ from grasslands in Zululand. Springtail species richness was not significantly different among biotope types in the Midlands ($F_{3, 68} = 1.23$, P = 0.306) (Fig. 3.2B) and in Zululand ($\chi2 = 4.57$, P = 0.102, df = 2) (Fig. 3.2B).

3.3.2. Objective 2a: Within-biotope assemblage dissimilarity

In both regions, ant and springtail assemblages showed high levels of total beta-diversity within each biotope type (Table 3.1). Total beta-diversity of ants ($F_{3, 396} = 38.23$, $P < 0.001$) and springtails ($F_{3, 396} = 60.87$, $P < 0.001$) in the Midlands, as well as ants ($F_{2, 297} = 30.42$, $P < 0.001$) and springtails in Zululand ($F_{2, 297} = 22.26$, $P < 0.001$), was significantly different between biotope types (Table 3.1). In the Midlands, eucalypt plantations had the highest overall ant beta-diversity, whereas grassland and indigenous forests had the highest springtail beta-diversity (Table 3.1). In Zululand, indigenous forests had the highest ant beta-diversity and grassland had the highest springtail beta-diversity (Table 3.1). These variations in assemblage composition was explained more by the turnover component, rather than the nestedness component of beta-diversity (Fig. 3.3), for both ants and springtails of both regions, within all of the biotope types. In the Midlands, both turnover ($F_{3, 396} = 104.70$, $P < 0.001$) and nestedness ($F_{3, 396} = 172.20$, $P < 0.001$) components of the ant assemblage differed significantly between biotope types (Fig. 3.3A). Here, pine and eucalypt compartments had the highest species turnover compared to indigenous forests and grasslands (Fig. 3.3A). In addition, all biotopes differed significantly from each other in nestedness (Fig. 3.3A), the highest occuring within the grasslands and the lowest occuring within the pine compartments.

Table 3.1 Total beta-diversity of ants and springtails within each biotope per region. Analysis conducted separately for ants and springtails in each region. Letters in common between biotopes for each taxon do not show a significant difference at $p < 0.05$.

	Midlands		**Zululand**	
Biotope	**Formicidae**	**Collembola**	**Formicidae**	**Collembola**
Indigenous forests	0.77 ± 0.00^{a}	0.86 ± 0.01^{a}	0.86 ± 0.01^{a}	0.82 ± 0.01^{a}
Grasslands	0.80 ± 0.01^{b}	0.86 ± 0.01^{a}	0.81 ± 0.00^{b}	0.85 ± 0.00^{b}
Pine compartments	0.79 ± 0.00^{b}	0.81 ± 0.00^{b}		
Eucalypt compartments	0.83 ± 0.00^{c}	0.77 ± 0.01^{c}	0.82 ± 0.00^{b}	0.82 ± 0.00^{a}

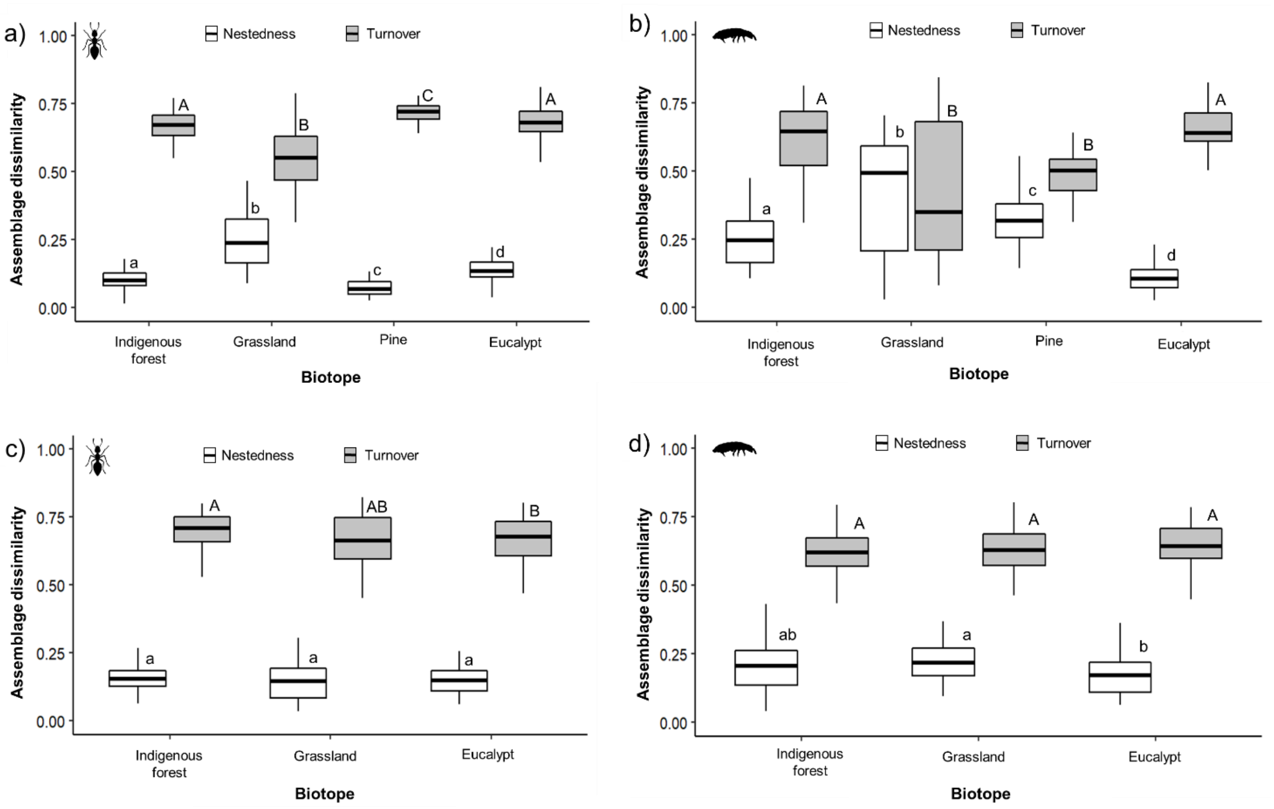

Figure 3.3 Boxplots of partitioned Bray-Curtis dissimilarity for nestedness (white) and turnover (grey), with central horizontal line indicating the median value, boxes indicating the interquartile range and the whiskers indicating standard deviation within each biotope. Illustrated are the nestedness and turnover components of a) ants and b) springtails in the Midlands, and c) ants and d) springtails in Zululand. Means with small letters (nestedness) and capital letters (turnover) in common between biotopes, are not significantly different at $P < 0.05$.

For springtails in the Midlands, both the turnover ($F_{3, 396} = 45.87$, $P < 0.001$) and the nestedness ($F_{3, 396} = 108.20$, $P < 0.001$) components differed significantly between biotope types (Fig. 3.3B). Inidngeous forests and eucalypt compartments had significantly higher species turnover compared to grasslands and pine compartments (Fig. 3.3B). There was, however, no difference in the species turnover between grasslands and pine compartments, nor between the indigenous forests and the eucalypt compartments (Fig. 3.3B). All biotopes differed significantly from each other regarding nestedness, the highest within the grasslands and the lowest within the eucalypt compartments (Fig. 3.3B).

In Zululand, the turnover ($F_{2, 297} = 3.42$, $P < 0.001$) component of the ant assemblage differed significantly between biotope types (Fig. 3.3C), but not in nestedness ($F_{2, 297} = 1.82$, $P = 0.164$). Indigenous forests had significantly higher species turnover than grasslands and eucalypt compartments. However, grasslands and eucalypt compartments did not significantly differ from each other (Fig. 3.3C). For springtails in Zululand, only the nestedness component of the assemblage differed signficantly between biotopes in Zululand ($F_{2, 297} = 7.83$, $P < 0.001$) (Fig. 3.3D). Grassland had higher springtail nestedness compared to indigenous forests and eucalypt compartments, however was only signficantly different from eucalypt compartments (Fig. 3.3D). The turnover component within each biotope type for springtails did not differ between biotope types in Zululand ($F_{2, 297} = 2.17$, P = 0.147) (Fig. 3.3D).

3.3.3. Objective 2b: Within-biotope environmental variation

Environmental variables showed high variation between sites in both the Midlands (Appendix H) and Zululand (Appendix I) based on the standard deviatation (SD) values per biotope. However, in the Midlands, site-related variables were more variable than the soil- and landscape-related variables based on the coefficient of variation (CV) values (i.e. CV > 1) (Appendix H). Similar results were found for Zululand when examining the CV values (Appendix I). Variation in grass cover was high within indigenous forest, while the variation in rock, dead wood and shrub cover was high within grassland in the Midlands (Appendix H). Furthermore, the variation in rock, herbaceous, shrub and grass cover was high within the pine compartments of the Midlands (Appendix I). Additionally, variation in rock, vegetation, herbaceous, grass and bare ground cover, and the vegetation height was high for the eucalypt compartments in the Midlands (Appendix H). In Zululand, the variation in bare ground cover was high within indigenous forest, while the variation in bare ground cover, soil carbon, nitrogen and sulphur content was high within the grasslands (Appendix I). Additionally, variation in site elevation, herbaceous, shrub and bareground cover was high within the eucalypt compartments in Zululand (Appendix I).

Table 3.2 Beta-diversity and its components (nestedness and turnover) between paires of biotope types in the Midlands and Zululand for ants (Formicidae) and springtails (Collembola). Biotopes indicated as indigenous forest (For), grassland (Grass), pine compartments (Pine) and eucalypt compartments (Euc). The proportional contribution of each component to total beta-diversity is indicated in brackets.

Between	**Formicidae**			**Collembola**		
Biotopes	**Beta-diversity**	**Nestedness**	**Turnover**	**Beta-diversity**	**Nestedness**	**Turnover**
Midlands						
For - Grass	0.89	0.83 (94.12%)	0.05 (5.88%)	0.69	0.22 (32.32%)	0.47 (67.68%)
For - Pine	0.69	0.50 (78.40%)	0.14 (21.60%)	0.63	0.28 (44.52%)	0.35 (55.64%)
For - Euc	0.70	0.15 (22.32%)	0.53 (77.68%)	0.87	0.83 (95.06%)	0.04 (4.94%)
Grass - Pine	0.94	0.94 (99.79%)	0.01 (0.21%)	0.73	0.47 (64.67%)	0.26 (35.33%)
Grass - Euc	0.94	0.87 (93.98%)	0.06 (6.02%)	0.93	0.89 (95.79%)	0.04 (4.10%)
Pine - Euc	0.76	0.38 (52.07%)	0.35 (47.93%)	0.75	0.71 (95.58%)	0.03 (4.42%)
Zululand						
For - Grass	0.34	0.06 (18.75%)	0.27 (81.25%)	0.47	0.25 (53.62%)	0.22 (46.17%)
For - Euc	0.63	0.45 (72.64%)	0.17 (27.36%)	0.54	0.46 (84.13%)	0.09 (15.68%)
Grass - Euc	0.68	0.50 (74.10%)	0.17 (25.90%)	0.46	0.23 (50.77%)	0.22 (49.23%)

3.3.4. Objective 3: Between-biotope assemblage dissimilarity

Total beta-diversity between pairs of biotopes was higher within the Midlands than in Zululand, for both ants and springtails (Table 3.2). In general, most of the variation in total beta-diversity was due

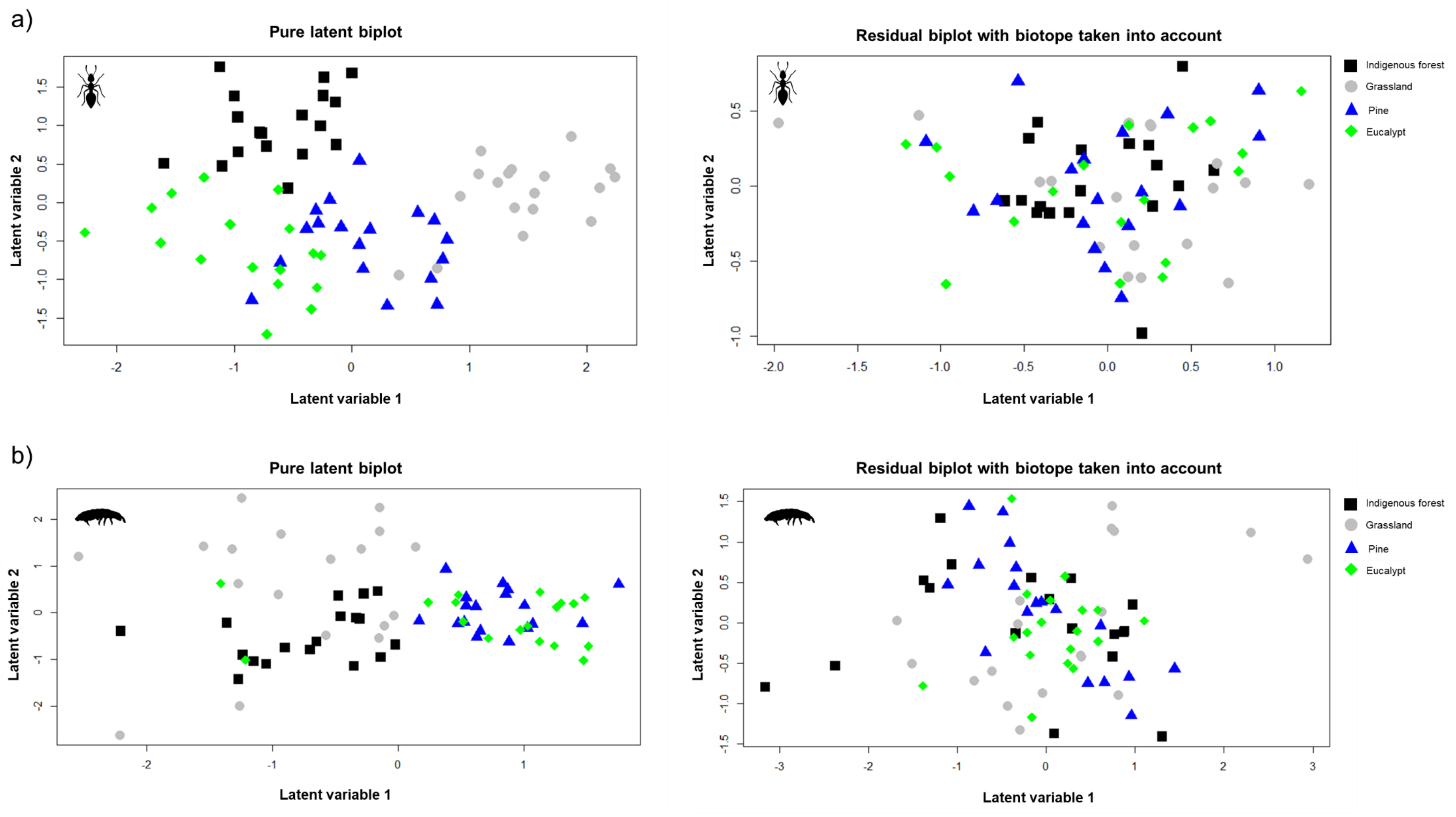

Figure 3.4 Model-based pure (left) and residual (right) ordination for a) ant and b) springtail assemblages in the Midlands, between indigenous forest, grassland, pine and eucalypt compartments. Pure biplots are without the influence of biotope type, whereas the residual bioplot included the influence of biotope type.

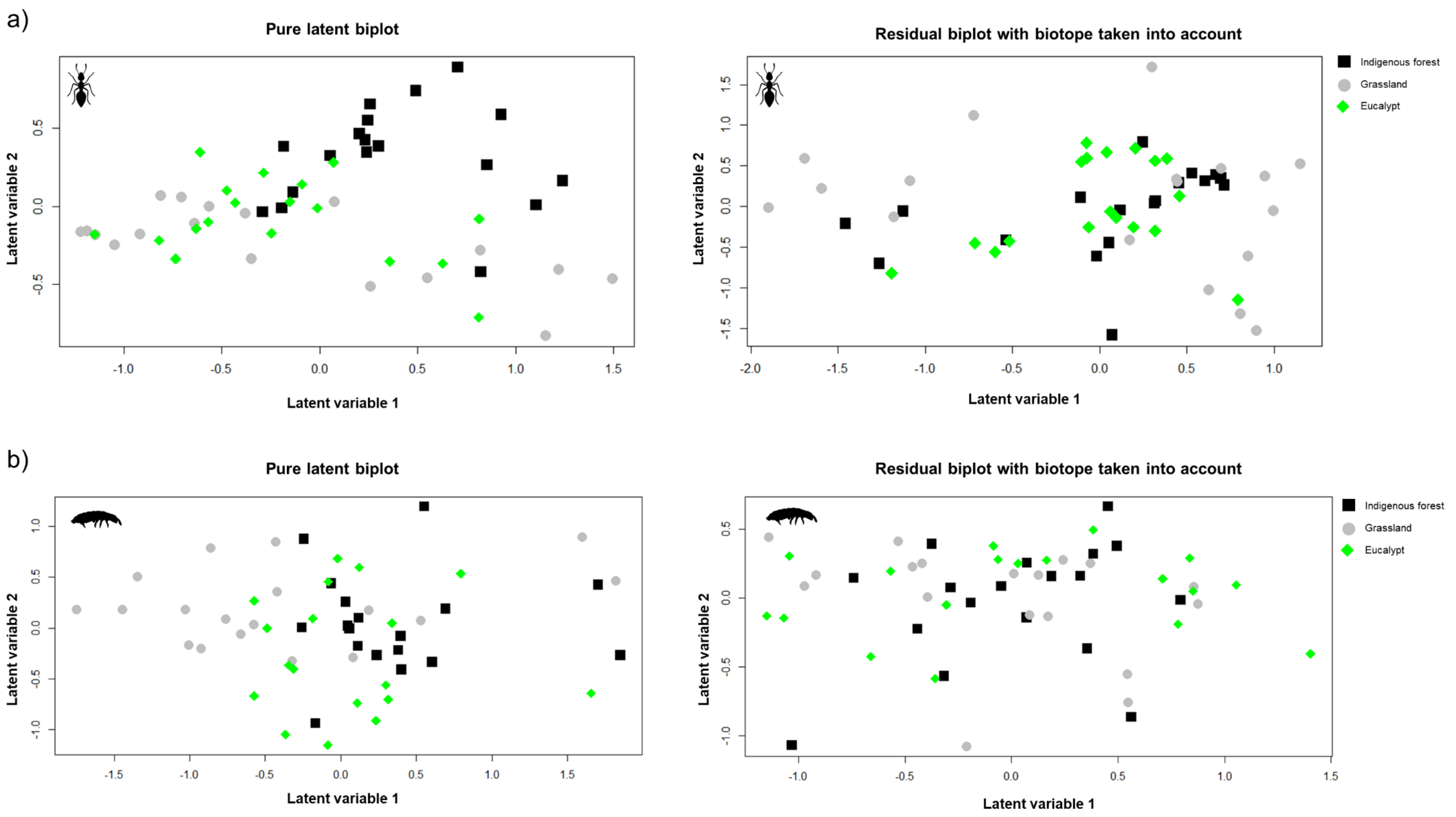

Figure 3.5 Model-based pure (left) and residual (right) ordination for a) ant and b) springtail assemblages in Zululand, between indigenous forest, grassland and eucalypt compartments. Pure biplots are without the influence of biotope type, whereas the residual bioplot included the influence of biotope type.

to nestedness, rather than turnover for most between-biotope pairings (Table 3.2). However, in certain cases, turnover was the main contributing factor towards the variation in total beta-diversity (Table 3.3). This occurred for 1) ants in the Midlands between indigenous forests and eucalypt compartments, 2) ants in Zululand between indigenous forest and grassland, 3) springtails in the Midlands between indigenous forest and grassland, and 4) springtails in the Midlands between indigenous forest and pine compartments (Table 3.2). Nestedness was the main factor contributing to the total variation in total beta-diversity in the remaining biotope pairs (Table 3.2).

Table 3.3 Proportion shared ant (Formicidae) and springtail (Collembola) species between indigneous forests, grasslands, pine compartments and eucalypt compartments within the Midlands and Zululand. The actual number of species shared, is indicated in brackets.

	Indigenous forest	**Grassland**	**Pine block**
Midlands Formicidae			
Grassland	47.22% (17)		
Pine	65.22% (15)	47.22% (17)	
Eucalypt	64.00% (16)	51.35% (19)	46.43% (13)
Midlands Collembola			
Grassland	58.49% (31)		
Pine	55.36% (31)	56.14% (32)	
Eucalypt	61.82% (34)	51.67% (31)	62.07% (36)
Zululand Formicidae			
Grassland	75.86% (22)		
Eucalypt	82.14% (23)	71.43% (20)	
Zululand Collembola			
Grassland	48.15% (13)		
Eucalypt	63.64% (14)	61.54% (16)	

When examining the assemblage composition, biotope had a significant effect on both ant (LRT = 813.30, $P < 0.001$, df = 68) (Fig. 3.4A) and springtail (LRT = 814.00, $P < 0.001$, df = 68) (Fig. 3.4B) assemblages in the Midlands. Interestingly, all biotopes differed from each other for both the ant and springtail assemblages. In Zululand, similar patterns were observed, with biotope having a significant effect on both ants (LRT = 200.10, $P < 0.001$, df = 51) (Fig. 3.5A) and springtails (LRT = 182.90, $P < 0.001$, df = 51) (Fig. 3.5B), and all biotopes differing from each other regarding their ant and springtail assemblages. Despite overall assemblage dissimilarity among biotopes, there were relatively high numbers of shared species between all biotopes for both ants and springtails in both regions (Table 3.3). In the Midlands, 46.–3 - 65.22% of the ants, and 51.67 – 62.07% of springtails, were shared among the different biotope pairs (Table 3.3). In Zululand, 75.–0 - 78.57% of the ants, and 48.–5 - 63.64% of springtails, were shared among the different biotope pairs (Table 3.3).

In addition, few species were highly associated with a particular biotope (Appendix L). In the Midlands, two ant species were characteristic of indigenous forest, while eleven species were characteristic of grassland (Appendix L). No ant species were characteristic of pine or eucalypt compartments in the Midlands. In Zululand, four ant species were characteristic of indigenous forest, and 1 species each of grassland and eucalypt compartments (Appendix L). For springtails in the Midlands, four species were characteristic of indigenous forest, five to grassland, four to pine compartments and 1 to eucalypt compartments (Appendix L). In Zululand, three springtail species were characteristic of grassland, with one species being characteristic of eucalypt compartments. No springtail species were characteristic of indigenous forest in Zululand (Appendix L).

3.4. Discussion

3.4.1. Objective 1: Alpha diversity amongst natural areas and plantations

Plantations are often viewed as systems that are ecological and biological barren, mainly due to their low structural complexity and compositional diversity compared to natural habitats, such as indigenous forest (Brockerhoff et al. 2008). Nonetheless, plantations can provide valuable habitat for some species (Brockerhoff et al. 2008), and are expected to have some level of diversity, although generally lower compared to natural ecosystems (Pryke and Samways 2009; Lucey et al. 2014; Eckert et al. 2019). Here, the plantations in both the Midlands and Zululand generally supported equally high local species richness as both the indigenous forest and grassland. I found that *Eucalyptus* plantations had similar levels of ant species richness as in forest or grassland in both the Midlands and Zululand, which was surprising. However, *Pinus* plantations had significantly lower ant species richness compared to all other biotopes in the Midlands. Studies have shown that *Eucalyptus* plantations can increase the movement and dispersal of some species by improving connectivity across the landscape more efficiently than other non-forests anthropogenic land use types (Klomp and Grabham 2002; Lindenmayer and Hobbs 2004), and therefore, could contain similar diversities as naturally forested systems (Barlow et al. 2007; Martello et al. 2018). Environmental heterogeneity, i.e the variation in biotic and abiotic conditions, is an important driver of species diversity (Stein and Kreft 2015). As studies have shown a positive relationship between environmental heterogeneity and species richness (Curd et al. 2018; Walters et al. 2020), it is possible that environmental conditions within the eucalypts may have been more complex compared to the pines (e.g., less shade, litter cover and barer ground; Appendix H), resulting in higher species richness estimates as more species are able to coexist with greater available niche space.

3.4.2. Objective 2: Within-biotope assemblage dissimilarity and environmental variation

I expected plantations to have lower levels of beta-diversity, i.e. low change in species assemblage, compared to natural systems. This was mainly expected due to the homogenous nature of the litter layer compared to natural systems, as found in Lui et al. (2016). Lui et al. (2016) showed rubber plantations had lower litter-dwelling ant beta-diversity compared to nearby forest habitat. In Brazil, ant assemblage composition within eucalypts was distinct from those in native rainforest, and they were more varied among sites (Martello et al. 2018). This may be due to the lower quantity and moisture of the leaf litter within the eucalypts driving homogenization of the ant assemblage composition compared to the forests, based on similar findings by Winck et al. (2017) for springtails. However, I did not observe this pattern in my study. In contrast, beta-diversity was high within all the biotope types, and plantations held similar levels of beta-diversity as natural biotopes for both ants and springtails, except for springtails in the Midlands where the eucalypt compartments had significantly lower levels of beta-diversity compared to grasslands, but similar to the indigenous forests. These results were surprising as patterns in beta-diversity may differ among taxa and regions, with higher levels of beta-diversity expected for less mobile organisms in more heterogeneous environments (Soininen et al. 2007). Oxbrough et al. (2016) showed different epigaeic arthropod groups responded differently to stand type and that beta-diversity was greater within single-species stands compared to mixed-stands. Additionally, studies such as Dahms et al. (2010) and Kataja-aho et al. (2016), showed that ants and springtails do not show similar trends in terms of their alpha- and beta-diversity patterns. However, I found that the overall trends were similar for both ants and springtails in the Midlands and Zululand.

When further examining overall beta-diversity patterns within each of the biotope types, it was expected that species nestedness, rather than species turnover, would play a greater role in driving the change in species between plantation sites, whereas the opposite was expected for natural sites. Here, I assumed that a small group of generalist species would consistently vary across sites within the plantations, rather than the replacement of unique, specialist species. This would concord with Knop (2016), who found that urbanization had large-scale homogenizing effects on leafhopper and bug assemblages due to reduced species turnover. Surprisingly, this was not the case in this study, and the turnover component contributed greatly to change in assemblages within the biotope types, regardless of taxon, biotope, or region. Although my study only examined taxonomic diversity, my results are in line with Martello et al. (2018) showing turnover contributed the most to changes in taxonomic diversity within both the forest and plantations, while nestedness contributed the most to changes in functional diversity within each of these systems. Others have also reported the replacement of species, i.e. species turnover, to contribute greatly to differences between sites and/or amongst different landuses (Bishop et al. 2015; Schmidt et al. 2017; Janion-Scheepers et al. 2020).

Environmental variation has been suggested to be an important factor in driving high levels of species replacement, even among the sites in the transformed habitats (Karp et al. 2012; Hammond et al.

2018; Sambhu et al. 2018), as it determines the distribution of species. Similarly, studies have shown habitat heterogeneity plays an important role as a driver of species variations for ants (Schmidt et al. 2017; Santoandré et al. 2019; Wendt et al. 2021) and springtails (Perez et al. 2013; Bairdet al. 2019) between different habitats. The high total beta-diversity, and the high contribution from species replacement for ants and springtails, may therefore have been explained by the high environmental variation observed within each biotope (Appendix H, I). Santoandré et al. (2019) suggested that environmental gradients lead to changes in species identities, which are coupled with changes in their functional characteristics. Findings in my study may therefore be a result of environmental filtering which is allowing some species to persist within some sites, while allowing other species to occur within the other sites (Gilbert and Lechowicz 2004; Santoandré et al. 2019). This concept suggests that not all species are able to establish and persist across all environmental conditions. This may have been a contributing factor, as shifts in species traits between sites may have added to the high overall dissimilarity between sites. Additionally, as species have different niche requirements, the high environmental variation within sites may have offered different suitable niches for the arthropods to use, thus resulting in an overall variation of suitable and available ecological niches across the sites. This may have allowed species with different identities and traits to co-exist (Arnan et al. 2011; Fowler et al. 2013; de Menezes and Schmidt 2020). As a result, this may also explain the high dissimilarity of ant and springtail assemblages between the sites.

However, a study in the Cape Fynbos found springtail beta-diversity was high among all sites and the result of species replacement rather than nestedness (Janion-Scheepers et al. 2020). They concluded that the high species turnover of springtails between sites was not likely to have been due to vegetation characteristics, as springtails are not strongly associated to specific plant species (Hopkin 1997; Salamon et al. 2004), but rather climatic gradients or landscape features. It is therefore possible that other environmental gradients are playing a role in the observed patterns. However, studies that examine mechanisms responsible for beta-diversity patterns are limited (Olden 2006). To efficiently conserve local biodiversity, we need a better understanding on the processes and environmental factors which shape alpha- and beta-diversity patterns, especially within agricultural landscapes. As this was not formally assessed within the current study, future studies should focus on examining possible specific drivers (from fine- to landscape-scale) of alpha- and beta-diversity, which are needed to make informed conservation and management decisions (Olden 2006; Socolar et al. 2016).

3.4.3. Objective 3: Between-biotope assemblage dissimilarity

Species migration from natural areas into plantations may also have contributed to the high diversity in plantations. My study found a high percentage species being shared between the biotope types, even though all assemblages were significantly different, which is similar to previous results from the KZN Midlands (Yekwayo et al. 2016, 2017). This suggests soil arthropods may colonize the plantations from the natural biotopes. Additionally, Basset et al. (2017) showed changes in assemblage composition between indigenous forest and plantations are less extreme for termites than for butterflies. Furthermore, Pryke and Samways (2012) showed highly mobile, above-ground arthropod taxa (e.g. butterflies, dragonflies and grasshoppers) respond more strongly to contrast differences between habitat types, in comparison to less mobile, surface-dwelling taxa (e.g. ants, beetles and spiders). As soil arthropods are more sensitive to factors such as leaf litter and soil structure or composition (Almeida et al. 2013; Martello et al. 2018), it is possible that the soil arthropods selected for this study are less influenced by structural contrast than above-ground fauna, allowing species to colonize the plantations from the nearby natural areas. This means that the high percentage of shared species indicates that these plantations are playing a supportive role in supporting species from both the indigenous forest and grassland. Likewise, Santoandré et al. (2019) showed young plantations resembled grassland in terms of environmental similarity (e.g. higher temperature and thermal variation), while mature plantations resembled indigenous forest in terms of their environmental similarity (e.g. lower temperatures and lower thermal variability). This could also explain why a subset of species are being shared between the plantations, grassland and indigenous forest, as the change in the maturity of the plantation can cause some species to persist, while others are lost, resulting in plantations sharing species with both the grasslands and indigenous forests. However, these plantations are not true extensions, as they do not support all the species that occur within either the indigenous forest or grassland (as in Yekwayo et al. 2017).

Another possible reason for the high faunal diversity in plantations could be the survival capabilities of the focal taxa within the plantations, coupled with the long period of limited disturbance between harvesting events. These plantations were initially natural vegetation and transformed into plantations many years ago (Samways et al. 2010). Today, these plantations are intensively managed only during the harvesting and replanting periods, and which involves soil disturbance by vehicles and the burning of harvest residue. Additionally, herbicide applications for weed control and the pruning of trees occur within the first five years after replanting. Thereafter, the compartment remains unmanaged until the end of the rotation, which is on average 10 years, when it can be harvested again. Additionally, soil-dwelling arthropods have a greater chance to survive disturbance events compared to surface-dwelling arthropods, as they can burrow into the soil for protection (Moretti et al. 2006; Gongalsky and Persson 2013). Inherently, levels of soil arthropods seem to recover faster than most surface-dwelling arthropods in some systems (Gongalsky and Persson 2013). It is possible that ants and springtails are more resilient than anticipated and species can survive and recover after implementation of management practices. However, as this was not examined in this study, it would require further examination to make robust conclusions.

Furthermore, although environmental conditions between plantations and natural biotopes may be allowing some species to move into the plantations from the nearby or neighboring natural vegetation types, the identities of the species were not assessed within this study. The environmental gradients may act as filters, allowing a species with a specific set of traits to occur within one habitat, but not in another (Wiescher et al. 2012; Santoandré et al. 2019). Thus, species can persist within habitat-specific conditions when their functional traits are compatible with that particular environment (Wiescher et al. 2012). Liu et al. (2012) found pine plantations had significantly higher springtail abundance and species richness compared to the Cape Flats Sand Fynbos (CFSF), although, these were mostly invasive species. As functional diversity was not assessed in my study, this suggests that future research could examine the species traits which allow them to colonize and persist within the plantation compartments. Further examination is required to determine whether these are specialist or endemic species rather than generalist, cosmopolitan or invasive species that are capable of moving across habitat boundaries and surviving in a wider range of habitats compared to range-restricted, specialist species (Harper et al. 2005; Yekwayo et al. 2016b).

3.5. Conclusion

It is important to understand how local- and landscape-scale soil biodiversity patterns differ between regions, land use types and taxa to protect local diversity and to improve conservation strategies (Socolar et al. 2016; Cameron et al. 2019). Here, alpha and beta-diversity within the plantations were relatively high and similar to the natural biotopes in some cases, with species replacement being the main driver for assemblage composition changes within plantations and natural systems. In addition, the high segregation among the biotopes at the overall assemblage level indicates that there are probably some specialized species that are spatially restricted to the natural areas, while the relatively high percentage of shared species indicates that there are some naturally occurring species that can be sustained by the plantations.

The concept of ecological networks (ENs) within these timber production landscapes, particularly at the large spatial scale of landscape mosaic, focuses on the land-sparing approach where conservation activities are primarily focused on the natural systems within these landscapes, while production is concentrated in the commercial timber compartment. Here, at least for these functionally important soil arthropod groups that are linked to soil health maintenance (Baretta et al. 2008; Venuste et al. 2018), the production areas show high levels of species diversity and turnover between sites.

Additionally, there were species unique to the natural areas and their conservation is vital to regional biodiversity.

Lastly, arthropods are sensitive to environmental change (Kotze and Samways 2001) and could react differently to changes in the landscape (Yekwayo et al. 2017), and so conservation approaches may not be the same for below- and above-ground biodiversity (Cameron et al. 2019). Therefore, more research is needed to determine how (dis)similar below- and above-ground arthropod diversity responds to contrasting environmental conditions within different land use types, which could improve conservation practices within this type of landscape. These results here provide support for the establishment of ecological networks (ENs) as beneficial for conserving and maintaining soil biodiversity within a plantation landscape by providing propagules for recolonization into the plantations (Meloni et al. 2020).

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CHAPTER 4

Trait divergence among soil arthropods in an agro-ecological land mosaic

ABSTRACT

Functional rather than taxonomic homogenization is of great concern for stability and functioning of ecosystems, with functional diversity essential for long-term ecosystem resilience. I assess the taxonomic and functional diversity, as well as trait composition, of ants and springtails, to determine whether there are significant shifts in taxonomic and functional diversity in an agro-ecological system with both natural vegetation (indigenous forests and grasslands) and transformed (*Eucalyptus* plantations) biotopes. The study was in two geographically and environmentally contrasting regions: high elevation clay soils of the Midlands, as well as the costal sandy soils of Zululand, both in KwaZulu-Natal, South Africa. Species richness and Shannon's entropy was assessed for taxonomic diversity, whereas functional and Rao's quadratic entropy were assessed for functional diversity. Additionally, I assess shifts in species-specific traits in natural vs. transformed biotopes. Surprisingly, the exotic *Eucalyptus* tree compartments generally had similar levels of taxonomic and functional diversity to both indigenous forests and/or grasslands, indicating seemingly high levels of ecosystem stability and functioning. However, there were significant shifts in species-specific traits between the two biotopes and at both elevations, indicating that environmental filtering may allow some species with a unique set of traits to persist within these contrasting biotopes, yet others are excluded. Certain traits are representative of natural biotopes, which emphasises the importance of having these natural biotopes interspersed between the managed biotopes to conserve functionally unique species. Plantations retain high functional diversity, due to the adaptiveness of their soil fauna, which is essential to the functioning of these soils. However, presence of natural biotopes and their soils is critical for the stability, resilience and functioning of soil ecosystems at the landscape level.

Key words: Collembola; Eucalypt; Forest; Formicidae; Functional diversity; Grassland; Landscape transformation

4.1. Introduction

The rapid increase of anthropogenic activities, such as the conversion of natural ecosystems into agricultural systems, can lead to changes in environmental conditions, which can have significant effects on biodiversity, both locally and regionally (Foley et al. 2005; Walther 2010; Isbell et al. 2015). In conjunction with studies monitoring the status of biodiversity (Scholes et al. 2008), we also require monitoring of the functional changes in species assemblages (Palmer and Febria 2012), due to habitat characteristics which drive both the taxonomic and functional composition of communities (Fichaux et al. 2019). Changes in the composition of faunal assemblages that occur due to changes in the complexity of the habitat, are dependent on the traits of the species (Wiescher et al. 2012). These traits are often related to the morphology, phenology and physiology of the species, which influences its performance and functioning within the environment (Violle et al. 2007; Pey et al. 2014). With land-use intensification, environmental filtering may lead to the exclusion of species with traits poorly adapted to a specific environment and yield communities with more similar traits which are ecologically redundant (Cornwell et al. 2006). In other words, environmental conditions will filter species assemblages so they contain a limited set of traits (i.e. functional homogenization), with more species performing similar functions, which leads to a decrease in functional diversity (Olden and Rooney 2006; Tecco et al. 2010; Rigal et al. 2018). This in turn, may have detrimental effects on the functioning of the ecosystem (Cardinale et al. 2012; Butterfield and Suding 2013). For example, functional homogenization of flower visiting assemblages can have consequences on services such as pollination (Hoehn et al. 2008; Frund et al. 2013), which can lead to decreased crop yields. Thus, understanding the response of functional diversity to environmental change could further enable us to understand and predict the consequences of land-use change on ecosystem functioning (Violle et al. 2007; Pillar et al. 2009; Winck et al. 2017).

Functional diversity can be calculated using different alpha diversty indices, namely functional richness (FRich), evenness (FEve), divergence (FDiv) (Mason et al. 2005), and Rao's quadratic entropy (RQ) (Sivadas et al. 2020). Rao's quadratic is an abundance-based approach, measuring the functional differences between species (Botta-Dukát 2005; de Bello et al. 2013; Gusmao et al. 2016). A high RQ value indicates that the community of species is functionally different, and deviates well above the mean trait composition of the community (Ricotta and Moretti 2011; Mouillot et al. 2013). Functional richness, FEve and FDiv are complementary (Villeger et al. 2008) and describe the distribution of species abundances within functional space (Mouchet et al. 2010). FRich defines how the species assemblage occupies the functional space (Mouchet et al. 2010). According to Mason et al. (2005), low FRich indicates that some potentially available niches are unused in the community which can significantly reduce productivity (Petchey 2003; Mason et al. 2005). In contrast, high FRich indicates a community with functionally unique species (Kuebbing et al. 2017). Nevertheless, studies on the change in functional diversity across ecosystems are still scarce (Bihn et al. 2010; Lohbeck et al. 2012), especially for soil fauna (Salmon and Ponge 2012; Salmon et al. 2014). Therefore, more studies on the response of soil fauna to biotic and abiotic conditions, along with fundamental studies on their traits are still needed (Abgrall et al. 2017).

Soil fauna play an important role within natural and agroecosystems (Wagg et al. 2014; Marsden et al. 2020), especially as their functions determine soil health (Kibblewhite et al. 2008). For example, the activity of detritivorous mesofauna such as Collembola play an important role in nutrient cycling, while ants are ecosystem engineers that play an important role in the maintenance of the soil structure (Jouquet et al. 2006; Marsden et al. 2020). As the taxonomic diversity of these taxa can be sensitive to changes in soil properties and micro-habitat characteristics (Bharti et al. 2013; Abgrall et al. 2017; Fichaux et al. 2019), functional diversity is also expected to be sensitive to these changes (Abgrall et al. 2017; Fichaux et al. 2019; Fontanilla et al. 2019). Functional traits are linked to species-specific preferences and tolerances of environmental conditions (Ekroos et al. 2013; Cadotte et al. 2015; Moretti et al. 2017). Therefore, we can expect species traits to vary across environmental gradients (Wright and Sutton-Grier 2012). Although studies have investigated changes in functional diversity of soil arthropods within agroecosystems (Martello et al. 2018; Marsden et al. 2020) or within natural systems (Fichaux et al. 2019; Fontanilla et al. 2019), very few studies have examined the change in functional diversity across both (Winck et al. 2017; Fichaux et al. 2019; Santoandré et al. 2019; Saifutdinov et al. 2020; Yin et al. 2020).

Here, I examine the change in taxonomic and functional alpha-diversity, as well as assemblage trait composition, of ants and springtails across a landscape mosaic comprising commercial exotic forestry compartments interspersed with remnant natural vegetation. Being of lower habitat complexity and diversity compared to natural systems, monocultures of large-scale timber compartments generally have negative effects on local biodiversity (Brockerhoff et al. 2008), although, they can contain some levels of diversity and offer additional habitat for species (Brockerhoff et al. 2008, 2013; Irwin et al. 2014). Ecological networks (ENs) are remnant corridors of natural vegetation that are conserved among the timber production areas and in South Africa consists primarily of grasslands and indigenous forests (Samways and Pryke 2016). Previous work within these ENs has shown aboveground taxonomic arthropod diversity (e.g. butterflies, dragonflies and grasshoppers) can be low within the plantation compartments (Pryke and Samways 2012a,b). In contrast, soil-based springtail and ants' alpha and beta diversity are relatively high within the plantation compartments relative to the natural areas (see Chapter 3). However, significant shifts in assemblage composition between transformed and untransformed areas suggest that plantations may still impact functional diversity and species traits, and so needs further investigation.

Understanding the response of soil arthropods to changes in environmental conditions and to which conditions they are most adapted to, can assist plantation managers in conservation and landscape planning, ensuring the continued presence and services these functionally important fauna provide within the soil ecosystem. Therefore, the first aim of this study is to determine if ant and springtail taxonomic and functional richness, change from natural (i.e., grasslands and indigenous forests) to transformed (i.e. eucalypt compartments) biotopes within an EN. As these landscape elements are structurally and environmentally different from that of timber plantations (Pryke and Samways 2001; Pryke and Samways 2012a,b; Eckert et al. 2019), it is expected that the taxonomic and functional richness of ants and springtails would be significantly different between these contrasting biotopes. As natural areas have higher environmental complexity, especially regarding their litter layer (Liu et al. 2016; Winck et al. 2017; Martello et al. 2018), offering greater niche space and resources to exploit

(Fowler et al. 2013; Santoandré et al. 2019; de Menezes and Schmidt 2020), I would expect both taxonomic and functional richness within the natural areas to be significantly higher compared to that in the plantation compartments.

The second aim of this study is to determine whether there are significant shifts in species-specific traits from these natural biotopes to the transformed biotope for ants and springtails. The third aim of this study is to determine whether there are traits that are species-specific and are highly associated to each biotope. Additionally, I would expect differences in environmental conditions to drive shifts in species traits between these biotopes, as part of environmental filtering (Gilbert and Lechowicz 2004; Santoandré et al. 2019). It is therefore expected that each of these biotopes would consist of species assemblages with specific traits that enable them to colonize or survive particular environmental conditions. For ants, I expect the grasslands would consist of species more adapted to open-habitat, less complex environments (i.e., large bodied, long femur length specimens), compared to closed-canopy, more complex environments (e.g. small bodied, short femur length specimens) (Farji-Brener et al. 2004; Wiescher et al. 2012; Gibb and Parr 2013). I also expect cooler environments to contain ant species of darker colour, whereas warmer environments will contain species of lighter colour, as a factor of thermoregulation (Gibb et al. 2015; Bishop et al. 2016). Additionally, I would expect to find omnivorous species to be dominant within the plantations, as species with unspecialized diets can have a wide range of habitat tolerance and are less sensitive to disturbances than species with specialized diets (Andersen 1995). When examining springtails, I would expect that specimens more adapted to simpler, more open environments, e.g. the grasslands, to be characterized by species that are adapted for above-ground surface living (i.e. larger bodies with well-developed furcas and pigmentation) (Salmon et al. 2014), whereas in more complex environments, e.g. the indigenous forests and eucalypt compartments, I would expect to find species that are more adapted for litter and below-ground surface living (i.e. smaller bodies with absence or reduction of eyes, furcas and pigmentation) (Salmon and Ponge et al. 2012; Salmon et al. 2014). Lastly, springtails with chewing or grinding mandibles are expected to dominate within the eucalypt compartments, as it is more associated with a generalist diet (Hoskins et al. 2015). In contrast, I would expect to find springtails with suctorial or piercing mandibles within the natural areas, as it is more associated with a specialist diet (Hoskins et al. 2015; Coulibaly et al. 2019).

4.2. Materials and methods

4.2.1. Study area and design

This study was conducted in two environmentally different geographical areas, namely the Midlands and Zululand (from here on referred to as regions) (Fig. 4.1), in KwaZulu-Natal, South Africa. The high contrast in environmental conditions such as elevation, vegetation, soil types, and topographical complexity between these two regions, allow for an assessment of the responses of soil arthropods to environmental gradients. Study sites were selected within three different biotopes (landscape elements), namely indigenous forest (Southern Mistbelt Forest in the Midlands; Northern Coastal Forest and Swamp Forest in Zululand), grassland (Midlands Mistbelt Grassland and Mooi River Highland Grassland in the Midlands; Maputaland Wooded Grassland and Maputaland Coastal Belt in Zululand) and eucalypt compartments (*Eucalyptus* spp.) across several plantation estates within each region (Mucina and Rutherford 2006) (Fig. 4.1). The plantation estates used in the Midlands were: Batchelors (30°09'12.77"S, 29°47'53.37"E), Cottingham (30°07'23.7"S, 29°47'14.49"E), Fabershill (29°40'13.3"S, 29°55'59.5"E), Harcourt (29°51'00.2"S, 30°10'36.1"E), Maybole (30°13'53.64"S, 29°44'8.95"E), Mkhuzane (29°49'33.9", 30°18'10.8"E) and Mount Shannon (29°41'11.8"S, 29°58'43.0"E) (Fig. 4.1A). For Zululand, plantation estates were Canewood (32°05'42.84"S, 28°37'56.52"E), Mcilrath (31°58'38.14"S, 28°42' 53.61"E), Montigny (32°11' 9.12"S, 28°35'41.9"E), Port Dunford (31°50'16.7"S, 28°53'30.92"E) and SiyaQhubeka Kwambonambi (32°10'27.06"S, 28°39'26.68"E) (Fig. 4.1B). Only plantation compartments in a mature growth stage were selected, i.e. > 6 years old. For each biotope type, 18 sites were selected to maximize on landscape variation, totaling to 108 sites (Fig. 4.1). Sites occurred within the elevation range of 917-1496 m a.s.l. in the Midlands, and 26-131 m a.s.l. in Zululand, with sites within the same biotope being > 250 m apart. Sampling was conducted in the summer months of these regions, January-February 2018 for Midlands and November-December 2018 for Zululand, when arthropods are most active.

4.2.2. Arthropod sampling and identification

Various sampling methods were used to ensure the greatest capture success. With pitfall trapping (Prasifka et al. 2007), four 300 ml plastic cups (9.5 cm diameter and 8 cm deep) were placed in a 2 m^2 grid at each site. The traps were placed with the rim of the trap level with the soil surface and filled with 50 ml of 60% ethylene glycol (containing a small amount of detergent to break the surface tension). Traps were left in the field for seven days, after which they were collected. Secondly, arthropods were collected using hand-collection (i.e. direct sampling) (Zanetti et al. 2016), which complement pitfall trapping by collecting arthropods which are not as readily captured by the pitfall trapping method (Mesibov et al. 1995). Within each site, a 1 m^2 quadrat was placed at random. Within the quadrat, the top 2 cm of the litter and soil was turned over to collect arthropods using an aspirator within these layers. This was conducted for 10 min by two people. Thirdly, arthropods were extracted from the soil using a modified Tullgren-Berlese extraction technique (Bird et al. 2004). At each site, 10 x 100 g subsamples were randomly collected and combined to form 1 L of soil, which was then

Figure 4.1 The focal plantation estates in a) the Midlands and b) Zululand, KwaZulu-Natal, South Africa. Illustrated are the study sites within indigenous forests (★), grasslands (◆) and eucalypt compartments (●). Plantation compartments (grey), non-plantation areas (white) and estate names indicated.

placed on top of a mesh (0.5 mm aperture size) and placed within a funnel. Below the funnel, a 130 ml plastic jar of 75% ethanol was attached. The soil samples were left for seven days within the funnel, allowing the soil to dry out and arthropods to be extracted into the attached jar. Specimens collected from all sampling methods were sorted into morphospecies (from here on referred to as ‘species’) and counted. Springtail specimens were identified by a taxonomic expert, while ants were identified to genus level using Hölldobler and Wilson (1990), Bolton (1994), Picker (2012), Fisher and Bolton (2016) and Slingsby (2017), and later verified by a taxonomic expert.

4.2.3. Functional traits

For this study, I divided the traits for ants and springtails into three categories: 1) morphological traits, 2) feeding strategy, and 3) habitat position (i.e., microhabitat occurrence). I also assessed patterns of separate taxonomic groupings, i.e., subfamily level for ants and family level for springtails, as some traits may have strong phylogenetic links. For ants, traits used in the analysis (Appendix M) were derived from the literature (eye size, habitat position, feeding strategy and subfamily) (Appendix N) or estimated in the laboratory (body length, femur length and darkness). For springtails, body length was measured in the laboratory, and all other traits (eye size, furca development, feeding strategy, habitat position and family) (Appendix O) were provided by the taxonomic expert based on available keys (Fjellberg 1998, Potapov 2001, Fjellberg 2007). Body length (ants and springtails) and femur length (ants) was measured using a Leica MZ7s dissecting microscope (Leica Microsystems, Germany). Where possible, six individuals per species were measured, and an average body length or femur length was calculated. For polymorphic ants, individuals of varying sizes were selected, and an average body length calculated for those species. The body length of each ant species was measured dorsally from the tip of the mandible to the tip of the gaster, whereas femur length was measured in anterior view as it is a good proxy for overall leg length (Queiroz et al. 2015), and only the hind femur was measured. Ant colour was examined by the same method proposed by Bishop et al. (2016), using HSV (hue, saturation and value). Here hue describes the dominant wavelength, saturation indicates the amount of hue present in the colour and the value sets the amount of light in the colour (Bishop et al. 2016). For this study, only lightness (v, or value, in HSV) is analyzed, ranging from 0-100, and a low V indicates a dark specimen, and a high V indicates a light specimen (pers. comm. T. Bishop). For springtails, body length measurements were taken either dorsally (species belonging to Poduromorpha) or laterally (species belonging to Entomobryomorpha and Symphypleona) from the tip of the mandible to the tip of the last abdominal segment. Appendages such as antennae, furcas and ovipositors were excluded in measurements for accuracy (Hódar 1996). Justification for traits included for this study can be seen in Table 4.1, and references thereof in Appendix N.

Table 4.1 Justification for springtail (Collembola) and ant (Formicidae) traits included in the analysis. Traits selected have either ecological or physiological significance.

Taxon	Trait	Description	Reference
Collembola	Body size	Correlated with dispersal ability, habitat preference and drought tolerance of the individual.	Berg et al. (1998) and Ponge et al. (2006)
	Furca development	The presence and size of the furca is correlated with the individual's dispersal ability and habitat preference.	Ponge et al. (2006) and Salmon et al. (2014)
	Eye size	Play a sensory role and is correlated with light sensitivity, habitat preference and defence against predators.	Hopkin (1997), Salmon et al. (2014) and Ruiz et al. (2017)
	Feeding strategy	Correlated with food preference. Type and size of mouthpart can restrict the type and size of resource that can be ingested.	Fjellberg (1985)
	Habitat position	Correlated with habitat preference, ecophysiology, and dispersal ability (i.e. euedaphic, hemiedaphic or atmobiotic)	Ponge et al. (2006)
	Family	Correlated with habitat preference, ecophysiology, dispersal ability and feeding habits of different families.	Ponge (2000) and Lensing et al. (2005)
Formicidae	Body size	Correlated with the dispersal ability, amount and type resources exploited and physiological/ecological tolerances, which is associated with habitat complexity.	Kaspari and Weiser (1999), Ness et al. (2004), Bihn et al. (2010), Arnan et al. (2013) and Bishop et al. (2015)
	Colour	Correlated with habitat preference and climate tolerance.	Bishop et al. (2016)
	Femur length	Correlated with dispersal ability, foraging efficiency and coping with foraging surface temperature, which is associated with habitat complexity	Feener et al. (1988), Kaspari and Weiser (1999), Weiser and Kaspari (2006), Bihn et al. (2010) and Guilherme et al. (2019).
	Eye size	Correlated with dispersal ability, feeding behaviour (when and where) and efficiency.	Weiser and Kaspari (2006) and Moretti et al. (2017)
	Feeding strategy	Correlated with type and size of food resource exploited.	Boet et al. (2020)
	Habitat position	Correlated with habitat/microclimatic preference and feeding behaviour (i.e. soil-, litter- or vegetation-dwelling)	Bihn et al. (2008)
	Family	Correlated with feeding habits and habitat preference	Samways (1983) and Sosiak and Barden (2021)

4.2.4. Biotic and abiotic environmental variables

To account for small-scale variations in soil parameters within each site, ten 100 g soil subsamples were collected at random and combined into a 1 L soil sample (i.e. the sample unit). From the sample unit, a 500 g sub-sample was taken (i.e. the representative sample) which was kept at room temperature and sent to a soil analytical laboratory (The Institute for Commercial Forestry Research; ICFR) for element analysis. From the representative sample, the following information was extracted: carbon (C), calcium (Ca), magnesium (Mg), nitrogen (N), phosphorus (P), potassium (K), sodium (Na) and sulphur (S). The Dumas combustion approach using a Leco Trumac CNS analyzer (Leco, USA) was used to analyze C, N and S, while the Bray II Phosphorus method was used to analyze P. Ca, K, Na and Mg was analyzed using an Agilent 4100 Microwave Plasma Atomic Emission Spectrometer (MP-AES) (Agilent, USA). Analysis was conducted by the Institute for Commercial Forestry Research (ICFR). Means (with standard deviations) of these soil elements are given in Appendix H for the Midlands, and Appendix I for Zululand. To record other biotic and abiotic variables at each site, a 1 m^2 quadrat was randomly placed three times and the average of these estimates were used in further analysis. These variables included vegetation height (m), vegetation cover (%), number of plant species, bare ground cover (%), leaf litter cover (%) and leaf litter depth (cm) and compositional characteristics (percentage of herbaceous, shrub and grass cover). The soil compaction, moisture and pH of each site was recorded using a soil penetrometer (Lang Penetrometer, Inc.) and a soil moisture and pH meter (Kelway, Inc.) within the quadrat. In a 5 m radius surrounding the quadrat (within 80 m^2), the amount of shade (%), deadwood cover (%) and rock cover (%) was estimated and recorded. Landscape variables including site elevation (m), site slope (°), site aspect (North or South-facing), terrain roughness (TR), terrain ruggedness index (TRI), amount of focal biotope (estimated as the percentage of the sampled biotope type in a 1 km radius around each site), and percentage transformed landscape (estimated as the percentage of plantation within a 1 km radius of each site) was calculated using QGIS (version 2.18.0) (QGIS Development Team 2009) and a Digital Elevation Model (DEM) of 1 m resolution. Within-site environmental variation is an important aspect to consider for biodiversity assessments (Lessard et al. 2011; Hansen et al. 2016a,b). However, as my study was conducted within a highly complex landscape consisting of different biotopes at a landscape-scale, emphasis was given more to habitat-level variation (i.e. between-site variation) rather than site-level variation (i.e. within-site variation), to gain baseline information regarding possible drivers of diversity within each biotope. Means with standard error (SE) and standard deviation (SD) of all recorded variables were calculated for the Midlands (Appendix H) and Zululand (Appendix I). Coefficient of variation (CV) (Reed et al. 2002), which is the standard deviation divided by the mean, was calculated for each environmental variable to determine the extent of variability in relation to the mean of environmental variables within a given biotope, with variables with CV < 1 indicating low variation and 1 < CV indicating high variation (Appendix H, I).

Table 4.2 Data normality, spatial autocorrelation, family distribution and model build results for each response variable for ants (Formicidae) and springtails (Collembola) in the Midlands and Zululand.

Group	Response variable	Data normality	Spatially autocorrelated	Family distribution	Model build
Midlands					
Formicidae	Species richness	No	Yes	Poisson	GLMM
	Shannon's entropy	No	Yes	Gamma	GLMM
	Functional richness	No	No	Gamma	GLM
	Rao's quadratic entropy	Yes	No	Gaussian	LM
Collembola	Species richness	Yes	No	Gaussian	LM
	Shannon's entropy	Yes	No	Gaussian	LM
	Functional richness	No	No	Gamma	GLM
	Rao's quadratic entropy	No	No	Gamma	GLM
Zululand					
Formicidae	Species richness	No	No	Poisson	GLM
	Shannon's entropy	Yes	No	Gaussian	LM
	Functional richness	No	No	Gamma	GLM
	Rao's quadratic entropy	Yes	No	Gaussian	LM
Collembola	Species richness	No	No	Poisson	GLM
	Shannon's entropy	No	No	Gamma	GLM
	Functional richness	Yes	No	Gaussian	LM
	Rao's quadratic entropy	Yes	No	Gaussian	LM

Model build: Linear models (LMs), generalized linear models (GLMs) or generalized linear mixed models (GLMMs).

4.2.5. Data analyses

Data analyses were performed separately for springtails and ants of each region, using pooled data from all sampling methods. Species accumulation curves were created for each arthropod taxon, separately per biotope and region, using the *iNEXT* package (Hsieh et al. 2019) (Appendix A) in R (version 3.6.3) (R Core Team 2016), to determine whether sampling was sufficient (Gotelli and Colwell 2001). Species richness estimators were calculated using the *fossil* package in R (Vavrek 2012). Chao2 and Jackknife2 were selected as they are suitable for estimating species diversity of highly diverse communities (Colwell and Coddington 1994). Ants collected are listed in Appendix C, and springtails in Appendix D.

4.2.5.1. Objective 1: Change in taxonomic and functional richness from plantation compartments to natural areas

Local species richness (SRich) was estimated for each site using morpho-species richness (from here on referred to as ‘species richness’). Functional richness (FRich) was calculated in R using the *dbFD* function of the *FD* package (Laliberte and Legendre 2010; Laliberte and Shipley 2011), whereas Shannon’s entopy (representing taxonomic evenness; ShanE) and Rao’s quadratic entropy (representing alpha-functional diversity; RQ) was calculated using *hillR* package in R (Li et al. 2014; Li 2018). Traits used for the calculation of FRich and RQ can be seen in Appendix M for ants and Appendix O for springtails. For SRich, ShanE, FRich and RQ, data normality distribution was assessed using Shapiro-Wilk tests using the *nortest* package in R (Gross and Gross 2009), and family distribution was assessed with the *car* and *MASS* packages in R using quantile-quantile plots (Fox et al. 2012; Ripley et al. 2013), and spatial autocorrelation was assessed based on Mantel tests using the *ade4* package in R (Dray and Dufour 2007). Linear models (LMs), generalized linear models (GLMs) or generalized linear mixed models (GLMMs) were then conducted using the *lme4* package (Bates et al. 2014) in R and post-hoc tests conducted using the *multcomp* package in R (Bretz et al. 2008). Model selection for each response variable can be seen in Table 4.2. Biotope type was included as a fixed parameter in all models and plantation estate as a random parameter within the GLMM models to account for spatial autocorrelation (Fig. 4.2). Plantation estate was sufficient as a random parameter, as based on plotted spline correlograms of model residuals after using the package *NCF* (Bjørnstad 2020), in the Midlands (Appendix P) and Zululand (Appendix Q). Boxplots were constructed using the *ggpubr* package (Kassambara 2017) in R.

4.2.5.2. Objective 2 and 3: Shifts in traits between biotopes and their associated traits

To determine the relationship between the traits of species and biotope type, a fourth-corner analysis (Dray and Legendre 2008; ter Braak et al. 2012) was conducted using a trait generalized linear model (traitglm) with the *mvabund* package (Wang et al. 2020) in R. These models were constructed using three data sets: an abundance matrix, biotope type matrix, and the trait matrix of the assemblage. The abundance matrix best fitted a negative binomial distribution. To account for species with a small number of individuals, all models included the LASSO penalty to reduce the trait-biotope association coefficients to 0 when the effects were small (Wang et al. 2020). The *lattice* package (Sarkar and Sarkar 2007) in R was used to visually show the relationship and its strength between a single trait and biotope type. Fourth-corner analysis was conducted separately for the following categories: morphological traits, feeding strategy, habitat preference and family/subfamily. Traits used within these analyses can be seen in Appendix M for ants and Appendix O for springtails. Analyses was conducted separately for springtails and ants for each region.

Table 4.3 Number of collected species (N) and species estimators Chao2 and Jacknife2 for ants (Formicidae) and springtails (Collembola) within each biotope type in the Midlands and Zululand.

	Formicidae			**Collembola**		
	N	**Chao2**	**Jacknife2**	**N**	**Chao2**	**Jacknife2**
Midlands						
Indigenous forests	24	30.25	27.99	50	54.65	56.00
Grasslands	75	112.56	102.99	57	65.45	72.00
Eucalypt compartments	33	37.00	39.98	64	100.45	87.97
Zululand						
Indigenous forest	56	68.03	67.99	25	49.00	29.98
Grassland	31	37.40	32.00	35	45.08	46.98
Eucalypt compartments	39	120.00	53.97	21	31.67	22.00

4.3. Results

Observed species richness of the different responses were similar to Chao2 and Jacknife2 species estimates, nearly reaching asymptotes in both regions (Table 4.3, Appendix A). Midland's samples consisted of 15 678 ant individuals, in 87 morphospecies belonging to 19 genera in 6 sub-families. Zululand samples consisted of 10 053 ant individuals, consisting of 74 morphospecies belonging to 25 genera in 6 sub-families. Regarding ants, *Tetramorium* (17 spp.), *Camponotus* (14 spp.), and *Crematogaster* (11 spp.) were the most speciose genera in the Midlands, while *Tetramorium* (12 spp.), *Camponotus* (7 spp.) and *Trichomyrmex* (6 spp.) were the most speciose genera in Zululand. For springtails, Midlands samples consisted of 63 719 individuals, in 87 morphospecies belonging to 11 families and 3 sub-orders. Zululand's samples consisted 5 119 springtail individuals, in 47 morphospecies belonging to 11 families and 3 sub-orders. Regarding springtails, Entomobryidae (44 spp.), Katiannidae (12 spp.) and Hypogastruridae (7 spp.) were the most speciose families in the Midlands, while Entomobryidae (27 spp.), Neanuridae (4 spp.) were the most speciose families in Zululand.

4.3.1. Objective 1: Effect of biotope type on taxonomic and functional richness

4.3.1.1. Formicidae

Ant SRich (χ^2 = 72.41, P < 0.001, df = 2) (Fig. 4.2A) and ShanE (χ^2 = 10.10, P = 0.006, df = 2) (Fig. 4.2B) was significantly different between biotopes in the Midlands, with grasslands having significantly more ant species compared to both the indigenous forests and eucalypt compartments. Ant SRich also differed significantly between biotopes in Zululand (χ^2 = 7.87, P < 0.001, df = 2) (Fig. 4.2A), with indigenous forests having significantly more ant species compared to both the grasslands and eucalypt compartments. ShanE in Zululand was also significantly different between biotopes ($F_{2, 51}$= 6.01, P = 0.005) (Fig. 4.2B), with indigenous forests being significantly higher from grasslands, but eucalypt compartments not differing from either indigenous forests or grasslands. Ant FRich in the Midlands differed significantly between biotopes (χ^2 = 4.37, P < 0.001, df = 2) (Fig. 4.2C), with eucalypt compartments being significantly lower than both indigenous forests and grasslands. In Zululand, no significant difference was found for ant FRich between biotopes (χ^2 = 0.72, P = 0.145, df = 2) (Fig. 4.2C). Ant RQ in the Midlands was significantly different between biotopes ($F_{2, 51}$= 24.95, P < 0.001) (Fig. 4.2D), being significantly higher within the indigenous forests compared to both the grasslands and eucalypt compartments. In Zululand, ant RQ also differed significantly between biotopes (χ^2 = 2.27, P = 0.002, df = 2) (Fig. 4.2D), with eucalypt compartments being significantly higher compared to the grasslands, while indigenous forests did not differ from either the grasslands or eucalypt compartments.

4.3.1.2. Collembola

Springtail SRich did not differ significantly between biotopes in the Midlands ($F_{2, 51}$= 0.71, P = 0.498) (Fig. 4.2A). Springtail SRich did differ between biotopes in Zululand (χ^2 = 7.32, P = 0.023, df = 2) (Fig. 4.2A), with grassland being significantly higher compared to the indigenous forests, while the eucalypt compartments did not differ from either the indigenous forests or grasslands. Springtail ShanE differed significantly between biotopes in the Midlands ($F_{2, 51}$= 3.20, P = 0.049) (Fig. 4.2B), with eucalypt compartments being significantly higher compared to the grasslands, while the indigenous forests did not differ significantly from either the grasslands or eucalypt compartments. Springtail ShanE did not differ significantly between biotopes in Zululand (χ^2 = 3.96, P = 0.138, df = 2) (Fig. 4.2B). Springtail FRich did not differ significantly between biotopes in the Midlands ($F_{2, 51}$= 2.32, P = 0.108) and Zululand ($F_{2, 51}$= 1.14, P = 0.327) (Fig. 4.2C). Springtail RQ was significantly different between biotopes in the Midlands (χ^2 = 2.27, P = 0.002, df = 2) (Fig. 4.2D), with indigenous forests being significantly higher than grasslands, but eucalypt compartments not differing from either grasslands or indigenous forests. No significant difference between biotopes were found in Zululand for springtail RQ ($F_{2, 51}$= 0.35, P = 0.709) (Fig. 4.2D).

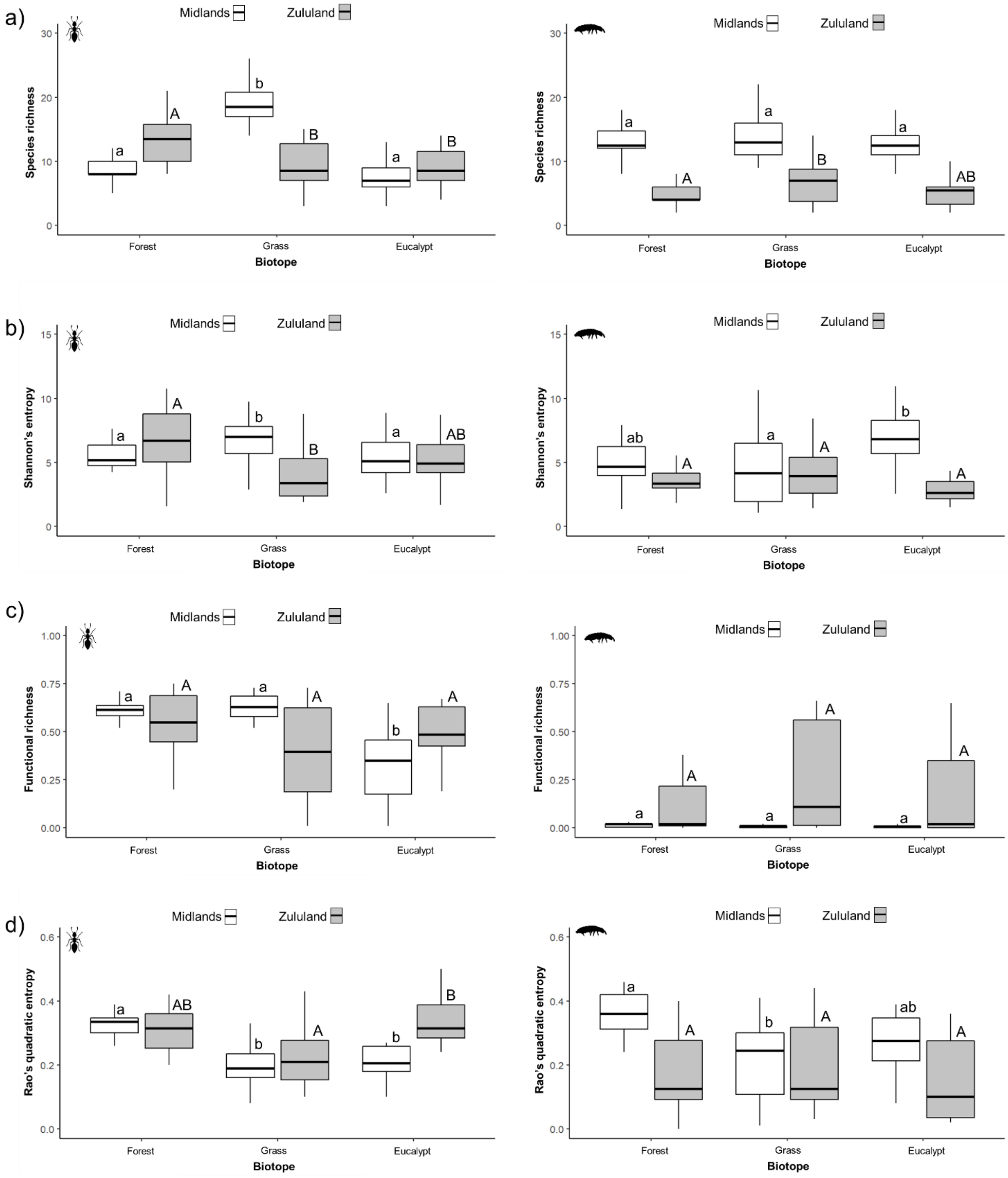

Figure 4.2 Boxplots with central horizontal line indicating the median value, the boxes indicating the interquartile range, and the whiskers indicating standard deviation within each biotope. Illustrated is the a) species richness (SRich), b) Shannon's entropy (ShanE), c) functional richness (FRich) and d) Rao's quadratic entropy (RQ) of ants and springtails in the Midlands and Zululand. Means with small letters for Midlands and capital letters for Zululand in common between biotopes, are not significantly different at $P < 0.05$.

4.3.2. Objective 2 and 3: Trait-association of Formicidae and Collembola to biotope type

4.3.2.1. Formicidae

Generally, specific taxonomic and trait associations with the biotopes varied between the two regions. However, there were clear shifts in trait composition between biotopes in both regions. In the Midlands, Proceratiinae was positively associated, while Dorylinae was negatively associated, with the eucalypt compartments (Fig. 4.3A). Ponerinae and Dorylinae was positively associated, while Formicinae was negatively associated, with the indigenous forests (Fig. 4.3A). Formicinae and Dolichoderinae was positively associated, while Proceratiinae and Ponerinae was negatively associated, with the grasslands (Fig. 4.3A). In Zululand, Ponerinae was positively associated with the eucalypt compartments (Fig. 4.3A). Proceratiinae and Dolichoderinae was positively associated, while Dorylinae was negatively associated, with the indigenous forests (Fig. 4.3A). Formicinae and Dorylinae was positively associated with the grasslands (Fig. 4.3A). Darker ants and those with reduced eyes were associated with the indigenous forests, while ants with longer legs but smaller bodies were associated with the eucalypt compartments in the Midlands (Fig. 4.3B). Ants of lighter colour and those with larger bodies and eyes that are present, were associated with the grasslands in the Midlands (Fig. 4.3B). In Zululand, ants with shorter legs, larger bodies and moderate eyes were associated with the eucalypts, while darker ants with larger eyes were associated with the indigenous forests (Fig. 4.3B). Ants of lighter colour, longer legs but smaller bodies were associated with the grasslands in Zululand (Fig. 4.3B). In the Midlands, predatory ants were associated with the indigenous forests and saprovores with the grasslands (Fig. 4.3C), while no association was found for the eucalypt compartments (Fig. 4.3B). In Zululand, predatory ants were associated with the eucalypt compartments and saprovores with the grasslands (Fig. 4.3C), while no association was found for the indigenous forests (Fig. 4.3B). Epigaeic litter-dwelling ants were associated with the indigenous forests, but negatively associated with the grasslands in the Midlands (Fig. 4.3D), while no association was found for the eucalypt compartments (Fig. 4.3D). In Zululand, epigaeic soil-dwelling ants were positively associated with the grasslands, but negatively associated with the indigenous forests (Fig. 4.3D), while no association was found for the eucalypt compartments (Fig. 4.3D).

4.3.2.2. Collembola

Sminthurididae, Neanuridae, Katiannidae, Hypogastruridae and Brachystomellidae were positively associated, while Sminthuridae, Odeontellidae, Isotomidae and Dicyrtomidae were negatively associated with the eucalypt compartments in the Midlands (Fig. 4.4A). Onychiuridae, Odontellidae and Entomobryidae were positively associated, while Neanuridae, Katiannidae and Hypogastruridae were negatively associated, with the indigenous forests in the Midlands (Fig. 4.4A). Sminthuridae and Isotomidae were positively associated, while Sminthurididae, Onychiuridae and Brachystomel-

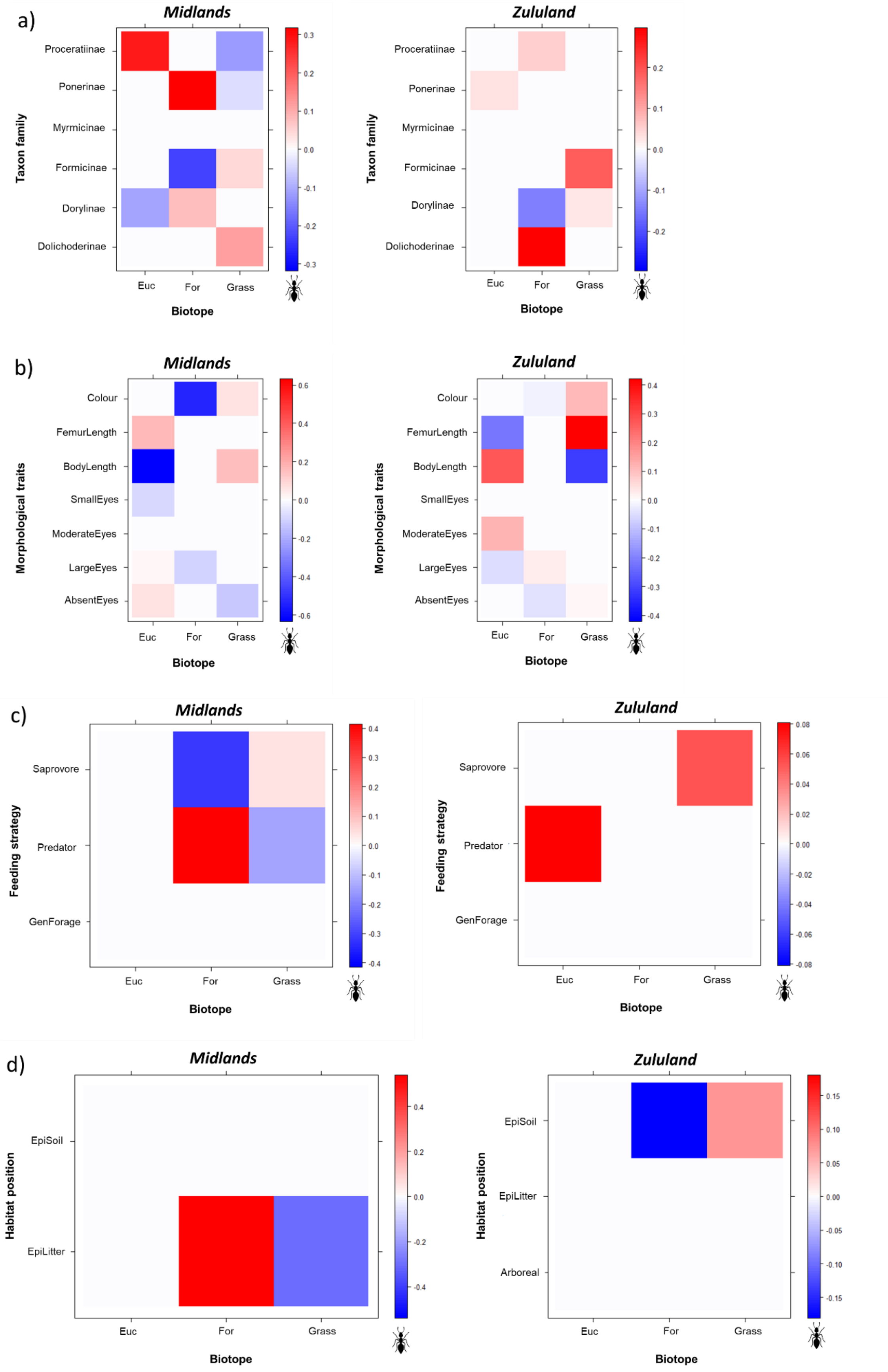

Figure 4.3 Fourth-corner analysis results of a) taxon family, b) morphological traits, c) feeding strategy and d) habitat position of ants in the Midlands and Zululand between indigenous forests (For), grasslands (Grass) and eucalypt compartments (Euc). Red indicates a positive association and blue indicates a negative association, with the colour intensity showing the strength of the relationship.

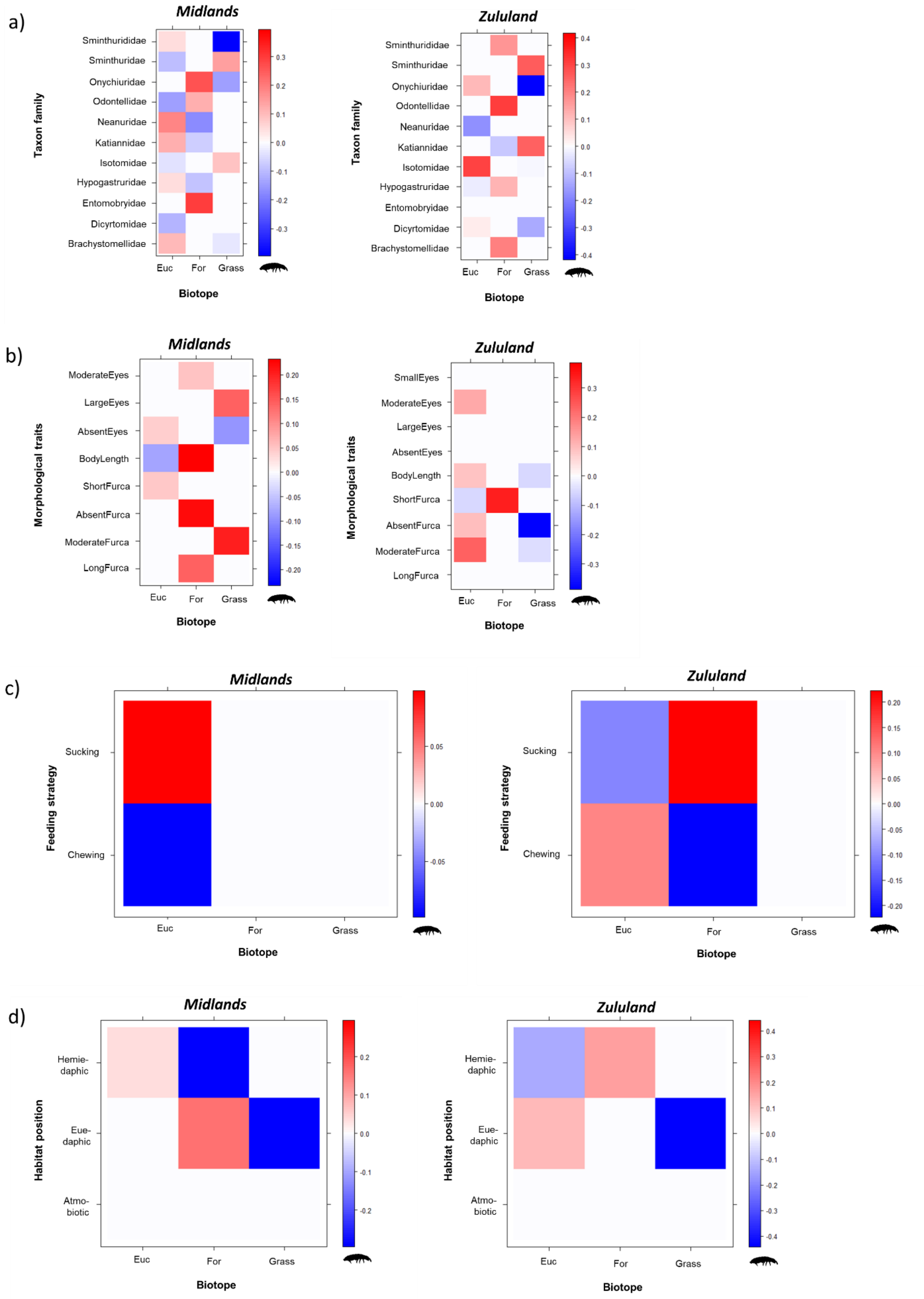

Figure 4.4 Fourth-corner analysis results of a) taxon family, b) morphological traits, c) feeding strategy and d) habitat position of springtails in the Midlands and Zululand between indigenous forests (For), grasslands (Grass) and eucalypt compartments (Euc). Red indicates a positive association and blue indicates a negative association, with the colour intensity showing the strength of the relationship.

mellidae were negatively associated, with the grasslands in the Midlands (Fig. 4.4A). Onychiuridae, Isotomidae and Dicyrtomidae were positively associated, while Neanuridae and Hypogastruridae were negatively associated, with the eucalypt compartments in Zululand (Fig. 4.4A). Sminthurididae, Odontellidae, Hypogastruridae and Brachystomellidae were positively associated, while Katiannidae were negatively associated, with the indigenous forests in Zululand (Fig. 4.4A). Sminthuridae, Katinannidae were positively associated, while Onychiuridae and Dicyrtomidae was negatively associated, with the grasslands in Zululand (Fig. 4.4A). Springtails with small bodies, short furcas and absent eyes were associated with the eucalypt compartments in the Midlands (Fig. 4.4B). Springtails with larger bodies, moderate eyes and larger/absent furcas were associated with the indigenous forests in the Midlands (Fig. 4.4B), while springtails with large eyes and moderate furcas were associated with the grasslands in the Midlands (Fig. 4.4B). Springtails with moderate eyes, larger bodies and absent/moderate furcas were associated with the eucalypt compartments in Zululand (Fig. 4.4B). Springtails with short furcas were associated with the indigenous forests in Zululand (Fig. 4.4B), while springtails with smaller bodies with furcas present were associated with the grasslands in Zululand (Fig. 4.4B). Springtails with sucking mouth parts were positively associated with the eucalypt compartments in the Midlands, and no associations found for the indigenous forests or grasslands (Fig. 4.4C). In Zululand, springtails with chewing mouth parts were associated with the eucalypt compartments, and springtails with sucking mouth parts associated with the indigenous forests (Fig. 4.4C). No association was found for the grasslands in Zululand (Fig. 4.4C). Hemidaphic springtails were postively associated with the eucalypt compartments, but negatively associated with the indigenous forests in the Midlands (Fig. 4.4D). Futhermore, euedaphic springtails were positively associated with the indigenous forests, but negatively associated with the grasslands in the Midlands (Fig. 4.4D). In Zululand, hemiedaphic springtails were positively associated with the indigenous forests, but negatively associated with the eucalypt compartments (Fig. 4.4D). Furthermore, euedaphic springtails were positively associated with the eucalypt compartments, but negatively associated with the grasslands in Zululand (Fig. 4.4D).

4.4. Discussion

4.4.1. Objective 1: Taxonomic and functional alpha-diversity in contrasting biotopes

Biological homogenization (i.e. increased similarity of species composition between sites; lower β-diversity) is a major conservation concern (Olden and Rooney 2006; Mitchell et al. 2015). In the previous chapter, I showed that in general, plantations have high levels of alpha- and beta-diversity, as well as major compositional changes between natural and transformed biotopes (Chapter 3). However, of conservation concern is functional homogenization (i.e. increased similarity of species functional traits between sites), as species functional traits have a greater link to ecosystem functioning, such as productivity (Hooper et al. 2005), compared to the taxonomic identities of species (Cadotte et al. 2011; Mori et al. 2013; Mori et al. 2015). The loss of functionally unique species results in lower functional diversity which may decrease ecosystem stability (Bregman et al. 2016) and have severe effects on the functioning of the ecosystem (Cardinale et al. 2006).

Taxonomic and/or functional alpha-diversity is generally higher within more heterogeneous, diverse systems, such as indigenous forests (Ponge et al. 2003; da Silva et al. 2016; Winck et al. 2017). However, my results show that *Eucalyptus* plantations can harbour similar levels compared to either indigenous forests or grasslands (or in some cases both) for ants and springtails, even though it is a transformed and relatively homogenous system. Winck et al. (2017) reported similar results, with functional diversity of springtails being significantly higher within the indigenous forests, with grasslands and eucalypts showing no difference, although assemblage compositions can still differ (Winck et al. 2017; Chapter 3). These findings support the hypothesis that communities respond to habitat complexity (i.e. in terms of biotic and abiotic factors) which lead to trait convergence or divergence within different land-use systems (Winck et al. 2017). Furthermore, based on my findings, the *Eucalyptus* plantations in this study are performing well in terms of their taxonomic and functional diversity compared to the indigenous forests and grasslands, in most cases, indicating potentially good ecosystem stability and functioning. However, the question remains, what are the functional traits that enable species to persist within these contrasting biotopes?

4.4.2. Objective 2 and 3: Functional trait adaptions in contrasting biotopes

Within similar biotope types, but contrasting regions, significant shifts in both ant and springtail traits occurred. Zululand has a sub-tropical climate, with high humidity and annual temperatures (Fairbanks et al. 2001; Viero 2007), whereas the Midlands have a temperate climate and lower annual temperatures (Fairbanks et al. 2001). Additionally, heavy mist frequently occurs in the Midlands, providing additional moisture within the area (Fairbanks et al. 2001; Mucina and Rutherford 2006). Additionally, the less complex landscape topography in Zululand contrasts to the highly complex landscape topography in the Midlands (Bazelet and Samways 2012). Lastly, soil type can also have significant effects on soil arthropod assemblages (Boulton et al. 2005; Andersen et al. 2015; Oliveira et al. 2017). As the Midlands have humic soils that are deep and nutrient rich compared to the shallow, nutrient poor sandy soils in Zululand, soil type may have also contributed to shifts in species traits. The collective differences in the above-mentioned factors, therefore, may contribute to environmental and microclimate variances that favour a completely different set of traits within similar biotopes, but in different regions.

Studies have shown habitat complexity can act as a filter and select species compositions based on their morphological traits (Gibb and Parr 2013). Species persistence in each environment is regulated by the compatibility of the species' traits to the environmental conditions therein (Wiescher et al. 2012). Environmental filtering can therefore hinder the persistence or establishment of certain species under specific environmental conditions (Keddy 1992), resulting in species traits becoming divergent (e.g. in different habitats) (Schofield et al. 2016) or convergent (e.g. in similar habitats) (Salmon et al. 2014). The fitness of the species is therefore regulated by its traits, whether morphological or physiological, which in turn can have significant impacts on the functioning of the ecosystem (Petchy and Gaston 2006). For this study, it should be noted that I focussed only on between-site environmental variation, within each biotope, as a possible driver of shifts in morphological and physiological traits. Here, due to the complex nature of environmental conditions between biotopes at landscape-scale, the idea was to gain baseline information regarding possible drivers of trait divergence/convergence between biotopes. I therefore recognize that within-site variation in environmental conditions could also have played an important role (Lessard et al. 2011; Hansen et al. 2016a,b), and should thus also be considered in future studies. It is therefore recommended that future research focus on environmental variation (within and between sites) to determine which environmental factors are responsible for shifts in species assemblages (and their respective traits) and under which conditions they persist.

4.4.2.1. Formicidae

At sub-family level, ant morphological characteristics and habitat preferences can differ significantly (Fisher and Bolton 2016). A common observation in ant trait-based approach studies, is that in a cooler, closed-canopy environment, individuals are larger and darker in colour, whereas the opposite is observed in warmer, open environments (Clusella-Trullas et al. 2008; Gibb and Parr 2013; Gibb et al. 2015). Body size and colour are partly related to thermoregulation, as larger bodies enable organisms to lose heat slower than smaller bodied organisms, while darker coloured organisms heat up faster compared to lighter coloured organisms (Bishop et al. 2016; Spicer et al. 2017). My results concord with these findings in several instances, e.g. ants in the indigenous forests were darker than in grassland in the Midlands and Zululand. Regarding femur length, several studies suggest ground cover complexity (in terms of vegetation, bare and leaf litter cover) is correlated to femur lengths (Kaspari and Weiser 1999; Parr et al. 2003; Wiescher et al. 2012), with shorter femur lengths expected in more complex environments. I found strong shifts in femur lengths and body size within the eucalypts, between regions. In the Midlands, ants with long legs and smaller bodies were associated with the eucalypt compartments, whereas in Zululand ants with short legs but larger bodies were associated with the eucalypt compartments. This may have resulted from variations in environmental conditions between the regions and a need for higher mobility in the Midlands *Eucalyptus* compartments. For example, the eucalypt compartments in Zululand has lower litter cover but more shade cover, whereas the opposite was found for the Midlands (Appendix H, I). Additionally, ants in the grasslands of Zululand had longer legs, but no association to grasslands were found in the Midlands. This may also reflect the environmental differences between the two regions (Appendix H, I), resulting in differential adaptions for each environment. Gibb and Parr (2013) also observed shorter and longer femur lengths in complex and simpler environments, respectively. Shifts in morphological traits link with the shifts in habitat position, i.e. where the ants occur. As smaller bodies are more beneficial in more complex environments (Farji-Brener et al. 2004), the reduction in body size and the association of epigaeic litter dwelling ants in indigenous forests and not the grasslands in the Midlands, may be linked to the high leaf litter cover within this biotope. Additionally, the environmental conditions in Zululand relating to moisture, vegetation and litter cover may have been favourable to epigaeic soil ants in the grasslands. Surprisingly, in both regions, there was no strong association between biotope type and habitat position (i.e. microhabitat occurrence) for ants within the eucalypt compartments.

Generalist foraging ants dominate in grassland systems (Wills and Landis 2018). As grasslands are structurally less complex, have no tree canopy cover, and experience burning as part of the management regime (Bazelet and Samways 2012), generalist foraging ants would be better adapted for these conditions than ants with more specialized diets. Species with unspecialized diets can have a wide range of habitat tolerance, and are less sensitive to disturbances than species with specialized diets (Andersen 1995). However, I found saprovores dominated in both regions within the grasslands. In contrast, complex environments can provide a greater variety of resources to exploit (Pacheco and Vasconcelos 2012), with lower inter-annual disturbance. Here, predatory ants were associated with the indigenous forests and eucalypt compartments in the Midlands and Zululand, respectively. Although indigenous forests and eucalypt compartments may be physically similar in terms of presence of canopy cover, other habitat conditions may have been more favourable in the eucalypt compartments than the indigenous forests in Zululand. For example, the lower soil moisture content and higher leaf litter cover within the eucalypts may have provided a more suitable habitat and resources to exploit compared to the indigenous forest.

4.4.2.2. Collembola

Morphological characteristics also differ significantly between springtail families (Hopkin 1997), and are often used to determine the habitat position of springtails, i.e. where the specimen occurs (Gisin 1943). Generally, springtails in simpler, more open environments (such as grasslands) are characterized with larger bodies with well-developed eyes and furcas (Kærsgaard et al. 2004; Salmon et al. 2014), aiding in predator detection and avoidance. In contrast, springtails in more complex, closed environments (such as woodlands) are characterized with smaller bodies, absence or reduction of eyes and furcas (Salmon and Ponge et al. 2012; Salmon et al. 2014). Body size is linked with protection against desiccation and frost (Kærsgaard et al. 2004; Bokhorst et al. 2012), with larger bodies being better adapted to surface living and is more protected against these factors. Surface-dwelling species are well adapted for environmental conditions aboveground as the soil conditions can be more variable and often drier than below ground (Makkonen et al. 2011). Therefore, surface-dwelling species have higher desiccation resistance and are more drought-tolerant than belowground euedaphic species (Kærsgaard et al. 2004; Makkonen et al. 2011). Observations from these studies correspond with the habitat position (i.e. life-form) traits of springtails in both regions from this study. Here, when purely examining life-forms (i.e. eudaphic, hemiedaphic or atmobiotic), it is clear that springtails associated with subterranean life, i.e. eudaphic species, are not associated with the grasslands, in either the Midlands and Zululand, whereas eudaphic or hemiedaphic species are more associated with the indigenous forests and eucalypt compartments. Environmental conditions between these contrasting biotopes may have explained this (Appendix H, I), as they may have offered differential suitable conditions and resources for the life-forms to persist in and exploit.

However, in terms of morphological traits and phylogeny, my findings do not correspond with other studies as mentioned above. For example, larger bodied springtails were associated with the indigenous forest biotope, smaller bodied springtails were associated with the eucalypt compartments and showed no association was found for the grassland in the Midlands. In contrast, larger bodied springtails were associated with the eucalypt compartments, smaller bodied springtails associated with the grasslands and no association was found for the indigenous forest in Zululand. A possible reason for the contrast in my findings to other studies, is that the majority of the springtails collected consisted of Entomobryomorpha and Symphypleona, with the minority consisting of Poduromorpha (Appendix D). Entomobryomorpha and Symphypleona are more litter- or vegetation-dwelling, whereas Poduromorpha are mainly soil-dwelling (Orgiazzi et al. 2016). Additionally, the environmental variation within- and between-sites may have contributed to the contrast in findings of my study to others. Santoandré et al. (2019) suggested that environmental gradients lead to changes in species identities, which are coupled with changes in their functional characteristics. In other words, environmental filtering suggests that environmental conditions may lead to the exclusion of species with traits poorly adapted to a specific environment (Cornwell et al. 2006; Santoandré et al. 2019). The fact that traits showed contrasting patterns between the regions, highlight that most traits are regionally-dependent, resulting in assemblages with very distinct assemblages. In this case, environmental filtering within each region may have played a role by offering very different conditions, which resulted in species trait shifts that are not commonly observed. I therefore highly recommend further examination on the effects of within- and between-site environmental variation, especially between contrasting regions, on species-specific shifts and adaptations. This could further enable an understanding the consequences of environmental change on species assemblages, and in turn, possible ecosystem functioning (Winck et al. 2017).

Of all the morphological traits, phylogeny is a poor proxy for mandibular traits (Malcicka et al. 2017; Raymond-Leonard et al. 2019), as taxonomically close species can have very different mandible structures, and taxonomically distant species can have similar mandible structures. Additionally, mandibular traits are more often associated with resource availability, distribution and quality, and less with habitat preferences (Holmstrup et al. 2018; Brousseau et al. 2019; Raymond-Leonard et al. 2019). Chewing/grinding mandibles are associated with a generalist diet (Hoskins et al. 2015), and can consist of harder items such as plant tissue and leaf litter (Dellinger and Day 2017; Malcicka et al. 2017), whereas suctorial/piercing mandibles are associated with feeding on liquids (Hopkin 1997; Berg et al. 2004) from micro-organisms such as fungi, mould, lichens, or bacteria (Jørgensen et al. 2005; Hoskins et al. 2015; Coulibaly et al. 2019). Leaf litter layer not only offers protection against predation (Hossie and Murray 2010), but also offers a greater variety of food resources for springtails (Salmon and Ponge 2001). However, I found springtails with suctorial/piercing mandibles to be positively associated with the *Eucalyptus* plantations in the Midlands, and positively associated with the indigenous forests in Zululand. Additionally, springtails with chewing mandibles were positively associated with the eucalypt compartments in Zululand. Therefore, I suspect that leaf litter cover may not have been a contributing factor to these shifts, and other factors may have played a more important role in providing the optimal conditions for resource availability and quality. For example, Erlandson et al. (2016) found that soil fungal species richness positively correlated with soil phosphorus, and community composition is strongly affected by soil moisture and pH. Suctorial/piercing mandibles may have been more positively associated to these biotopes as environmental conditions, such as soil phosphorus content, which favour fungal growth and provide optimal resource availability, benefitting the fungal feeding species (Fujii and Takeda 2012). In contrast, the lower soil phosphorus content within the indigenous forests in Midlands, may have limited fungal growth and so hinder the presence of springtails with suctorial/piercing mandibles.

4.5. Conclusion

Although plantations are structurally and environmentally less complex compared to natural systems at a large scale (Fayle et al. 2010; Wang and Foster 2015), environmental heterogeneity at smaller scale can still be high within the plantations (e.g. in terms of soil conditions) (Appendix H, I), which may be beneficial to soil biodiversity. From a taxonomic and functional point of view, *Eucalyptus* plantations are seemingly performing as well as the indigenous forests and grasslands. In some cases, the *Eucalyptus* plantations had similar values of taxonomic and functional diversity to both the indigenous forests and grasslands. This indicates that ecosystem stability and functioning may be high in these *Eucalyptus* plantations. Therefore, although these landscape elements (i.e. the natural areas and the plantation compartments) are environmentally different (Appendix H, I), they can be seen as an agro-ecological land mosaic, consisting of various environmental conditions suitable for different sets of soil arthropods, which contributing to overall landscape biodiversity.

This chapter further demonstrates a key reason for this high diversity, i.e. that certain traits allow a variety of species to persist in the transformed biotopes. I show that variations in environmental conditions within contrasting biotopes and regions are driving trait divergence. Environmental filtering may be allowing species with a unique set of traits to persist within these environments, while others are excluded. Some species were favoured by conditions within the *Eucalyptus* plantations, whereas others were favoured by the conditions within the indigenous forests or grasslands. Additionally, shifts in traits were highly regionally-dependent. As the effects of environmental variation between regions, along with within- and between-site environmental variation amongst biotopes, were not assessed within this study, I highly recommended further examination into this concept, which will aid in understanding the mechanisms behind species trait shifts, which may possibly lead to altered ecosystem processes.

Having natural, non-crop areas within an agricultural system may be beneficial for not only providing suitable refuge habitat for common species, but also for specialized species with habitat-specific requirements (Dauber and Wolters 2005), increasing not only species diversity across the landscape, but also functional diversity. Similar findings have been reported for ecological network-plantation landscape mosaics for arthropods such as dragonflies, butterflies, grasshoppers, spiders and beetles (Pryke and Samways 2012a,b; Kietzka et al. 2015). Here, I show that these remnant natural vegetation types interspersed between the plantations are also beneficial for increasing soil arthropod taxonomic and functional diversity, highlighting the importance of the ecological networks for conserving soil taxonomic diversity, but also functional diversity, which is important for the stability, resilience and functioning of these soil ecosystems. Furthermore, I show that these contrasting biotopes within the landscape can contain soil arthropod communities with very distinct functional traits adapted to survive and persist within these different environments.

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CHAPTER 5

Arthropod diversity and activity in nutrient-rich clay soils when subjected to various timber slash management practices

Abstract

To sustainably manage soils, we need to understand the impact that management practices have on soil biota. One of the greatest disturbances in commercial tree plantations is management of woody residue that remains *in situ* after harvesting. I examine the impact of different harvest residue management practices on soil biota in a timber production landscape in KwaZulu-Natal, South Africa on nutrient-rich high-resilience clay soils. I assess four different management practices and an unmanaged grassland control in a replicated experiment, at three time periods: prior to implementation of residue management, directly after implementation, and one year after implementation. Management practices include 1) on-site retention of residue, 2) removal of residue, 3) stacking and burning of residue (high intensity burn due to high fuel loads), and 4) spreading and burning of residue (low intensity burn due to lower fuel loads). I examine ant and springtail taxonomic diversity (Shannon's entropy; ShanE), and functional diversity (Rao's quadratic entropy; RQ), and soil biological activity. Overall, biological activity was higher in grasslands than in plantations. However, there was no difference in faunal diversity among the four management treatments at any time, although assemblage composition changed significantly across all sites over time. Biological activity declined post-treatment, although recovered up to 50% in the plantations one year later. There were no differences in overall biological activity, or in activity at different soil depths among management treatments at any time. Thus, soil biota responded similarly between treatments regardless of major treatment differences.

Keywords: Collembola, Formicidae, Eucalyptus, Residue management, Silviculture, Soil health

5.1. Introduction

Sustainable agriculture requires greater attention to the soil, with increased efforts towards improving or maintaining soil health (Maharjan et al. 2020). A critical aspect of maintaining soil health is to preserve soil biodiversity (Karlen 2012). Soil biota can have a direct impact on agricultural productivity and ecosystem services (Hou et al. 2020), such as nutrient and organic matter cycling (Maisto et al. 2017). Management practices that are detrimental to the functioning of the soil should be avoided, and needs to be sustainable, allowing both resilience and persistence of the system (Butler et al. 2007; Cardinale et al. 2012; Garibaldi et al. 2017). Timber plantations are intensively managed during certain periods of the timber rotation (Brockerhoff et al. 2008). There is therefore a need to understand the impacts of a wide range of management practices, starting from harvesting until the canopy closes (Smith and du Toit 2005).

A rotation is defined as the period between the establishment of new seedlings until the final harvest (Sappi 2017). The rotation starts by planting seedlings, followed by weed management (Sappi 2017;

Little et al. 2018). Weed management occurs in the first three years of establishment, and is done manually or chemically (Seifert et al. 2007). Thereafter, tree thinning (Esteban et al. 2020; Tavankar et al. 2020) can also occur until canopy closure to remove smaller, poor-quality trees and to reduce tree density, giving better growing conditions for better performance (Ferraz Filho et al. 2018; Esteban et al. 2020; Tavankar et al. 2020). The compartment then remains undisturbed until harvesting, occurring between 15-22 years for *Pinus* and 7-10 years for *Eucalyptus* species in South Africa, depending on the region of occurrence and harvesting product (pulpwood or saw logs) (Mondi 2007). The harvesting of timber can be done mechanically, or manually with chainsaws (Moskalik et al. 2017; Labelle and Lemmer 2019), with the latter currently being less frequently used than in the past (Ackerman and Upfold 2017; Labelle and Lemmer 2019). Today, mechanical harvesting is mostly practiced for increased productivity (Liepiņš et al. 2015) through lower time consumption rates (van Wyk 2018; Labelle and Lemmer 2019) and improved worker safety (Bell 2002; Gerasimov and Sokolov 2014; van Wyk 2018). The harvesting of timber alone can change environmental factors such as the microclimate and structure, as well as quality and quantity of the leaf litter (Edlund et al. 2013). However, site preparation for the next rotation can have further significant effects on the soil environment (Ballard 2000). An important component of this is the management of non-utilizable tree biomass (residue or slash) which remains after harvesting, which includes treetops, branches, twigs, bark, and needles/leaves.

Residue management is important as it can increase site access, increase planting success, and reduce fire risk (Ackerman and Upfold 2017; Sappi 2017). In addition, residue management can also be seen as nutrient management (Skovsgaard et al. 2021), which is important for the long-term sustainability of the timber compartment. Harvest residue can be managed in several ways, depending on site characteristics (including slope and soil type) and weather conditions (Sappi 2017). One method is the removal of harvest residue for bioenergy production (Grodsky et al. 2018). However, this method can have negative effects on the site's productivity, as it leads to decreased nutrient availability (du Toit and Scholes 2002; Saint-André et al. 2008; Dovey 2009). Short-term productivity of a site can therefore be compromised by residue removal, compared to other residue management practices such as the retention or burning of residue (Gonçalves et al. 2007). The retention of residue post-harvest is recommended, as it can help retain nutrients and aid in minimizing soil and water loss (Forestry South Africa 2019), while offering more slow-release nutrients (Li et al. 2018, 2020). Furthermore, fire is often used as a silvicultural management tool (Arno 1996; Grigal 2000), although best practice guidelines recommend using only cool to moderate intensity burns when conditions permit its implementation. Yet, fires can have large effects on the site's productivity (Grigal 2000). The severity of a fire event at a site depends on the intensity of the fire, the fuel load, soil type and moisture content, the slope of the site, and the area burned (Neary et al. 1999; Certini 2005). Furthermore, depending on the severity of the fire, soil properties, both physical and chemical, can experience short-term, long-term, or permanent changes (Certini 2005). Through means of mechanized harvesting, harvest residue generally remains as an evenly spread layer on the soil surface after harvesting (Mendham et al. 2003; Kumaraswamy et al. 2014). This is a fire risk, and therefore the residue needs to be burned under a controlled environment to prepare the compartment for the next plantation rotation. As such, broadcast burning (i.e. prescribed cool to moderate intensity fire across the entire compartment) is implemented (Page-Dumroese et al. 2017). However, this type of burning method is often limited by factors such as fire complexity (i.e. unpredictable fire behavior, intensity and severity due to fuel load), weather conditions, increased risk, and the need for expertise (Wright et al. 2010; Page-Dumroese et al. 2017). Therefore, the piling and burning of residue is often practiced (Page-Dumroese et al. 2017; Mott et al. 2021), requiring a smaller work force which decreases fire safety risks (Wright et al. 2010). Thus, land managers can burn larger quantities of residue under more controlled environments using the pile-burning method in comparison to the broadcast-burning method (Korb et al. 2004). However, the piling and burning of residue can have localized soil impacts which can be short- or long-term in duration (Korb et al. 2004; Page-Dumroese et al. 2017).

To assess the effect of management practices, land managers need to assess changes in soil quality and functioning using tools that are cost- and time-efficient as well as easily applied (Bai et al. 2018). The effects of management practices on the chemical or physical (Ballard 2000; Norström et al. 2012; Scheepers and du Toit 2016; Venanzi et al. 2016) components of the soil have received much greater attention compared to the biological component (Gongalsky et al. 2012; Puga et al. 2017). Yet soil biota are excellent indicators of soil quality, as they respond rapidly to anthropogenic disturbances (Paz-Ferreiro et al. 2007). In addition to using taxonomic groups as indicators of soil condition, the bait laminae method developed by Von Törne (1990) is a standard international test (Römbke et al. 2006) to measure soil quality. This method can be applied under various environmental conditions (Kratz 1998) and is used to measure the feeding activity of a wide variety of soil arthropods (Jänsch et al. 2017), including taxa such as earthworms, termites, and micro-organisms (Helling et al. 1998; Van Gestel et al. 2003; Römbke et al. 2006). The bait laminae method has been applied in several studies under natural conditions (Hamel et al. 2007; Birkhofer et al. 2011; Klimek et al. 2015) or to examine its response to management practices in agricultural systems (Diekötter et al. 2010; Rożen et al. 2010; Podgaiski et al. 2014). It has the additional capability for measuring feeding activity at different soil depths, allowing for a more three-dimensional assessment of impacts on the soil. It therefore a useful tool for monitoring soil health in timber production landscapes.

This study aims to determine how different residue management practices after tree harvesting operations influence soil faunal diversity and soil biological activity within a timber production landscape. To do this, I conduct a field-based experiment of replicated harvest residue treatments in a 6.43 ha timber compartment. Four different residue management treatments that are commonly used within the industry are examined: 1) on-site retention of unburned harvest residue, representing the greatest amount of fresh organic matter (retention), 2) stacking and burning of residue, representing a high intensity burn (stacking), 3) complete removal of residue (removal), and 4) burning of remaining, evenly spread residue after harvesting, representing a low intensity burn (spread). The objectives of this study are 1) to determine which residue treatment has the most severe impact on ant and springtail taxonomic and functional alpha-diversity directly after the implementation, and to examine which treatment allows for greatest short-term recovery in ant and springtail taxonomic and functional alpha-diversity a year after implementation, 2) how soil biological activity is influenced by the residue management treatments at different soil depths directly after the implementation, and to examine which treatment allows for greatest short-term recovery in soil biological activity a year after implementation and 3) to determine how ant and springtail assemblage composition differs amongst the residue management treatments, and to examine which treatment allows for the assemblage structure to become most similar to the initial assemblage a year after implementation. Here, I expect residue management treatments which include burning to have the most severe effect on arthropod assemblages which reside in the topsoil and litter layers, as opposed to treatments which do not include the use of fire. These predictions are based on previous studies showing differential responses of arthropods to fire that result from community differences in their physiology, dispersal capabilities and/or habitat requirements (Bengtsson 2002; Gongalsky et al. 2012; Zaitsev et al. 2014) and that arthropods within the topsoil and litter layer can be more severely affected by fire than those residing within the deeper layers of the soil (Zaitsev et al. 2014; Korobushkin et al. 2017). Similar findings are therefore also expected for soil biological activity within this study, as biological activity can be negatively affected where burning occurs (Santana et al. 2018). Determining the best residue management practice would be valuable for land managers for promoting soil function through sustainable management of soil for the long-term.

5.2. Materials and methods

5.2.1. Study area and design

This study was conducted on Inverness estate (29°09'29.99"S, 30°23'22.62"E) in KwaZulu-Natal, South Africa (Fig. 5.1A), which consists of a mosaic of commercial eucalypt plantations and grassland conservation corridors (Fig. 5.1B). Eight reference sites were selected in a nearby grassland conservation corridor to assess variation in arthropod diversity and biological activity over

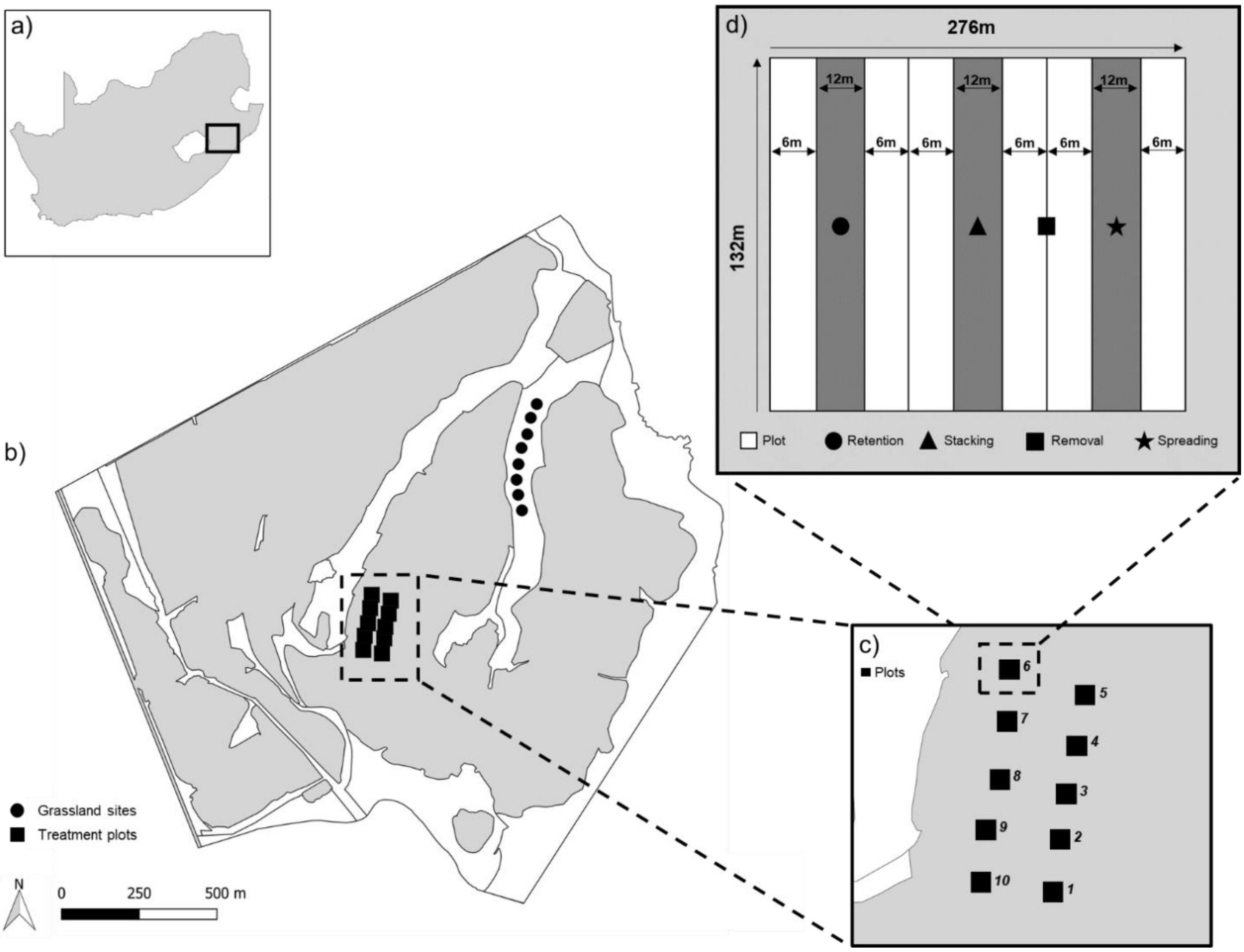

Figure 5.1 The focal plantation estate Inverness in KwaZulu-Natal, South Africa (a). Illustrated are the treatment plots (■) and grassland reference sites (●) within the estate (b). Plantation compartments (grey), non-plantation areas (white) and estate names indicated. A treatment plot was replicated ten times within the plantation compartment (c), each containing four different residue management practices (d).

the sampling period due to natural seasonal fluctuation (Fig. 5.1B). Within a timber compartment (which was 6.43 ha), ten plots were used to replicate residue management treatments (Fig. 5.1C, D). A plot was 132 m wide and 276 m long (Fig. 5.1D). Each plot contained four different residue management treatments, including: 1) retention of residue after harvesting (from here on referred to as the retention treatment), 2) stacking and burning of residue after harvesting (from here on referred to as the stacking treatment), 3) complete removal of residue after harvesting (from here on referred to as the removal treatment), and 4) burning of residue as it remained after harvesting (from here on referred to as the spread treatment) (Fig. 5.1D). In total, this gave ten sites per treatment and eight sites for the grassland control. Sampling was conducted over three sampling events: prior to harvesting of compartment (January 2019), one month after harvesting and implementation of the management treatments (August 2019) and after one year (February 2020), to monitor the short-term effects of each residue management treatment.

5.2.2. Arthropod collection and identification

At each site, arthropods were collected using the pitfall trapping method (Prasifka et al. 2007) and the Tullgren-Berlese extraction technique (Bird et al. 2004). For pitfall trapping, four 300 ml plastic cups (9.5 cm diameter and 8 cm deep) were placed in a 2 m^2 grid at each site. The traps were placed with the rim of the trap level with the soil surface and filled with 50 ml of 60% ethylene glycol (containing a small amount of detergent to break the surface tension). Traps were left in the field for seven days, after which they were collected. For the extraction technique, 10 x 100 g subsamples were randomly collected at each site and combined to form 1 L of soil, which was then placed on top of a mesh (0.5 mm aperture size) and placed within a funnel. Below the funnel, a 130 ml plastic jar with 75% ethanol was attached. The soil samples were left for seven days within the funnel, allowing the soil to dry out and arthropods to be extracted into the attached jar.

Focal taxa for this study were ants (Formicidae) and springtails (Collembola) as they play important roles in the soil ecosystem. Ants are important soil ecosystem engineers (Jouquet et al. 2006), while springtails are important decomposers within the soil ecosystem (Pollierer and Scheu 2021). Differences in mobility, habitat preference, disturbance sensitivity and dietary requirements of these focal taxon can give a better indication of how different soil arthropod groups respond to management practices. Specimens collected from all sampling methods were sorted into morphospecies (from here on referred to as ‘species’) and counted. Springtail specimens were identified by a taxonomic expert, while ants were identified to genus level using Hölldobler and Wilson (1990), Bolton (1994), Picker (2012), Fisher and Bolton (2016) and Slingsby (2017), and later verified by a taxonomic expert.

5.2.3. Soil biological activity

The bait laminae method consisted of modified plastic strips (150 mm long, 18 mm wide and 2 mm thick), with 25 perforated holes (1.5 mm diameter and 5 mm apart) (Birkhofer et al. 2011). At each site, four bait-laminae strips were placed at each site, arranged 10 cm apart and vertically inserted into the soil. Jelly, unlike agar-agar in a preliminary test to select bait-material, allowed the bait to securely remain within the perforated holes. Therefore, the bait material in this study consisted of cellulose powder, active charcoal, and flavored powdered jelly (70:5:25), made into a paste by adding a small amount of water. The bait laminae strips were left in the field for seven days, the biological activity was examined by categorizing the holes as fully empty (i.e., ‘eaten’) or intact. As the number of empty holes is an indication of biological activity, it was expressed as an overall percentage for each site.

5.2.4. Biotic and abiotic environmental variables

At each site, a 1 m^2 quadrat was placed at random three times within the site. Within the quadrat, a soil moisture and pH meter (Kelway, Inc.) and a soil penetrometer (Lang Penetrometer, Inc.) were used to measure soil moisture, pH, and soil compaction. Additionally, vegetation characteristics such as vegetation height (m), vegetation cover (%), number of plant species, leaf litter cover (%), leaf litter depth (cm), herbaceous cover (%), shrub cover (%), grass cover (%) and bare ground cover (%) were recorded. Additionally, in a 5 m radius surrounding the quadrat (an area of 80 m^2), amount of shade (%) and dead wood cover (%) was recorded. The average and total precipitation (mm) that occurred during the sampling period was also recorded. Means and standard errors of environmental variables for each treatment, within each sampling event, are given in Appendix M.

5.2.5. Data analyses

All data analyses were performed in R version 3.6.3 (R Core Team 2016). Data analyses were performed separately for springtails and ants, using pooled data from all sampling methods. The *iNEXT* package (Hsieh et al. 2019) was used to create species accumulation curves, to determine whether sampling was sufficient (Gotelli and Colwell 2001). This was done for each treatment, across the sampling events (Appendix N). The *fossil* package (Vavrek 2012) was used to calculate species richness estimators, namely Chao2 and Jackknife2. These estimators were selected as they are suitable for estimating species diversity of highly diverse communities (Colwell and Coddington 1994).

5.2.5.1. Objective 1: Effect of residue management practice on taxonomic and functional alpha-diversity

As the weather was sub-optimal for pitfall sampling in February 2020, with heavy rains, all the data was rarefied using the *hillR* package (Li et al. 2014, 2018) to examine Shannon's entropy (representing taxonomic evenness; ShanE) and Rao's quadratic entropy (representing functional diversity; RQ). This was done for both taxa and accounted for potential unequal sampling efficacy in different treatments due to rain interference with traps, allowing for a direct comparison between treatments, within a sampling event. Traits used for the calculation of RQ are given in Appendix O for ants and Appendix P for springtails. Literature used for the identification of traits is given in Appendix K, while justification for traits included in the analysis is given in Chapter 4 (Table 4.1).

Univariate modelling was done for a dataset including the residue management treatments only to test the overall effect of treatment, sampling event, and their interaction on each biodiversity response (ant ShanE and RQ, springtail ShanE and RQ). Reference grassland sites were excluded to leave out their influence on the interaction, and to focus on between-treatment patterns only. Modelling was then done for each sampling event separately, for each response to further assess within-sampling event biodiversity responses to treatment across all sites. Data from reference grassland sites were included in these models. All data showed a non-normal distribution based on Shapiro-Wilk tests conducted using the *nortest* package (Gross and Gross 2009). The *car* and *MASS* packages using quantile-quantile plots (Fox et al. 2012; Ripley et al. 2013) was used to assess the family distribution of ShanE and RQ. The *ade4* package (Dray and Dufour 2007) was used to assess the spatial autocorrelation of the data based on Mantel tests, but none was detected. Generalized linear models (GLMs) was therefore conducted using the *lme4* package (Bates et al. 2014). Post-hoc tests were conducted using the *multcomp* package (Bretz et al. 2008) where significant effects occurred. Family was specified as gamma with specified log-link function for ShanE and RQ models. Using the *ggpubr* package (Kassambara 2017), boxplots were constructed.

5.2.5.2. Objective 2: Effect of residue management practice on soil biological activity

Univariate modelling was conducted for soil biological activity, following the same approach as in the previous section. A dataset including the residue management treatments only was used to test the overall effect of treatment, sampling event, and their interaction on soil biological activity. Data showed non-normal distribution (Shapiro-Wilk tests) and was not spatially autocorrelated (Mantel tests). Generalized linear models (GLMs) were conducted, along with post-hoc tests where significant effects occurred, which are visually presented using boxplots. Family distribution was specified as Poisson for biological activity within the GLMs. Differences between treatments in biological activity at different depths in the soil were also graphically assessed.

5.2.5.3. Objective 3: Effect of residue management practice on ant and springtail assemblage composition

Multivariate modelling was done using data including the residue management treatments only to test the overall effect of treatment, sampling event and their interaction on ant and springtail assemblage composition, and data for sampling event (excluding the grassland sites) separately, for both ants and springtails independently. This was calculated using multivariate generalized linear models (GLMs) with a negative binomial distribution of abundance data using the *mvabund* package (Wang et al. 2012) and the *manyglm* function. For unconstrained ordination and visualizing the differences in assemblage composition between the treatments, latent variable models (LVMs) using the *Boral* package (Hui 2016) were made, for each sampling event. These biplots show ordinations without (pure biplot) and with (residual biplot) the influence of environmental variables (Hui 2016). For these ordinations, I used treatment as my environmental variable.

5.3. Results

Observed species richness were similar to Chao2 and Jacknife2 species estimates, and accumulation curves nearly reached asymptotes (Table 5.1, Appendix N). Overall, samples consisted of 17 768 ant individuals and 54 species belonging to 19 genera in 5 sub-families, along with 10 846 springtail individuals and 87 species belonging to 11 families and 3 sub-orders.

Table 5.1 Number of collected species (N) and species estimators Chao2 and Jacknife2 for ants (Formicidae) and springtails (Collembola) within each sampling event.

	Formicidae			**Collembola**		
	N	**Chao 2**	**Jack 2**	**N**	**Chao 2**	**Jack 2**
January 2019	41	65.08	53.00	61	91.72	73.99
August 2019	15	18.60	9.02	43	64.13	44.00
February 2020	26	31.79	32.99	30	42.10	36.96

5.3.1. Objective 1: Effect of residue management practice on taxonomic and functional alpha-diversity

When all sampling events were assessed together, there was no significant interaction between residue management treatment and sampling event for ant RQ and ShanE, or springtail RQ and ShanE (Table 5.2). Here, sampling event played a significant role in each case in comparison to treatments (Table 5.2), with a decline in most of the arthropod responses from January to August 2019, and a further decline towards February 2020 (Fig. 5.2). Although grasslands were not included in the analysis (Table 5.2), recovery to similar levels occurred in the February 2020 compared to the January 2019 for most of the arthropod responses (Fig. 5.2). In the January 2019 sampling event, no significant difference between treatments were found for ant ShanE (Table 5.2; Fig. 5.2A), ant RQ

Table 5.2 Univariate results of overall and sampling event data sets. Overall includes all sampling events and treatments, showing the effect of treatment and sampling event, and their interaction, on measured response variables. Samping event illustrates the effect of treatment on the measured response variables, within each sampling event. Natural grassland reference sites were excluded from the data sets.

Overall	**Treatment**		**Sampling event**		**Interaction**	
	df	**χ^2**	**df**	**χ^2**	**df**	**χ^2**
Biological activity	3	0.03	2	41.33 ***	6	2.76
Formicidae RQ	3	0.32	2	47.11 ***	6	7.63
Formicidae ShanE	3	0.51	2	65.84 ***	6	0.01
Collembola RQ	3	0.04	2	26.40 ***	6	0.99
Collembola ShanE	3	0.37	2	27.50 ***	6	1.20

Sampling event	**January 2019**		**August 2019**		**February 2020**	
	df	**χ^2**	**df**	**χ^2**	**df**	**χ^2**
Biological activity	3	0.16	3	20.19***	3	8.68*
Formicidae RQ	3	0.08	3	1.01	3	9.11
Formicidae ShanE	3	0.18	3	0.05	3	3.82
Collembola RQ	3	0.10	3	0.06	3	1.65
Collembola ShanE	3	0.75	3	0.18	3	0.49

RQ = Rao’s quadratic entropy, ShanE = Shannon’s entropy. Significance codes: *p < 0.05, **p < 0.01, ***p < 0.001

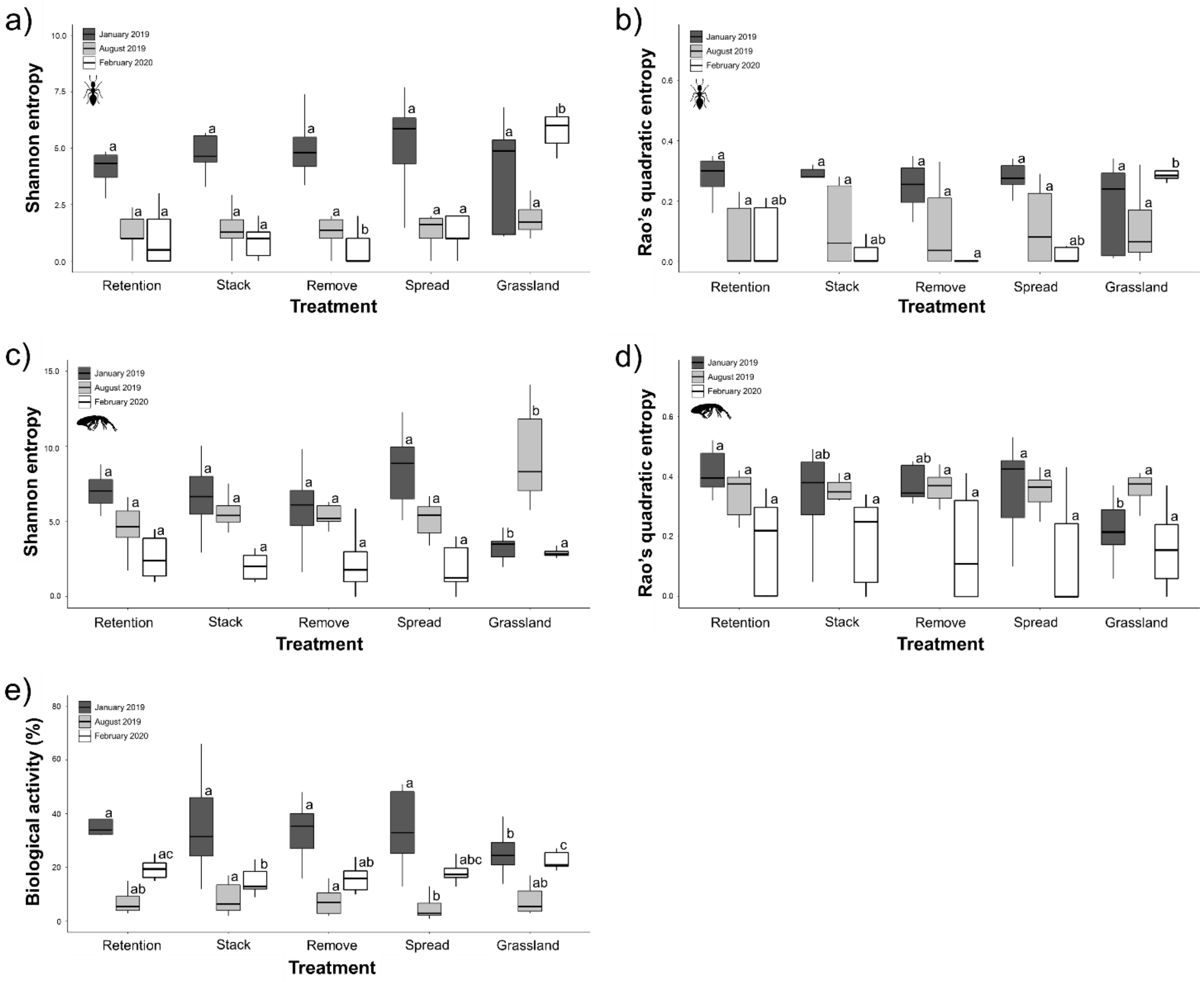

Figure 5.2 Boxplots with central horizontal line indicating the median value, the boxes indicating the interquartile range, and the whiskers indicating standard deviation within each treatment. Illustrated is the a) ant Shannon's entropy (ShanE), b) ant Rao's quadratic entropy (RQ), c) springtail Shannon's entropy (ShanE), d) springtail Rao's quadratic entropy (RQ) and e) soil biological activity, within each sampling event. Means with letters in common between the treatments for each sampling event, are not significantly different at $P < 0.05$.

(Table 5.2; Fig. 5.2B), springtail ShanE (Table 5.2; Fig. 5.2C) or springtail RQ (Table 5.2; Fig. 5.2D). In the August 2019 sampling event, no significant differences between treatments were found for ant ShanE (Table 5.2; Fig. 5.2A), ant RQ (Table 5.2; Fig. 5.2B) or springtail RQ (Table 5.2; Fig. 5.2D). A significant difference for springtail ShanE (Table 5.2; Fig. 5.2C) were found between treatments. Springtail ShanE was significantly higher within the grasslands compared to all management treatments, and there was no significant difference between management treatments (Fig. 5.2C). In the February 2020 sampling event, no significant difference between treatments were found for ant ShanE (Table 5.2; Fig. 5.2A), springtail ShanE (Table 5.2; Fig. 5.2C) or springtail RQ (Table 5.2; Fig. 5.2D). A significant difference for Ant RQ (Table 5.2; Fig. 5.2B) was found between treatments, with ant RQ being significantly higher within the grasslands compared to all management treatments, and there was no significant difference between management treatments (Fig. 5.2B).

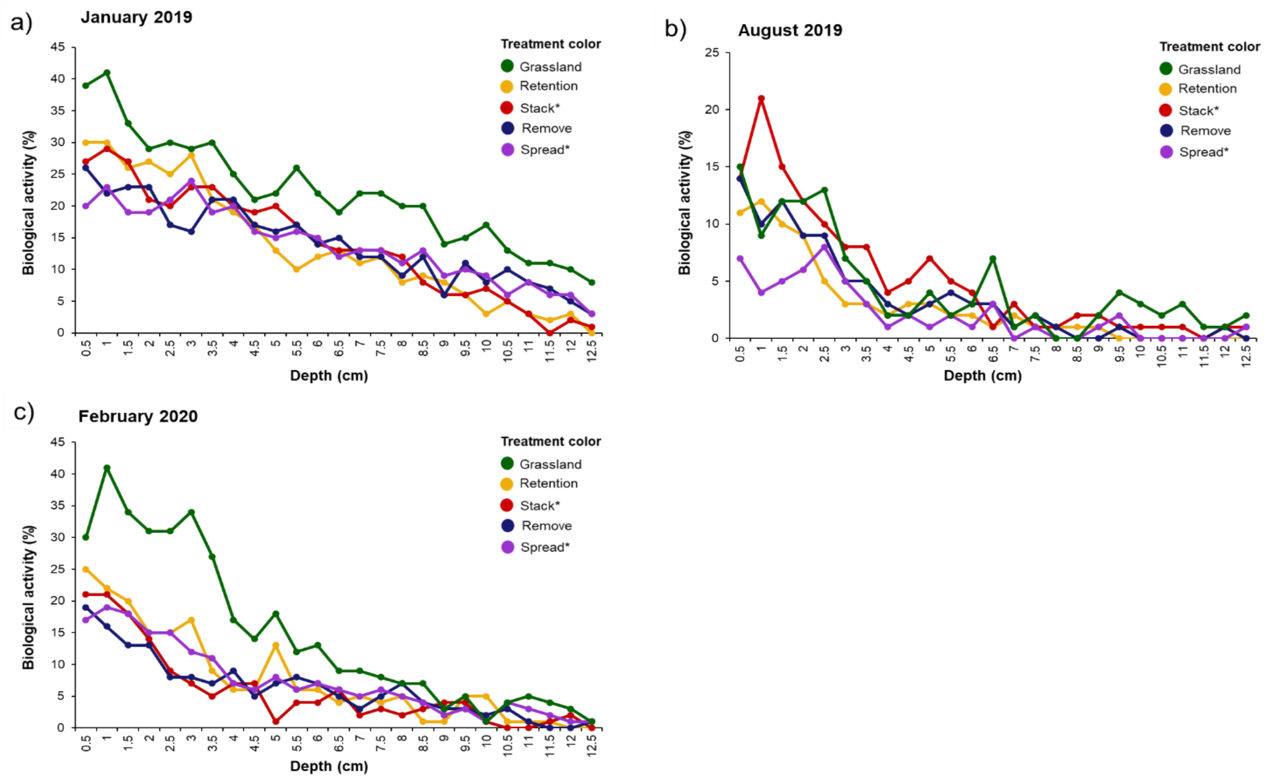

Figure 5.3 Biological activity (%) at different depths within the soil for each sampling event across the different treatments. Sampling events indicated as a) sampling prior to harvest (January 2019) and to post-residue management samples at b) August 2019 and c) February 2020. Also indicated is where burning as a management tool for the residue occurred with * after the treatment name.

5.3.2. Objective 2: Effect of residue management practice on soil biological activity

When all sampling events were assessed together, there was no significant interaction between residue management treatment and sampling event for soil biological activity (Table 5.2). Here, event played a significant role in comparison with treatment when grasslands were excluded from the dataset (Table 5.2). Biological activity declined from the January to August 2019, but recovered to about 50% of the January 2019 level by February 2020 (Fig. 5.2E). Additionally, grassland biological activity in February 2020 recovered to similar levels of January 2019 (Fig. 5.2E). In the January 2019 event (Table 5.2; Fig. 5.2E), a significant difference between treatments, with biological activity being significantly lower within the grasslands compared to all management treatments, and there was no significant difference between management treatments (Fig. 5.2E). In the August 2019 event (Table 5.2; Fig. 5.2E), a significant difference was found between treatments, with all management treatments not being significantly different from the grasslands, but did show differences amongst each other. The spread management treatment has significantly lower biological activity compared to the stacking and removal treatments, but was not different from the retention treatment (Fig. 5.2E). In the February 2020 event (Table 5.2; Fig. 5.2E), a significant difference was found between treatments. Biological activity was higher within the grasslands, but was not significantly different from that within the retention and spread management treatments (Fig. 5.2E). The stacking treatment

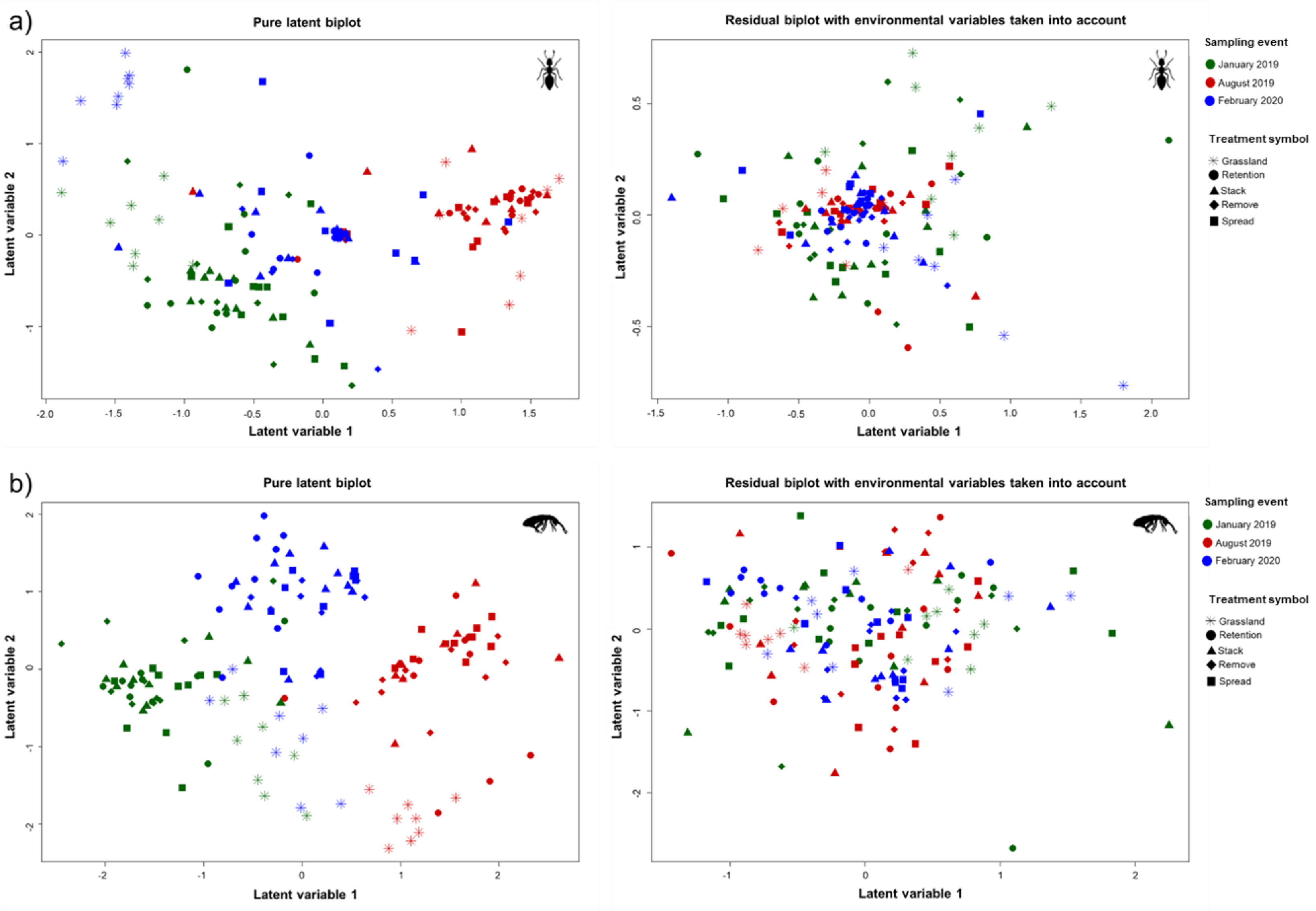

Figure 5.4 Model-based pure (left) and residual (right) ordination of a) ant and b) springtail assemblages between the different treatments and sampling events. Pure biplots are without the influence of treatment and sampling event as environmental variables, whereas the residual bioplot included the influence of treatment and sampling event as environmental variables.

has significantly lower biological activity compared to the retention treatment and the grasslands, but was not significantly different from the removal and spread management treatment (Fig. 5.2E). Additionally, the greatest amount of soil biological activity resides in the topsoil (Fig. 5.3).

Table 5.3 Multivariate results of overall and sampling event data sets. Analysis conducted separately for springtails (Collembola) and ants (Formicidae). Overall includes all sampling events and treatments, and shows the effect of treatment and sampling event, and their interaction, on measured response variables. Sampling event illustrates the effect of treatment on the measured response variables, within each sampling event. Natural grassland reference sites were excluded from the data sets.

Overall	**Treatment**		**Sampling event**		**Interaction**	
	df	**Dev**	**df**	**Dev**	**df**	**Dev**
Collembola assemblage	116	240.40	114	1394.20 ***	108	180.60 ***
Formicidae assemblage	116	122.30	114	781.20 ***	108	78.40 **

Sampling event	**January 2019**		**August 2019**		**February 2020**	
	df	**Dev**	**df**	**Dev**	**df**	**Dev**
Collembola assemblage	36	175.40	36	105.40	36	119.90***
Formicidae assemblage	36	108.90	36	30.96	36	51.58

Significance codes: *p < 0.05, **p < 0.01, ***p < 0.001

Table 5.4 Post-hoc pairwise results of ant and springtail assemblage composition between treatments, when data sets were analysed separately per sampling event.

Treatments	**Formicidae**			**Collembola**		
	January 2019	**August 2019**	**February 2020**	**January 2019**	**August 2019**	**February 2020**
Grassland - Remove	82.23**	26.25*	188.77***	104.57*	199.35**	62.51***
Grassland - Spread	80.08**	30.59*	185.28***	119.98*	230.24***	63.68***
Grassland - Retention	73.93**	32.88*	184.68***	133.54**	193.84**	58.29**
Grassland - Stack	71.94*	27.70*	169.36***	118.25*	196.50**	60.77**
Remove - Spread	40.00	3.38	14.97	51.74	26.49	20.23
Spread - Stack	32.11	7.88	18.94	52.24	23.21	27.50
Retention - Spread	30.07	11.41	16.39	53.30	38.66	51.56*
Remove - Retention	29.56	9.98	11.35	53.60	33.37	51.25*
Remove - Stack	28.74	6.83	11.48	46.44	25.71	25.18
Retention - Stack	25.07	12.88	10.26	57.10	42.59	47.06*

Significance codes: *p < 0.05, **p < 0.01, ***p < 0.001

5.3.3. Objective 3: Effect of residue management practice on ant and springtail assemblage composition

There was a significant interaction between residue management treatment and sampling events for ant and springtail assemblage composition (Table 5.3). From the ordination (Fig. 5.4) sampling event had a stronger effect on assemblage compositionthan treatment, with an especially clear segregation of the winter samples, including for grassland control sites. In the January 2019 and August 2019 sampling events, treatment did not have a significant effect on both ant (Table 5.3; Fig. 5.4A) and springtail (Table 5.3; Fig. 5.4B) assemblages. In both cases, the grassland assemblage differed significantly from all management treatments, while no difference occurred among the management treatments (Table 5.4). In the February 2020 sampling event, treatment had a significant effect on springtail (Table 5.3; Fig. 5.4B) assemblages, but not on the ant assemblages (Table 5.3; Fig. 5.4A). In both cases, the grassland assemblage differed significantly from all management treatments, while no difference occurred among the management treatments for ants (Table 5.4). However, the springtail assemblage in the retention treatment differed from all other management treatments (Table 5.4).

5.4. Discussion

The least sustainable management practice was hypothesized to be the complete removal of harvest residues, as this activity could possibly have negative effects on the soil environment and nutrient cycling (Helmisaari et al. 2011). At the other extreme, I expected residue retention would be most beneficial for the soil environment due to the availability of slow-release nutrients and added protection from soil erosion (Bautista et al. 2008; Li et al. 2020). Furthermore, differences in fire intensity was expected to play a major role (Mott et al. 2021). Previous studies have shown the removal of residue can have significant negative effects on the soil environment (Helmisaari et al. 2011). Others have shown the excessive removal of crop residues can lead to declines in soil organic carbon (Smith et al. 2012), increased soil erosion, and reduced water infiltration (Clay et al. 2019). Therefore, as the soil's chemical and physical properties can be inherently affected by the management of slash residues, including the removal (Helmisaari et al. 2011; Smith et al. 2012; Clay et al. 2019), retention (Keizer et al. 2018; Li et al. 2018, 2020), or burning of residue (Mott et al. 2021), it can therefore be expected that the biological component of the soil would also be negatively affected. Use of fire as a management tool significantly affects soil communities (Korobushkin et al. 2017), mainly due to removal of the leaf litter layer and a decrease in suitable post-fire habitat and resources (Kral et al. 2017). Additionally, these affects can be more detrimental with increased fire intensity (Gongalsky et al. 2012; Kral et al. 2017; Mott et al. 2021).

5.4.1. Objective 1: Effect of residue management practice on taxonomic and functional alpha-diversity

A meta-analysis across different natural and agricultural systems by Pressler et al. (2019), showed fire events significantly reduces soil biota abundance. Gongalsky et al. (2012) even suggested that abudance and biomass of soil fauna groups are more sensitive to fire than species richness. In another study, they also showed abundance and species richness was higher within unburned plots compared to burned plots shortly after the fire event (Gongalsky and Persson 2013). Castro-Huerta et al. (2021) even found differences in arthropod abundance between low, medium and high intensity fires, being significantly lower within the high intensity treatments. Others however, have shown no difference in arthropod abundance between different burning treatments (Nadel et al. 2007; Osabiya and Adeduntan 2020). It should be noted, that although this was not formally examined within this study, very large and clear declines occurred across all management treatments between the January 2019 and August 2019 sampling events, for both ants and springtails, and which had not recovered by February 2020 (Appendix N). Declines in population, i.e. the number of individuals, is a conservation concern, given that these declines may also have detrimental effects on ecosystem functioning (Ceballos et al. 2017; Harris et al. 2019). Seemingly, I can conclude these management practices (regardless of the inclusion or exclusion of fire) similarly resulted in significant declines in abundances directly after implementation, and have not recovered to similar levels after a year. Based on these results, recommendations on the most sustainable management practice cannot be made on arthropod abundance alone, and requires further examination on other components of biodiversity before conclusions can be made.

Surprisingly, I found soil taxonomic and functional diversity responded similarly among residue management treatments within each sampling event, showing no significant differences among the treatments, regardless of whether fire was included or excluded as a management tool, and regardless of the differences in amounts of woody biomass remaining after implementation. This contrasts with the findings of Korobushkin et al. (2017) and Saifutdinov et al. (2018), showing soil arthropods to be strongly impacted by burning events in forested ecosystems (i.e., plantations and indigenous forests) in Russia. Similarly, Mantoni et al. 2020 showed soil-dwelling arthropod diversity was lower within burned soils compared to unburned soils of both indigenous forests and grasslands in Italy. Additionally, Mott et al. (2021) and Smith et al. (2016) in the United States show the degree of fire intensity can negatively affect the soil’s physical, chemical, and biological components within forested ecosystems (i.e., indigenous forests and timber plantations). Therefore, it was surprising to see no differences in taxonomic or functional diversity between the spreading and stacking residue treatments in my study.

Osabiya and Adeduntan (2020) suggested that some species might be adapted to burrow into the soil, which can lead to no noticeable difference between their different burning treatments within indigenous forests and *Tectonia* plantations. This observation by Osabiya and Adeduntan (2020) may therefore explain why the focal taxa in my study was not as greatly affected as I expected, being physiologically or behaviourally adapted to survive that level of disturbance. On the other hand, Nadel et al. (2007) found soil arthropod diversity and composition was more influenced by season than by fire within *Eucalyptus* plantations in South Africa. Related to Nadel et al. (2007), it is important to note that my study was also conducted in the Midlands, which is characterized by nutrient rich, well-buffered clay soils (du Toit 2003, du Toit et al. 2004, 2008). Therefore, these clay soils may be more resilient to disturbances compared to other soil types, for example, nutrient poor, sandy soils (Smith and Du Toit 2005; Titshall et al. 2013). Soils that are unable to buffer disturbances may be at greater risk of soil degradation (Dovey et al. 2011), and therefore, residue management practices recommended and implemented in the Midlands may not have the same benefits in regions with other soil types. Therefore, further research is needed to determine appropriate and sustainable residue management practices for specific soil types and regions.

The results here on management practices coincided with austral winter, and arthropod diversity declined across all sites, including the grassland. It was therefore not possible to attribute this decline to the management practices per se. But, as the final sampling occurred after several months of warm, wet conditions, it was expected that there would be detectable recovery by following February, and possibly different rates of recovery among treatments. Surprisingly, neither taxonomic nor functional diversity showed any differences among the management treatments a year after they had been implemented. These findings contrast with the findings of da Cunha et al. (2020), showing most arthropod orders returned shortly after a fire event, but this was due to the return of vegetation after the first rains occurred. Even with vegetative regrowth (Appendix M), these responses were not observed in my study. On the other hand, Zaitsev et al. (2014) found recovery of arthropods after a fire is dependent on the remaining quality and quantity of the leaf litter layer. Thus, further decline in taxonomic and functional diversity a year after the management practices have been implemented could be attributed to the reduction in the leaf litter layer (Appendix M). It is possible that some species survived the management practices, but due to the significant alteration in microhabitat and the reduction of available resources (Coyle et al. 2017), a further decline occurred. Alternatively, the decline may have been caused by the weather event (i.e., heavy rainfall) that occurred in the final sampling event (February 2020).

5.4.2. Objective 2: Effect of management practices on soil biological activity

As the assessment of soil biological activity contributes to a better understanding of the ecosystem functioning of a wider array of taxa, I expected soil biological activity to show a significant response to management treatments, particularly those including and excluding fire as a management tool, which have been reported to affect soil properties (Musso et al. 2014; Butenko et al. 2017) and ultimately the diversity and activity of soil micro-organisms (Bouchez et al. 2016; Panico et al. 2018). Santana et al. (2018) showed that fires significantly alter soil chemical properties at the surface layer, but also below the surface, but do not affect soil physical properties. Furthermore, they show fire affected soil biological activity up to 2 cm within the soil substrate. Here, I show that the top 2 cm of the soil of both the grasslands and plantations contains the highest amount of biological activity but was not affected by the presence or absence of fire, nor by the difference in fire intensity related to the stacking and spread burning management treatments.

Additionally, my results also contrast with Santana et al. (2018) who showed crop residue to have higher soil biological activity and Fuentes-Ramirez et al. (2018) that showed soil biological activity to be significantly higher within burned sites compared to unburned sites. My results do, however, agree with Cooperdock et al. (2020) and Goncharov et al. (2020), together with a review by Giorgis et al. (2021), showing no significant difference between burned and unburned conditions. However, compared to August 2019, soil biological activity was showing signs of recovery in February 2020 across all the plantation sites. This suggests that below-surface fauna responsible for these results (including earthworms, isopods, micro-organisms, and termites) (Van Gestel et al. 2003; Filzek et al. 2004; Römbke et al. 2006; Gongalsky et al. 2008) is showing more rapid recovery in plantations compared to the taxa examined in this study. Ants and springtail use both above- and below-ground realms may have been exposed to the disturbances to a greater degree. Additionally, it is possible that the bait-laminae was less affected by the weather event (i.e., heavy rainfall) being below the soil surface, in comparison to the exposed pitfall traps, in February 2020. As pitfall traps can become flooded due to extensive rainfall (van den Berghe 1992; Van Zoeren et al. 2018), this may have contributed to lower levels of diversity measures in February 2020 (Nadel et al. 2007).

5.4.1. Objective 3: Effect of residue management practice on ant and springtail assemblage composition

Nadel et al. (2007) found season to play a much larger role in shaping soil invertebrate assemblages between burnt and unburnt residue managements plots, compared to the fire event itself. In my study, this can clearly be seen in the grasslands, with their assemblages naturally fluctuating with season (i.e. the August 2019 sampling event being segregated from the January 2019 and February 2020 sampling events). Additionally, my results align with Nadel et al. (2007) showing strong seasonal effects within management treatments, and assemblages being less influenced by fire. Furthermore, no distinct differences in ant or springtail assemblages were observed between the January 2019 or August 2019 management treatments, showing they were equally affected by the different management practices. It is possible that some species were able to persist under these conditions due to traits relating to dispersal abilities and vertical distribution in the soil (Bengtsson 2002; van Dooremalen et al. 2013; Zaitsev et al. 2014), which could explain why no differences were found amongst the treatments. For example, species may have dispersed from the unburnt treatments to the burnt treatments (Gongalsky and Persson 2013) or may have ascended temporarily to deeper layers of the soil (Gongalsky et al. 2012). However, as this was not assessed within this study, further examination into trait-identies of post-fire communities could give better insight as to whether species were able to survive these disturbances.

Furthermore, ant assemblages did not show any recovery by February 2020, being no different from the January 2019 or August 2019 samples. However, springtail assemblages in the retention treatment of the February 2020 sample did differ from all other residue management treatments. This may be explained by the remaining litter that offered sufficient resources to the surface-dwelling springtails (Zaitsev et al. 2014). These results therefore indicate that while grassland assemblages fluctuate naturally with season and maintain their species composition, recovery of the plantation assemblages may take longer. Some studies have found post-fire recovery of soil parameters to be rapid, i.e. within a year (Antunes et al. 2009), however, the recovery of soil fauna communities may take a lot longer (Bengtsson 2002; Malmström et al. 2009; Gongalsky and Persson 2013). As these plantations undergo large disturbances every 7-10 years, it is expected that these assemblages may require more time to recover. Here, I recognize that the study period may have been too short to fully examine recovery and resilience of soil arthropod communities, as suggested by Bengtsson (2002). However, the focus of this study was more to determine the management practice with the most severe short-term effect on the communities. Thus, more research is needed to monitor the recovery of these assemblages over a longer time than was possible to monitor in this study.

5.5. Conclusion

I show that regardless of the inclusion or exclusion of fire as a management tool, the effects of residue management treatment, whether retention, removing, stacking (with burning) or spreading (with burning) was equally strong, resulting in no difference directly after the practices were implemented. Furthermore, one year after the management treatments had been implemented, there was still no significant difference between the residue management treatments, with responses declining further even after a year (except for soil biological activity). This means that it makes no difference which management practice is used. The lack of difference between the practices may have been attributable to the nutrient rich, high-resilience clay soils that occur within the area (du Toit 2003, du Toit et al. 2004, 2008), resulting in no clear distinction in the effect of residue management practice, regardless of fire effects that have been well-documented to effect arthropod assemblages elsewhere (Korobushkin et al. 2017; Saifutdinov et al. 2018; Pressler et al. 2019). Additionally, these results build on the continued use of fire as a management practice on these soils, as in Nadel et al. (2007). These findings may differ in other silvicultural regions with different soil conditions that are likely to be less resilient to disturbances.

Therefore, further assessment is required in the long-term to determine which of these residue management practice allows for greater recovery of these functionally important soil arthropods under different contrasting regions, with differential soil conditions. Additionally, I recommend further examinination on species-specific traits to determine the effects of management practices on the survivability and/or vulnerability of some species, and how this may affect important ecosystem processes. It is also important to increase sampling events in monitoring studies (Nooten et al. 2019), which may in the long-term, also aid in drawing stronger conclusions regarding the effects of these residue management practices.

5.6. References

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CHAPTER 6

General discussion

The focus of this dissertation was to gain a more in-depth understanding of two functionally important soil taxa, namely ants and springtails, regarding their diversity, distribution and response to environmental gradients and management practices. I approached this by examining these taxa within a timber plantation landscape mosaic, which also consists of remnant natural areas which are dispersed throughout the landscape.

Large-scale, monoculture timber landscapes have received much criticism over the possible negative effects that management practices may bring to local biodiversity (Brockerhoff et al. 2008). This has been extensively shown for aboveground arthropods (Kietzka et al. 2015; Pryke et al. 2015; Van Schalkwyk et al. 2017). However, less attention has been given to soil and litter arthropods (Yekwayo et al. 2016a,b; Eckert et al. 2019). Considering their functionally important roles within the soil, we need a better understanding of their diversity patterns and responses if we are to efficiently conserve them, and in turn, the soils.

Overall, the results of my dissertation can be divided into four main themes. Under each theme, I discuss my findings, their implications and management recommendations, along with suggestions for focal research areas in the future. A summary of overall findings (Fig 6.1) is presented.

6.1. Large remnant areas conserve critical soil biodiversity

Specifically in KwaZulu-Natal, South Africa, previous studies in this region have shown that the natural areas within the timber plantation landscape have great conservation value for soil biodiversity compared to the plantation compartments (Yekwayo et al. 2016a,b; Eckert et al. 2019). Expanding on this, I show that in terms of taxonomic diversity (Chapter 2), landscape-level species turnover (Chapter 3) and functional diversity of soil organisms (Chapter 4), these remnant areas exhibit high biodiversity and functional value within timber-plantation landscapes. These results were consistent between two climatically and topographically different regions (KwaZulu-Natal and Midlands), on two very distinct soil types, for two ecologically different taxonomic groups. Additionally, the natural remnant areas harbor rare and unique species that do not occur elsewhere in the landscape (Chapter 3 and 4). My results show the crucial value of this land-sparing approach (i.e., instigating networks of conservation corridors) for the conservation of functionally important soil fauna. I therefore recommend this approach as a landscape-scale conservation strategy for maintaining the integrity of natural areas within these highly transformed landscapes so as to maintain irreplaceable biodiversity

(Gibson et al. 2011), as some species cannot persist or survive within simplified, intensively managed areas (Gámez-Virués et al. 2015; Phalan 2018). This approach is therefore highly effective for promoting biodiversity in managed landscapes locally in two contrasting regions on different soil types, and should therefore be considered in landscape planning for soil biodiversity conservation in other regions too.

Furthermore, very few studies have examined soil biological activity using the bait-laminae method within a plantation landscape context (Römbke et al. 2006; Woodham et al. 2019; Zhu et al. 2020). Römbke et al. (2006), for example, compared primary and secondary forests to mixed tree plantations, whereas Zhu et al. (2020) compared native forests to monoculture and mixed tree plantations. The use of the bait-laminae method to examine soil biological activity within the landscape context (i.e. remnant natural areas embedded within large-scale monoculture plantation landscapes) is a novel aspect of this dissertation. The fact that these remnant areas also exhibit high level of soil biological activity (Chapter 2), highlights their value in terms of soil functional integrity and functioning, as higher values of biological activity can indicate better ecosystem functioning (Reinecke et al. 2008; Simpson et al. 2012; Zhu et al. 2020), which puts further emphasis on the need to conserve the natural remnant areas across these plantation mosaics.

6.2. The importance of heterogeneity in the natural areas

In addition, one of the goals of Chapter 2 was to find common environmental drivers of biodiversity that could be used as indicators of soil biodiversity hotspots. As it turned out, this could not be achieved due to the high responsiveness of the soil fauna to natural heterogeneity, and that even among soil taxa, there can be varied responses to environmental drivers (Chapter 2). This is also indicated by the high species turnover within both the indigenous forests and grasslands (Chapter 3). My results, therefore, show that different taxonomic and functional groups can respond differentially to environmental drivers, as seen elsewhere (Birkhofer et al. 2017; de Graaff et al. 2019). Although Le Provost et al. (2021) show that landscape factors do influence soil fauna, I show that soil arthropods are most responsive to small-scale variables in these landscapes (i.e., plant and soil related variables) than landscape-scale variables (Chapter 2), highlighting that small-scale environmental heterogeneity greatly supports arthropod biodiversity (Foord et al. 2003; Nielsen et al. 2010). I recommend that land managers should focus on conserving as much heterogeneity as possible across the landscape, which is not only important for conserving aboveground biodiversity (Bazelet and Samways 2011; Joubert et al. 2016), but has most recently been shown to also be beneficial for belowground diversity (Burton and Eggleton 2016; García-Tejero and Taboada 2016). Furthermore, environmental conditions shape communities, which in turn, can have impacts on ecosystem functioning (Cardinale et al. 2000; Ratcliffe et al. 2016). Therefore, managing and conserving small-scale heterogeneity would therefore maximally benefit a wide range of soil organisms. Conserving as many taxonomic and functionally unique species as possible is crucial, as this would lead to different species that perform different ecosystem functions, thereby enhancing ecosystem health and performance (Wolters 2001; Tilman et al. 2014; Wagg et al. 2019). In contrast, the loss of functionally unique species could lead to impaired ecosystem functioning (Wolters 2001; Wagg et al. 2019).

In addition, a high degree of assemblage dissimilarity between indigenous forests and grasslands was found in both study regions on contrasting soil types (Chapter 2 and 3). These results highlight the importance of landscape planning to include both grassland and indigenous forest patches in conservation corridors. Therefore, from a landscape planning perspective, corridors with a high level of environmental heterogeneity in terms of soil type, topography and vegetation type, for example, would be of high conservation priority. In addition, management practices can be applied non-uniformly to achieve heterogeneity by, for example, mowing, grazing, or burning, that follow a mosaic management strategy allowing both managed and undisturbed conditions within a plantation estate. Although I did not assess management options and feasibilities here, the effect of management practices in conservation corridors (i.e. more specifically the grasslands) on the soil biota, would be a high priority in future research.

6.3. Timber plantations support unexpectedly high soil biodiversity

Lower levels of biodiversity are often observed within timber plantations for aboveground, mobile taxa such as butterflies, dragonflies, grasshoppers and beetles (Pryke and Samways 2012b, 2015). In terms of soil arthropods, local studies have shown that timber plantations can have lower levels of diversity compared to nearby, natural remnant areas (Yekwayo et al. 2016b; Eckert et al. 2019). Furthermore, and importantly, I show that timber plantations (more specifically *Eucalyptus* plantations compared to *Pinus* plantations), can support similar levels of both soil arthropod alpha- and beta-diversity (Chapter 3) and functional diversity (Chapter 4) compared to indigenous forests and grasslands. This was observed in the two geographically, topographically and climatically different regions with different soil types (i.e. clay and sand). Although assemblage composition differed between the natural areas and plantation compartments, as expected, the commercial blocks did not lead to large-scale homogenization of soil biodiversity, as expected. This contrasts with the findings of Mori et al. (2015a,b) showing lower beta-diversity in the plantations in terms of litter-dwelling arthropods. However, my findings concord rather with Martello et al. (2018) showing species turnover contributed the most to changes in taxonomic diversity between plantation compartments, and with Winck et al. (2017) and Martello et al. (2018) showing *Eucalyptus* compartments can have similar levels of functional diversity compared to indigenous forests and/or grasslands. My results provide strong evidence that distribution patterns and stressors on belowground biodiversity do not mirror that of aboveground biodiversity at local scales, which has been demonstrated by Le Provost et al. (2021) and Cameron et al. (2019). This suggests that conservation strategies for aboveground biodiversity may not be appropriate to conserve belowground biodiversity.

My findings also enabled identification of potential mechanisms for the high level of biodiversity in the plantations. I show a relatively high degree of shared species between the natural and plantation areas (Chapter 3). As matrix quality (Boesing et al. 2018; Arroyo-Rodrıguez et al. 2020) is important for local biodiversity, and in return regional biodiversity, based on my findings a landscape consisting of both natural and plantation areas cannot be seen as habitat versus non-habitat, but as a mosaic of varied suitability for different species (Ingham and Samways 1996). This builds further on my recommendation to conserve natural areas within production landscapes as part of the land-sparing approach. This conclusion comes from the presence of the natural areas in the surrounding areas of the plantations having seemingly contributed to the high levels of species turnover and functional diversity within the plantations through species spill-over, as suggested by Yekwayo et al. (2016a,b), Basset et al. (2017) and Santoandré et al. (2019).

Additionally, the high environmental variation in vegetation and soil properties observed between the plantations may also have contributed to the high species turnover between plantations (Gibson et al. 2017). An important future research question related to within-plantation heterogeneity, is the effect of large-scale felling of plantations across whole estates vs. that of rotational harvesting. Rotational harvesting leads to a mosaic of plantation age classes, offering greater environmental heterogeneity throughout the planted areas and greater resources for arthropods to utilize when some compartments have been harvested. Based on the responsiveness of soil fauna to heterogeneity observed in this study, rotational harvesting would be expected to be beneficial. This has not yet been assessed for soil fauna, but may become increasingly important as mechanization, and resulting large-scale felling in the industry, is increasing, and therefore of concern.

Furthermore, I show a high degree of trait divergence between the natural areas and the plantation compartments, indicating an environmental filtering effect between these contrasting biotopes (Chapter 4). However, it further shows that, even under the highly transformed conditions in the plantations, soil assemblages are composed of species with varied adaptations to survive within those conditions. This may have contributed to the high functional diversity found within the plantation compartments (Chapter 4). Moreover, functional diversity has been found to be a better indication or measure of ecosystem functioning compared to taxonomic diversity (Goswami et al. 2017; Finney and Kaye 2017; Abonyi et al. 2018), and that any change in functional diversity may lead to changes in ecosystem stability, productivity, and functioning (Goswami et al. 2017; Finney and Kaye 2017). Results of Chapter 3 and 4 together indicate that these plantations are doing well in terms of their soil biodiversity, and that they can contribute to enhanced soil biodiversity across the landscape (Yekwayo et al. 2016a,b; Eckert et al. 2019). However, although this was not formally investigated within my dissertation, the high functional diversity suggests that these plantations have seemingly high levels of ecosystem stability and functioning. Yet, shifts in trait composition can lead to changes in ecosystem processes (Gámez-Virués et al. 2015) such as litter breakdown and nutrient cycling. Further examination of soil ecosystem functioning in these systems would enable us to make more robust conclusions on the effects of species trait shifts and soil functioning between the natural and plantation areas.

6.4. Soil faunal diversity and activity response to timber slash management practices

An important part of nutrient management in timber plantation landscapes is the management of timber residue after harvesting (Skovsgaard et al. 2021). Studies on the effects of residue management on nutrient dynamics have received much attention (Scheepers and du Toit 2016; Venanzi et al. 2016), while the biological component has been neglected (Nadel et al. 2007; Gongalsky et al. 2012; Puga et al. 2017). Within agricultural systems, most of its biodiversity resides within the soil (Brussaard et al. 2007) and generally exceeds aboveground biodiversity (Thiele-Bruhn et al. 2012). Therefore, as the soil biodiversity is crucially linked to the functioning of the soil, ecosystem stability and ecosystem services (Thiele-Bruhn et al. 2012; Hou et al. 2020), management practices need to be identified that allow both the reliance and persistence of the soil ecosystem (Garibaldi et al. 2017), especially within timber production landscapes.

In Chapter 5, I focussed on the residue management of the genus *Eucalyptus*, as it is one of the most widely planted trees in the world (Albaugh et al. 2013; Attia et al. 2018), due to its fast-growing and drought-tolerant nature (Nadel et al. 2007; Liu and Li 2010; Zaiton et al. 2018). Before harvesting, taxonomic and functional diversity within the *Eucalyptus* compartment was like that of a nearby natural grassland. It has been suggested that species richness does not imply greater resilience of a community (i.e. the ability of a community to absorb disturbance and retain the same structure, functioning), but rather relies on the community based species traits (Elmqvist et al. 2003; Fischer et al. 2009). This indicates that the compartment had seemingly high levels of ecosystem stability and functioning prior to harvesting, as shown by its high functional diversity based on species trait diversity. Similar results were also found for soil biological activity, with the highest level of activity occurring in the topsoil layer for both the natural reference grassland and the *Eucalyptus* compartment. This emphasizes the importance of the topsoil layer for soil biodiversity and functioning, and that management practices which have destructive effects on the topsoil layer should be avoided, as it can have detrimental effects on the functioning and productivity of the soils (Obalum et al. 2011).

Furthermore, the recovery of communities after a disturbance depends on their behavioural or physical traits (Gongalsky et al. 2012). This means that community response to disturbances (e.g., fires) is therefore expected to vary greatly among taxa (Ferrenberg et al. 2006; Maleque et al. 2009; Yekwayo et al. 2018). Additionally, studies have shown aboveground fauna are more vulnerable to disturbances (e.g., fires) compared to belowground fauna (Wikars and Schimmel 2001; Gongalsky and Persson 2013; Zaitsev et al. 2014). This may explain why soil biological activity, arthropod abundance, taxonomic and functional diversity were equally (negatively) affected by the different management treatments in my study, and were not significantly different from one another directly after implementation and even a year later (Chapter 5), as soil-dwelling invertebrates can survive disturbances by descending further down into the soil profile (Gongalsky et al. 2012; Verma and Jayakumar 2012; Korobushkin et al. 2017). Although not significantly different among the management treatments, soil biological activity did increase a year after the treatments were implemented, suggesting that below-surface fauna responsible for soil biological activity (including earthworms, isopods, micro-organisms, and termites) (Van Gestel et al. 2003; Filzek et al. 2004; Römbke et al. 2006; Gongalsky et al. 2008) is indicating more rapid recovery compared to the taxa examined in this study (i.e., ants and springtails).

Therefore, for optimal soil biodiversity conservation, I recommend a multi-taxon approach (Pryke and Samways 2012a; Yekwayo et al. 2018), that is, examining several arthropod taxa with different habitat requirements and traits sharing the same habitat stratum (Kotze and Samways 1999), to gain a better understanding of the response and recovery of different soil arthropods to disturbances, and to enhanced management and conservation strategies for soil biodiversity (Pressler et al. 2019). It should also be noted that this study (Chapter 5) only examined the immediate and short-term recovery success of ant and springtails after the implementation of common residue management practices within a timber production landscape. In the short-term, I found that it makes no difference which residue management practice is used, regardless of the inclusion or exclusion of fire nor whether residue is retained and/or removed. Even after a year, the most sustainable practice in this context could not be identified. However, the study period (Chapter 5) may have been too short to fully examine recovery and resilience of soil arthropod communities to confidently recommend the most sustainable residue management practice in this type of context, as suggested by Bengtsson (2002). I thus recommend that studies examining the effects of residue management monitor the recovery of these assemblages over a longer time period to enable us to determine whether there are legacy effects of the different management practices on the soil fauna and the functioning of the soil, which is inherently linked (Yan et al. 2012; Orgiazzi et al. 2016).

Additionally, soil resilience (i.e., capacity of soil to recover functional and structural integrity after a disturbance) (Adaikwu et al. 2017; Ludwig et al. 2018) is linked to soil type (Kawy and Ali 2012; Lal 2015). Nadel et al. (2007), for example, encouraged the continuous use of fire as a management tool in *Eucalyptus* plantations. It is important to note, that their findings and mine (Chapter 5), are based on studies conducted on clay soils. As in Nadel et al. (2007), I show that residue management practices which include the use of fire is acceptable on clay soils. Others have found clay soils are more resilient to disturbances in comparison to other soil types, such as sandy soils (Prasad and Power 1997; Smith and Du Toit 2005; Titshall et al. 2013). Soil types respond differently to disturbances (Rietz 2010), mostly due to their differences of their chemical and physical characteristics (Searle and Bitnere 2017). Therefore, as the resilience of soils may be specific to the soil type in question (Adaikwu et al. 2017), soils that are not able to buffer disturbances are at greater risk of soil degradation (Dovey et al. 2011). Therefore, as we are losing our soils and soil biodiversity is declining (Wall et al. 2015), expanding research across a range of major soil types is crucial to make soil type-based recommendations to efficiently manage our soils and their functioning (Kome et al. 2018; de Paul Obade et al. 2019; Amelung et al. 2020), both locally (Rietz 2010), and globally.

6.5. Concluding remarks

The overall purpose of this dissertation was to gain an in-depth understanding of two important soil arthropod taxa, namely ants (Formicidae) and springtails (Collembola), regarding their diversity, distribution and responses to land-use and management practices, within South African forestry landscapes which comprise mosaics of remnant natural habitat along with timber production areas. As expected, I show that soil arthropod taxa, more specifically ants and springtails, respond differentially to landuse cover and environmental gradients, and that these responses are region-specific. Additionally, I show that small-scale factors (e.g. variations in soil and habitat properties) play a greater role than landscape-scale factors. This was expected given how these taxa are dependent on the soil environment for their survival. What I did not expect to find, was that these plantation compartments can have similar levels of taxonomic and functional alpha-diversity, and that there are species adapted to persist and surive within these transformed conditions. This highlights the crucial need for sustainable management practices within the compartments to ensure the continued presence of these organisms, and their important functional roles. To address this, I examined the effect of different residue management practices on these taxa, as it forms a major part of nutrient management within these compartments for future rotations. Here, I focused on management practices which are most common within the industry and either includes or excludes the use of fire. Contrary to expectations, the selected residue management practices equally affected the abundance, taxonomic and functional alpha-diversity of ants and springtails directly after implementation, and showed no difference between treatments a year after. Therefore, within this landscape-context and on this specific soil type (i.e. clay soils), either of these studied residue management practices can be implemented, as they show no short-term differences.

In conclusion, although there is still much to examine and understand about soil arthropods and their functioning, my dissertation makes a significant contribution within the soil ecology community by addressing some research gaps and shortfalls regarding soil biodiversity. The results (summarized in Fig. 6.1) and recommendations (summarized in Fig 6.2) made throughout this dissertation can be used as base-line information on how best to conserve and maintain functionally important soil taxa within a timber production landscape, ensuring the continued functioning of their soils.

Conservation of ant (Formicidae) and springtail (Collembola) diversity in South African timber production landscapes

Grassland

Forest

Large remnant areas conserve critical soil biodiversity

Remnant areas exhibit high biodiversity and functional value within timber-plantation landscapes, containing rare and unique species that do not occur elsewhere in the landscape. Assemblages differed between these natural areas within and between regions, with species traits being context- and regionally-specific. With high soil biological activity, taxonomic and functional alpha diversity, the land-sparing approach is effective for conserving soil arthropod taxa that are not capable of persisting or surviving within the disturbed, intensively managed areas.

Timber plantations support unexpectedly high soil biodiversity

Although not true extensions of remnant areas, plantations can have similar levels of ant and springtail taxonomic and functional alpha-diversity. Assemblages within the compartments are also composed of species with varied adaptations to survive within those conditions. This may have contributed to their high functional diversity estimates, which indicate seemingly high levels of ecosystem stability and functioning. Additionally, although assemblage composition differed between natural and planted areas, the plantation compartments did not lead to large-scale homogenization of soil biodiversity as expected, given their high beta-diversity and large contribution of species turnover between the plantation compartments.

Pine

Eucalypt

Environment

The importance of environmental heterogeneity for soil biodiversity conservation

Conservation practices for aboveground biodiversity may be insufficient to conserve belowground biodiversity. Therefore, finding common drivers of soil biodiversity, could be used as indicators for soil biodiversity hotspots. However, no common environmental drivers could be found for taxa within and between biotopes, nor across regions. This builds on the fact that different taxonomic and functional groups responding differentially to environmental drivers. Small-scale environmental heterogeneity, especially in terms of plant and soil related variables, is therefore important to these functionally important taxa, and perhaps others, to conserve the most diversity. Promoting environmental heterogeneity would therefore enable more species to persist and/or co-exist, which could contribute to enhanced ecosystem functioning.

Soil faunal diversity and activity response to timber residue management practices

Management practices which have destructive effects on the topsoil layer should be avoided at all costs, as it can have detrimental effects on the functioning and productivity of the soils. Here, regardless of the inclusion or exclusion of fire as a management tool, the effects of residue management treatment, whether retention, removing, stacking (with burning) or spreading (with burning) was equally strong, resulting in no difference directly after the practices were implemented. Furthermore, one year after the management treatments had been implemented, there was still no significant difference between the residue management treatments. On the contrary, soil biological activity showed signs of recovery a year after the implementation of management practices, although was not significantly different between treatments. Arthropods within the deeper layers of the soil, which were responsible for biological activity measurements, may have not been as severely impacted by the management treatments as the focal taxa of this study.

Management

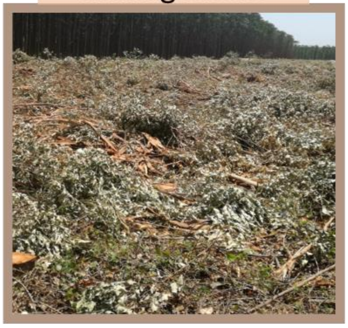
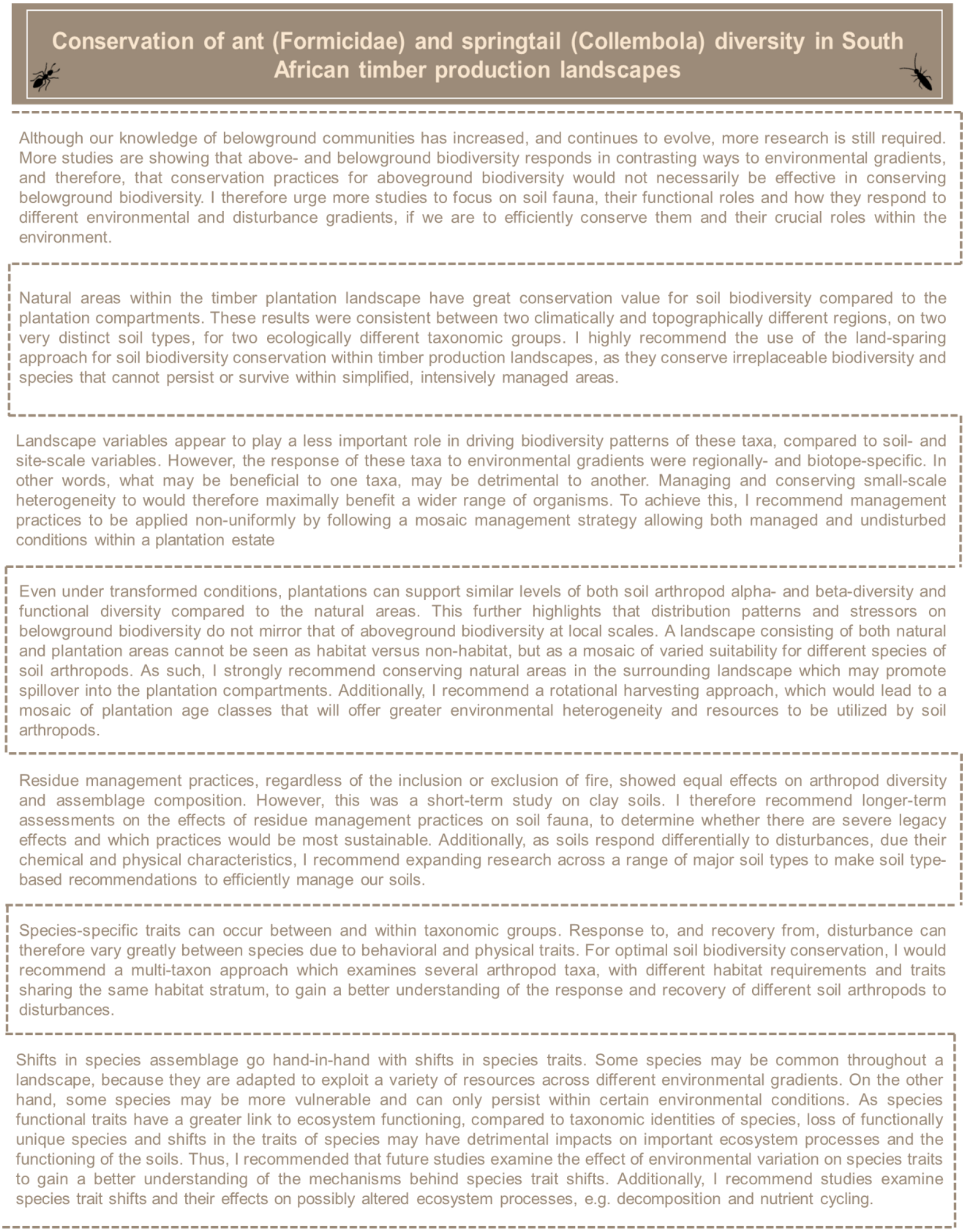


Figure 6.1 Summary of overall findings of the dissertation.



Conservation of ant (Formicidae) and springtail (Collembola) diversity in South African timber production landscapes

Although our knowledge of belowground communities has increased, and continues to evolve, more research is still required. More studies are showing that above- and belowground biodiversity responds in contrasting ways to environmental gradients, and therefore, that conservation practices for aboveground biodiversity would not necessarily be effective in conserving belowground biodiversity. I therefore urge more studies to focus on soil fauna, their functional roles and how they respond to different environmental and disturbance gradients, if we are to efficiently conserve them and their crucial roles within the environment.

Natural areas within the timber plantation landscape have great conservation value for soil biodiversity compared to the plantation compartments. These results were consistent between two climatically and topographically different regions, on two very distinct soil types, for two ecologically different taxonomic groups. I highly recommend the use of the land-sparing approach for soil biodiversity conservation within timber production landscapes, as they conserve irreplaceable biodiversity and species that cannot persist or survive within simplified, intensively managed areas.

Landscape variables appear to play a less important role in driving biodiversity patterns of these taxa, compared to soil- and site-scale variables. However, the response of these taxa to environmental gradients were regionally- and biotope-specific. In other words, what may be beneficial to one taxa, may be detrimental to another. Managing and conserving small-scale heterogeneity to would therefore maximally benefit a wider range of organisms. To achieve this, I recommend management practices to be applied non-uniformly by following a mosaic management strategy allowing both managed and undisturbed conditions within a plantation estate

Even under transformed conditions, plantations can support similar levels of both soil arthropod alpha- and beta-diversity and functional diversity compared to the natural areas. This further highlights that distribution patterns and stressors on belowground biodiversity do not mirror that of aboveground biodiversity at local scales. A landscape consisting of both natural and plantation areas cannot be seen as habitat versus non-habitat, but as a mosaic of varied suitability for different species of soil arthropods. As such, I strongly recommend conserving natural areas in the surrounding landscape which may promote spillover into the plantation compartments. Additionally, I recommend a rotational harvesting approach, which would lead to a mosaic of plantation age classes that will offer greater environmental heterogeneity and resources to be utilized by soil arthropods.

Residue management practices, regardless of the inclusion or exclusion of fire, showed equal effects on arthropod diversity and assemblage composition. However, this was a short-term study on clay soils. I therefore recommend longer-term assessments on the effects of residue management practices on soil fauna, to determine whether there are severe legacy effects and which practices would be most sustainable. Additionally, as soils respond differentially to disturbances, due their chemical and physical characteristics, I recommend expanding research across a range of major soil types to make soil type-based recommendations to efficiently manage our soils.

Species-specific traits can occur between and within taxonomic groups. Response to, and recovery from, disturbance can therefore vary greatly between species due to behavioral and physical traits. For optimal soil biodiversity conservation, I would recommend a multi-taxon approach which examines several arthropod taxa, with different habitat requirements and traits sharing the same habitat stratum, to gain a better understanding of the response and recovery of different soil arthropods to disturbances.

Shifts in species assemblage go hand-in-hand with shifts in species traits. Some species may be common throughout a landscape, because they are adapted to exploit a variety of resources across different environmental gradients. On the other hand, some species may be more vulnerable and can only persist within certain environmental conditions. As species functional traits have a greater link to ecosystem functioning, compared to taxonomic identities of species, loss of functionally unique species and shifts in the traits of species may have detrimental impacts on important ecosystem processes and the functioning of the soils. Thus, I recommended that future studies examine the effect of environmental variation on species traits to gain a better understanding of the mechanisms behind species trait shifts. Additionally, I recommend studies examine species trait shifts and their effects on possibly altered ecosystem processes, e.g. decomposition and nutrient cycling.

Figure 6.2 Summary of recommendations based on findings of the dissertation.

6.6. References

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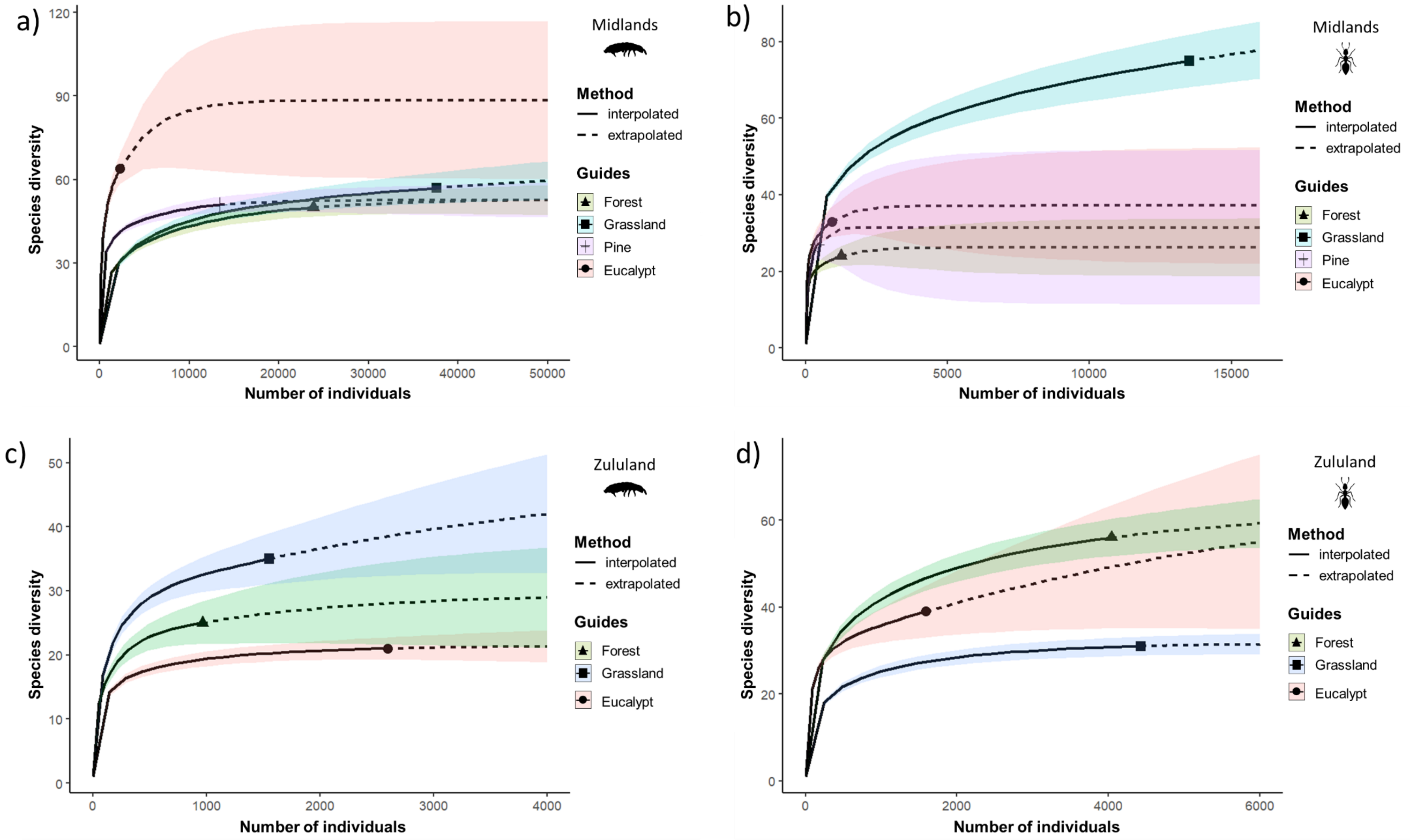
Appendix A Species accumulation curves of all species collected across all biotopes (indigenous forest, grassland, pine and eucalypt compartments) in the Midlands and Zululand. Midlands illustrated as a) springtails, and b) ants, with Zululand illustrated as c) springtails and d) ants.



Appendix B Environmental variables included in uni- and multi-variate models based on environmental parameter elimination using VIF ≤ 3. Environmental variables categorized into landscape, site and soil variables for each region. Uni- and multi-variate models were conducted separately for ants and springtails, within the indigenous forests and grasslands for the Midlands and Zululand.

Dataset	Description	Landscape variables	Site variables	Soil variables
Midlands Forest	Within biotope	Site slope (°), site aspect, site elevation (m), site terrain roughness index (TRI) and focal biotope (%) and transformed biotope (%)	Rock cover (%), deadwood cover (%), shade cover (%), vegetation height (m), number of plant species, leaf litter cover (%), shrub cover (%) and grass cover (%)	Soil moisture (%), soil compaction (psi), soil pH, P (mg/kg), C (mg/kg) and N (mg/kg)
Midlands Grassland	Within biotope	Site slope (°), site aspect, site elevation (m), site terrain roughness index (TRI) and focal biotope (%)	Rock cover (%), vegetation height (m), number of plant species, leaf litter cover (%), herbaceous cover (%), shrub cover (%) and bare ground cover (%)	Soil moisture (%), soil compaction (psi), soil pH, P (mg/kg), C (mg/kg), N (mg/kg) and S (mg/kg)
Zululand Forest	Within biotope	Site slope (°), site aspect, site elevation (m) and focal biotope (%)	Shade cover (%), vegetation height (m), number of plant species, leaf litter cover (%), shrub cover (%), grass cover (%) and bare ground cover (%)	Soil moisture (%), soil compaction (psi), soil pH, P (mg/kg), C (mg/kg), N (mg/kg) and S (mg/kg)
Zululand Grassland	Within biotope	Site slope (°), site aspect, site elevation (m), site terrain roughness index (TRI) and focal biotope (%)	Vegetation height (m), number of plant species, leaf litter cover (%), herbaceous cover (%) and bare ground cover (%)	Soil moisture (%), soil compaction (psi), soil pH, P (mg/kg), C (mg/kg) and N (mg/kg)

Appendix C Ants recorded during the study period. Sub-family and genus of each collected specimen is indicated, along with the mean abundance ± standard error (SE) for indigenous forests (For), grasslands (Grass), pine (Pine) and eucalypt (Euc) compartments within the Midlands and Zululand.

			Midlands								**Zululand**					
ID	**Sub-family**	**Genus**	**For**		**Grass**		**Pine**		**Euc**		**For**		**Grass**		**Euc**	
			Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
sp012F	Myrmicinae	Monomorium sp. 1	7.56	2.18	12.78	3.37	3.44	2.02	3.89	1.44	11.22	6.91	14.06	3.07	27.56	9.26
sp013F	Myrmicinae	Tetramorium sp. 1	12.17	3.31	23.61	21.08	6.61	1.27	1.22	0.57	16.78	4.40	1.78	0.95	4.00	1.53
sp014F	Myrmicinae	Strumigenys sp. 1	1.39	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp015C	Ponerinae	Leptogenys sp. 1	2.11	1.08	0.11	0.11	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp020F	Myrmicinae	Monomorium sp. 2	0.67	0.35	0.00	0.00	0.78	0.72	4.61	2.68	4.89	2.29	0.06	0.06	1.78	0.76
sp021F	Ponerinae	Bothroponera sp. 1	4.67	1.14	4.06	0.90	0.28	0.23	1.06	0.83	0.56	0.29	0.94	0.26	1.11	0.40
sp022F	Ponerinae	Leptogenys sp. 2	14.39	4.35	0.00	0.00	0.00	0.00	1.72	0.80	6.06	2.02	1.33	0.73	3.56	0.81
sp033F	Myrmicinae	Tetramorium sp. 2	2.89	0.98	0.28	0.14	0.17	0.17	8.89	2.11	9.11	3.51	9.89	2.33	5.50	2.92
sp034F	Myrmicinae	Trichomyrmex sp. 1	4.11	1.32	3.22	1.43	0.00	0.00	8.28	2.84	85.78	45.01	92.50	31.46	13.83	3.45
sp035F	Formicinae	Paratrechina sp. 1	1.06	0.45	1.17	0.49	0.67	0.35	1.83	0.66	4.44	1.61	17.78	5.16	0.78	0.34
sp036F	Myrmicinae	Crematogaster sp. 1	2.94	1.35	21.61	18.99	0.06	0.06	0.00	0.00	0.00	0.00	0.17	0.12	0.00	0.00
sp044F	Formicinae	Camponotus sp. 1	2.11	0.48	3.44	1.59	0.06	0.06	0.28	0.19	2.11	0.77	3.50	1.17	0.56	0.20
sp052F	Myrmicinae	Crematogaster sp. 2	1.78	0.97	0.39	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp065F	Myrmicinae	Crematogaster sp. 3	1.67	1.50	4.06	1.56	1.11	0.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp067F	Myrmicinae	Crematogaster sp. 4	0.11	0.08	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp070F	Myrmicinae	Crematogaster sp. 5	1.94	1.30	8.56	4.88	0.00	0.00	0.00	0.00	1.56	0.65	0.00	0.00	0.00	0.00
sp077F	Formicinae	Camponotus sp. 2	6.78	1.76	169.61	44.31	0.33	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp086F	Dorylinae	Aenictus sp. 1	0.06	0.06	0.28	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.28	0.00	0.00
sp087F	Formicinae	Camponotus sp. 3	0.00	0.00	116.28	41.98	0.17	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp088F	Formicinae	Camponotus sp. 4	0.00	0.00	91.28	25.69	0.17	0.12	0.17	0.09	0.00	0.00	0.00	0.00	0.00	0.00
sp093F	Myrmicinae	Meranoplus sp. 1	0.06	0.06	137.72	54.87	0.06	0.06	0.89	0.67	0.00	0.00	0.00	0.00	0.00	0.00
sp094F	Myrmicinae	Strumigenys sp. 2	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp095F	Formicinae	Plagiolepis sp. 1	0.00	0.00	21.67	18.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp096F	Myrmicinae	Tetramorium sp. 3	0.00	0.00	2.78	1.39	0.00	0.00	0.83	0.83	0.00	0.00	0.00	0.00	0.78	0.78
sp097F	Myrmicinae	Tetramorium sp. 4	0.00	0.00	15.39	12.75	0.78	0.51	0.00	0.00	0.44	0.39	4.61	2.02	2.67	2.67
sp099F	Ponerinae	Paltothyreus sp. 1	0.00	0.00	0.83	0.34	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp100F	Ponerinae	Paltothyreus sp. 2	0.00	0.00	0.61	0.20	0.00	0.00	0.00	0.00	0.22	0.22	0.00	0.00	0.00	0.00
sp101F	Dolichoderinae	Tapinoma sp. 1	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp102F	Myrmicinae	Tetramorium sp. 5	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp125F	Formicinae	Camponotus sp. 5	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.17	0.12	0.00	0.00	0.00	0.00
sp126F	Formicinae	Camponotus sp. 6	0.00	0.00	0.94	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp127F	Formicinae	Camponotus sp. 7	0.00	0.00	2.78	1.32	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.67	0.67
sp128F	Myrmicinae	Tetramorium sp. 6	0.00	0.00	0.22	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp129F	Myrmicinae	Tetramorium sp. 7	0.11	0.11	6.00	2.70	0.17	0.17	0.61	0.56	0.78	0.45	0.56	0.40	0.56	0.32
sp130F	Formicinae	Lepisiota sp. 1	0.28	0.16	3.17	1.02	0.56	0.25	2.22	0.87	0.89	0.32	1.72	1.44	1.56	1.01
sp142F	Formicinae	Camponotus sp. 8	0.00	0.00	0.33	0.28	0.00	0.00	0.06	0.06	0.00	0.00	0.06	0.06	0.00	0.00
sp143F	Myrmicinae	Tetramorium sp. 8	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp144F	Formicinae	Camponotus sp. 9	0.00	0.00	0.50	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp145F	Formicinae	Plagiolepis sp. 2	0.00	0.00	0.50	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.28
sp165F	Formicinae	Camponotus sp. 10	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp166F	Myrmicinae	Pheidole sp. 1	0.00	0.00	0.11	0.11	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00
sp167F	Myrmicinae	Crematogaster sp. 6	0.00	0.00	0.39	0.28	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix C continued

ID	Sub-family	Genus	Midlands								Zululand					
			For		Grass		Pine		Euc		For		For		Grass	
			Mean	SE	Mean	SE	Mean	Mean	SE	SE	Mean	SE	Mean	SE	Mean	SE
sp168F	Myrmicinae	Trichomyrmex sp. 2	0.00	0.00	0.67	0.40	0.00	0.00	3.11	2.15	0.00	0.00	0.00	0.00	1.50	1.50
sp169F	Myrmicinae	Crematogaster sp. 7	0.00	0.00	19.83	6.30	0.00	0.00	0.50	0.44	0.00	0.00	0.00	0.00	0.28	0.23
sp170F	Myrmicinae	Solenopsis sp. 1	0.00	0.00	4.17	2.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp171F	Myrmicinae	Solenopsis sp. 2	0.00	0.00	19.17	9.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp172F	Myrmicinae	Pheidole sp. 2	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp190F	Formicinae	Lepisiota sp. 2	0.00	0.00	1.00	0.73	0.06	0.06	0.00	0.00	0.00	0.00	0.11	0.08	0.06	0.06
sp191F	Myrmicinae	Monomorium sp. 3	0.00	0.00	0.28	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp200F	Formicinae	Camponotus sp. 11	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp201F	Formicinae	Camponotus sp. 12	0.00	0.00	2.44	1.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp202F	Myrmicinae	Tetramorium sp. 9	0.00	0.00	2.39	1.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp203F	Myrmicinae	Tetramorium sp. 10	0.00	0.00	13.56	9.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp204F	Ponerinae	Parasyscia sp. 1	0.33	0.20	0.44	0.27	0.11	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp205F	Myrmicinae	Solenopsis sp. 3	0.00	0.00	1.00	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp206F	Myrmicinae	Crematogaster sp. 8	0.00	0.00	0.17	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp207F	Myrmicinae	Solenopsis sp. 4	0.00	0.00	1.06	0.85	0.11	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp208F	Formicinae	Lepisiota sp. 3	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp209F	Formicinae	Lepisiota sp. 4	0.06	0.06	2.39	0.95	0.17	0.09	2.17	1.22	0.00	0.00	0.00	0.00	0.00	0.00
sp210F	Dolichoderinae	Tapinoma sp. 2	0.00	0.00	0.17	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp211F	Myrmicinae	Pheidole sp. 3	0.00	0.00	0.17	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp212F	Myrmicinae	Crematogaster sp. 9	0.00	0.00	10.67	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp213F	Myrmicinae	Trichomyrmex sp. 3	0.39	0.39	5.39	3.03	0.00	0.00	2.50	1.18	0.00	0.00	0.00	0.00	1.72	1.72
sp226F	Myrmicinae	Pheidole sp. 4	0.00	0.00	0.22	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp227F	Myrmicinae	Crematogaster sp. 10	0.00	0.00	4.94	1.98	4.11	0.99	0.11	0.08	0.00	0.00	0.00	0.00	0.00	0.00
sp231F	Myrmicinae	Tetramorium sp. 11	0.00	0.00	0.11	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp232F	Myrmicinae	Tetramorium sp. 12	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp233F	Myrmicinae	Crematogaster sp. 11	0.00	0.00	0.11	0.08	0.00	0.00	0.00	0.00	1.89	1.89	0.00	0.00	0.00	0.00
sp234F	Myrmicinae	Tetramorium sp. 13	0.00	0.00	2.06	1.78	2.22	0.76	0.50	0.29	2.61	1.83	0.11	0.11	0.00	0.00
sp235F	Formicinae	Lepisiota sp. 5	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp240F	Formicinae	Lepisiota sp. 6	0.00	0.00	1.61	0.82	0.11	0.08	1.44	0.92	0.00	0.00	0.00	0.00	0.00	0.00
sp246F	Formicinae	Camponotus sp. 13	0.00	0.00	0.17	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp247F	Formicinae	Camponotus sp. 14	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.11	0.11	0.61	0.23	0.94	0.45
sp254F	Myrmicinae	Solenopsis sp. 5	0.00	0.00	0.00	0.00	0.17	0.12	0.67	0.46	0.00	0.00	0.00	0.00	0.00	0.00
sp258F	Myrmicinae	Monomorium sp. 4	0.00	0.00	0.00	0.00	0.11	0.11	1.56	0.62	5.17	3.19	0.00	0.00	0.00	0.00
sp284F	Formicinae	Paratrechina sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp289F	Myrmicinae	Pheidole sp. 5	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp294F	Formicinae	Plagiolepis sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.46	0.22	0.17	0.00	0.00	0.00	0.00
sp301F	Myrmicinae	Tetramorium sp. 14	0.00	0.00	0.17	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp302F	Formicinae	Paratrechina sp. 3	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp324F	Formicinae	Lepisiota sp. 7	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.39	0.00	0.00	0.00	0.00	0.00	0.00
sp325F	Myrmicinae	Tetramorium sp. 15	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.08	0.00	0.00	0.00	0.00	0.00	0.00
sp326F	Myrmicinae	Tetramorium sp. 16	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.11	0.00	0.00	0.00	0.00	0.00	0.00
sp329F	Myrmicinae	Strumigenys sp. 3	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp331F	Myrmicinae	Tetramorium sp. 17	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp332F	Formicinae	Lepisiota sp. 8	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp337F	Proceratiinae	Probolomyrmex sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.56	0.35	0.06	0.06	0.00	0.00	0.11	0.11

Appendix C continued

			Midlands								Zululand					
ID	Sub-family	Genus	For		Grass		Pine		Euc		For		For		Grass	
			Mean	SE	Mean	SE	Mean	Mean	SE	SE	Mean	SE	Mean	SE	Mean	SE
sp344F	Myrmicinae	Tetramorium sp. 18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	2.44
sp345F	Myrmicinae	Trichomyrmex sp. 4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.29	0.00	0.00	0.06	0.06
sp346F	Formicinae	Plagiolepis sp. 4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.50	0.70	2.78	2.06	0.00	0.00
sp347F	Formicinae	Camponotus sp. 15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00
sp348F	Myrmicinae	Tetramorium sp. 19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	1.77	2.22	2.22	0.22	0.22
sp349F	Myrmicinae	Myrmicaria sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	25.17	14.48	40.17	14.66	4.22	1.69
sp350F	Myrmicinae	Trichomyrmex sp. 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.28	0.28	0.23	2.11	2.11
sp351F	Ponerinae	Bothroponera sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.12	0.00	0.00	0.39	0.24
sp352F	Formicinae	Paratrechina sp. 4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.17	0.22	0.22	0.00	0.00
sp353F	Ponerinae	Bothroponera sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.56	0.28	0.61	0.23	1.39	0.80
sp355F	Dorylinae	Aenictus sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.15	0.61	0.45
sp356F	Ponerinae	Leptogenys sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.06	1.59	2.00	0.74	3.06	1.29
sp358F	Myrmicinae	Trichomyrmex sp. 6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	44.44	18.03	0.00	0.00
sp359F	Formicinae	Lepisiota sp. 9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06
sp360F	Myrmicinae	Tetramorium sp. 20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.11	0.00	0.00	2.44	1.26
sp361F	Ponerinae	Parasyscia sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06
sp362F	Myrmicinae	Pheidole sp. 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06
sp363F	Myrmicinae	Pheidole sp. 6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.67	2.11	1.09	0.06	0.06
sp364F	Myrmicinae	Solenopsis sp. 6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.39	8.40	0.00	0.00	1.00	0.65
sp366F	Formicinae	Polyrhachis sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06
sp367F	Formicinae	Polyrhachis sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.11	0.08	0.06	0.06
sp368F	Formicinae	Lepisiota sp. 10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.61	1.12	0.44	0.44	0.17	0.17
sp370F	Formicinae	Anoplolepis sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.22	0.00	0.00
sp381F	Myrmicinae	Cataulacus sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.08	0.00	0.00	0.00	0.00
sp381F	Myrmicinae	Cataulacus sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.08	0.00	0.00	0.00	0.00
sp382F	Myrmicinae	Crematogaster sp. 12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.17	0.00	0.00	0.00	0.00
sp383F	Myrmicinae	Tetramorium sp. 21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.44	3.29	0.00	0.00	0.00	0.00
sp384F	Ponerinae	Anochetus sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00
sp385F	Proceratiinae	Probolomyrmex sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.44	0.00	0.00	0.00	0.00
sp387F	Formicinae	Polyrhachis sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00
sp388F	Myrmicinae	Tetramorium sp. 22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.67	1.15	0.00	0.00	0.00	0.00
sp389F	Ponerinae	Bothroponera sp. 4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.08	0.00	0.00	0.00	0.00
sp390F	Proceratiinae	Discothyrea sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.08	0.00	0.00	0.00	0.00
sp391F	Ponerinae	Parasyscia sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00
sp392F	Dolichoderinae	Tapinoma sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.11	1.11	0.00	0.00	0.00	0.00
sp394F	Dolichoderinae	Tapinoma sp. 4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.22	3.22	0.00	0.00	0.00	0.00
sp395F	Myrmicinae	Tetramorium sp. 23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.22	0.00	0.00	0.00	0.00
sp396F	Ponerinae	Boloponera sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00
sp398F	Ponerinae	Bothroponera sp. 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00
sp399F	Formicinae	Anoplolepis sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.54	0.00	0.00	0.00	0.00
sp400F	Formicinae	Camponotus sp. 16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.17	0.00	0.00	0.00	0.00
sp401F	Ponerinae	Hypoponera sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.17	0.00	0.00	0.00	0.00
sp402F	Dorylinae	Aenictus sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.08	0.00	0.00	0.00	0.00

Appendix D Springtails recorded during the study period. Sub-order and family of each collected specimen is indicated, along with the mean abundance ± standard error (SE) for indigenous forests (For), grasslands (Grass), pine (Pine) and eucalypt (Euc) compartments within the Midlands and Zululand.

			Midlands								**Zululand**					
ID	**Sub-order**	**Family**	**For**		**Grass**		**Pine**		**Euc**		**For**		**For**		**Grass**	
			Mean	**SE**	**Mean**	**SE**	**Mean**	**Mean**	**SE**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
sp001C	Poduromorpha	Onychiuridae sp.1	546.28	378.36	0.56	0.50	1.17	0.85	5.06	4.48	0.72	0.67	0.00	0.00	6.44	6.05
sp002C	Entomobryomorpha	Entomobryidae sp.1	2.17	0.64	2.56	0.76	47.00	10.89	2.11	0.75	0.00	0.00	0.00	0.00	0.00	0.00
sp005C	Entomobryomorpha	Entomobryidae sp.2	199.17	140.66	10.33	2.12	78.56	23.89	7.78	2.11	13.89	3.11	32.83	9.74	36.61	7.85
sp006C	Poduromorpha	Hypogastruridae sp.1	96.50	23.96	121.39	87.68	213.11	60.84	33.83	4.95	0.00	0.00	0.00	0.00	0.00	0.00
sp023C	Symphypleona	Dicyrtomidae sp.1	6.06	2.65	1.44	0.44	1.00	0.66	2.94	0.72	1.39	0.62	0.89	0.50	0.00	0.00
sp024C	Symphypleona	Sminthuridae sp.1	0.17	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp027C	Entomobryomorpha	Entomobryidae sp.3	1.33	0.50	177.06	175.47	1.83	0.56	0.94	0.52	0.00	0.00	0.17	0.17	0.00	0.00
sp028C	Entomobryomorpha	Isotomidae sp.1	245.11	97.28	1332.50	453.72	52.00	25.97	7.06	3.31	11.67	8.40	18.11	7.91	58.22	22.42
sp049C	Entomobryomorpha	Entomobryidae sp.4	0.78	0.29	1.44	0.95	3.61	3.44	0.00	0.00	0.00	0.00	0.39	0.24	0.00	0.00
sp050C	Entomobryomorpha	Entomobryidae sp.5	0.67	0.20	2.22	1.99	3.94	3.37	0.11	0.08	0.00	0.00	0.00	0.00	0.00	0.00
sp051C	Symphypleona	Dicyrtomidae sp.2	38.17	15.43	104.39	86.68	24.17	14.72	1.33	0.56	2.94	1.06	1.00	0.35	6.50	3.07
sp060C	Entomobryomorpha	Entomobryidae sp.6	4.44	2.09	0.11	0.08	11.89	6.36	4.00	1.26	0.06	0.06	0.33	0.33	0.11	0.11
sp064C	Entomobryomorpha	Entomobryidae sp.7	0.11	0.08	0.22	0.13	0.28	0.28	0.06	0.06	0.22	0.22	0.00	0.00	0.00	0.00
sp069C	Symphypleona	Dicyrtomidae sp.3	0.28	0.19	1.00	0.49	8.22	7.28	0.22	0.22	0.00	0.00	0.00	0.00	0.00	0.00
sp072C	Entomobryomorpha	Entomobryidae sp.8	1.06	0.47	2.61	1.18	3.72	2.26	0.00	0.00	8.78	2.07	1.39	0.53	7.89	3.31
sp073C	Entomobryomorpha	Entomobryidae sp.9	0.72	0.48	1.78	0.92	1.50	0.69	0.00	0.00	0.17	0.17	0.06	0.06	0.17	0.17
sp074C	Entomobryomorpha	Entomobryidae sp.10	0.94	0.38	0.22	0.13	0.83	0.37	0.00	0.00	0.67	0.67	0.00	0.00	0.94	0.54
sp080C	Symphypleona	Katiannidae sp.1	0.11	0.08	12.17	10.43	8.11	4.51	1.83	0.67	0.00	0.00	2.83	1.77	0.17	0.12
sp089C	Entomobryomorpha	Entomobryidae sp.11	0.06	0.06	4.11	2.42	0.22	0.17	1.00	0.65	0.00	0.00	0.00	0.00	0.00	0.00
sp090C	Symphypleona	Dicyrtomidae sp.4	0.00	0.00	0.50	0.32	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp092C	Entomobryomorpha	Entomobryidae sp.12	0.00	0.00	1.17	0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.28	0.00	0.00
sp111C	Symphypleona	Katiannidae sp.2	0.00	0.00	0.22	0.13	0.00	0.00	0.17	0.12	0.00	0.00	0.00	0.00	0.00	0.00
sp112C	Entomobryomorpha	Entomobryidae sp.13	2.28	0.99	5.22	1.12	3.72	1.03	0.56	0.32	2.72	0.89	1.00	0.42	4.00	0.91
sp113C	Symphypleona	Dicyrtomidae sp.5	0.00	0.00	0.94	0.53	0.11	0.11	0.22	0.17	0.00	0.00	0.33	0.23	2.72	2.66
sp114C	Poduromorpha	Hypogastruridae sp.2	0.11	0.11	4.89	3.19	0.56	0.40	0.11	0.08	1.39	0.95	0.22	0.15	0.72	0.72
sp117C	Poduromorpha	Hypogastruridae sp.3	0.00	0.00	25.50	22.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp118C	Entomobryomorpha	Isotomidae sp.2	0.00	0.00	0.78	0.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp119C	Symphypleona	Dicyrtomidae sp.6	0.00	0.00	0.17	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp120C	Poduromorpha	Hypogastruridae sp.4	0.00	0.00	0.06	0.06	0.00	0.00	0.28	0.28	0.00	0.00	0.00	0.00	0.00	0.00
sp131C	Poduromorpha	Neanuridae sp.1	0.17	0.17	10.06	6.64	0.56	0.56	0.72	0.61	0.00	0.00	7.17	4.84	1.00	0.63
sp132C	Poduromorpha	Hypogastruridae sp.5	106.94	37.28	226.89	174.71	136.39	42.08	18.28	4.66	2.61	1.36	2.89	2.66	0.22	0.22
sp133C	Entomobryomorpha	Isotomidae sp.3	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.00	8.00
sp160C	Entomobryomorpha	Entomobryidae sp.14	0.00	0.00	0.28	0.16	13.61	13.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp161C	Entomobryomorpha	Entomobryidae sp.15	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp162C	Entomobryomorpha	Entomobryidae sp.16	3.33	1.97	1.56	0.44	39.56	14.21	8.72	2.81	0.00	0.00	1.89	1.49	1.83	1.30
sp163C	Entomobryomorpha	Entomobryidae sp.17	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp180C	Symphypleona	Sminthuridae sp.2	0.06	0.06	10.89	10.71	0.00	0.00	0.56	0.45	0.00	0.00	3.00	1.66	0.00	0.00
sp181C	Symphypleona	Katiannidae sp.3	0.17	0.17	0.44	0.35	0.00	0.00	0.22	0.22	0.00	0.00	0.00	0.00	0.00	0.00
sp182C	Symphypleona	Sminthuridae sp.4	0.11	0.08	7.06	6.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp183C	Symphypleona	Katiannidae sp.4	0.33	0.20	0.61	0.26	1.06	1.06	0.22	0.17	0.00	0.00	1.33	0.66	0.00	0.00
sp196C	Entomobryomorpha	Entomobryidae sp.18	0.00	0.00	0.44	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.17	0.00	0.00
sp197C	Symphypleona	Katiannidae sp.5	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp198C	Entomobryomorpha	Entomobryidae sp.19	0.00	0.00	0.28	0.14	10.83	10.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

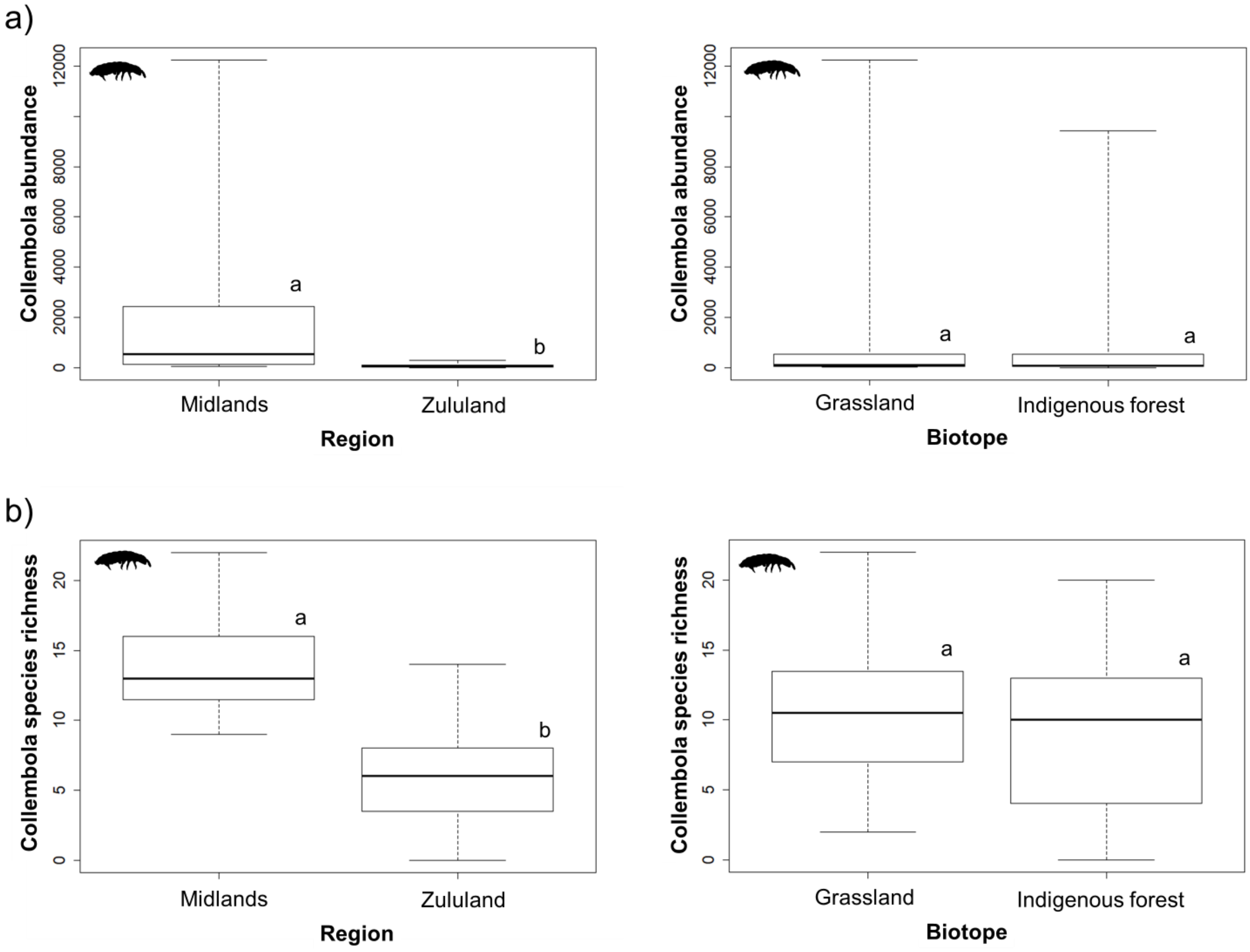
Appendix D continued

ID	Sub-family	Genus	Midlands								Zululand					
			For		Grass		Pine		Euc		For		For		Grass	
			Mean	SE	Mean	SE	Mean	Mean	SE	SE	Mean	SE	Mean	SE	Mean	SE
sp219C	Symphypleona	Katiannidae sp.6	0.00	0.00	0.56	0.35	1.67	1.61	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp220C	Poduromorpha	Odontellidae sp.1	36.67	25.07	11.72	8.25	0.00	0.00	0.33	0.33	1.83	1.78	0.00	0.00	0.00	0.00
sp221C	Entomobryomorpha	Entomobryidae sp.20	0.00	0.00	1.17	0.95	2.61	0.99	0.17	0.12	0.00	0.00	0.00	0.00	0.00	0.00
sp228C	Entomobryomorpha	Isotomidae sp.4	0.00	0.00	0.28	0.23	0.00	0.00	0.44	0.26	0.00	0.00	0.00	0.00	0.00	0.00
sp244C	Entomobryomorpha	Entomobryidae sp.21	0.00	0.00	0.28	0.23	0.89	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp250C	Entomobryomorpha	Entomobryidae sp.22	0.17	0.12	0.00	0.00	0.11	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp251C	Entomobryomorpha	Entomobryidae sp.23	0.00	0.00	0.06	0.06	0.44	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp252C	Symphypleona	Sminthuridae sp.3	0.06	0.06	0.28	0.28	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp253C	Entomobryomorpha	Entomobryidae sp.24	0.00	0.00	0.00	0.00	8.11	4.33	6.78	2.85	0.00	0.00	0.00	0.00	0.00	0.00
sp256C	Symphypleona	Katiannidae sp.7	0.06	0.06	0.00	0.00	0.06	0.06	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp265C	Poduromorpha	Neanuridae sp.2	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.28	0.00	0.00	0.00	0.00	0.00	0.00
sp266C	Poduromorpha	Neanuridae sp.3	0.00	0.00	0.00	0.00	7.56	4.55	2.28	1.39	0.00	0.00	0.00	0.00	0.00	0.00
sp275C	Symphypleona	Sminthurididae sp.1	0.00	0.00	0.00	0.00	1.06	1.06	0.28	0.23	0.00	0.00	0.00	0.00	0.00	0.00
sp276C	Symphypleona	Katiannidae sp.8	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.15	0.00	0.00	0.00	0.00	0.00	0.00
sp280C	Poduromorpha	Hypogastruridae sp.6	0.00	0.00	0.00	0.00	22.00	11.93	1.50	1.01	0.00	0.00	0.00	0.00	0.00	0.00
sp281C	Symphypleona	Katiannidae sp.9	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.22	0.00	0.00	0.00	0.00	0.00	0.00
sp282C	Symphypleona	Katiannidae sp.10	0.00	0.00	0.00	0.00	0.17	0.17	0.17	0.17	0.00	0.00	0.00	0.00	0.00	0.00
sp295C	Entomobryomorpha	Entomobryidae sp.25	0.00	0.00	0.00	0.00	19.72	14.23	0.44	0.22	0.00	0.00	0.44	0.32	0.00	0.00
sp296C	Poduromorpha	Hypogastruridae sp.7	0.00	0.00	0.00	0.00	4.61	3.82	7.72	2.93	0.00	0.00	0.06	0.06	0.00	0.00
sp297C	Entomobryomorpha	Entomobryidae sp.26	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.39	0.00	0.00	0.28	0.23	0.00	0.00
sp298C	Entomobryomorpha	Entomobryidae sp.27	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.17	0.11	0.11	0.00	0.00	0.00	0.00
sp303C	Entomobryomorpha	Entomobryidae sp.28	0.00	0.00	0.17	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp304C	Entomobryomorpha	Entomobryidae sp.29	2.56	1.85	0.00	0.00	5.22	2.05	3.28	1.60	2.67	1.04	4.89	2.24	0.50	0.50
sp305C	Entomobryomorpha	Entomobryidae sp.30	4.00	2.20	0.00	0.00	0.06	0.06	0.28	0.28	0.00	0.00	0.00	0.00	0.00	0.00
sp307C	Entomobryomorpha	Entomobryidae sp.31	0.22	0.22	0.00	0.00	0.06	0.06	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp308C	Entomobryomorpha	Entomobryidae sp.32	0.22	0.15	0.06	0.06	0.11	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp309C	Entomobryomorpha	Entomobryidae sp.33	1.00	0.70	0.00	0.00	2.17	1.62	0.11	0.11	0.06	0.06	0.94	0.94	1.56	0.87
sp311C	Entomobryomorpha	Entomobryidae sp.34	11.17	3.41	0.00	0.00	0.00	0.00	0.28	0.14	0.00	0.00	0.00	0.00	0.00	0.00
sp312C	Entomobryomorpha	Entomobryidae sp.35	0.11	0.11	0.00	0.00	0.00	0.00	0.83	0.49	0.28	0.28	0.00	0.00	5.33	1.68
sp313C	Entomobryomorpha	Entomobryidae sp.36	8.17	3.25	0.00	0.00	0.00	0.00	0.22	0.17	0.00	0.00	0.00	0.00	0.00	0.00
sp314C	Entomobryomorpha	Entomobryidae sp.37	1.22	0.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp315C	Symphypleona	Sminthurididae sp.2	0.06	0.06	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp316C	Entomobryomorpha	Entomobryidae sp.38	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp317C	Entomobryomorpha	Entomobryidae sp.39	0.56	0.35	0.06	0.06	0.00	0.00	0.39	0.24	0.00	0.00	0.00	0.00	0.00	0.00
sp318C	Symphypleona	Sminthurididae sp.3	0.28	0.23	0.00	0.00	0.00	0.00	0.67	0.50	0.22	0.17	0.00	0.00	0.00	0.00
sp322C	Entomobryomorpha	Entomobryidae sp.40	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp323C	Entomobryomorpha	Entomobryidae sp.41	0.00	0.00	0.00	0.00	0.11	0.11	0.06	0.06	0.17	0.09	0.00	0.00	0.00	0.00
sp328C	Symphypleona	Dicyrtomidae sp.7	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp334C	Entomobryomorpha	Entomobryidae sp.42	0.00	0.00	0.11	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sp336C	Poduromorpha	Brachystomellidae sp.1	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.33	0.33	0.00	0.00	0.00	0.00
sp339C	Symphypleona	Katiannidae sp.11	0.00	0.00	0.00	0.00	0.06	0.06	0.28	0.28	0.00	0.00	0.00	0.00	0.00	0.00
sp340C	Symphypleona	Katiannidae sp.12	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp341C	Entomobryomorpha	Entomobryidae sp.43	0.00	0.00	0.00	0.00	0.17	0.12	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00

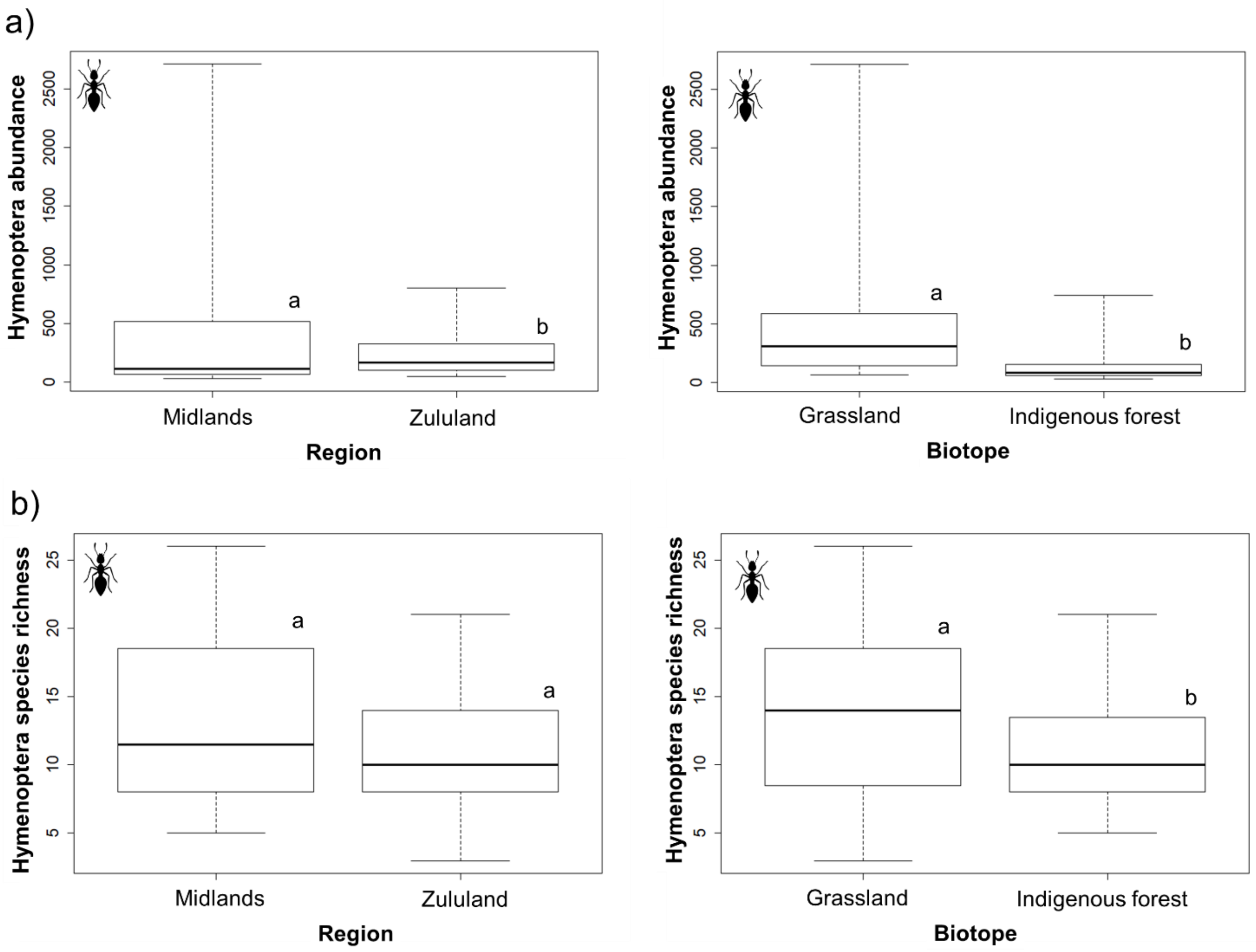
Appendix D continued

			Midlands								Zululand					
ID	**Sub-family**	**Genus**	**For**		**Grass**		**Pine**		**Euc**		**For**		**For**		**Grass**	
			Mean	**SE**	**Mean**	**SE**	**Mean**	**Mean**	**SE**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
sp342C	Entomobryomorpha	Entomobryidae sp.44	0.00	0.00	0.00	0.00	0.11	0.08	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
sp354C	Entomobryomorpha	Entomobryidae sp.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.28	1.28
sp357C	Entomobryomorpha	Entomobryidae sp.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00
sp365C	Poduromorpha	Neanuridae sp.4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.58	0.06	0.06
sp371C	Entomobryomorpha	Entomobryidae sp.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.17	0.00	0.00
sp372C	Entomobryomorpha	Entomobryidae sp.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00
sp373C	Entomobryomorpha	Entomobryidae sp.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.28	0.74	0.00	0.00
sp374C	Entomobryomorpha	Entomobryidae sp.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.40	0.00	0.00
sp375C	Entomobryomorpha	Entomobryidae sp.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.22	0.22	0.13	0.00	0.00
sp379C	Entomobryomorpha	Entomobryidae sp.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00
sp380C	Entomobryomorpha	Isotomidae sp.5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00
sp386C	Poduromorpha	Neanuridae sp.5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.29	0.00	0.00	0.00	0.00
sp393C	Poduromorpha	Neanuridae sp.6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.22	0.00	0.00	0.00	0.00

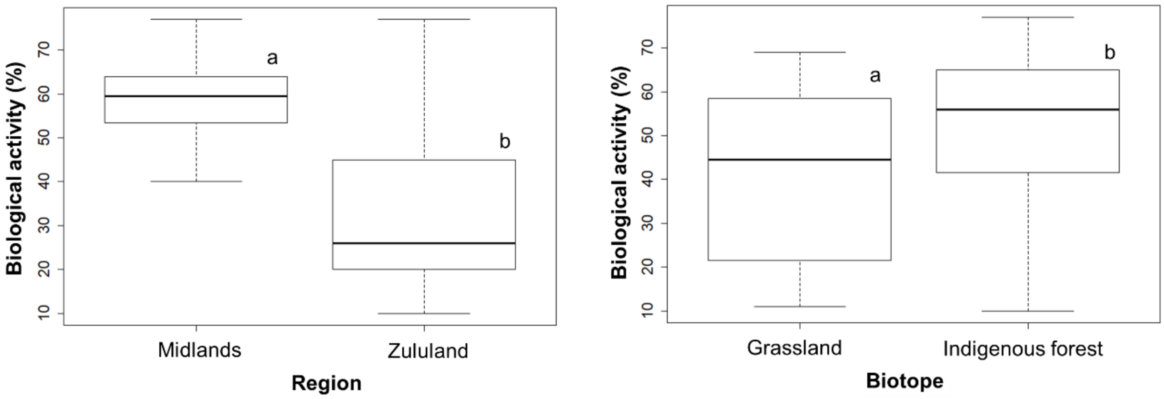
Appendix E Boxplots with central horizontal line indicating the median value, the boxes indicating the interquartile range and the whiskers indicating standard deviation within each biotope. Boxplots show overall springtail a) abundance and b) species richness between regions and biotope types, separately. Means with letters in common between biotopes, are not significantly different at $P < 0.05$.



Appendix F Boxplots with central horizontal line indicating the median value, the boxes indicating the interquartile range and the whiskers indicating standard deviation within each biotope. Boxplots show overall ant a) abundance and b) species richness between regions and biotope types, separately. Means with letters in common between biotopes, are not significantly different at $P < 0.05$.



Appendix G Boxplots with central horizontal line indicating the median value, the boxes indicating the interquartile range and the whiskers indicating standard deviation within each biotope. Boxplots show overall biological activity between regions and biotope types, separately. Means with letters in common between biotopes, are not significantly different at $P < 0.05$.



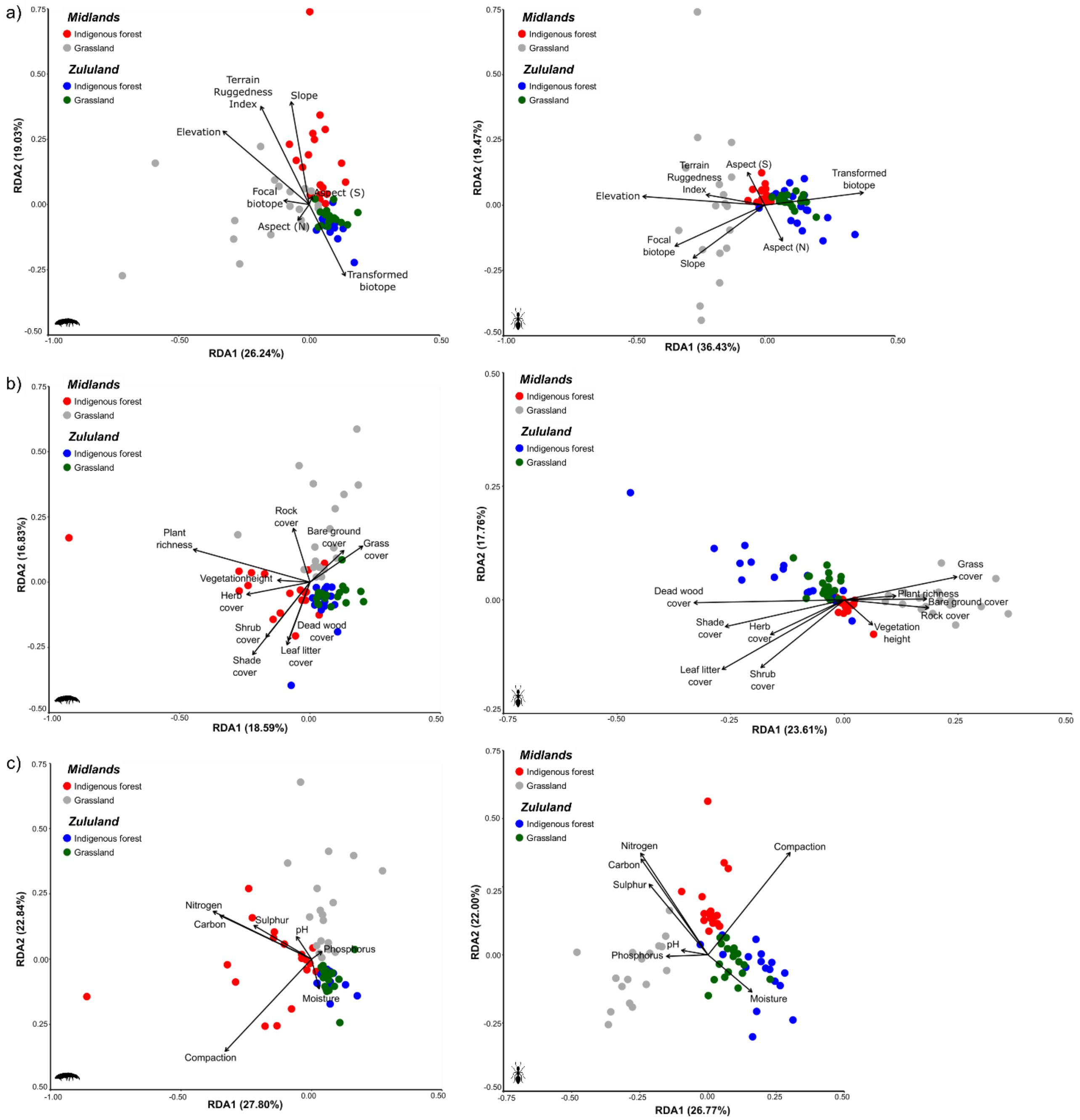
Appendix H Mean with standard error (SE) and deviation (SD), and the coefficient of variation (CV) of all recorded environmental variables within the indigenous forests, grasslands, pine and eucalypt compartments in the Midlands. CV values greater than "1" indicated in bold.

Environmental variables	**Indigenous forest**				**Grassland**				**Pine compartment**				**Eucalypt compartment**			
	Mean	**SE**	**SD**	**CV**	**Mean**	**SE**	**SD**	**CV**	**Mean**	**SE**	**SD**	**CV**	**Mean**	**SE**	**SD**	**CV**
Landscape variables																
Site elevation (m)	1243.78	15.89	67.43	0.05	1286.11	33.34	141.44	0.11	1398.06	20.68	87.74	0.06	1063.22	25.14	106.66	0.10
Site slope (º)	15.83	0.93	3.96	0.25	10.72	1.84	7.80	0.73	7.83	1.49	6.32	0.81	10.39	1.17	4.97	0.48
Site aspect (North)	1 site				12 sites				12 sites				8 sites			
Site aspect (South)	17 sites				6 sites				6 sites				10 sites			
Terrain Roughness	22.72	1.36	5.76	0.25	13.11	2.02	8.59	0.66	11.00	2.00	8.51	0.77	15.78	1.83	7.76	0.49
Terrain ruggedness index	7.17	0.44	1.89	0.26	4.00	0.54	2.30	0.58	3.39	0.62	2.62	0.77	4.67	0.55	2.35	0.50
Focal biotope (%)	47.22	3.00	12.74	0.27	57.22	4.19	17.76	0.31	71.11	1.96	8.32	0.12	70.00	3.02	12.83	0.18
Transformed biotope (%)	20.56	3.43	14.54	0.71	26.94	3.16	13.41	0.50	71.11	1.96	8.32	0.12	70.00	3.02	12.83	0.18
Site variables																
Rock cover (%)	9.72	1.83	7.76	0.80	7.50	2.60	11.01	**1.47**	3.33	1.67	7.07	**2.12**	0.83	0.45	1.92	**2.31**
Dead wood cover (%)	14.72	1.54	6.52	0.44	0.56	0.56	2.36	**4.21**	24.17	3.62	15.36	0.64	56.11	2.93	12.43	0.22
Shade cover (%)	70.56	3.21	13.60	0.19	0.00	0.00	0.00	0.00	38.33	1.90	8.04	0.21	36.11	1.83	7.78	0.22
Tree density (%)	52.50	4.21	17.84	0.34	0.00	0.00	0.00	0.00	26.11	2.12	9.00	0.34	26.11	1.18	5.02	0.19
Vegetation height (cm)	45.00	2.49	10.57	0.23	39.44	3.02	12.82	0.33	5.39	1.00	4.24	0.79	8.33	3.05	12.95	**1.55**
Vegetation cover (%)	69.17	5.18	21.98	0.32	88.06	1.62	6.89	0.08	5.83	1.23	5.22	0.90	2.78	1.01	4.28	**1.54**
Number of plant species	7.72	0.55	2.32	0.30	5.78	0.30	1.26	0.22	1.00	0.16	0.69	0.69	0.56	0.22	0.92	**1.64**
Leaf litter cover (%)	30.83	5.18	21.98	0.71	3.06	0.59	2.51	0.82	94.17	1.23	5.22	0.06	96.11	1.03	4.39	0.05
Leaf litter depth (cm)	4.83	0.12	0.51	0.11	0.94	0.21	0.87	0.93	3.33	0.11	0.49	0.15	3.00	0.00	0.00	0.00
Herbaceous cover (%)	46.39	5.33	22.61	0.49	18.33	3.26	13.83	0.75	3.39	0.80	3.38	**1.00**	1.39	0.68	2.87	**2.06**
Shrub cover (%)	7.78	1.41	6.00	0.77	0.56	0.38	1.62	**2.89**	0.28	0.28	1.18	**4.21**	0.00	0.00	0.00	0.00
Grass cover (%)	18.61	4.66	19.76	**1.06**	68.61	3.59	15.22	0.22	2.17	0.53	2.26	**1.04**	0.83	0.61	2.57	**3.10**
Bare ground cover (%)	0.00	0.00	0.00	0.00	8.89	1.59	6.76	0.76	0.00	0.00	0.00	0.00	1.11	0.65	2.74	**2.47**
Soil variables																
Soil moisture (%)	26.39	2.99	12.70	0.48	30.56	3.08	13.05	0.43	30.00	2.86	12.13	0.40	35.56	3.81	16.17	0.45
Soil compaction (psi)	126.33	8.85	37.53	0.30	65.33	4.15	17.63	0.27	131.22	2.20	9.33	0.07	81.11	5.69	24.13	0.30
Soil pH	6.09	0.14	0.59	0.10	5.81	0.04	0.19	0.03	5.17	0.06	0.27	0.05	5.32	0.14	0.61	0.11
CA (mg/kg)	2581.30	249.80	1059.83	0.41	974.21	62.88	266.76	0.27	687.85	94.19	399.60	0.58	1124.57	245.80	1042.86	0.93
MG (mg/kg)	354.32	54.31	230.41	0.65	248.99	28.63	121.45	0.49	136.13	17.10	72.56	0.53	172.37	39.38	167.08	0.97
K (mg/kg)	318.78	28.93	122.74	0.39	217.78	13.26	56.24	0.26	123.47	18.12	76.88	0.62	164.28	33.57	142.42	0.87
NA (mg/kg)	17.28	1.12	4.74	0.27	10.13	0.80	3.40	0.34	7.66	0.58	2.47	0.32	22.82	2.21	9.37	0.41
P (mg/kg)	3.47	0.25	1.05	0.30	5.28	0.95	4.01	0.76	7.35	1.91	8.10	**1.10**	6.15	1.40	5.96	0.97
C (mg/kg)	9.88	0.77	3.28	0.33	6.11	0.34	1.44	0.24	8.56	0.71	3.00	0.35	9.15	1.10	4.68	0.51
N (mg/kg)	0.71	0.05	0.21	0.30	0.41	0.02	0.09	0.22	0.48	0.03	0.13	0.27	0.56	0.07	0.28	0.50
S (mg/kg)	0.09	0.01	0.03	0.33	0.07	0.00	0.02	0.29	0.06	0.00	0.01	0.17	0.08	0.01	0.03	0.38

Appendix I Mean with standard error (SE) and deviation (SD), and the coefficient of variation (CV) of all recorded environmental variables within the indigenous forests, grassland and eucalypt compartments in Zululand. CV values greater than “1” indicated in bold.

Environmental variables	**Indigenous forest**				**Grassland**				**Eucalypt compartment**			
	Mean	**SE**	**SD**	**CV**	**Mean**	**SE**	**SD**	**CV**	**Mean**	**SE**	**SD**	**CV**
Landscape variables												
Site elevation (m)	57.67	2.25	9.54	0.17	56.06	2.46	10.43	0.19	109.34	54.79	232.46	**2.13**
Site slope (º)	3.15	0.70	2.95	0.94	2.71	0.42	1.79	0.66	2.96	0.45	1.89	0.64
Site aspect (North)	8 sites				7 sites				6 sites			
Site aspect (South)	10 sites				11 sites				12 sites			
Terrain Roughness	5.17	1.00	4.23	0.82	5.00	0.80	3.38	0.68	4.83	0.68	2.90	0.60
Terrain ruggedness index	1.65	0.31	1.29	0.78	1.50	0.26	1.08	0.72	1.49	0.22	0.91	0.61
Focal biotope (%)	40.00	3.52	14.95	0.37	26.67	2.29	9.70	0.36	78.89	3.12	13.23	0.17
Transformed biotope (%)	60.00	3.52	14.95	0.25	61.11	3.32	14.10	0.23	78.89	3.12	13.23	0.17
Site variables												
Rock cover (%)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dead wood cover (%)	25.56	2.71	11.49	0.45	0.00	0.00	0.00	0.00	26.11	3.15	13.35	0.51
Shade cover (%)	56.67	2.29	9.70	0.17	0.00	0.00	0.00	0.00	44.44	1.66	7.05	0.16
Tree density (%)	44.44	3.98	16.88	0.38	0.00	0.00	0.00	0.00	33.33	1.14	4.85	0.15
Vegetation height (cm)	50.28	7.66	32.52	0.65	17.78	2.66	11.27	0.63	11.67	1.94	8.22	0.70
Vegetation cover (%)	58.89	5.11	21.66	0.37	83.33	2.89	12.25	0.15	29.44	6.44	27.33	0.93
Number of plant species	5.56	0.37	1.58	0.28	4.06	0.29	1.21	0.30	2.17	0.36	1.54	0.71
Leaf litter cover (%)	40.83	5.21	22.11	0.54	5.83	1.09	4.62	0.79	70.00	6.35	26.95	0.39
Leaf litter depth (cm)	3.06	0.24	1.00	0.33	0.94	0.15	0.64	0.68	3.17	0.22	0.92	0.29
Herbaceous cover (%)	44.44	4.22	17.90	0.40	4.72	1.31	5.55	**1.18**	16.67	4.78	20.29	**1.22**
Shrub cover (%)	8.61	1.80	7.63	0.89	0.00	0.00	0.00	0.00	6.67	3.31	14.04	**2.10**
Grass cover (%)	10.28	1.31	5.55	0.54	78.33	3.23	13.72	0.18	8.89	1.74	7.39	0.83
Bare ground cover (%)	0.28	0.28	1.18	**4.21**	10.83	2.22	9.43	0.87	0.56	0.38	1.62	**2.89**
Soil variables												
Soil moisture (%)	47.78	3.92	16.65	0.35	27.22	2.89	12.27	0.45	26.11	3.15	13.35	0.51
Soil compaction (psi)	94.67	2.55	10.80	0.11	84.67	4.17	17.69	0.21	158.00	10.86	46.06	0.29
Soil pH	5.46	0.15	0.62	0.11	5.86	0.18	0.77	0.13	5.71	0.13	0.54	0.09
CA (mg/kg)	446.53	69.92	296.65	0.66	350.48	58.97	250.20	0.71	187.99	39.96	169.55	0.90
MG (mg/kg)	56.78	5.82	24.68	0.43	40.72	3.67	15.58	0.38	27.82	3.32	14.09	0.51
K (mg/kg)	94.44	15.28	64.85	0.69	76.53	14.74	62.53	0.82	38.62	4.14	17.58	0.46
NA (mg/kg)	13.59	1.35	5.74	0.42	15.13	2.51	10.63	0.70	8.38	1.02	4.31	0.51
P (mg/kg)	2.80	0.51	2.18	0.78	5.79	1.34	5.69	0.98	3.61	0.42	1.78	0.49
C (mg/kg)	2.53	0.31	1.30	0.51	2.83	1.02	4.34	**1.53**	1.11	0.22	0.95	0.86
N (mg/kg)	0.17	0.02	0.07	0.41	0.15	0.04	0.16	**1.07**	0.06	0.01	0.04	0.67
S (mg/kg)	0.03	0.00	0.01	0.33	0.04	0.01	0.06	**1.50**	0.02	0.00	0.01	0.50

Appendix J Redundancy analysis (RDA) biplots showing amount of variation in springtail and ant assemblage composition explained by environmental variables along the first two RDA axes. Analysis was conducted separately for a) landscape-, b) site- and c) soil-related variables recorded in each site within the Midlands and Zululand, consisting of both indigenous forest and grassland biotopes. Black arrows within each biplot represent the explanatory variables, which are plotted as vectors.



Appendix K Table showing the number of sites (N), the mean ± standard deviation (SD), as well as the minimum (Min) and maximum (Max) distance in kilometers between sites within a biotope type, for both the Midlands and Zululand.

Midlands	**N**	**Mean ± SD**	**Min**	**Max**
Indigenous forest	18	9.75 ± 7.38	0.42	26.36
Grassland	18	15.55 ± 10.57	0.33	34.06
Pine compartment	18	9.72 ± 5.12	0.32	16.54
Eucalypt compartment	18	5.04 ± 2.57	0.81	11.21

Zululand	**N**	**Mean ± SD**	**Min**	**Max**
Indigenous forest	18	23.18 ± 17.08	0.88	54.52
Grassland	18	24.66 ± 16.98	0.59	53.27
Eucalypt compartment	18	23.44 ± 16.43	1.07	53.80

Appendix L Indicator species of ants and springtails within each biotope type in the Midlands and Zululand. Biotopes indicated as indigenous forests (Forest), grasslands (Grass), pine compartments (Pine) and eucalypt compartments (Euc).

	Midlands				**Zululand**		
Species	**Forest**	**Grass**	**Pine**	**Euc**	**Forest**	**Grass**	**Euc**
Formicidae							
Leptogenys sp. 2 (Ponerinae)	0.833***						
Leptogenys sp. 1 (Ponerinae)	0.507**						
Anoplolepis sp. 1 (Formicinae)		0.962***					
Meranoplus sp. 3 (Myrmicinae)		0.939***					
Camponotus sp. 5 (Formicinae)		0.810***					
Crematogaster sp. 3 (Myrmicinae)		0.698***					
Paltothyreus spp. 2 (Ponerinae)		0.667***					
Tetramorium sp. 4 (Myrmicinae)		0.667***					
Pheidole sp. 3 (Myrmicinae)		0.624***					
Solenopsis sp. 2 (Myrmicinae)		0.577***					
Paltothyreus spp. 1 (Ponerinae)		0.559**					
Camponotus sp. 3 (Formicinae)		0.527**					
Camponotus sp. 6 (Formicinae)		0.471*					
Tetramorium sp. 1 (Myrmicinae)					0.847***		
Nesomyrmex sp. 3 (Myrmicinae)					0.682**		
Crematogaster sp. 5 (Myrmicinae)					0.593**		
Plagiolepis sp. 4 (Formicinae)					0.471*		
Trichomyrmex sp. 1 (Myrmicinae)						0.624***	
Tetramorium sp. 10 (Myrmicinae)							0.461*
Collembola							
Onychiuridae sp. 1 (Poduromorpha)	0.845***						
Entomobryidae sp. 28 (Entomobryomorpha)	0.807***						
Entomobryidae sp. 30 (Entomobryomorpha)	0.698***						
Entomobryidae sp. 24 (Entomobryomorpha)	0.555***						
Entomobryidae sp. 12 (Entomobryomorpha)		0.577***					
Entomobryidae sp. 11 (Entomobryomorpha)		0.545***					
Neanuridae sp. 2 (Poduromorpha)		0.540*					
Hypogastruridae sp. 3 (Poduromorpha)		0.471*					
Dicyrtomidae sp. 5 (Symphypleona)		0.453*					
Entomobryidae sp. 1 (Entomobryomorpha)			0.881***				
Entomobryidae sp. 17 (Entomobryomorpha)			0.664***				
Hypogastruridae sp. 5 (Poduromorpha)			0.510*				
Entomobryidae sp. 18 (Entomobryomorpha)			0.411*				
Entomobryidae sp. 29 (Entomobryomorpha)				0.443*			0.727***
Sminthuridae sp. 1 (Symphypleona)						0.624***	
Katiannidae sp. 1 (Symphypleona)						0.606**	
Katiannidae sp. 4 (Symphypleona)						0.577**	

Significance codes: *p < 0.05, **p < 0.01, ***p < 0.001

Appendix M Trait identities used in the analysis of ants in the Midlands and Zululand.

ID	Sub-family	Genus	Forage strategy	Habitat position	Eye Size	Body length (mm)	Femur length (mm)	Colour value (V)
sp012	Myrmicinae	Monomorium sp. 1	GenForager	EpiLitter	Moderate	1.00	0.50	64
sp013	Myrmicinae	Tetramorium sp. 1	GenForager	EpiSoil	Large	1.00	0.50	6
sp014	Myrmicinae	Strumigenys sp. 1	Pred	EpiLitter	Moderate	1.00	0.50	6
sp015	Ponerinae	Leptogenys sp. 1	Pred	EpiSoil	Large	3.00	2.50	2
sp020	Myrmicinae	Monomorium sp. 2	GenForager	EpiLitter	Moderate	0.50	0.25	42
sp021	Ponerinae	Bothroponera sp. 1	Pred	EpiLitter	Small	1.50	1.00	2
sp022	Ponerinae	Leptogenys sp. 2	Pred	EpiSoil	Large	3.00	2.00	4
sp033	Myrmicinae	Tetramorium sp. 2	GenForager	EpiSoil	Large	0.50	0.50	52
sp034	Myrmicinae	Trichomyrmex sp. 1	GenForager	EpiSoil	Moderate	1.00	1.00	49
sp035	Formicinae	Paratrechina sp. 1	GenForager	EpiSoil	Large	1.00	1.00	29
sp036	Myrmicinae	Crematogaster sp. 1	GenForager	EpiSoil	Moderate	1.50	1.00	25
sp044	Formicinae	Camponotus sp. 1	GenForager	EpiSoil	Moderate	3.50	5.00	2
sp052	Myrmicinae	Crematogaster sp. 2	GenForager	EpiSoil	Moderate	2.00	1.00	12
sp065	Myrmicinae	Crematogaster sp. 3	GenForager	EpiSoil	Moderate	1.50	1.00	11
sp067	Myrmicinae	Crematogaster sp. 4	GenForager	EpiSoil	Moderate	1.50	1.00	4
sp070	Myrmicinae	Crematogaster sp. 5	GenForager	EpiSoil	Moderate	1.50	1.00	49
sp077	Formicinae	Camponotus sp. 2	GenForager	EpiSoil	Moderate	2.00	2.00	15
sp086	Dorylinae	Aenictus sp. 1	Pred	EpiSoil	Absent	0.50	0.25	38
sp087	Formicinae	Camponotus sp. 3	GenForager	EpiSoil	Moderate	3.00	2.00	49
sp088	Formicinae	Camponotus sp. 4	GenForager	EpiSoil	Moderate	1.50	1.50	27
sp093	Myrmicinae	Meranoplus sp. 1	GenForager	EpiSoil	Large	1.00	1.00	33
sp094	Myrmicinae	Strumigenys sp. 2	Pred	EpiLitter	Moderate	1.50	0.50	13
sp095	Formicinae	Plagiolepis sp. 1	Sap	EpiLitter	Large	0.50	0.25	30
sp096	Myrmicinae	Tetramorium sp. 3	GenForager	EpiSoil	Large	1.00	0.50	32
sp097	Myrmicinae	Tetramorium sp. 4	GenForager	EpiSoil	Large	0.50	0.50	44
sp099	Ponerinae	Paltothyreus sp. 1	Pred	EpiSoil	Large	5.00	3.00	8
sp100	Ponerinae	Paltothyreus sp. 2	Pred	EpiSoil	Large	5.00	3.00	12
sp101	Dolichoderinae	Tapinoma sp. 1	GenForager	EpiLitter	Large	1.50	0.50	7
sp102	Myrmicinae	Tetramorium sp. 5	GenForager	EpiSoil	Large	3.00	2.50	28
sp125	Formicinae	Camponotus sp. 5	GenForager	EpiSoil	Moderate	2.50	2.00	53
sp126	Formicinae	Camponotus sp. 6	GenForager	EpiSoil	Moderate	2.00	1.50	50
sp127	Formicinae	Camponotus sp. 7	GenForager	EpiSoil	Moderate	2.00	1.50	15
sp128	Myrmicinae	Tetramorium sp. 6	GenForager	EpiSoil	Large	1.00	0.50	47
sp129	Myrmicinae	Tetramorium sp. 7	GenForager	EpiSoil	Large	1.50	1.00	63
sp130	Formicinae	Lepisiota sp. 1	GenForager	EpiSoil	Moderate	1.00	0.50	32
sp142	Formicinae	Camponotus sp. 8	GenForager	EpiSoil	Moderate	2.00	2.00	48
sp143	Myrmicinae	Tetramorium sp. 8	GenForager	EpiSoil	Large	1.00	0.50	52
sp144	Formicinae	Camponotus sp. 9	GenForager	EpiSoil	Moderate	2.00	1.50	26
sp145	Formicinae	Plagiolepis sp. 2	Sap	EpiLitter	Large	1.00	0.50	45
sp165	Formicinae	Camponotus sp. 10	GenForager	EpiSoil	Moderate	3.00	3.00	50
sp166	Myrmicinae	Pheidole sp. 1	GenForager	EpiSoil	Small	1.00	1.00	70
sp167	Myrmicinae	Crematogaster sp. 6	GenForager	EpiSoil	Moderate	1.00	1.00	40
sp168	Myrmicinae	Trichomyrmex sp. 2	GenForager	EpiSoil	Moderate	1.00	0.50	70
sp169	Myrmicinae	Crematogaster sp. 7	GenForager	EpiSoil	Moderate	1.00	0.25	53
sp170	Myrmicinae	Solenopsis sp. 1	GenForager	EpiSoil	Small	1.00	1.00	72
sp171	Myrmicinae	Solenopsis sp. 2	GenForager	EpiSoil	Small	1.00	0.25	57
sp172	Myrmicinae	Pheidole sp. 2	GenForager	EpiSoil	Small	1.50	1.00	77
sp190	Formicinae	Lepisiota sp. 2	GenForager	EpiSoil	Moderate	0.50	0.50	33
sp191	Myrmicinae	Monomorium sp. 3	GenForager	EpiLitter	Moderate	0.50	0.25	33
sp200	Formicinae	Camponotus sp. 11	GenForager	EpiSoil	Moderate	4.00	2.00	33
sp201	Formicinae	Camponotus sp. 12	GenForager	EpiSoil	Moderate	2.50	1.50	29
sp202	Myrmicinae	Tetramorium sp. 9	GenForager	EpiSoil	Large	1.50	1.00	53
sp203	Myrmicinae	Tetramorium sp. 10	GenForager	EpiSoil	Large	2.00	1.00	50
sp204	Ponerinae	Parasyscia sp. 1	Pred	EpiLitter	Small	1.00	0.50	52
sp205	Myrmicinae	Solenopsis sp. 3	GenForager	EpiSoil	Small	1.00	0.50	53
sp206	Myrmicinae	Crematogaster sp. 8	GenForager	EpiSoil	Moderate	1.00	0.50	34
sp207	Myrmicinae	Solenopsis sp. 4	GenForager	EpiSoil	Small	0.50	0.25	22
sp208	Formicinae	Lepisiota sp. 3	GenForager	EpiSoil	Moderate	1.00	0.50	53
sp209	Formicinae	Lepisiota sp. 4	GenForager	EpiSoil	Moderate	0.50	0.50	28
sp210	Dolichoderinae	Tapinoma sp. 2	GenForager	EpiLitter	Large	1.00	1.00	31
sp211	Myrmicinae	Pheidole sp. 3	GenForager	EpiSoil	Small	1.50	1.00	59
sp212	Myrmicinae	Crematogaster sp. 9	GenForager	EpiSoil	Moderate	1.00	0.50	60
sp213	Myrmicinae	Trichomyrmex sp. 3	GenForager	EpiSoil	Moderate	1.00	0.50	30
sp226	Myrmicinae	Pheidole sp. 4	GenForager	EpiSoil	Small	2.00	1.50	45
sp227	Myrmicinae	Crematogaster sp. 10	GenForager	EpiSoil	Moderate	1.00	0.50	28

Abbreviations: GenForager = Generalist forager, Pred = Predator, Sap = Saprovore, EpiSoil = Epigaeic soil-dweller, EpiLitter = Epigaeic litter-dweller.

Appendix M continued

ID	Sub-family	Genus	Forage strategy	Habitat position	Eye Size	Body length (mm)	Femur length (mm)	Colour value (V)
sp231	Myrmicinae	Tetramorium sp. 11	GenForager	EpiSoil	Large	1.50	1.50	25
sp232	Myrmicinae	Tetramorium sp. 12	GenForager	EpiSoil	Large	2.00	2.00	29
sp233	Myrmicinae	Crematogaster sp. 11	GenForager	EpiSoil	Moderate	1.00	0.50	30
sp234	Myrmicinae	Tetramorium sp. 13	GenForager	EpiSoil	Large	1.00	1.00	28
sp235	Formicinae	Lepisiota sp. 5	GenForager	EpiSoil	Moderate	1.50	0.50	30
sp240	Formicinae	Lepisiota sp. 6	GenForager	EpiSoil	Moderate	0.50	0.50	25
sp246	Formicinae	Camponotus sp. 13	GenForager	EpiSoil	Moderate	2.00	2.00	66
sp247	Formicinae	Camponotus sp. 14	GenForager	EpiSoil	Moderate	3.00	2.00	71
sp254	Myrmicinae	Solenopsis sp. 5	GenForager	EpiSoil	Small	1.00	0.25	60
sp258	Myrmicinae	Monomorium sp. 4	GenForager	EpiLitter	Moderate	1.00	1.00	71
sp284	Formicinae	Paratrechina sp. 2	GenForager	EpiSoil	Large	1.00	0.50	35
sp289	Myrmicinae	Pheidole sp. 5	GenForager	EpiSoil	Small	0.50	0.25	36
sp294	Formicinae	Plagiolepis sp. 3	Sap	EpiLitter	Large	1.00	0.50	65
sp301	Myrmicinae	Tetramorium sp. 14	GenForager	EpiSoil	Large	1.50	0.50	58
sp302	Formicinae	Paratrechina sp. 3	GenForager	EpiSoil	Large	1.00	1.00	70
sp324	Formicinae	Lepisiota sp. 7	GenForager	EpiSoil	Moderate	1.00	0.50	14
sp325	Myrmicinae	Tetramorium sp. 15	GenForager	EpiSoil	Large	1.00	0.50	46
sp326	Myrmicinae	Tetramorium sp. 16	GenForager	EpiSoil	Large	1.00	0.50	32
sp329	Myrmicinae	Strumigenys sp. 3	Pred	EpiLitter	Moderate	2.00	1.00	52
sp331	Myrmicinae	Tetramorium sp. 17	GenForager	EpiSoil	Large	1.00	0.50	56
sp332	Formicinae	Lepisiota sp. 8	GenForager	EpiSoil	Moderate	2.00	1.00	36
sp337	Proceratiinae	Probolomyrmex sp. 1	Pred	EpiLitter	Absent	1.00	0.25	59
sp344	Myrmicinae	Tetramorium sp. 18	GenForager	EpiSoil	Large	1.00	0.50	50
sp345	Myrmicinae	Trichomyrmex sp. 4	GenForager	EpiSoil	Moderate	1.00	1.00	68
sp346	Formicinae	Plagiolepis sp. 4	Sap	EpiLitter	Large	0.50	0.30	68
sp347	Formicinae	Camponotus sp. 15	GenForager	EpiSoil	Moderate	3.00	2.00	25
sp348	Myrmicinae	Tetramorium sp. 19	GenForager	EpiSoil	Large	1.00	1.00	26
sp349	Myrmicinae	Myrmicaria sp. 1	GenForager	EpiSoil	Large	2.50	3.00	71
sp350	Myrmicinae	Trichomyrmex sp. 5	GenForager	EpiSoil	Moderate	1.00	1.50	49
sp351	Ponerinae	Bothroponera sp. 2	Pred	EpiLitter	Small	5.00	4.00	35
sp352	Formicinae	Paratrechina sp. 4	GenForager	EpiSoil	Large	2.50	1.50	65
sp353	Ponerinae	Bothroponera sp. 3	Pred	EpiLitter	Small	3.00	2.50	24
sp355	Dorylinae	Aenictus sp. 2	Pred	EpiSoil	Absent	1.00	0.50	65
sp356	Ponerinae	Leptogenys sp. 3	Pred	EpiSoil	Large	2.50	2.00	29
sp358	Myrmicinae	Trichomyrmex sp. 6	GenForager	EpiSoil	Moderate	1.50	1.00	66
sp359	Formicinae	Lepisiota sp. 9	GenForager	EpiSoil	Moderate	0.10	0.50	18
sp360	Myrmicinae	Tetramorium sp. 20	GenForager	EpiSoil	Large	1.00	0.50	61
sp361	Ponerinae	Parasyscia sp. 2	Pred	EpiLitter	Small	0.50	0.25	67
sp362	Myrmicinae	Pheidole sp. 5	GenForager	EpiSoil	Small	1.00	0.50	66
sp363	Myrmicinae	Pheidole sp. 6	GenForager	EpiSoil	Small	1.50	1.00	65
sp364	Myrmicinae	Solenopsis sp. 6	GenForager	EpiSoil	Small	0.50	0.30	71
sp366	Formicinae	Polyrhachis sp. 1	GenForager	EpiSoil	Large	3.00	2.50	25
sp367	Formicinae	Polyrhachis sp. 2	GenForager	EpiSoil	Large	3.00	2.50	28
sp368	Formicinae	Lepisiota sp. 10	GenForager	EpiSoil	Moderate	1.50	1.50	32
sp370	Formicinae	Anoplolepis sp. 1	GenForager	EpiLitter	Large	0.50	0.50	62
sp381	Myrmicinae	Cataulacus sp. 1	Sap	Arboreal	Large	1.50	0.50	16
sp382	Myrmicinae	Crematogaster sp. 12	GenForager	EpiSoil	Moderate	1.50	1.00	38
sp383	Myrmicinae	Tetramorium sp. 21	GenForager	EpiSoil	Large	1.50	0.50	34
sp384	Ponerinae	Anochetus sp. 1	Pred	EpiLitter	Large	1.00	1.00	63
sp385	Proceratiinae	Probolomyrmex sp. 2	Pred	EpiLitter	Absent	1.50	1.00	77
sp387	Formicinae	Polyrhachis sp. 3	GenForager	EpiSoil	Large	3.00	2.50	26
sp388	Myrmicinae	Tetramorium sp. 22	GenForager	EpiSoil	Large	1.00	1.00	43
sp389	Ponerinae	Bothroponera sp. 4	Pred	EpiLitter	Small	2.50	2.00	22
sp390	Proceratiinae	Discothyrea sp. 1	Pred	EpiLitter	Small	1.00	0.25	59
sp391	Ponerinae	Parasyscia sp. 3	Pred	EpiLitter	Small	1.00	0.50	61
sp392	Dolichoderinae	Tapinoma sp. 3	GenForager	EpiLitter	Large	1.00	0.50	36
sp394	Dolichoderinae	Tapinoma sp. 4	GenForager	EpiLitter	Large	1.00	1.00	24
sp395	Myrmicinae	Tetramorium sp. 23	GenForager	EpiSoil	Large	1.00	0.50	57
sp396	Ponerinae	Boloponera sp. 1	Pred	EpiLitter	Absent	1.00	1.00	48
sp398	Ponerinae	Bothroponera sp. 5	Pred	EpiLitter	Small	2.50	2.50	21
sp399	Formicinae	Anoplolepis sp. 2	GenForager	EpiLitter	Large	0.50	0.25	54
sp400	Formicinae	Camponotus sp. 16	GenForager	EpiSoil	Moderate	3.00	2.00	19
sp401	Ponerinae	Hypoponera sp. 1	Pred	EpiLitter	Small	2.00	1.00	21
sp402	Dorylinae	Aenictus sp. 3	Pred	EpiSoil	Absent	1.50	1.00	58

Abbreviations: GenForager = Generalist forager, Pred = Predator, Sap = Saprovore, EpiSoil = Epigaeic soil-dweller, EpiLitter = Epigaeic litter-dweller.

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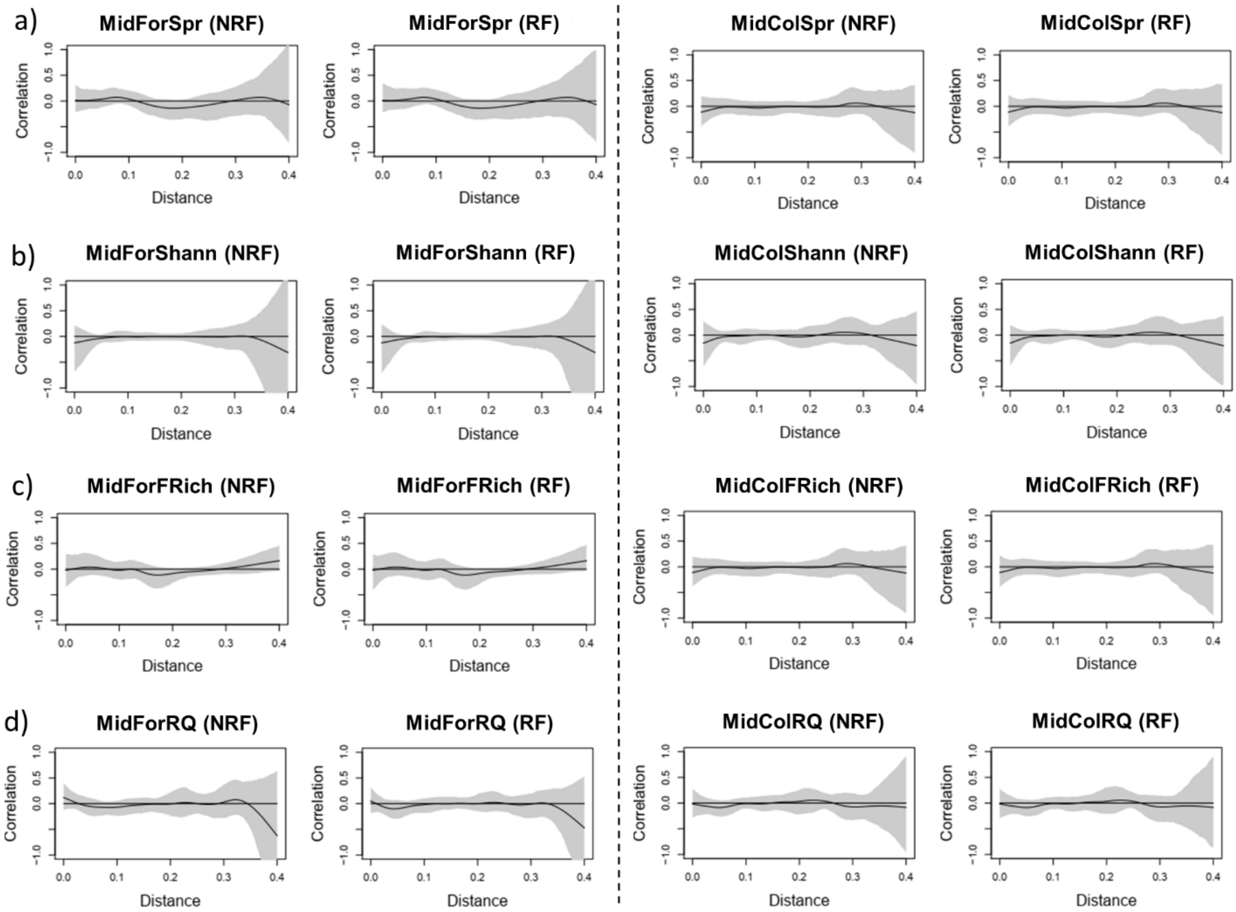
Appendix O Trait identities used in the analysis of springtails in the Midlands and Zululand.

ID	Sub-order	Family	Fruca development	Body length (mm)	Eye size	Habitat position	Feeding strategy
sp001	Poduromorpha	Onychiuridae sp.1	Absent	1.84	Absent	Euedaphic	Chew
sp002	Entomobryomorpha	Entomobryidae sp.1	Long	1.35	Large	Atmobiotic	Chew
sp005	Entomobryomorpha	Entomobryidae sp.2	Long	2.15	Large	Atmobiotic	Chew
sp006	Poduromorpha	Hypogastruridae sp.1	Short	0.80	Large	Hemiedaphic	Chew
sp023	Symphypleona	Dicyrtomidae sp.1	Long	1.20	Large	Atmobiotic	Chew
sp024	Symphypleona	Sminthuridae sp.1	Long	1.28	Large	Atmobiotic	Chew
sp027	Entomobryomorpha	Entomobryidae sp.3	Long	2.00	Large	Atmobiotic	Chew
sp028	Entomobryomorpha	Isotomidae sp.1	Moderate	1.10	Moderate	Hemiedaphic	Chew
sp049	Entomobryomorpha	Entomobryidae sp.4	Long	1.50	Large	Atmobiotic	Chew
sp050	Entomobryomorpha	Entomobryidae sp.5	Long	1.50	Large	Atmobiotic	Chew
sp051	Symphypleona	Dicyrtomidae sp.2	Long	0.88	Large	Atmobiotic	Chew
sp060	Entomobryomorpha	Entomobryidae sp.6	Long	1.00	Moderate	Atmobiotic	Chew
sp064	Entomobryomorpha	Entomobryidae sp.7	Long	1.38	Large	Atmobiotic	Chew
sp069	Symphypleona	Dicyrtomidae sp.3	Long	0.40	Large	Atmobiotic	Chew
sp072	Entomobryomorpha	Entomobryidae sp.8	Long	1.00	Large	Atmobiotic	Chew
sp073	Entomobryomorpha	Entomobryidae sp.9	Long	0.86	Large	Atmobiotic	Chew
sp074	Entomobryomorpha	Entomobryidae sp.10	Long	0.80	Large	Atmobiotic	Chew
sp080	Symphypleona	Katiannidae sp.1	Long	0.38	Large	Atmobiotic	Chew
sp089	Entomobryomorpha	Entomobryidae sp.11	Long	0.90	Large	Atmobiotic	Chew
sp090	Symphypleona	Dicyrtomidae sp.4	Long	0.26	Large	Atmobiotic	Chew
sp092	Entomobryomorpha	Entomobryidae sp.12	Long	1.00	Large	Atmobiotic	Chew
sp111	Symphypleona	Katiannidae sp.2	Long	0.32	Large	Atmobiotic	Chew
sp112	Entomobryomorpha	Entomobryidae sp.13	Long	1.50	Large	Atmobiotic	Chew
sp113	Symphypleona	Dicyrtomidae sp.5	Long	0.46	Large	Atmobiotic	Chew
sp114	Poduromorpha	Hypogastruridae sp.2	Short	0.30	Large	Hemiedaphic	Chew
sp117	Poduromorpha	Hypogastruridae sp.3	Short	0.58	Large	Hemiedaphic	Chew
sp118	Entomobryomorpha	Isotomidae sp.2	Moderate	0.70	Large	Hemiedaphic	Chew
sp119	Symphypleona	Dicyrtomidae sp.6	Long	1.10	Large	Atmobiotic	Chew
sp120	Poduromorpha	Hypogastruridae sp.4	Short	0.60	Large	Hemiedaphic	Chew
sp131	Poduromorpha	Neanuridae sp.1	Short	0.54	Large	Hemiedaphic	Suck
sp132	Poduromorpha	Hypogastruridae sp.5	Short	1.00	Large	Hemiedaphic	Chew
sp133	Entomobryomorpha	Isotomidae sp.3	Moderate	0.90	Moderate	Hemiedaphic	Chew
sp160	Entomobryomorpha	Entomobryidae sp.14	Long	1.88	Large	Hemiedaphic	Chew
sp161	Entomobryomorpha	Entomobryidae sp.15	Long	1.05	Large	Atmobiotic	Chew
sp162	Entomobryomorpha	Entomobryidae sp.16	Long	1.38	Large	Atmobiotic	Chew
sp163	Entomobryomorpha	Entomobryidae sp.17	Long	1.50	Large	Atmobiotic	Chew
sp180	Symphypleona	Sminthuridae sp.2	Long	0.66	Large	Atmobiotic	Chew
sp181	Symphypleona	Katiannidae sp.3	Long	1.12	Large	Atmobiotic	Chew
sp182	Symphypleona	Sminthuridae sp.4	Long	0.50	Large	Atmobiotic	Chew
sp183	Symphypleona	Katiannidae sp.4	Long	1.00	Large	Atmobiotic	Chew
sp196	Entomobryomorpha	Entomobryidae sp.18	Long	0.75	Large	Hemiedaphic	Chew
sp197	Symphypleona	Katiannidae sp.5	Long	1.00	Large	Atmobiotic	Chew
sp198	Entomobryomorpha	Entomobryidae sp.19	Long	0.80	Large	Atmobiotic	Chew
sp219	Symphypleona	Katiannidae sp.6	Long	0.50	Large	Atmobiotic	Chew
sp220	Poduromorpha	Odontellidae sp.1	Short	0.36	Large	Hemiedaphic	Suck
sp221	Entomobryomorpha	Entomobryidae sp.20	Long	1.25	Large	Atmobiotic	Chew
sp228	Entomobryomorpha	Isotomidae sp.4	Moderate	0.75	Large	Hemiedaphic	Chew
sp244	Entomobryomorpha	Entomobryidae sp.21	Long	1.30	Large	Atmobiotic	Chew
sp250	Entomobryomorpha	Entomobryidae sp.22	Long	1.35	Large	Atmobiotic	Chew
sp251	Entomobryomorpha	Entomobryidae sp.23	Long	1.38	Large	Hemiedaphic	Chew
sp252	Symphypleona	Sminthuridae sp.3	Long	0.60	Large	Atmobiotic	Chew
sp253	Entomobryomorpha	Entomobryidae sp.24	Long	0.92	Large	Atmobiotic	Chew
sp256	Symphypleona	Katiannidae sp.7	Long	0.80	Large	Atmobiotic	Chew
sp265	Poduromorpha	Neanuridae sp.2	Short	0.48	Absent	Euedaphic	Suck
sp266	Poduromorpha	Neanuridae sp.3	Short	0.36	Large	Hemiedaphic	Suck
sp275	Symphypleona	Sminthurididae sp.1	Long	0.92	Large	Atmobiotic	Chew
sp276	Symphypleona	Katiannidae sp.8	Long	0.80	Large	Atmobiotic	Chew
sp280	Poduromorpha	Hypogastruridae sp.6	Short	1.00	Large	Hemiedaphic	Chew
sp281	Symphypleona	Katiannidae sp.9	Long	0.38	Large	Atmobiotic	Chew
sp282	Symphypleona	Katiannidae sp.10	Long	0.50	Large	Atmobiotic	Chew
sp295	Entomobryomorpha	Entomobryidae sp.25	Long	0.63	Large	Hemiedaphic	Chew
sp296	Poduromorpha	Hypogastruridae sp.7	Short	1.04	Large	Hemiedaphic	Chew
sp297	Entomobryomorpha	Entomobryidae sp.26	Long	1.38	Large	Atmobiotic	Chew
sp298	Entomobryomorpha	Entomobryidae sp.27	Long	0.46	Large	Hemiedaphic	Chew
sp303	Entomobryomorpha	Entomobryidae sp.28	Long	1.13	Large	Atmobiotic	Chew
sp304	Entomobryomorpha	Entomobryidae sp.29	Long	0.53	Large	Atmobiotic	Chew

Appendix O continued

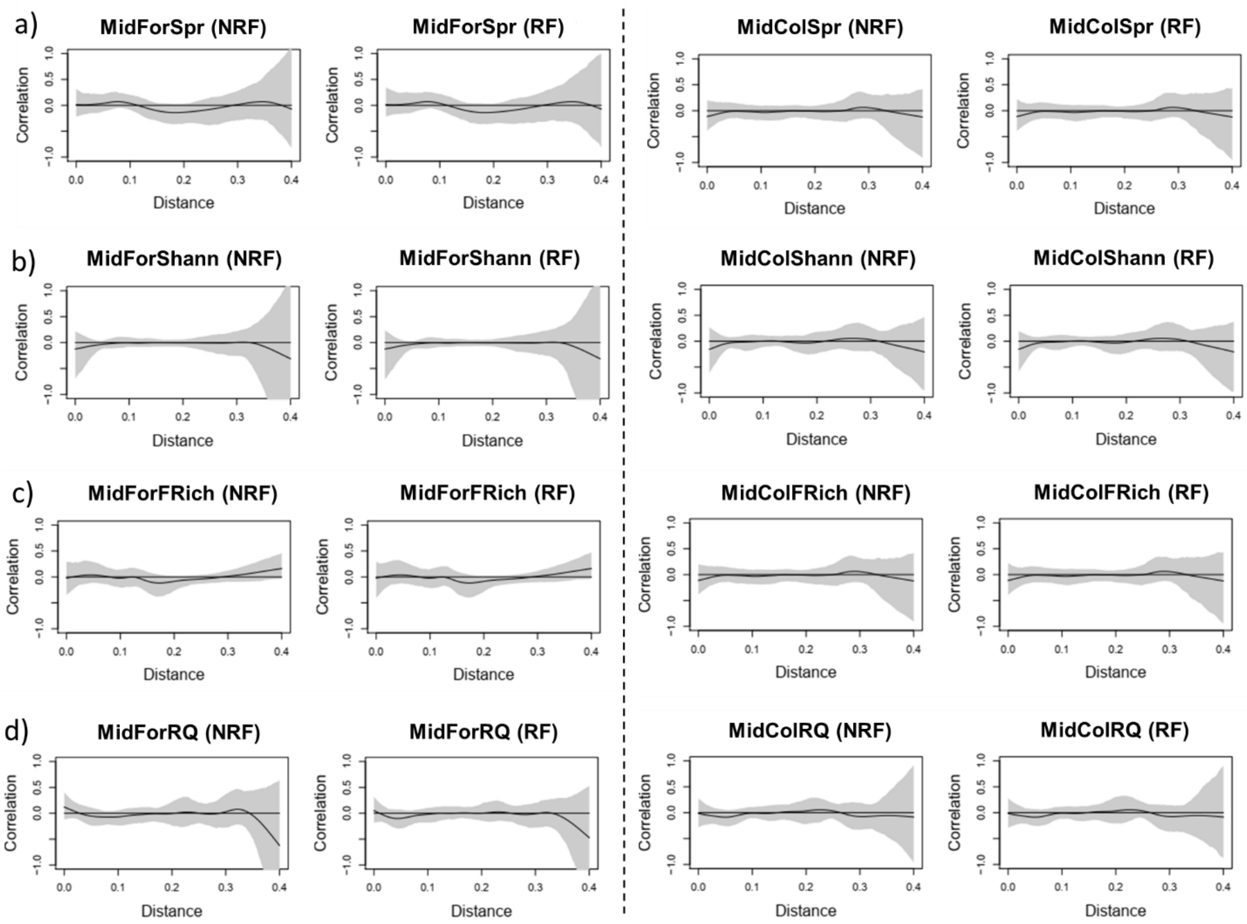
ID	Sub-order	Family	Fruca development	Body length (mm)	Eye size	Habitat position	Feeding strategy
sp305	Entomobryomorpha	Entomobryidae sp.30	Long	1.25	Large	Atmobiotic	Chew
sp307	Entomobryomorpha	Entomobryidae sp.31	Long	1.30	Large	Atmobiotic	Chew
sp308	Entomobryomorpha	Entomobryidae sp.32	Long	0.93	Large	Atmobiotic	Chew
sp309	Entomobryomorpha	Entomobryidae sp.33	Long	1.08	Large	Atmobiotic	Chew
sp311	Entomobryomorpha	Entomobryidae sp.34	Long	1.33	Large	Atmobiotic	Chew
sp312	Entomobryomorpha	Entomobryidae sp.35	Long	1.40	Large	Atmobiotic	Chew
sp313	Entomobryomorpha	Entomobryidae sp.36	Long	1.08	Large	Atmobiotic	Chew
sp314	Entomobryomorpha	Entomobryidae sp.37	Long	0.40	Large	Atmobiotic	Chew
sp315	Symphypleona	Sminthurididae sp.2	Long	0.90	Large	Atmobiotic	Chew
sp316	Entomobryomorpha	Entomobryidae sp.38	Long	0.80	Large	Atmobiotic	Chew
sp317	Entomobryomorpha	Entomobryidae sp.39	Long	0.24	Large	Atmobiotic	Chew
sp318	Symphypleona	Sminthurididae sp.3	Long	0.98	Large	Atmobiotic	Chew
sp322	Entomobryomorpha	Entomobryidae sp.40	Long	1.38	Large	Atmobiotic	Chew
sp323	Entomobryomorpha	Entomobryidae sp.41	Long	0.80	Large	Atmobiotic	Chew
sp328	Symphypleona	Dicyrtomidae sp.7	Long	0.66	Large	Atmobiotic	Chew
sp334	Entomobryomorpha	Entomobryidae sp.42	Long	0.28	Large	Atmobiotic	Chew
sp336	Poduromorpha	Brachystomellidae sp.1	Short	0.56	Large	Hemiedaphic	Suck
sp339	Symphypleona	Katiannidae sp.11	Long	0.28	Large	Atmobiotic	Chew
sp340	Symphypleona	Katiannidae sp.12	Long	0.60	Large	Atmobiotic	Chew
sp341	Entomobryomorpha	Entomobryidae sp.43	Long	0.80	Large	Hemiedaphic	Chew
sp342	Entomobryomorpha	Entomobryidae sp.44	Long	1.05	Large	Atmobiotic	Chew
sp354	Entomobryomorpha	Entomobryidae sp.45	Long	1.13	Large	Atmobiotic	Chew
sp357	Entomobryomorpha	Entomobryidae sp.46	Long	1.15	Large	Atmobiotic	Chew
sp365	Poduromorpha	Neanuridae sp.4	Short	0.60	Large	Hemiedaphic	Suck
sp371	Entomobryomorpha	Entomobryidae sp.47	Long	0.93	Large	Atmobiotic	Chew
sp372	Entomobryomorpha	Entomobryidae sp.48	Long	0.93	Small	Hemiedaphic	Chew
sp373	Entomobryomorpha	Entomobryidae sp.49	Long	0.60	Large	Hemiedaphic	Chew
sp374	Entomobryomorpha	Entomobryidae sp.50	Long	1.30	Large	Atmobiotic	Chew
sp375	Entomobryomorpha	Entomobryidae sp.51	Long	1.13	Large	Atmobiotic	Chew
sp379	Entomobryomorpha	Entomobryidae sp.52	Long	0.93	Large	Atmobiotic	Chew
sp380	Entomobryomorpha	Isotomidae sp.5	Moderate	0.43	Large	Hemiedaphic	Chew
sp386	Poduromorpha	Neanuridae sp.5	Short	0.92	Large	Hemiedaphic	Suck
sp393	Poduromorpha	Neanuridae sp.6	Short	0.56	Large	Hemiedaphic	Suck

Appendix P Spline correlograms for a) species richness, b) Shannon Entropy, c) functional richness and d) Rao's entropy, for both ants and springtails in the Midlands, across all biotopes (i.e. indigenous forest, grassland and eucalypt compartment). Spline correlograms were created without (NRF) and with (RF) the inclusion of selected random factor plantation estate". Distance is shown in degrees.



Abbreviations: Mid = Midlands, For = Formicidae, Col = Collembola, Spr = species richness, Shann = Shannon entropy, FRich = functional richness, RQ = Rao's entropy, NRF = no random factor inlcuded, RF = random factor included.

Appendix Q Spline correlograms for a) species richness, b) Shannon Entropy, c) functional richness and d) Rao’s entropy, for both ants and springtails in the Zululand, across all biotopes (i.e. indigenous forest, grassland and eucalypt compartment). Spline correlograms were created without (NRF) and with (RF) the inclusion of selected random factor “plantation estate”. Distance is shown in degrees.



Abbreviations: Mid = Midlands, For = Formicidae, Col = Collembola, Spr = species richness, Shann = Shannon entropy, FRich = functional richness, RQ = Rao’s entropy, NRF = no random factor inlcuded, RF = random factor included.

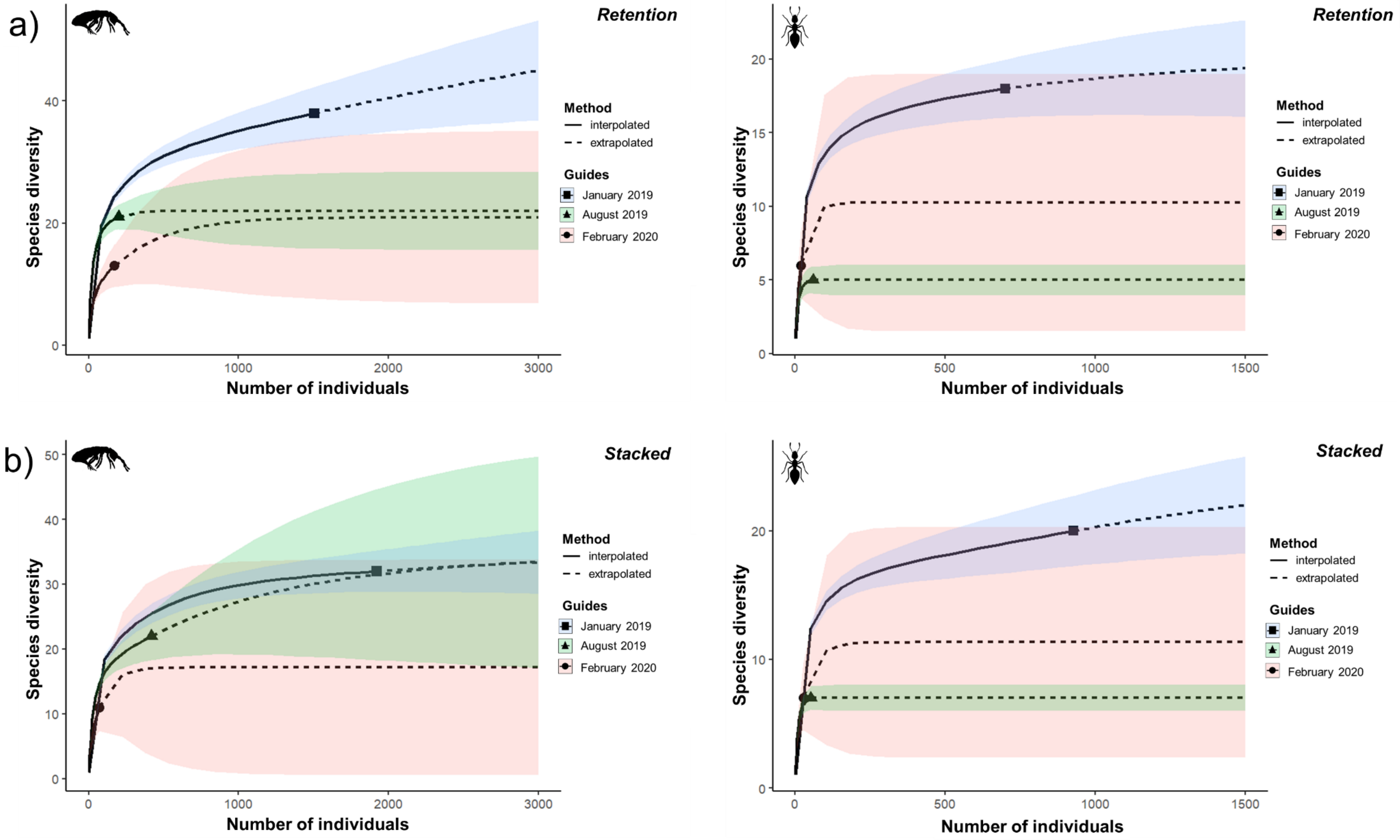
Appendix R Mean and standard error (SE) of recorded variables across natural grassland reference sites and residue management treatments, per sampling event.

Season	January 2019										August 2019									
Treatment	**Grass**		**Remove**		**Retention**		**Spread**		**Stack**		**Grass**		**Remove**		**Retention**		**Spread**		**Stack**	
Stat	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
DWC	0.00	0.00	24.00	1.63	24.00	1.63	24.00	2.21	20.00	2.11	0.00	0.00	0.00	0.00	63.00	1.53	0.00	0.00	0.00	0.00
SC	0.00	0.00	36.00	1.63	35.00	1.67	38.00	1.33	36.00	1.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MP	0.20	0.00	0.56	0.00	0.56	0.00	0.56	0.00	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TP	14.45	0.51	11.85	0.08	11.85	0.08	11.85	0.08	11.85	0.08	2.00	0.00	2.00	0.00	2.00	0.00	2.00	0.00	2.00	0.00
VH	40.63	3.83	3.00	2.00	1.50	1.50	5.50	2.29	2.00	1.33	52.50	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
VC	89.38	1.48	6.00	4.99	1.00	1.00	6.00	3.06	4.00	2.67	86.88	1.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
VSP	4.75	0.45	0.30	0.21	0.10	0.10	0.70	0.30	0.60	0.40	4.50	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LLC	4.38	0.63	86.00	7.02	93.00	2.13	87.00	3.96	88.00	5.73	5.63	0.63	39.00	7.37	70.00	4.22	11.00	5.67	7.00	1.53
LLD	0.88	0.13	2.60	0.22	2.50	0.17	2.30	0.15	2.30	0.21	1.00	0.00	1.45	0.24	2.10	0.18	0.55	0.20	0.45	0.12
HERB	15.63	4.57	0.00	0.00	1.00	1.00	3.00	1.53	3.00	2.13	10.63	1.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SHRUB	1.25	1.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GRASS	72.50	4.53	6.00	4.99	0.00	0.00	3.00	2.13	1.00	1.00	76.25	2.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BG	6.25	1.25	8.00	4.90	6.00	2.21	7.00	3.96	8.00	3.89	6.25	1.25	57.50	6.55	26.00	4.00	74.00	4.76	65.00	5.63
MOIST	37.50	3.66	33.00	4.96	42.00	5.93	32.00	2.00	35.00	5.82	20.00	0.00	11.00	0.67	11.50	0.76	11.00	0.67	11.50	0.76
PH	6.33	0.21	6.64	0.07	6.26	0.16	6.64	0.04	6.50	0.14	6.98	0.06	6.92	0.04	6.94	0.03	6.94	0.05	6.92	0.05
COMP	141.00	10.58	134.40	8.91	140.40	8.77	123.60	7.17	130.80	10.19	109.50	3.54	85.20	5.20	70.80	4.18	76.80	6.97	82.80	5.20
P	13.88	6.57	6.12	0.63	5.27	0.53	5.63	0.74	17.37	11.56	4.88	0.56	6.32	1.34	4.90	0.66	15.76	7.75	6.45	0.52
C	9.97	1.21	7.01	0.51	7.06	0.38	7.02	0.92	6.58	0.22	8.67	0.57	6.08	0.29	5.99	0.12	6.19	0.21	6.23	0.32
N	4.53	1.02	1.14	0.41	0.91	0.24	1.28	0.63	1.29	0.63	3.60	0.37	0.73	0.25	0.48	0.16	1.28	0.43	0.66	0.10
S	0.25	0.04	0.05	0.01	0.05	0.01	0.05	0.01	0.05	0.01	0.26	0.02	0.05	0.01	0.04	0.01	0.06	0.01	0.05	0.00

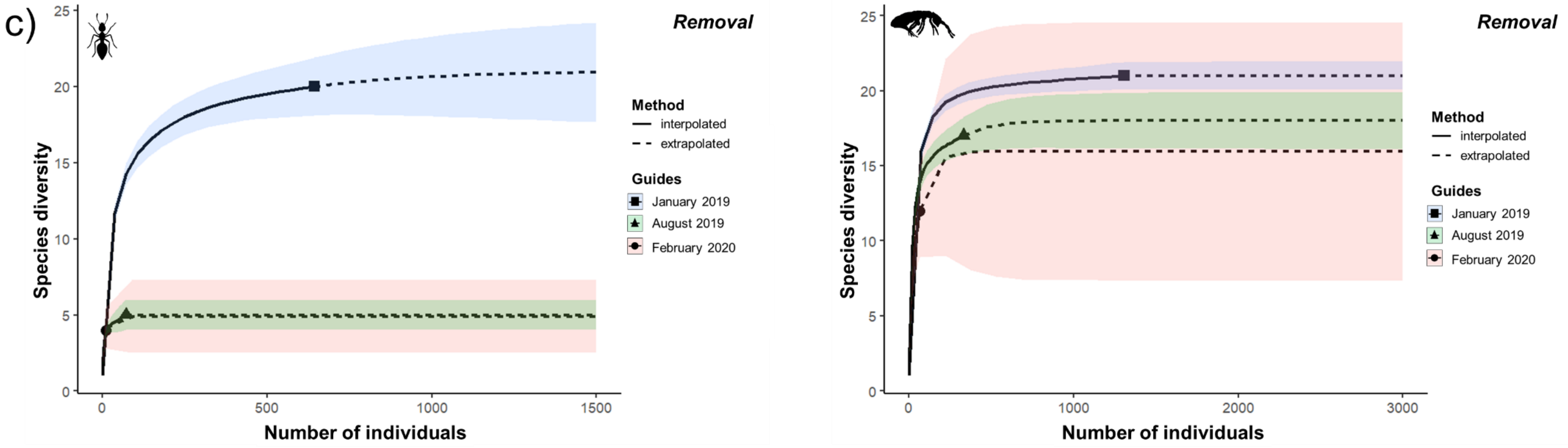
Season	February 2020									
Treatment	**Grass**		**Remove**		**Retention**		**Spread**		**Stack**	
Stat	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
DWC	0.00	0.00	0.00	0.00	59.00	5.04	0.00	0.00	0.50	0.50
SC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AP	15.00	0.00	15.60	0.16	16.00	0.00	15.00	0.00	14.20	0.13
TP	122.00	0.00	124.40	0.65	126.00	0.00	122.00	0.00	114.80	1.20
VH	42.50	3.13	22.50	2.14	9.50	3.83	23.50	2.79	20.50	2.73
VC	89.38	1.48	33.50	4.95	5.00	2.11	35.00	5.00	31.00	5.21
VSP	5.63	0.26	2.50	0.17	1.00	0.39	2.50	0.27	2.40	0.27
LLC	0.00	0.00	3.50	1.50	72.50	3.89	2.00	1.33	5.50	2.41
LLD	0.00	0.00	0.40	0.16	2.10	0.28	0.20	0.13	0.40	0.16
HERB	10.63	0.63	14.50	2.41	3.50	1.30	15.00	2.69	17.00	3.00
SHRUB	2.50	1.64	4.00	1.63	0.00	0.00	6.00	1.63	4.00	1.63
GRASS	76.25	1.83	8.00	1.33	3.00	1.70	7.00	2.13	6.00	1.45
BG	10.63	1.48	63.00	4.23	19.50	3.61	63.00	4.23	61.50	4.22
MOIST	10.00	0.00	12.00	1.33	12.00	1.33	12.00	1.33	12.00	1.33
PH	7.00	0.00	6.98	0.05	6.24	0.69	6.92	0.03	6.98	0.04
COMP	104.50	2.82	84.80	3.17	76.60	4.34	83.80	2.52	87.00	2.44
P	10.57	3.36	7.85	0.91	17.29	6.45	14.66	5.58	5.30	3.24
C	7.22	0.35	7.15	0.46	6.87	0.48	7.58	0.29	5.89	0.27
N	0.48	0.02	0.49	0.04	0.47	0.03	0.48	0.02	0.36	0.02
S	0.06	0.00	0.07	0.00	0.07	0.00	0.12	0.01	0.09	0.00

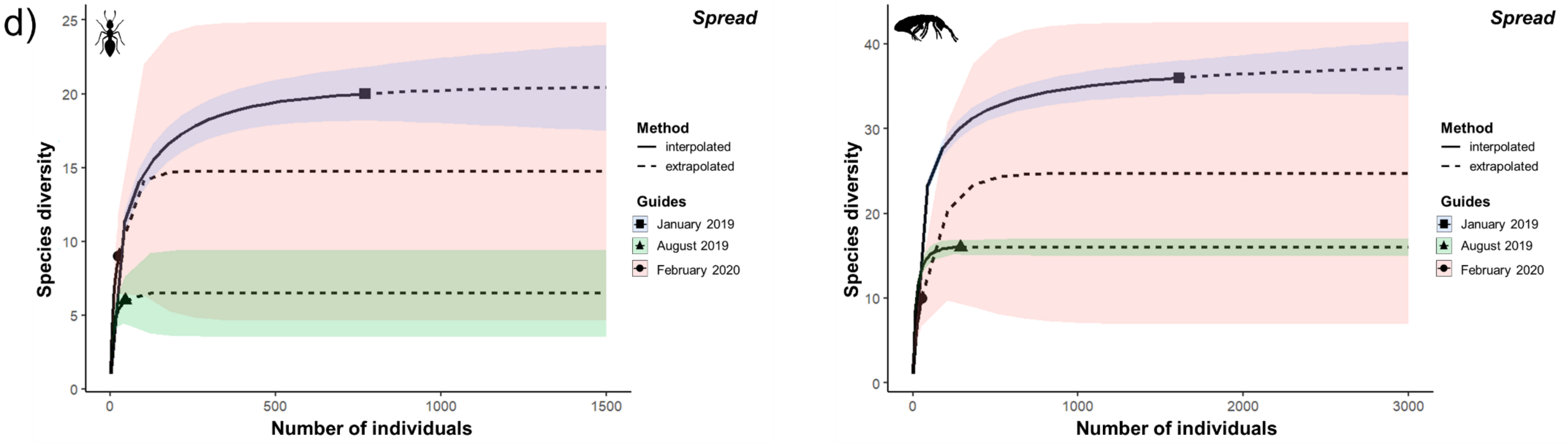
Abbreviations: Deadwood cover (DWC), shade cover (SC), average precipitation (AP), total precipitation (TP), vegetation height (VH), vegetation cover (VC), number of plant species (VSP), leaf litter cover (LLC), leaf litter depth (LLD), herbaceous cover (HERB), shrub cover (SHRUB), grass cover (GRASS), bare ground (BG) cover, soil moisture (MOIST), soil pH (PH), soil compaction (COMP), soil Phosphorus (P), Carbon (C), Nitrogen (N) and Sulphur (S) content.

Appendix S Species accumulation curves showing species collected across treatments and sampling events for ants and springtails. Treatments illustrated as a) retention, b) stacked, c) removal, d) spread and e) grasslands.



Appendix S continued





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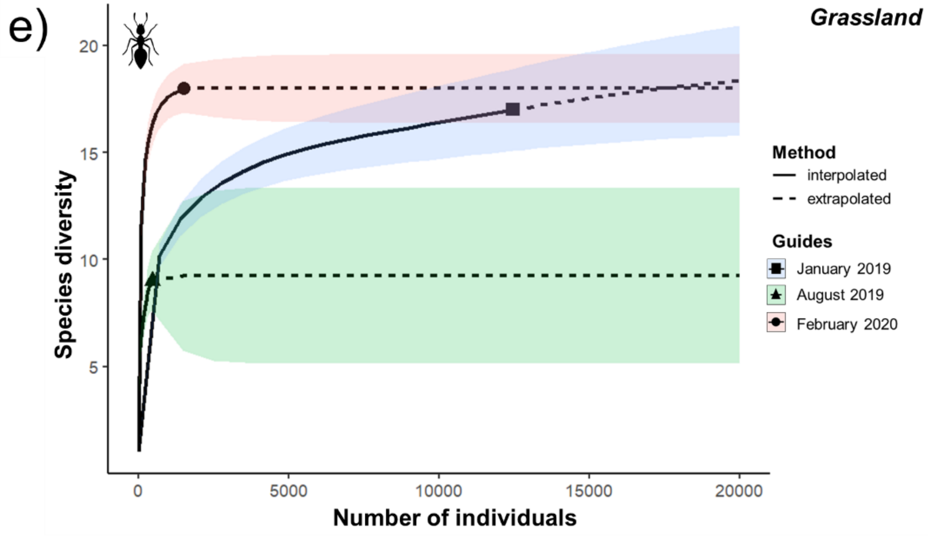

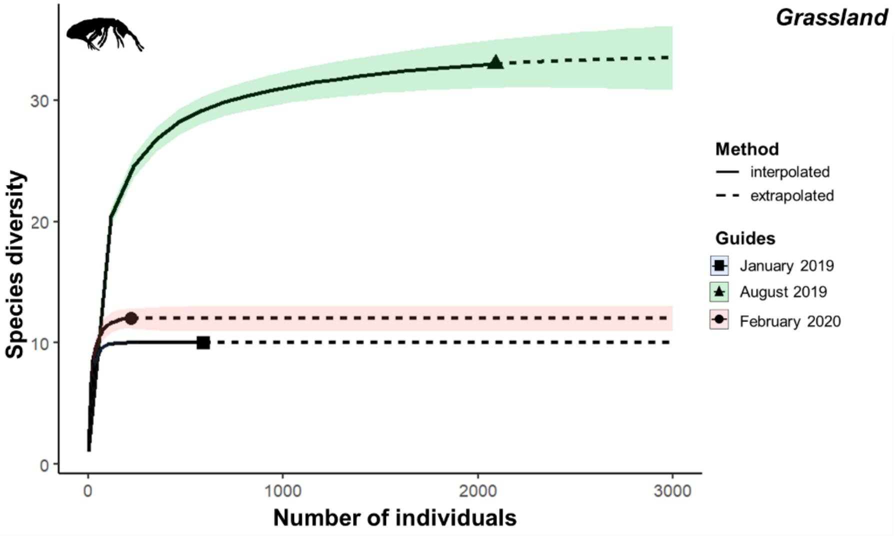

Appendix T Traits included in the calculation of ant Rao's quadratic entropy.

ID	**Sub-family**	**Genus**	**Eye size**	**Body length (mm)**	**Femur length (mm)**	**Colour (V)**	**Forage strategy**	**Habitat**
sp012	Myrmicinae	*Monomorium* sp. 1	Moderate	1.00	0.50	64	GenForager	EpiLitter
sp013	Myrmicinae	*Tetramorium* sp. 1	Large	1.00	0.50	6	GenForager	EpiSoil
sp020	Myrmicinae	*Monomorium* sp. 2	Moderate	0.50	0.25	42	GenForager	EpiLitter
sp021	Ponerinae	*Bothroponera* sp. 1	Small	1.50	1.00	2	Pred	EpiLitter
sp033	Myrmicinae	*Tetramorium* sp. 2	Large	0.50	0.50	52	GenForager	EpiSoil
sp034	Myrmicinae	*Trichomyrmex* sp. 1	Moderate	1.00	1.00	49	GenForager	EpiSoil
sp035	Formicinae	*Paratrechina* sp. 1	Large	1.00	1.00	29	GenForager	EpiSoil
sp044	Formicinae	*Camponotus* sp. 1	Moderate	3.50	5.00	2	GenForager	EpiSoil
sp052	Myrmicinae	*Crematogaster* sp. 2	Moderate	2.00	1.00	12	GenForager	EpiSoil
sp065	Myrmicinae	*Crematogaster* sp. 3	Moderate	1.50	1.00	11	GenForager	EpiSoil
sp067	Myrmicinae	*Crematogaster* sp. 4	Moderate	1.50	1.00	4	GenForager	EpiSoil
sp088	Formicinae	*Camponotus* sp. 4	Moderate	1.50	1.50	27	GenForager	EpiSoil
sp093	Myrmicinae	*Meranoplus* sp. 1	Large	1.00	1.00	33	GenForager	EpiSoil
sp094	Myrmicinae	*Strumigenys* sp. 2	Moderate	1.50	0.50	13	Pred	EpiLitter
sp096	Myrmicinae	*Tetramorium* sp. 3	Large	1.00	0.50	32	GenForager	EpiSoil
sp099	Ponerinae	*Paltothyreus* sp. 1	Large	5.00	3.00	8	Pred	EpiSoil
sp125	Formicinae	*Camponotus* sp. 5	Moderate	2.50	2.00	53	GenForager	EpiSoil
sp128	Myrmicinae	*Tetramorium* sp. 6	Large	1.00	0.50	47	GenForager	EpiSoil
sp142	Formicinae	*Camponotus* sp. 8	Moderate	2.00	2.00	48	GenForager	EpiSoil
sp144	Formicinae	*Camponotus* sp. 9	Moderate	2.00	1.50	26	GenForager	EpiSoil
sp145	Formicinae	*Plagiolepis* sp. 2	Large	1.00	0.50	45	Sap	EpiLitter
sp166	Myrmicinae	*Pheidole* sp. 1	Small	1.00	1.00	70	GenForager	EpiSoil
sp191	Myrmicinae	*Monomorium* sp. 3	Moderate	0.50	0.25	33	GenForager	EpiLitter
sp202	Myrmicinae	*Tetramorium* sp. 9	Large	1.50	1.00	53	GenForager	EpiSoil
sp203	Myrmicinae	*Tetramorium* sp. 10	Large	2.00	1.00	50	GenForager	EpiSoil
sp205	Myrmicinae	*Solenopsis* sp. 3	Small	1.00	0.50	53	GenForager	EpiSoil
sp208	Formicinae	*Lepisiota* sp. 2	Moderate	1.00	0.50	53	GenForager	EpiSoil
sp211	Myrmicinae	*Pheidole* sp. 3	Small	1.50	1.00	59	GenForager	EpiSoil
sp212	Myrmicinae	*Crematogaster* sp. 9	Moderate	1.00	0.50	60	GenForager	EpiSoil
sp231	Myrmicinae	*Tetramorium* sp. 11	Large	1.50	1.50	25	GenForager	EpiSoil
sp233	Myrmicinae	*Crematogaster* sp. 11	Moderate	1.00	0.50	30	GenForager	EpiSoil
sp246	Formicinae	*Camponotus* sp. 13	Moderate	2.00	2.00	66	GenForager	EpiSoil
sp258	Myrmicinae	*Monomorium* sp. 4	Moderate	1.00	1.00	71	GenForager	EpiLitter
sp289	Myrmicinae	*Pheidole* sp. 5	Small	0.50	0.25	36	GenForager	EpiSoil
sp294	Formicinae	*Plagiolepis* sp. 3	Large	1.00	0.50	65	Sap	EpiLitter
sp301	Myrmicinae	*Tetramorium* sp. 14	Large	1.50	0.50	58	GenForager	EpiSoil
sp326	Myrmicinae	*Tetramorium* sp. 16	Large	1.00	0.50	32	GenForager	EpiSoil
sp329	Myrmicinae	*Strumigenys* sp. 3	Moderate	2.00	1.00	52	Pred	EpiLitter
sp348	Myrmicinae	*Tetramorium* sp. 19	Large	1.00	1.00	26	GenForager	EpiSoil
sp349	Myrmicinae	*Myrmicaria* sp. 1	Large	2.50	3.00	71	GenForager	EpiSoil
sp350	Myrmicinae	*Trichomyrmex* sp. 5	Moderate	1.00	1.50	49	GenForager	EpiSoil
sp353	Ponerinae	*Bothroponera* sp. 3	Small	3.00	2.50	24	Pred	EpiLitter
sp355	Dorylinae	*Aenictus* sp. 2	Absent	1.00	0.50	65	Pred	EpiSoil
sp356	Ponerinae	*Leptogenys* sp. 3	Large	2.50	2.00	29	Pred	EpiSoil
sp358	Myrmicinae	*Trichomyrmex* sp. 6	Moderate	1.50	1.00	66	GenForager	EpiSoil
sp360	Myrmicinae	*Tetramorium* sp. 20	Large	1.00	0.50	61	GenForager	EpiSoil
sp364	Myrmicinae	*Solenopsis* sp. 6	Small	0.50	0.30	71	GenForager	EpiSoil
sp385	Proceratiinae	*Probolomyrmex* sp. 2	Absent	1.50	1.00	77	Pred	EpiLitter
sp395	Myrmicinae	*Tetramorium* sp. 23	Large	1.00	0.50	57	GenForager	EpiSoil
sp403	Formicinae	*Lepisiota* spp. 11	Moderate	0.50	0.50	37	GenForager	EpiSoil
sp417	Myrmicinae	*Monomorium* sp. 5	Moderate	1.00	1.00	11	GenForager	EpiLitter
sp418	Ponerinae	*Bothroponera* sp. 6	Small	3.00	2.50	19	Pred	EpiLitter
sp423	Formicinae	*Lepisiota* sp. 12	Moderate	0.50	0.50	16	GenForager	EpiSoil
sp429	Ponerinae	*Odontomachus* sp. 1	Large	2.00	1.50	18	Pred	EpiLitter

Abbreviations: GenForager = Generalist forager, Pred = Predator, Sap = Saprovore, EpiSoil = Epigaeic soil-dweller, EpiLitter = Epigaeic litter-dweller.

Appendix U Traits included in the calculation of springtail Rao's quadratic entropy.

ID	Order	Family	Body length (mm)	Eye size	Fruca development	Feeding strategy	Habitat
sp002	Entomobryomorpha	Entomobryidae sp. 1	2.15	Large	Long	Chew	Atmobiotic
sp005	Entomobryomorpha	Entomobryidae sp. 2	2.15	Large	Long	Chew	Atmobiotic
sp006	Poduromorpha	Hypogastruridae sp. 1	0.80	Large	Short	Chew	Hemiedaphic
sp023	Symphypleona	Dicyrtomidae sp. 1	1.20	Large	Long	Chew	Atmobiotic
sp028	Entomobryomorpha	Isotomidae sp. 1	1.10	Moderate	Moderate	Chew	Hemiedaphic
sp049	Entomobryomorpha	Entomobryidae sp. 3	1.50	Large	Long	Chew	Atmobiotic
sp050	Entomobryomorpha	Entomobryidae sp. 4	1.50	Large	Long	Chew	Atmobiotic
sp051	Symphypleona	Dicyrtomidae sp. 2	0.88	Large	Long	Chew	Atmobiotic
sp060	Entomobryomorpha	Entomobryidae sp. 5	1.00	Moderate	Long	Chew	Atmobiotic
sp064	Entomobryomorpha	Entomobryidae sp. 6	1.38	Large	Long	Chew	Atmobiotic
sp072	Entomobryomorpha	Entomobryidae sp. 7	1.00	Large	Long	Chew	Atmobiotic
sp073	Entomobryomorpha	Entomobryidae sp. 8	0.86	Large	Long	Chew	Atmobiotic
sp074	Entomobryomorpha	Entomobryidae sp. 9	0.80	Large	Long	Chew	Atmobiotic
sp080	Symphypleona	Katiannidae sp. 1	0.38	Large	Long	Chew	Atmobiotic
sp089	Entomobryomorpha	Entomobryidae sp. 10	0.90	Large	Long	Chew	Atmobiotic
sp090	Symphypleona	Dicyrtomidae sp. 3	0.26	Large	Long	Chew	Atmobiotic
sp091	Entomobryomorpha	Entomobryidae sp. 11	1.13	Large	Long	Chew	Atmobiotic
sp111	Symphypleona	Katiannidae sp. 2	0.32	Large	Long	Chew	Atmobiotic
sp113	Symphypleona	Dicyrtomidae sp. 4	0.46	Large	Long	Chew	Atmobiotic
sp114	Poduromorpha	Hypogastruridae sp. 2	0.30	Large	Short	Chew	Hemiedaphic
sp117	Poduromorpha	Hypogastruridae sp. 3	0.58	Large	Short	Chew	Hemiedaphic
sp118	Entomobryomorpha	Isotomidae sp. 2	0.70	Large	Moderate	Chew	Hemiedaphic
sp131	Poduromorpha	Neanuridae sp. 1	0.54	Large	Short	Suck	Hemiedaphic
sp132	Poduromorpha	Hypogastruridae sp. 4	1.00	Large	Short	Chew	Hemiedaphic
sp133	Entomobryomorpha	Isotomidae sp. 3	0.90	Moderate	Moderate	Chew	Hemiedaphic
sp161	Entomobryomorpha	Entomobryidae sp. 12	1.05	Large	Long	Chew	Atmobiotic
sp162	Entomobryomorpha	Entomobryidae sp. 13	1.38	Large	Long	Chew	Atmobiotic
sp183	Symphypleona	Katiannidae sp. 3	1.00	Large	Long	Chew	Atmobiotic
sp196	Entomobryomorpha	Entomobryidae sp. 14	0.75	Large	Long	Chew	Hemiedaphic
sp197	Symphypleona	Katiannidae sp. 4	1.00	Large	Long	Chew	Atmobiotic
sp219	Symphypleona	Katiannidae sp. 5	0.50	Large	Long	Chew	Atmobiotic
sp220	Poduromorpha	Odontellidae sp. 1	0.36	Large	Short	Suck	Hemiedaphic
sp221	Entomobryomorpha	Entomobryidae sp. 15	1.25	Large	Long	Chew	Atmobiotic
sp251	Entomobryomorpha	Entomobryidae sp. 16	1.38	Large	Long	Chew	Hemiedaphic
sp253	Entomobryomorpha	Entomobryidae sp. 17	0.92	Large	Long	Chew	Atmobiotic
sp275	Symphypleona	Sminthurididae sp. 1	0.92	Large	Long	Chew	Atmobiotic
sp276	Symphypleona	Katiannidae sp. 6	0.80	Large	Long	Chew	Atmobiotic
sp280	Poduromorpha	Hypogastruridae sp. 5	1.00	Large	Short	Chew	Hemiedaphic
sp295	Entomobryomorpha	Entomobryidae sp. 18	0.63	Large	Long	Chew	Hemiedaphic
sp296	Poduromorpha	Hypogastruridae sp. 6	1.04	Large	Short	Chew	Hemiedaphic
sp298	Entomobryomorpha	Entomobryidae sp. 19	0.46	Large	Long	Chew	Hemiedaphic
sp304	Entomobryomorpha	Entomobryidae sp. 20	0.53	Large	Long	Chew	Atmobiotic
sp307	Entomobryomorpha	Entomobryidae sp. 21	1.30	Large	Long	Chew	Atmobiotic
sp308	Entomobryomorpha	Entomobryidae sp. 22	0.93	Large	Long	Chew	Atmobiotic
sp309	Entomobryomorpha	Entomobryidae sp. 23	1.08	Large	Long	Chew	Atmobiotic
sp312	Entomobryomorpha	Entomobryidae sp. 24	1.40	Large	Long	Chew	Atmobiotic
sp313	Entomobryomorpha	Entomobryidae sp. 25	1.08	Large	Long	Chew	Atmobiotic
sp314	Entomobryomorpha	Entomobryidae sp. 26	0.40	Large	Long	Chew	Atmobiotic
sp316	Entomobryomorpha	Entomobryidae sp. 27	0.80	Large	Long	Chew	Atmobiotic
sp317	Entomobryomorpha	Entomobryidae sp. 28	0.24	Large	Long	Chew	Atmobiotic
sp318	Symphypleona	Sminthurididae sp. 2	0.98	Large	Long	Chew	Atmobiotic
sp322	Entomobryomorpha	Entomobryidae sp. 29	1.38	Large	Long	Chew	Atmobiotic
sp336	Poduromorpha	Brachystomellidae sp. 1	0.56	Large	Short	Suck	Hemiedaphic
sp340	Symphypleona	Katiannidae sp. 7	0.60	Large	Long	Chew	Atmobiotic
sp342	Entomobryomorpha	Entomobryidae sp. 30	1.05	Large	Long	Chew	Atmobiotic
sp357	Entomobryomorpha	Entomobryidae sp. 31	1.15	Large	Long	Chew	Atmobiotic
sp374	Entomobryomorpha	Entomobryidae sp. 32	1.30	Large	Long	Chew	Atmobiotic
sp378	Entomobryomorpha	Entomobryidae sp. 33	0.50	Large	Long	Chew	Hemiedaphic
sp380	Entomobryomorpha	Isotomidae sp. 4	0.43	Large	Moderate	Chew	Hemiedaphic
sp404	Entomobryomorpha	Entomobryidae sp. 34	2.00	Large	Long	Chew	Atmobiotic
sp405	Symphypleona	Bourletiellidae sp. 1	1.15	Large	Long	Chew	Atmobiotic
sp406	Entomobryomorpha	Entomobryidae sp. 35	2.50	Large	Long	Chew	Atmobiotic
sp407	Entomobryomorpha	Entomobryidae sp. 36	1.60	Large	Long	Chew	Atmobiotic
sp408	Entomobryomorpha	Entomobryidae sp. 37	1.90	Large	Long	Chew	Atmobiotic
sp409	Entomobryomorpha	Entomobryidae sp. 38	2.00	Large	Long	Chew	Atmobiotic
sp410	Entomobryomorpha	Entomobryidae sp. 39	1.35	Large	Long	Chew	Hemiedaphic
sp411	Entomobryomorpha	Entomobryidae sp. 40	1.75	Large	Long	Chew	Atmobiotic
sp412	Entomobryomorpha	Entomobryidae sp. 41	2.55	Large	Long	Chew	Atmobiotic

Appendix U continued

ID	Order	Family	Body length (mm)	Eye size	Fruca development	Feeding strategy	Habitat
sp413	Entomobryomorpha	Entomobryidae sp. 42	2.50	Large	Long	Chew	Hemiedaphic
sp415	Entomobryomorpha	Entomobryidae sp. 43	0.70	Large	Long	Chew	Atmobiotic
sp416	Poduromorhpha	Brachystomellidae sp. 2	0.75	Large	Short	Suck	Hemiedaphic
sp419	Entomobryomorpha	Entomobryidae sp. 44	0.25	Moderate	Long	Chew	Hemiedaphic
sp420	Symphypleona	Sminthuridae sp. 1	0.65	Large	Long	Chew	Atmobiotic
sp422	Entomobryomorpha	Entomobryidae sp. 45	0.60	Large	Long	Chew	Hemiedaphic
sp424	Entomobryomorpha	Entomobryidae sp. 46	0.80	Large	Long	Chew	Hemiedaphic
sp425	Entomobryomorpha	Entomobryidae sp. 47	1.25	Large	Long	Chew	Atmobiotic
sp426	Entomobryomorpha	Entomobryidae sp. 48	1.00	Large	Long	Chew	Atmobiotic
sp427	Entomobryomorpha	Entomobryidae sp. 49	1.25	Large	Long	Chew	Atmobiotic
sp430	Entomobryomorpha	Entomobryidae sp. 50	1.50	Large	Long	Chew	Atmobiotic
sp431	Entomobryomorpha	Entomobryidae sp. 51	2.00	Large	Long	Chew	Atmobiotic
sp432	Entomobryomorpha	Entomobryidae sp. 52	0.90	Large	Long	Chew	Atmobiotic
sp433	Entomobryomorpha	Entomobryidae sp. 53	2.00	Large	Long	Chew	Atmobiotic
sp434	Entomobryomorpha	Entomobryidae sp. 54	1.75	Large	Long	Chew	Atmobiotic
sp435	Symphypleona	Katiannidae sp. 8	1.90	Large	Long	Chew	Atmobiotic
sp436	Symphypleona	Katiannidae sp. 9	1.90	Large	Long	Chew	Atmobiotic
sp437	Symphypleona	Katiannidae sp. 10	1.90	Large	Long	Chew	Atmobiotic
sp438	Symphypleona	Bourletiellidae sp. 2	0.50	Large	Long	Chew	Atmobiotic