Community diversity and composition of ground-dwelling arthropods in major habitat types of the KwaZulu-Natal Sandstone Sourveld

By

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INYUVESI YAKWAZULU-NATALI

Preface

The research contained in this dissertation was completed by the candidate while based in the Discipline of Ecological Sciences, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg Campus, South Africa. The research was financially supported by the National Research Foundation (NRF) and the fieldwork was funded by Durban Research-Action Partnership (D'RAP).

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

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Declaration: plagiarism

I, Nokukhanya Mhlongo, declare that:

(i)   the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii)   this dissertation has not been submitted in full or in part for any degree or examination to any other university;

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(vi)   this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

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Signed: Nokukhanya Mhlongo

Date: 18 August 2023

Dedication

I dedicate this work to my daughter, uNkazimulo Ntombela. I hope you surround yourself with people who think you CAN, people who have your best interests at heart. Without such people, this work was going to remain a dream and only that. It took time, a lot of strength, and hard work to complete this task. My patience and resilience were truly tested through this work. But guess what? I finished! Greatness comes at a cost and through great sacrifices. Nkazimulo, I hope you learn a thing or two from the resilience and hard work I exerted on this study.

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Abstract

Grasslands constitute over 25% of the global land surface and close to one-third of southern Africa. Natural and semi-natural grasslands are recognized globally for their high biodiversity value and their important contribution to the provision of ecosystem services, including provisioning services such as carbon sequestration, water catchments, and grazing for livestock and wildlife. Nonetheless, grasslands are consistently reduced and threatened by anthropogenic activities and invasive alien plants. Invasive alien plants may hinder the growth of natural vegetation by overconsumption of resources. The impact of invasive alien plants on natural vegetation may indirectly affect plant-to-animal interactions such as specialized pollination and seed dispersal syndromes which may ultimately disturb ecosystem processes. The Sandstone Sourveld in KwaZulu-Natal province of South Africa is a threatened grassland ecosystem as a result of various anthropogenic disturbances. Knowledge of arthropod response to differences in habitat types may be essential for an improved understanding of the structure and functioning of ecosystems, which is relevant for informing conservation practice. The aim of this study was to investigate the composition and diversity patterns of ground-dwelling arthropods (ants, beetles, Orthopterans, and spiders) in three habitat types (forest, intact grassland, and disturbed grassland) at Springside and Tanglewood Nature Reserves, which occur in the KwaZulu-Natal Sandstone Sourveld (KZNSS). The objectives were: (i) to document the response of the ground-dwelling arthropod community in different habitat types, (ii) to determine the impacts of seasonal change on the abundance and richness of ground-dwelling arthropods at the two sites, and (iii) to determine the correlation between the distribution of ground-dwelling arthropods and soil characteristics in the KZNSS. Ground-dwelling arthropods were sampled in Springside and Tanglewood Nature Reserves using pitfall traps in each habitat type. Soil parameters in the habitats were also assessed. Analysis of variance was used to test for differences in arthropod morphospecies richness and abundance

across the habitat types and between seasons. The Shannon-Weiner diversity index was computed and used to compare the diversity of ground-dwelling arthropods between the two sites and among habitat types. Ground-dwelling arthropods showed varying patterns in response to habitat characteristics and the disturbance gradient at Springside and Tanglewood. Intact grassland was the most diverse habitat in both Springside and Tanglewood. In Tanglewood, the abundance of ants was greater in disturbed grassland which consisted of a variety of alien invasive shrubs, the high abundance was explained by the "intermediate disturbance hypothesis". However, alien invasion showed more negative than positive impacts on the abundance and composition of ground-dwelling arthropods when there was a significant decrease in the abundance and composition of ants, beetles and spiders. Species richness of ants and beetles was higher in the wet than dry season whereas Orthopterans and spiders showed no significant difference between seasons. In all arthropod groups, a greater number of species were correlated to soil potassium, soil pH, and soil bulk density. Overall, the intact grassland had the highest species richness and abundance followed by the forest and lastly the disturbed grassland. The greater abundance of ants, beetles, and spiders in the pristine grasslands of KZNSS shows that there is still a need to conserve the remnants of the KZNSS vegetation. Therefore, the conservancy management is urged to consider the eradication of alien invasive plants. Future studies are recommended to consider the volant and vegetation canopy arthropods as they are all interdependent with ground-dwelling arthropods to form a whole community of arthropods in an ecosystem.

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Abbreviations

ACE: Abundance–based Coverage Estimator

AIPs: Alien Invasive Plants

CCA: Constrained Correspondence Analysis

GLMs: General Linear Models

KZNSS: KwaZulu-Natal Sandstone Sourveld

nMDS: non-metric Multidimensional Scaling

PAST: Paleontological Statistics Software Package

SIMPER: Similarity Percentage

SNR: Springside Nature Reserve

TNR: Tanglewood Nature Reserve

Chapter One: Introduction

1.1 Background

1.1.1 Arthropod services in natural ecosystems

Arthropods provide several ecological services in natural ecosystems, including economic benefits from an agricultural perspective (Isaacs et al. 2009). Services such as pollination and pest control may increase agricultural productivity and reduce the use of pesticides, respectively. In the Unites State alone, arthropod mediated ecosystem services such as pollination and pest control are worth approximately $8 billion per year (Isaacs et al. 2009). Arthropods are prey to a variety of vertebrates, predators to other arthropods of smaller body sizes, and important plant pollinators and seed dispersers (McCormick and Polis 1982, Montero-Castaño and Vila 2012, Valdez 2020). Ground-dwelling arthropods are involved in decomposition and accelerate the rate of nutrient recycling from plant litter to inorganic nutrients, producing nutrient-rich soils and improving soil fertility (Vitousek et al. 1996, Menta et al. 2011). In cases of biodiversity-threatened ecosystems such as grasslands, ground-dwelling arthropods may be used as bioindicators of the environmental change in an ecosystem (van der Merwe et al. 2020). In particular, insects are sensitive to environmental changes, and their relatively short life span may explain their quick response to environmental or anthropogenic changes, and because of this, they are considered good bioindicators (McGeoch 2007). However, due to their small body size and the fact that they occur in high abundance, the impact of ground-dwelling arthropods can be easily underestimated (Cardoso et al. 2011).

1.1.2 Arthropod-plant interactions

Changes in vegetation type and soil characteristics may be detrimental for ground-dwelling

arthropods, particularly arthropod groups with species-specific host plants or limited mobility (Genes and Dirzo 2022). Ecosystem services supplied by ground-dwelling arthropods are constantly reduced due to direct and indirect threats, such as habitat modification resulting from invasion by alien plants (Mgobozi et al. 2008, Litt et al. 2014, Chikowore et al. 2021). Bottom-up effect have been evident in the studies of arthropod diversity, where the diversity of arthropods is affected by vegetation type, plant species diversity and the type of soil. (Ebeling et al. 2020). Variety of plants provide food for various arthropod groups, while soil provides a habitat for ground-dwelling arthropods (Kaur et al. 2019). Invasive alien plants can suppress the growth of indigenous plants and alter plant species composition, which changes habitat structure (Vilà et al. 2011). Invasions by alien plants may modify soil characteristics such as soil pH, soil salinity, and soil temperature and these soil parameters may regulate the reproductive success of arthropods (Talley et al. 2012).

An increase in invasive alien plants may promote high vegetation cover, increase vegetation density and biomass, and decrease bare ground (Spyreas et al. 2010). Vegetation height might also change depending on the plant species type which dominates the vegetation (Spyreas et al. 2010). Such structural alterations may negatively distort microclimates of the vegetation, changing the acquired temperature, the amount of light available and the moderate moisture content within vegetation (Wolkovich et al. 2009). It has been observed that habitats that invasive alien plants dominate have a relatively reduced abundance and richness of ground-dwelling arthropods (Samways et al. 1996, Hickman et al. 2006, Wolkovich et al. 2009, Litt and Steidl 2010). However, in some instances, arthropod abundance and species richness remained the same, or where change was mostly influenced by seasonality rather than the vegetation composition (Greenwood et al. 2004, Fork 2010). Seasonal variation often relates to temperature and precipitation, which may

influence soil temperature and the amount of water available for plant growth. Ground-dwelling arthropods may increase, decrease or remain the same with seasonality depending on the frequency of seasonal changes and the resilience of the species (Liu et al. 2013).

1.1.3 The grassland vegetation

Grasslands constitute over 25% of the global land surface and close to one-third of southern Africa. Grassland is one of the most species-rich vegetation in the world and it stands out for its high biodiversity value and important contribution to the provision of ecosystem services, including as sites of carbon sequestration, water catchments, and grazing for livestock and wildlife (Boval and Dixon 2012). In South Africa, the KwaZulu-Natal Sandstone Sourveld (KZNSS) is a species-rich grassland that occurs in the KwaZulu-Natal Province. KwaZulu-Natal Sandstone Sourveld constitutes a variety of flora but is mostly dominated by short grass species, shrubs, legumes, and trees (Mucina and Rutherford 2006). This vegetation is located within the eThekwini Municipality area and is of economic and ecological importance because it plays an integral role in livestock farming and provides many ecosystem services such as erosion control and flood attenuation (Taylor and Mathews 2017). It is a habitat for a variety of animals and a site for carbon sequestration. However, the significance of grasslands is not only ecological but expands to economic significance.

Grasslands are diverse and provide a broad range of ecosystem services and ecological infrastructure which positively contribute to livelihoods and economic growth (Carbutt and Kirkman 2022). Grasslands sustain agricultural practices, such as providing sites for row cropping and pastures for livestock grazing, which contributes significantly to South Africa's gross domestic product. Consequentially, the development pressures in South Africa are in a manner that grasslands are continuously transformed and impacted by several competing

land-use types (Carbutt and Kirkman 2022). Primarily, agricultural intensification, forestry plantation, urban development, and mining are the main drivers of grassland transformation, in addition to invasion by alien plants (Neke and Du Plessis 2004, Carbutt et al. 2011). These drivers have fragmented grassland habitats and threatened their sustainability so that approximately a third of the grassland biome has been transformed (Carbutt et al. 2011). Grasslands have been transformed to accommodate South African economic development goals, which include the development of big cities such as Bloemfontein and Johannesburg. Furthermore, in these big cities, it is where activities such as gold mining, coal reserves, diamond deposits, and agriculture are heavily practiced, all at the cost of the grassland transformation (Rutherford and Westfall 1994).

The same pattern is drawn for the KwaZulu-Natal Sandstone Sourveld which is threatened by urban sprawl in the eThekwini Municipality (Boon et al. 2016). The building of housing, industrial complexes, and soil mining is occurring at an accelerated rate (O'Connor and Kuyler 2009, Yusuf and Allopi 2010). Unfortunately, grasslands are the target for such development as they are seen as neglected open spaces with no value (Bond 2016). It is due to these reasons that the KZNSS is listed as endangered vegetation on the National Environmental Management: Biodiversity Act (Act 10 of 2004) of South Africa (Mucina and Rutherford 2006). It is also one of the most critically threatened ecosystems in southern Africa (Rutherford and Westfall 1994). In addition, only 0.2 % of the KZNSS grassland is protected (Boon et al. 2016). Due to the ecosystem's imperilment, there is a greater need to understand the occurrence of species and interactions among species and their environment.

1.1.4 Rationale

Most of the research carried out on the KZNSS is based on the floristics of the vegetation and utilisation of the grassland for grazing (O'Connor et al. 2011, Drury et al. 2016, Ramdhani et al. 2016, Morris and Scott-Shaw 2019). Apart from Hlongwane et al. (2019), there is limited published work done on the importance and contributions of ground-dwelling arthropod communities to the sustainability of the KZNSS ecosystem. Therefore, this study investigates the composition and diversity patterns of ground-dwelling arthropods such as ants, beetles, Orthopterans, and spiders in forest, intact grassland, and alien-invaded grassland at two sites in the KwaZulu-Natal Sandstone Sourveld.

1.1.5 Aim

The aim of the study was to investigate potential response of ground-dwelling arthropods to the habitat disturbance resulting from invasive alien plants in the KwaZulu-Natal Sandstone Sourveld.

1.1.6 Objectives

The objectives of the study were:

1. To determine the species composition of ground-dwelling arthropods in Tanglewood and Springside Nature Reserves,

2. To compare the abundance of ground-dwelling arthropods from the forest, intact grassland, and alien plant-invaded grassland in the two sites,

3. To determine the impacts of seasonal change on the abundance and species richness of ground-dwelling arthropods at the two sites, and

4. To determine the relationship between species composition and distribution of ground-

dwelling arthropods with the KwaZulu-Natal Sandstone Sourveld soil characteristics.

1.1.7 Hypotheses

1. The species composition of ground-dwelling arthropods will be similar in Tanglewood than in Springside Nature Reserves.

2. The alien plant-invaded grassland will have the least abundance and low species richness of ground-dwelling arthropods than the intact grassland and forest habitats.

3. The species richness and abundance of ground-dwelling arthropods will be greater in the wet season than in the dry season.

4. The KwaZulu-Natal Sandstone Sourveld soil characteristics will have no effect on the species composition and distribution of ground-dwelling arthropods.

1.1.8 Thesis structure

Chapter 1 consists of the general introduction, where I describe the importance of the study and state the aim, hypotheses, and objectives of the study. Chapter 2 entails the literature review, and I describe the response of ground-dwelling arthropods to the impact of alien invasive plants on grassland habitats as well as the impact of seasonal change on the abundance and composition of ground-dwelling arthropods. Chapter 3 describes the study sites and details the methods used to conduct the study. Chapter 4 consists of the results. Chapter 5 provides a discussion of the results and chapter 6 includes a general conclusion and recommendations that arise from the study.

Chapter Two: Literature Review

2.1   Importance of ground-dwelling arthropods

Ground-dwelling organisms play a pivotal role in supporting the ecological functions of ecosystems. Epigeic arthropods are important organic matter decomposers and pest control agents for crops (Herrick 2000, Gonçalves and Pereira 2012). They regulate the soil ecosystem by enhancing soil structure and mineralizing soil nutrients (Moore et al. 1988, Cornelissen et al. 2016). Arthropods are the most diverse and abundant group among soil organisms (Santos et al. 2007) and contribute approximately 85% of this composition (Decaëns et al. 2006). Ground-dwelling arthropods are prey to a variety of vertebrates. Multiple guilds of ground-dwelling arthropods are predators of other smaller body-sized arthropods (McCormick and Polis 1982, Prather et al. 2013). Additionally, ground-dwelling arthropods are involved in seed dispersal and pollination of plants (Culliney 2013).

The efficiency of ground-dwelling arthropods in regulating soil ecosystems has contributed to them being referred to as ecosystem engineers (Jones et al. 1994). Ecosystem engineers are organisms that can significantly modify habitat to balance the resources in an ecosystem (Jones et al. 1994). These organisms can change the ecosystem's organic matter composition, soil structure, hydrology, and minerals (Jones et al. 1994, Cornelissen et al. 2016). Within the three levels of soil food web organization, ground-dwelling arthropods are responsible for the breakdown of plant and animal litter (Lavelle et al. 1995). Of the total leaf litter produced yearly, 60% can be decomposed and processed by termites alone. Micro-organisms use the plant matter which is deposited in the faeces of herbivorous animals to convert the organic nutrients into simplified inorganic compounds available to plants through the process of mineralization (Culliney 2013).

The burrowing activities of arthropods such as ants and termites improve soil porosity and increase

aeration, which improves the water-holding capacity of the soil (Culliney 2013). In addition, the movement of ants and termites from their nests, which are usually below ground, to the ground surface, aids in the mixing of mineral and organic particles in the soil (Bagyaraj et al. 2016) The excreta of ground-dwelling arthropods form the basis of humus, stabilizing the soil and improving its ability to store nutrients (Bagyaraj et al. 2016).

2.2   Responses of ground-dwelling arthropods to disturbance

Land-use change is impacting arthropod communities worldwide. The cause is believed to be mainly anthropogenic activities which result in habitat loss (Goulson 2019). Natural habitats have been removed to build roads, houses, factories, recreational spaces, farming, and several other human-pleasing endeavours (Goulson 2019). Approximately 45% of arthropod species losses are due to anthropogenic activities such as agriculture, urban development, and deforestation. In addition to agricultural practices, exposure to pesticides and fertilizers account for another 23% of the insect population decline (Sánchez-Bayo and Wyckhuys 2019).

The common impact caused by these land-use activities is land degradation of natural habitat, resulting in patches of isolated fragments of land. Habitat fragmentation is the leading factor that causes species extinction in the world (Wilson 2002, Haddad et al. 2015). Species with limited dispersal abilities, for example, most of the ground-dwelling arthropods, are the most affected by habitat isolation and fragmentation compared to highly mobile groups such as birds and flying insects (Ewers and Didham 2006). A high rate of arthropod population declines, and possible future extinctions are expected as the impact of habitat loss and fragmentation is explained by the principles of island biogeography (Losos and Ricklefs 2009).

Globally, there has been a debate on the decline of arthropod populations. The majority of scholars

who have written on this topic have considered this decline as an "insect apocalypse" (Goulson 2019, Sánc-Bayo and Wyckhuys 2019, Salcido et al. 2020). In contrast, some scholars argue that the term "insect apocalypse" is an exaggeration since the studies are often site-specific and do not consider disturbances (Willig et al. 2019). For a clear understanding to how arthropod populations change over time, it is important to analyze and know the underlying drivers of the decline. However, each taxa of arthropods may exhibit diverse responses to a particular type of disturbance, depending on the physiology and life history traits of a species.

In a study conducted by Blaum et al. (2009) to investigate the response of ground-dwelling arthropods to grazing-induced shrub encroachment showed that some groups of arthropods showed an increase in abundance, some decreased, and others showed a bell-shaped response to a change in vegetation structure. While all groups of arthropods showed a decrease in abundance in response to shrub cover, dung beetles and ants abundance increased in correlation to shrub cover (Blaum et al. 2009).

Studies have shown that land-use change disturbance can affect the diversity, abundance, and composition of plants and animals in ecosystems. Swart et al. (2019) reported the response of arthropods to a disturbance caused by roads that cut through natural forests. The results showed a significant decline in arthropod species richness towards the road edge compared to areas far into the forest. This suggests that the movement of arthropods was limited by the road which acts as a barrier between habitats. Carabids and Lepidopterans are known to be the most affected by roads (Askling and Bergman 2003, Koivula and Vermeulen 2005). In contrast, there was high alpha diversity near road edges, but the species composition differed from arthropods found 10 m away from the road. The high diversity near road edges was explained by the movement of arthropod generalist species to the forest occupying the habitat of local arthropod specialists (Tscharntke et

al. 2002). These generalists could be invasive or carriers of diseases into the ecosystem. Therefore, habitat fragmentation may compromise the ecological integrity of the forest systems.

Apart from anthropogenic induced disturbances, the invasion by alien plants can be detrimental to arthropods. After habitat loss, alien invasion is the second major threat to biodiversity. Invasive alien plants have spread rapidly worldwide, impacting native species diversity, ecosystem services, and livelihoods (Vilà et al. 2011, Pyšek et al. 2012). The invasion by alien plants into natural habitats often negatively affects native fauna through habitat conversion and alteration of resources. Most studies show that the effect of alien plants will either be neutral or pose a significant decrease in native animal species richness (Garcia and Clusella-Trullas 2017).

2.3   The impact of invasive alien plants on natural vegetation and ground-dwelling arthropods

Invasive alien species have raised concerns in biodiversity conservation (Vitousek et al. 1996, Blossey 1999). Invasive alien plants negatively affect indigenous plants, reducing native vegetation diversity and abundance (Bakker and Wilson 2001). Most invasive alien plants have distinctive characteristics which benefit their proliferation. For example, invasive alien plants have enhanced growth and establishment rates over indigenous plants, can survive in extreme conditions, grow well in poor soils and disturbed environments, and are resilient to changing climatic conditions (Vitousek et al. 1996, Bodle and Hanlon 2001, Herrera and Dudley 2003). In certain invasive alien plants, allelopathic compounds may suppress the germination of indigenous plants species and impede the growth of the seedlings, while some invasive species overconsume natural resources (Kato-Noguchi 2020, Kato-Noguchi and Kurniadie 2021). For example,

Eucalyptus trees are known for transpiring hundreds of litres of water per plant per day. Most invasive alien plants commonly lack natural enemies, such as their native herbivores, and become dominant over indigenous plants (Tallamy 2004).

An increase in the abundance of invasive alien plants leads to an increase in vegetation cover and biomass and decreases the bare ground (Standish 2004, Wolkovich et al. 2009, Spyreas et al. 2010). An increase in vegetation biomass results in a high amount of plant litter which, through nutrient recycling, may promote plant growth and productivity (Standish 2004, Wolkovich et al. 2009). Alien plant invasions may alter the height of native vegetation. They may hinder the growth of native plants based on the level of dominance (Spyreas et al. 2010). These structural variations may negatively impact microclimatic conditions within vegetation by modifying soil moisture availability, the amount of light that penetrates through vegetation, and the ambient temperatures in the understory (Lindsay and French 2006). Invasive alien plants may also modify soil pH and salinity, making conditions unfavourable for native plant growth (Kappes et al. 2007, Topp et al. 2008).

Alteration of vegetation structure and soil composition by invasions of alien plants may be harmful to ground-dwelling arthropods due to their relatively limited dispersal abilities, and due to specificity to the certain host plant (Litt et al. 2014). Environmental factors such as soil pH, soil moisture, light intensity, and ambient temperatures are important in determining success in the reproduction and distribution of ground-dwelling arthropods. Therefore, altering these elements by alien plant invasions may change habitat quality and influence arthropod abundance and diversity (Antvogel and Bonn 2001, Lassau et al. 2005).

Various studies have assessed the impacts of invasive alien plants on species richness, abundance, species composition, and diversity of arthropods from different taxonomic groups. General results

showed that the diversity of arthropods was reduced where invasive alien plants were dominant as compared with areas where indigenous plants dominated (Samways et al. 1996, Ernst and Cappuccino 2005, Gerber et al. 2008, Wolkovich et al. 2009, Simao et al. 2010). However, there have been few studies where arthropods' species richness and abundance were greater, remained the same, or were determined by sampling method (Greenwood et al. 2004, Fork 2010).

In cases where one or few invasive alien plants dominate, the vegetation lacks diversity and becomes homogeneous. Vegetation homogeneity may limit habitat availability for most arthropods, specifically those which are host-specific (Haddad et al. 2001). Limited plant diversity may result in limited arthropod diversity (Hansen 2000). Ground-dwelling arthropods have microclimatic preferences, mostly determined by their life cycle stages. For example, arthropods may require a suitable environment for larval development, and protection in dry and extreme conditions (Samways et al. 1996). Overall, the alterations caused by invasive alien plants can be detrimental to many functional groups of arthropods in several ways depending on their needs for natural resources. Even when microclimate conditions are less crucial, the thickness of invasive plants may continuously impact growth and ultimately reduce the movement of arthropods and habitat availability (Samways et al. 1996). Alterations in the environment as a result of invasive plants may impact arthropod functional groups differently depending on the various specific requirements necessary for growth, reproduction and microclimate.

2.4   Response of ground-dwelling arthropods to seasonal changes

2.4.1   Interaction of arthropods with the environment

Arthropods are an integral part of an ecosystem and are a diverse group of animals that exist in utmost abundance worldwide (Stork 2018). Their abundance and diversity allow for diverse

important ecological roles in an ecosystem. They decompose dead debris of plants into organic matter which influences soil fertility. They form part of important functional groups in soil food webs, as important predators for pests and prey for other animal groups (McCormick and Polis 1982, Prather et al. 2013). The interaction of arthropods with the environment is influenced by resource availability and environmental conditions (Barahona-Segovia et al. 2019). The availability of resources and the environmental conditions can change over time due to seasonal changes. In the grassland biome, weather patterns change seasonally (Mucina and Rutherford 2006). The wet season occurs in summer when temperatures and rainfall are high, and the dry season occurs in winter when temperatures are low and with limited rainfall (Mucina and Rutherford 2006).

2.4.2 Seasonal change influences resource availability

Seasonal change influences the availability of resources for both plants and animals. In the wet season, there is high productivity in vegetation due to warm temperatures and high rainfall which supports the growth of plants (Uhey et al. 2020). The high plant productivity provides more food for arthropods, particularly herbivores, and detritivores. This means there is an increase in the density of arthropods in an ecosystem. In addition, predatory arthropods benefit from the high density of other arthropods of smaller size due to a high number of prey (Mavasa et al. 2022). Therefore, the abundance, richness, and composition of arthropods may be largely influenced by the amount and type of resources available in a particular season.

As seasons change, the availability of resources and environmental conditions also change. These changes may alter the emergence, reproduction, growth rate, and the spatial distribution of arthropods. In general, terrestrial arthropods are sensitive to changes in moisture and temperatures given their high surface-to-volume ratio. However, the response of arthropods to environmental

changes may differ among arthropod groups, depending on the intensity and type of environmental change (Uhey et al. 2020, Mavasa et al. 2022).

Under reduced rainfall, most ground-dwelling arthropods will escape desiccation by migrating to a more suitable environment. They would hide under rocks, dig holes, stay in the soil, and sometimes build a shelter using the debris of litter (Hoffmann et al. 2021). Another factor that may affect the abundance, species richness, and distribution of ground-dwelling arthropods in the dry season is choosing their preferred habitat for overwintering (Hoffmann et al. 2021). For example, wildflower areas are preferred by rove and carabid beetles and spiders as their overwintering habitat (Ganser et al. 2019). The choice could have been driven by the habitat characteristics of the wildflower area, such as high plant species diversity and the background cover (Hoffmann et al. 2021).

As seasons change, the temperature and precipitation also change (Tembe and Mukaratirwa 2020). In a grassland biome wet season comes with high rainfall coupled with high-heat weather patterns. During the season, the temperature can be too high that it is unbearable for ground-dwelling arthropods (Barahona-Segovia et al. 2019). Insects are ectotherms, their body temperature is highly dependent on external environmental conditions. As temperature increases, insect's body gets warm, and their metabolism and food demand increase (Youngsteadt et al. 2023). A forest ground-dwelling beetle *Ceroglossus chilensis* showed the highest physiological performance and species abundance at a thermal preference of 15 °C (Barahona-Segovia et al. 2019). In high-heat environmental conditions, many ground-dwelling arthropods might have physiological restrictions, which could severely impact important survival variables such as reproduction and dispersal abilities (Tuff et al. 2016).

Ants are one of the most active soil-surface arthropods, nest builders, and active foragers are

mostly exposed to the outside environment. A recent study conducted by Youngsteadt et al. (2023) revealed that ants rarely change their behaviour in response to high temperatures. Youngsteadt et al. (2023) tested ants behaviour in a controlled temperature environment, most ants choose a cooler environment. Contrary, when the experiment was done in a natural environment, most species were found in warmer temperatures with high productivity in terms of food, particularly the worker ants. This suggests that firstly, worker ants will prioritize their foraging duty over escaping the lethal temperatures, secondly, they may try to tolerate the heat for the sake of securing the colony. Lastly, it could be that they lack the behavioural flexibility to move to their preferred temperatures (Youngsteadt et al. 2023).

2.5   The importance of the KwaZulu-Natal Sandstone Sourveld

2.5.1   Characteristics of the vegetation

In southern Africa, the grassland biome covers approximately a third of the total land area, it is the second largest biome (Mucina and Rutherford 2006). Grasslands provide ecosystem services such as nutrient and water cycling, energy supply, carbon sequestration, and soil stability (Reyers et al. 2005, 2009). Egoh et al. (2020) reported an accelerating decline in ecosystem service worldwide due to land-cover change. Although grasslands are of high importance, only 2.8% of this biome is protected for formal conservation. South African grassland ecosystems are listed as critically endangered (Reyers et al. 2005).

The KZNSS consists mainly of grassland and savanna elements with small patches of scarp forests and occurs in the eThekwini municipality in the province of KwaZulu-Natal. KwaZulu-Natal Sandstone Sourveld originally covered 179 671 ha but has diminished in extent due to anthropogenic disturbances such as urban development, agricultural activities, and soil mining

(Jewitt 2018). It was initially classified as part of the Savanna Biome (Mucina and Rutherford 2006). However, its classification affiliation on Mucina and Rutherford (2006) is on the borderline of two vegetation types, portraying characters between savanna and grassland biomes. KwaZulu-Natal Sandstone Sourveld could, therefore, be considered a candidate for a grassland biome (Mucina and Rutherford 2006).

KwaZulu-Natal Sandstone Sourveld is described as species-rich grassland vegetation with short grasses, low shrubs that spread within the vegetation, and fewer scattered woody plants (Drury et al. 2016, Mucina and Rutherford 2006). The grass: tree ratio is not stable, and proportions are affected by various factors including natural and/or anthropogenic-induced disturbances (Boon et al. 2016). KwaZulu-Natal Sandstone Sourveld is distributed along well-drained shallow, acidic, sandy soils that are nutrient-poor, derived from Natal Group Sandstone (NGS). The mean annual precipitation of the region is 934 mm, and the mean annual temperature is 17.2 °C (Mucina and Rutherford 2006). It is found on heights lower than 450 m above sea level (Boon et al. 2016). Fog might be the moisture source for this vegetation, whereas frost is limited and infrequent (Boon et al. 2016).

2.5.2 Conservation status

KwaZulu-Natal Sandstone Sourveld houses several endemic species of plants. Approximately 11.4% of the total area of KZNSS remains as natural habitat and less than 0.2% is formerly protected (Jewitt 2012). Within the eThekwini municipality, only 0.74% (116 ha) of the KZNSS is protected and this is much lower than the conservation target of 3920 ha for this vegetation type (Jewitt 2012). The national conservation target for KZNSS is 25%, which would protect about 75% of plant species found there (Rouget et al. 2004). However, as more data is collected the target percentage will also change. Nationally, KZNSS is considered an endangered ecosystem

(Jewitt 2012).

The average percentage of natural habitat loss in KwaZulu-Natal (KZN) is high and estimated at 1.2% annually (Jewitt et al. 2015). Should the loss rate remain the same, by 2050 only 45% of the KZN landscape will be left as natural habitat. Jewitt et al. (2015) reported that in 2012 approximately 54% of natural vegetation in the city of Durban was modified and about 17% was reported as highly degraded. The major drivers of biodiversity loss in the KZNSS ecosystem are habitat fragmentation, biological invasions, infrastructural development (settlements and urban expansion, roads) mining, and agriculture. Also land use in the area is dominated by timber plantations and sugarcane, subsistence agriculture, and the urban sprawl of the eThekwini municipality (Mucina and Rutherford 2006). Approximately 68% of KZNSS is irreversibly transformed for cultivation, forestry, road building, and urban development, which is much higher than the national average of 18% transformation of all vegetation types (Boon et al. 2016). Boon et al. (2016) reported that approximately 90% of KZNSS is lost and the vegetation should be classified as critically endangered instead of endangered because the natural area left is smaller than the conservation target of this vegetation type.

The high level of ecosystem degradation and transformation with limited protection in the KZNSS has resulted in initiatives to undertake baseline research to improve understanding of the ecosystem. The eThekwini (Durban) municipality conservancy program is one such initiative. This research contributes to the municipal research strategy by exploring diversity patterns of ground-dwelling arthropods in two protected areas in the KZNSS. The protected areas may represent the characteristic vegetation communities (grassland, savanna, and forest) of the KZNSS.

Chapter Three: Material and Methods

3.1 Study area

The study was conducted in the KwaZulu-Natal Sandstone Sourveld (KZNSS), a small portion of the vast grasslands in South Africa. A significant part of the KZNSS is found in the eThekwini (Durban) municipal area, which is located on the east coast of the KwaZulu-Natal Province in South Africa. This study focuses on the two protected areas, whose vegetation comprises of remnants of the KZNSS. Springside Nature Reserve (SNR: 29°46'47.79"S, 30°46'19.88"E; altitude 447 m.s.l.) and the Tanglewood Nature Reserve (TNR: 29°48'37"S, 30°49'18"E; altitude 446 m.a.s.l.) are located in the eThekwini municipal area and are proximately 15 km apart (Fig. 3.1).

Springside Nature Reserve is a 21-ha conservation area of forest, grassland, and riverine forest elements. The reserve is co-managed by Hillcrest Conservancy, a suburban initiative on environmental advocacy, and the eThekwini Municipality. Springside receives an average daily temperature of 11.1 ℃ in July to 25.6 ℃ in October (NASA 2022). Tanglewood Nature Reserve is a 64.7 ha private nature reserve that consists of natural forest and grassland. Tanglewood has an average daily temperature of 18.8 ℃ in July and 24.1 ℃ October (NASA 2022). The mean annual precipitation for Springside and Tanglewood ranges from 951 to 1756 mm and falls mainly in summer (Oct-Mar) (NASA 2022). The climate of the whole area can be described as hot and wet summers and cool dry winters. The geology of the area consists of Ordovician sandstone overlain with shallow, skeletal, nutrient-poor sandy soils (Mucina and Rutherford 2006).
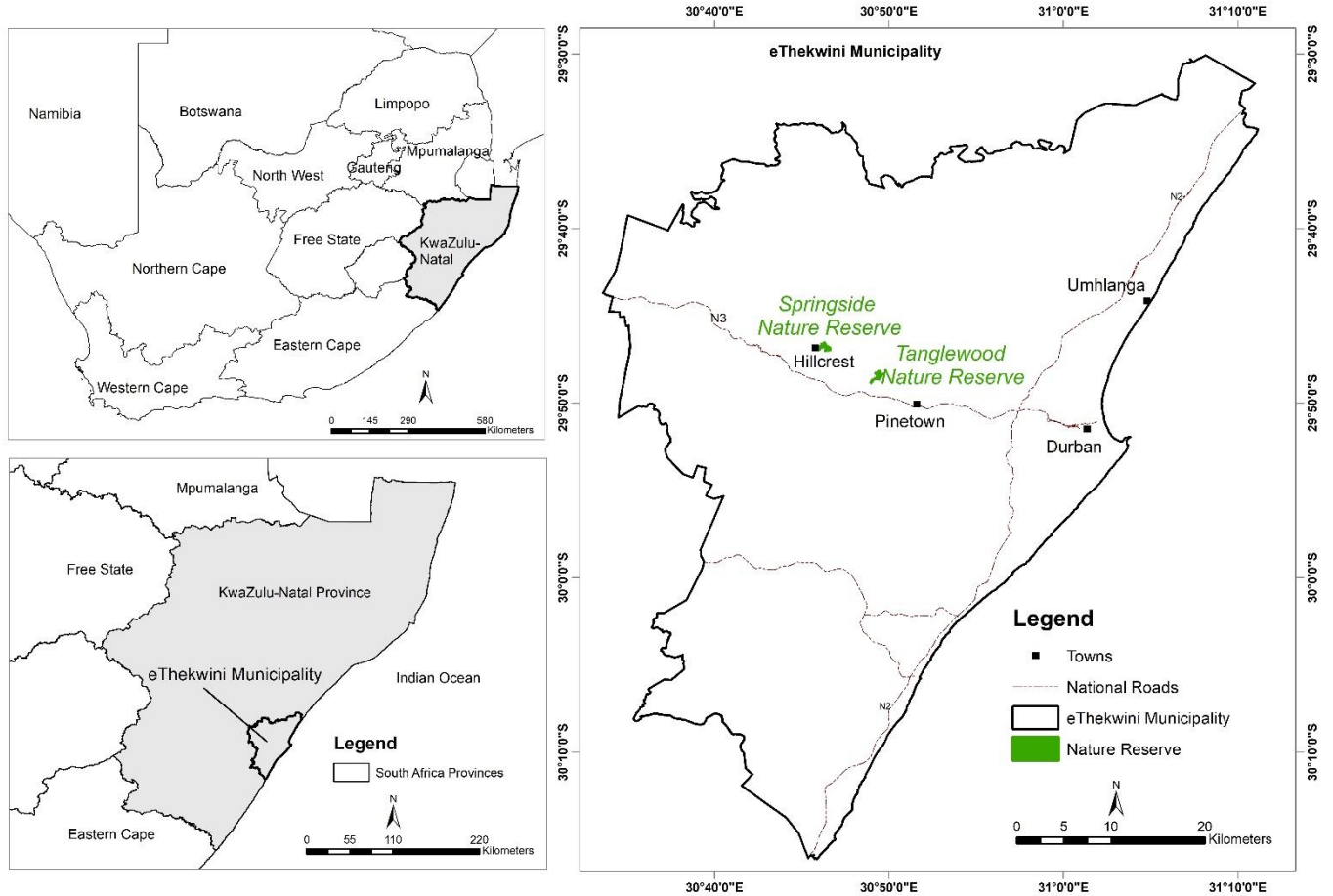
Figure 3.1. Location of the study sites in the eThekwini Municipality in KwaZulu-Natal, South Africa.

At each site, the vegetation was categorised as 1) forest, 2) intact grassland, and 3) alien plant-invaded grassland. The plant composition of Alien Invasive Plants (AIPs) patches differs between sampled nature reserves. In Springside Nature Reserve, AIPs vegetation was previously a grassland that is now a *Pinus patula* plantation that is interspersed with patches of native *Strelitzia nicolai.* In Tanglewood Nature Reserve, patches of invasive alien plants occur in the grassland and are dominated by *Lantana camara*, *Solanam nigrum, Diplocyclos palmatus* and *Tithonia diversifolia.* In both SNR and TNR, the intact grassland is dominated by *Aristida junciformis* and

Digitaria eriantha. However, TNR also had *Panicum maximum* while SNR had *Cymbopogon caesius*, *Setaria pallide-fusca* and *Monocymbium ceresiforme*. The forest at SNR is dominated by *Psychotria capensis* and *S. nicolai* while *S. nicolai* is dominant at TNR.

3.2   Sampling of ground-dwelling arthropods

Ground-dwelling arthropods were sampled from Tanglewood and Springside using pitfall traps. Three replicates per nature reserve were set for each habitat type (forest, intact grassland, alien plant-invaded grassland). Each replicate had 10 pitfall traps laid out in two rows of five traps that were spaced 10 m apart. Replicates of forest and alien plant-invaded grassland were not located in contiguous patches. The traps were made of 250 ml transparent honey jars (70 mm diameter, 150 mm height) which were inserted into the pits with their reams flush with the soil surface. The jars were one-quarter filled with propylene glycol, which neither repels nor attracts arthropods (Munyai and Foord 2015). Traps were set for five days during the dry (May-Jul) and wet (Oct-Dec) seasons of 2016 before samples were collected and transported to the laboratory. In the laboratory, specimens were washed, sorted, and stored in 70 % ethanol. Specimens were identified to morpho-species using an insect identification guide (Picker 2012). To identify ant species to genus level, Fisher and Bolton (2016) was used, and to check the validity of species names, AntCat (http://www.antcat.org) and AntWeb (http://antweb.org) were used. Ant specimens were identified to species level where possible, but many were identified to genus level and then assigned a morphospecies name. The insect reference collections housed at the University of KwaZulu-Natal in Pietermaritzburg and Westville campuses were also used for species identification. Dippenaar-Schoeman (2014) was used to identify spiders to genus level and then assigned a morphospecies name. Species that were difficult to identify to lower ranks were

identified at family level and then assigned to morphospecies.

3.3 Soil sampling and analysis

Soil samples were collected in March 2017 from forest, intact grassland, and alien plant invaded grassland in each nature reserve. To minimize bias and accommodate all possible soil heterogeneity, five soil samples were collected at depths of 0-50 mm from each replicate used for pitfall traps. Soil samples were bulked into a composite sample from each replicate and were analysed at the Soil Fertility and Analytical Services unit of the KwaZulu-Natal Department of Agriculture and Rural Development at Cedara. Samples were analysed for physico-chemical parameters using standard methods (Manson et al. 2020). Calcium (Ca) and magnesium (Mg) were extracted from a mixture of 2.5 mL of sampled soil with 25 mL of 1 M KCL solution and stirred at 400 r.p.m for 10 min. Whatman No.1 paper was used to filter the extracts and filtrate of 5 mL was diluted with 20 mL of 0.0356 M $SrCl_2$, Ca and Mg were then determined by atomic absorption. Soil acidity was determined using 10 mL of the filtrate which was diluted with 10 mL of de-ionised water with 2-4 drops of phenolphthalein and titrated with 0.005 M NaOH.

Phosphorus (P), potassium (K), zinc (Zn), copper (Cu), and manganese (Mn) were extracted using Ambic-2 extracting solution (0.25 M NH_4CO_3 + 0.01 M Na_2EDTA + 0.01 M NH_4F + 0.05 g l^{-1} Superfloc (N100) with pH adjusted to 8 and concentrated ammonia solution included. A mixture of 25 mL Ambic-2 extracting solution with 2.5 ml of sampled soil was stirred at 400 r.p.m for 10 minutes, extracts were filtered using Whatman No. 1 filter paper. From 2 mL of the filtrate, P was determined using a modification procedure by Murphy and Riley (1962). Potassium was quantified by atomic absorption on a filtrate after being diluted with de-ionised water. Zn, Cu, and Mn were quantified by the atomic absorption of the undiluted filtrate. Soil pH was obtained in 1

M KCL solution and was measured with a gel filled glass electrode while stirring. Percentage of acid saturation was calculated as acidity × 100/ (Ca + Mg + K + acidity). Organic carbon was estimated by the near-infrared reflectance. Clay content was estimated using a combination of near-infrared reflectance and measured bulk density. Total nitrogen was determined by the automated Dumas dry combustion method using a LECO CNS 2000 analyzer (Leco Corporation, Michigan, USA).

3.4   Data analysis

To gain a measure of the adequacy of sampling, species accumulation curves were drawn for each group of ground-dwelling arthropods at each site. Species accumulation curves were computed in EstimateS version 9.0 (Colwell and Elsensohn 2014) using a diversity estimator Chao 2 (Chao 1987) and an abundance–based coverage estimator (ACE) (Chao and Yang 1993). Chao 2 and ACE are recommended for incident-based richness data (Colwell and Elsensohn 2014).

To compare species diversity of each group across habitat types, Shannon's *H′* and Pileou's evenness indices were calculated (Magurran 2004). Indices and evenness were computed using Paleontological Statistics Software Package (PAST) version 3.18 (Hammer et al. 2001). To identify the percentage contribution of each taxon to the observed value of the Bray-Curtis dissimilarity between habitats, the Similarity Percentage (SIMPER) analysis was calculated (Clarke 1993) in PAST.

General linear models (GLMs) were used to test for significant differences in species richness and species abundance among habitat types and between seasons for each arthropod group. Normality and equality of variances of residuals of the data were tested using one-sample Kolmogorov-Smirnov and Levene's tests respectively. In cases where the assumptions of normality and equality

of variance were not met, data were transformed. The assumption of normality of residuals of the data is not expected for count data because abundance is often skewed and the values tend to be discrete (Anderson 2001). The log link function was used for data transformation, and the GLM analyses were repeated after data were transformed. When significance was obtained, a Tukey's post hoc test evaluated specific differences between habitat types. In cases where assumptions were not met after data transformation, a non-parametric Kruskal Wallis's test was performed. In all cases, the significance level was set at alpha = 0.05. All GLM data analysis was carried out in IBM SPSS version 27 (IBM SPSS Statistics 2020).

Non-metric multidimensional scaling (nMDS) in PAST3 was computed to present a visual representation of the influence of habitat types on the distribution of ground-dwelling arthropods. Environmental parameters and arthropods species composition data were analysed by computing a constrained ordination procedure which illustrates the main trends of variation of data sets regarding environmental factors and restrictions of inexplicable variation (Legendre and Legendre 2012). The ordination analysis was carried out using CANOCO version 5.1 (ter Braak and Šmilauer 2012). For each group of arthropods, two ordinations were computed representing the morphospecies sampled from the two sites. Canonical Correspondence Analysis (CCA) measures the variation of species distribution with reference to corresponding environmental factors (Borcard et al. 1992), which were soil variables in this study. This analysis determined the impact of soil parameters on the distribution and diversity of ground-dwelling arthropods (Krishnadas et al. 2016).

Chapter Four: Results

In total, 6 060 ground-dwelling arthropods from 145 morphospecies were collected from the Springside and Tanglewood Nature Reserves during the two sampling seasons. Ants were the most abundant and species-rich group, with 3 340 specimens from five subfamilies and 18 genera with 56 morphospecies. Subfamilies with the highest species richness were the Myrmicinae (15 morphospecies) and the Formicinae (14 morphospecies). The Dorylinae was the least species-rich, with one morphospecies of three individuals. The most abundant subfamilies were the Myrmicinae (79.9%) and the Formicinae (7.4%). A single morphospecies belonging to the genus *Pheidole* contributed 76.5% of individuals of the Myrmicinae.

There were 281 individuals of beetles from 14 families and 34 morphospecies. Order Orthoptera consisted of 119 individuals from seven families with 24 morphospecies, and lastly, spiders consisted of 153 individuals from 17 families with 31 morphospecies.

Sample-based species accumulation curves showed that the estimated species richness resembled the number of species observed at both Springside and Tanglewood (Fig. S1 to S3). Both estimators reached an asymptote indicating adequate sampling for all species groups except for spiders in Tanglewood, the curves for spiders showed that there was a possibility for more species provided extended sampling time (Fig. S4b).

4.1 The abundance and species richness of ground-dwelling arthropods

At Springside, the species richness and abundance of ants were significantly greater in intact grassland than in alien-invaded grassland and forest but were similar between the other two habitats (Table 4.1; Fig. S5a, b). Ants were more abundant and species-rich in the wet season than in the dry season (Table 4.1; Fig. S5c, d). For beetles, abundance was similar among habitat types

and between seasons while species richness was greater in the forest than in alien-invaded grassland (Table 1; Fig. S6a, c). However, the species richness of beetles was greater in the wet season than in the dry season (Table 1; Fig. S6d). At Tanglewood, the species richness and abundance of ants were similar among habitat types (Table 1). The abundance of ants was also similar between seasons (Table 1; Fig. S5c). In Tanglewood, species richness of ants was greater in the wet season than in the dry season when 25 species were not represented in the dry season (Table 1; Fig. S5d). For beetles, the species richness and abundance were significantly greater in the forest than in the other two habitats (Table 1; Fig. S6a, b) but were similar between seasons (Fig. S6c, d). At the two sites, the species richness and abundance of Orthopterans were similar among habitat types and between seasons (Fig. S7). At both sites, spider abundance was not significantly different among the three habitats (Fig. S8a) while species richness was greater in intact grassland than in alien-invaded grassland but not forest at Springside (Table 1; Fig. S8b). Compared between seasons, species richness and abundance of spiders were similar at both sites (Fig. S8c, d).

4.2 Shannon diversity and Pielou's evenness

Values of the Shannon diversity index showed that the intact grassland was the most diverse habitat for ants while the disturbed grassland had the least at Springside (Table 2). At Tanglewood, the disturbed grassland also had the least ant diversity and evenness (Table 2). Diversity of beetles was consistently highest in the forest, while evenness was greatest in disturbed grassland (Table 2). At both sites, alien-invaded grassland was the most diverse habitat for Orthopterans (Table 2). The diversity of spiders was greatest in intact grassland for both sites but with low evenness in Springside (Table 2).

4.3 Species composition of ground-dwelling arthropods

Patterns of species composition of ants at Springside and Tanglewood showed that the forest and intact grassland showed the most dissimilarity, and an ant morphospecies, *Pheidole* sp.02 (*megacephala* gp.) contributed most to the dissimilarity among habitats (Table S1). For beetles, the high dissimilarity in species composition between intact grassland and alien-invaded grassland was evident at both sites. A beetle morphospecies, *Curculionidae* sp.01, contributed most to the dissimilarity among habitat types in both Springside and Tanglewood (Table S12). Greater dissimilarity in species composition of Orthopterans was shown between forest and intact grassland in Springside. Orthopteran morphospecies, *Cophogryllus* sp.02, contributed most to the dissimilarity among habitats (Table S3). For spiders, high dissimilarity in species composition was observed between forest and alien-invaded grassland. An araneomorph spider morphospecies, *Pholcidae* sp.01 contributed most to the dissimilarity of the habitat types (Table S4). At Tanglewood, alien-invaded grassland and forest habitats showed a high percentage of dissimilarity. Another Orthoptera morphospecies, *Gryllidae* sp.07, contributed most to the dissimilarity of habitat types (Table S3). For spiders, forest and intact grassland showed a high percentage of dissimilarity. A wolf spider morphospecies, *Lycosidae* sp.05, contributed most to the dissimilarity between alien-invaded grassland and intact grassland, as well as between forest and intact grassland (Table S4).

At Springside, there was a close similarity between ants found in the forest and alien-invaded grassland. In contrast, intact grassland was isolated from the other habitats (Fig. 1a). For beetles, the similarity in species composition is shown between forest and intact grassland habitats (Fig. 2). For Orthopterans there was an overlap in the species composition of all three habitats (Fig. 3). In Tanglewood, ants composition was dissimilar across all habitats. The species of ants found in

each habitat were different from those of the other two habitats (Fig. 1b). For beetles, there was an overlap between species composition in forest and alien-invaded grassland (Fig. 2b). For Orthopterans and spiders, there was a close similarity in the species composition of taxa between forest and intact grassland (Figs. 3b and 4b).

4.4 Relationships between species composition and soil variables

At Springside and Tanglewood, the constrained correspondence analysis (CCA) revealed that the species composition of all groups of arthropods occurring in intact grassland was correlated to K, soil pH, and soil bulk density (Fig. 5-8). In forest, the species composition was correlated to Ca, Mg, and P. However, for beetles, species composition was correlated to N, in addition to Ca, Mg, and P. In alien-invaded grassland, the species composition of all arthropods was correlated to clay content, organic carbon, and N at both sites.

Table 4.1. *F* ratios and associated probabilities of the effect of habitat type and season on species richness and abundance of ants collected in Springside and Tanglewood. Significant p-values are in bold.

			Habitat			Season	
Ants		*F*	df_1, df_2	*P*	*F*	df_1, df_2	*P*
Springside	Abundance	11.53	2, 6	**0.009**	4.66	1, 16	**0.046**
	Species richness	11.51	2, 6	**0.009**	11.10	1, 16	**0.004**
Tanglewood	Abundance	3.47[#]	2, 6	0.177	3.26	1, 16	0.09
	Species richness	2.29	2, 6	0.182	8.22	1, 16	**0.011**
Beetles							
Springside	Abundance	2.724	2, 6	0.144	3.213	1, 13	0.096
	Species richness	6.152	2, 6	**0.035**	6.054	1, 13	**0.029**
Tanglewood	Abundance	7.240	2, 6	**0.025**	3.626	1, 14	0.078
	Species richness	11.485	2, 6	**0.009**	2.092	1, 14	0.170
Orthopterans							
Springside	Abundance	1.315	2, 5	0.348	0.116	1, 10	0.741
	Species richness	3.196[#]	2, 5	0.202	0.10	1, 10	0.923
Tanglewood	Abundance	1.969	2, 6	0.220	0.877	1, 12	0.367
	Species richness	3.658	2, 6	0.091	0.515	1, 12	0.487
Spiders							
Springside	Abundance	4.093	2, 6	0.076	0.155	1, 14	0.7
	Species richness	7.398	2, 6	**0.05**	0.024	1, 14	0.814
Tanglewood	Abundance	2.118	2, 6	0.201	1.885	1, 16	0.189
	Species richness	3.570	2, 6	0.095	0.640	1, 16	0.435

[#]The value of the test statistic shown is based on a Kruskal-Wallis test

Table 4.2. Values of Shannon-Weiner diversity and Pielou's evenness of ants found in Springside and Tanglewood.

	Characteristics		Habitat types		
			Forest	Grassland	Alien invaded grassland
Ants	Springside	Shannon (*H'*)	1.373	1.628	0.916
		Evenness	0.282	0.268	0.125
	Tanglewood	Shannon (H'*)	2.035	1.828	1.063
		Evenness	0.403	0.183	0.152
Beetles	Springside	Shannon (*H'*)	2.444	2.322	1.994
		Evenness	0.677	0.637	0.735
	Tanglewood	Shannon (*H'*)	2.635	1.587	1.846
		Evenness	0.774	0.543	0.905
Orthopterans	Springside	Shannon (*H'*)	0.637	1.677	2.034
		Evenness	0.945	0.892	0.849
	Tanglewood	Shannon (*H'*)	1.55	2.01	1.976
		Evenness	0.942	0.622	0.656
Spiders	Springside	Shannon (*H'*)	1.985	2.596	1.561
		Evenness	0.809	0.789	0.952
	Tanglewood	Shannon (*H'*)	1.979	2.626	2.152
		Evenness	0.905	0.727	0.662

Figure 4.1. nMDS plot of ants sampled among three habitat types in Springside (a) and Tanglewood (b) with stress of 0.109 and 0.095, respectively, based on the Jaccard's index. Colour-coding indicates alien-invaded grassland (red circle); forest (blue square); and intact grassland (green star).
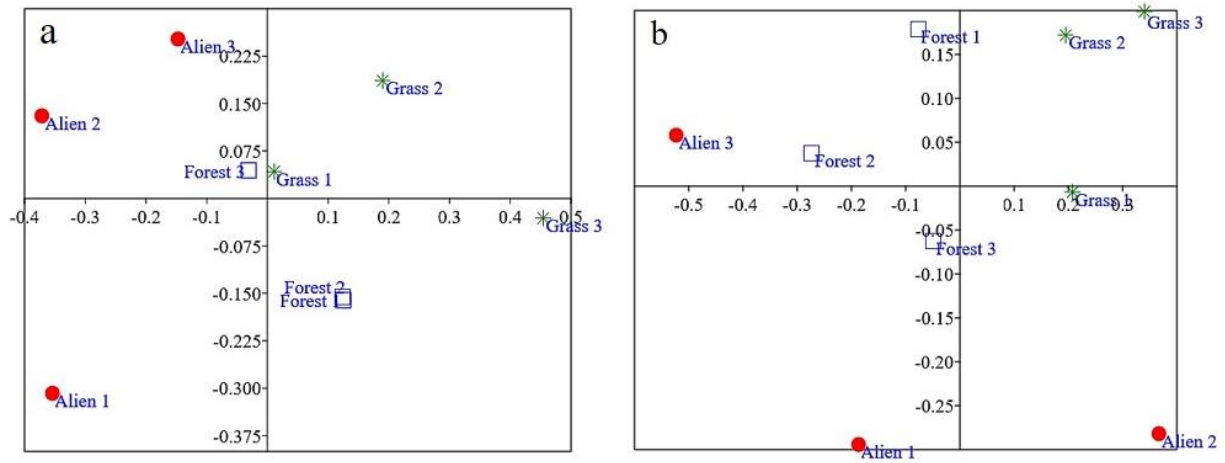
Figure 4.2. nMDS plot of beetles sampled among three habitat types in Springside (a) and Tanglewood (b) with stress of 0.1097 and 0.259, respectively, based on the Jaccard index. Colour-coding indicates alien-invaded grassland (red circle); forest (blue square); and intact grassland (green star).
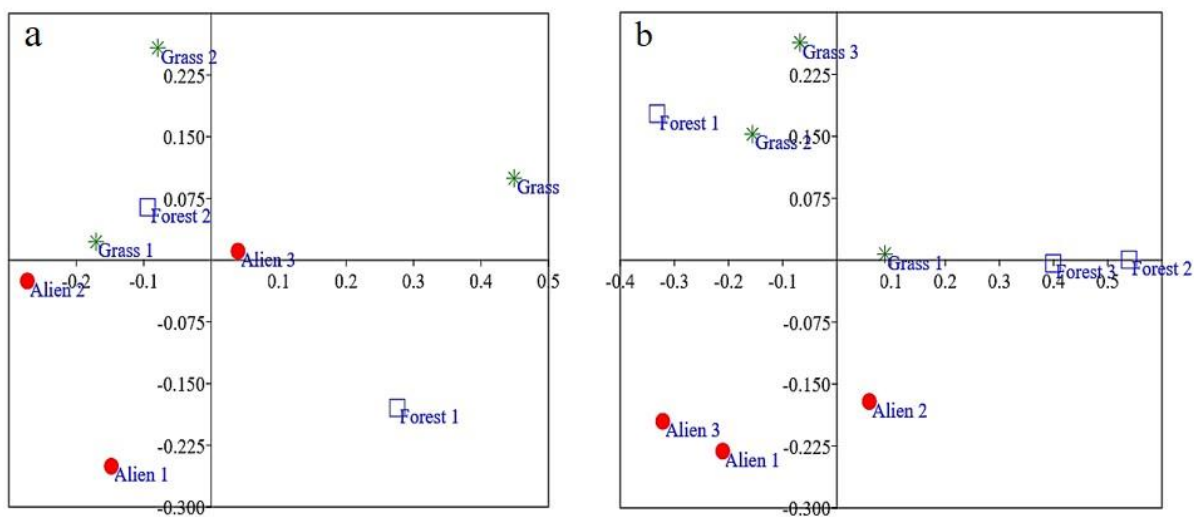
Figure 4.3. nMDS plot of crickets sampled among three habitat types in Springside (a) and Tanglewood (b) with stress of 0.4814 and 0.2753, respectively, based on the Jaccard index. Colour-coding indicates alien invaded grassland (red circle); forest (blue square); and intact grassland (green star).
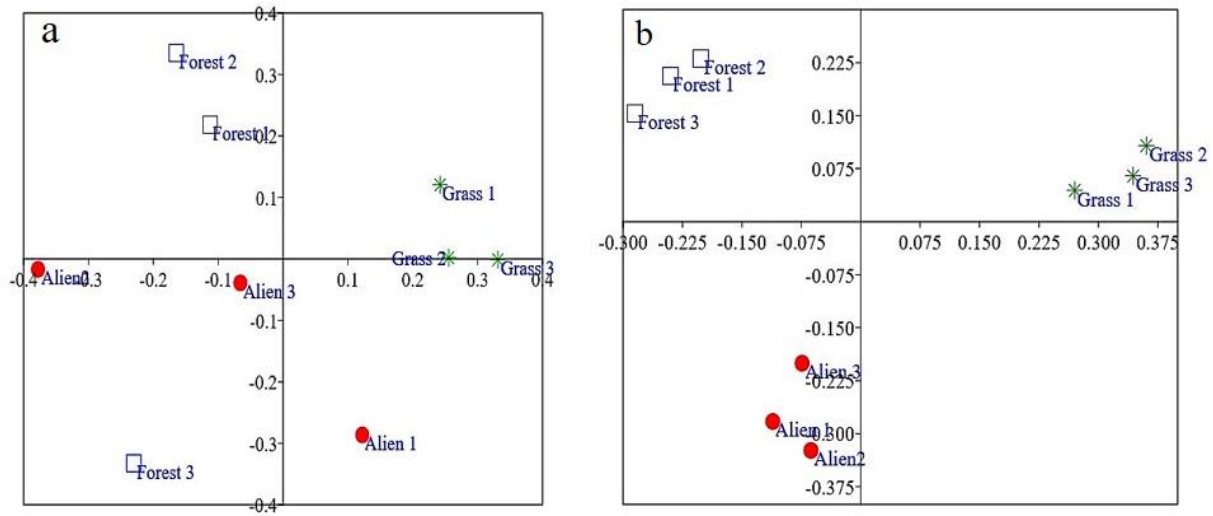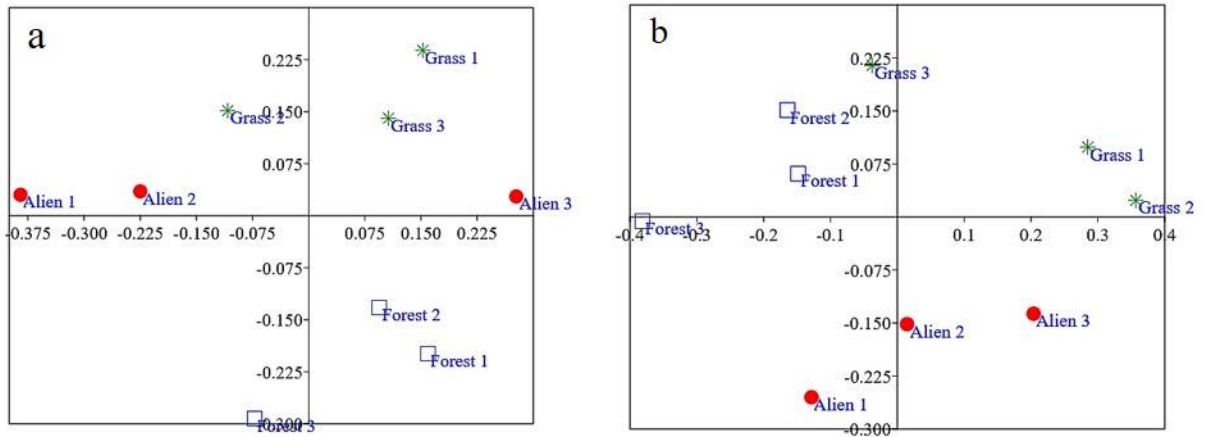
Figure 4.4. nMDS plot of spiders sampled among three habitat types in Springside (a) and Tanglewood (b) with stress of 0.2619 and 0.1351, respectively, based on the Jaccard index. Colour-coding indicates alien invaded grassland (red circle); forest (blue square); and intact grassland (green star).

Figure 4.5. Canonical correspondence analysis ordination (biplot, sample scaling) of soil variables that explained the frequency of ground-dwelling ants in forest, intact grassland, and alien invaded grassland in (a) Springside and (b) Tanglewood. Environmental variables are soil bulk density (g/mL), P (mg/L), K (mg/L), Ca (mg/L), Mg (mg/L), soil pH (KCL), organic C (%), N %, and amount of clay (%). The arrows indicate and point to the direction of maximum change. The length of arrows is proportional to the magnitude of change. The abbreviations indicate the first two letters of the genus and the number used to create the morphospecies name. See Table S5 for full names of morphospecies.
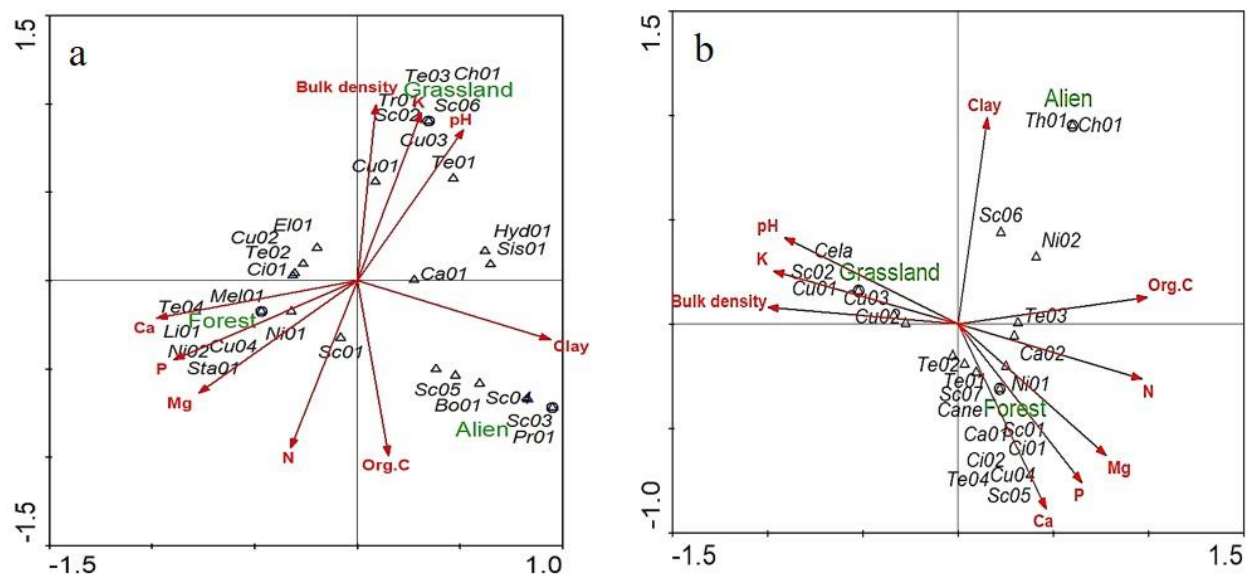
Figure 4.6. Canonical correspondence analysis ordination (biplot, sample scaling) of soil variables that explained the frequency of ground-dwelling beetles in forest, intact grassland, and alien invaded grassland in (a) Springside and (b) Tanglewood. Environmental variables are soil bulk density (g/mL), P (mg/L), K (mg/L), Ca (mg/L), Mg (mg/L), soil pH (KCL), organic C (%), N %, and amount of clay (%). The arrows indicate and point to the direction of maximum change. The length of arrows is proportional to the magnitude of change. The species abbreviations indicate the first two letters and the number used to create the morphospecies name, see Table S5 for full names of morphospecies.
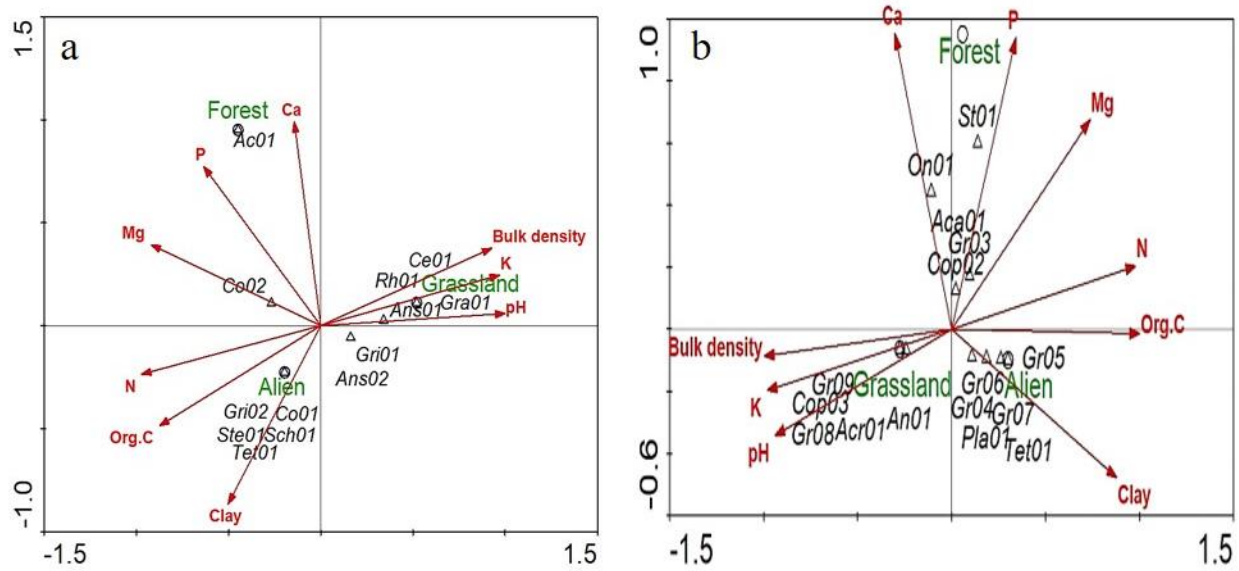
Figure 4.7. Canonical correspondence analysis ordination (biplot, sample scaling) of soil variables that explained the frequency of ground-dwelling Orthopterans in forest, intact grassland, and alien invaded grassland in (a) Springside and (b) Tanglewood. Environmental variables are soil bulk density (g/mL), P (mg/L), K (mg/L), Ca (mg/L), Mg (mg/L), soil pH (KCL), organic C (%), N %, and amount of clay (%). The arrows indicate and point to the direction of maximum change. The length of arrows is proportional to the magnitude of change. The species abbreviations indicate the first two letters and the number used to create the morphospecies name, see Table S5 for full names of morphospecies.
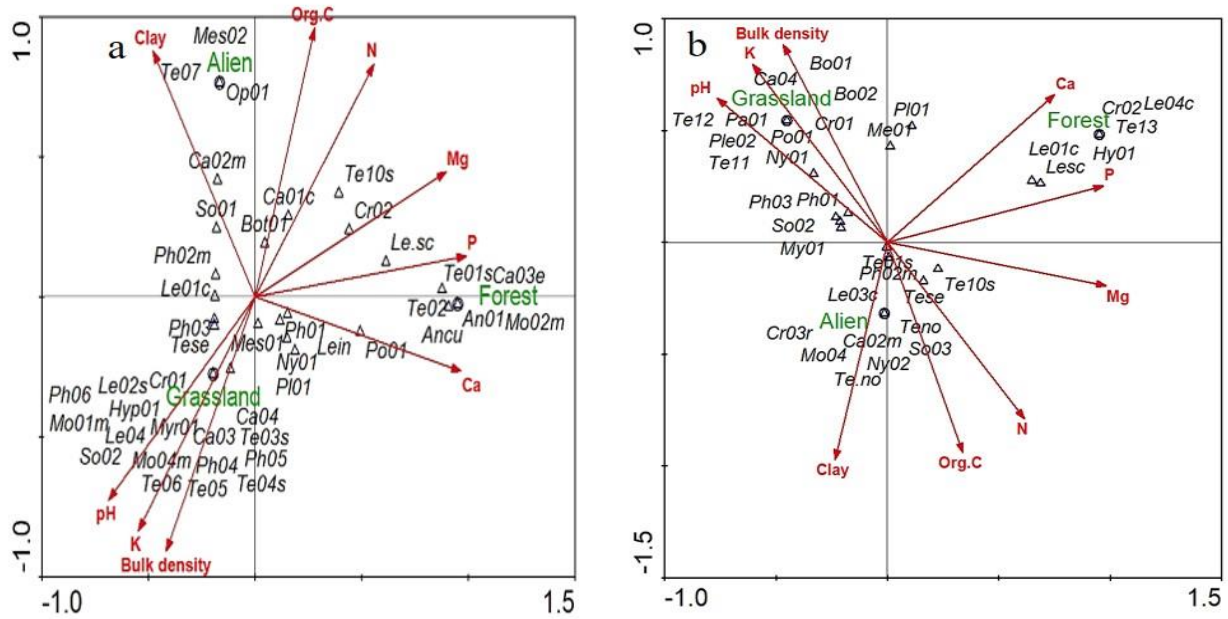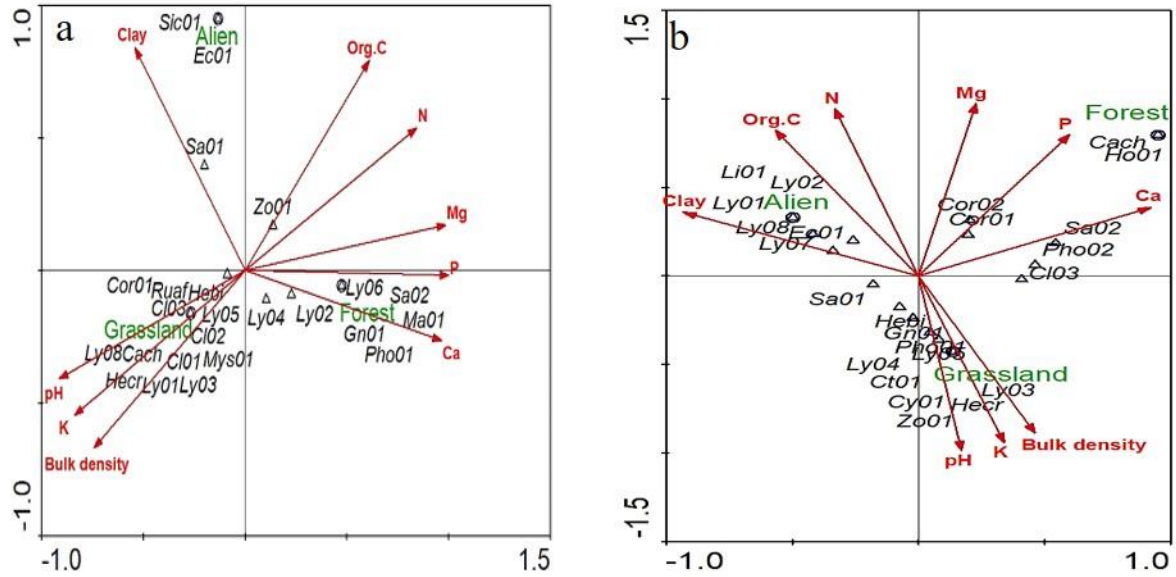
Figure 4.8. Canonical correspondence analysis ordination (biplot, sample scaling) of soil variables that explained the frequency of ground-dwelling spiders in forest, intact grassland, and alien invaded grassland in (a) Springside and (b) Tanglewood. Environmental variables are soil bulk density (g/mL), P (mg/L), K (mg/L), Ca (mg/L), Mg (mg/L), soil pH (KCL), organic C (%), N %, and amount of clay (%). The arrows indicate and point to the direction of maximum change. The length of arrows is proportional to the magnitude of change. The species abbreviations indicate the first two letters and the number used to create the morphospecies name, see Table S5 for full names of morphospecies.

Chapter Five: Discussion

5.1   The abundance and species richness of ground-dwelling arthropods

Ground-dwelling arthropods showed varying patterns in response to habitat characteristics and the disturbance gradient at Springside and Tanglewood. Some groups, e.g. Orthopterans showed a minimal to non-significant response to the presence of invasive alien plants as compared to other groups, such as ants and beetles. No families or subfamilies were specific to a particular habitat in this study. However, at the morphospecies level, some species of Orthoptera (e.g. *Gryllidae* sp. 07 and *Cophogryllus* sp.02) were more confined to alien-invaded grassland. In contrast, some species of beetles (e.g. *Nitidulidae* sp.01) were more confined in the forest, illustrating that alien-invasive vegetation may impact arthropods at the species level. This pattern is consistent with that of Samways et al. (1996), where certain species of Diptera (e.g. *Drosophila* spp.) were specific to exotic vegetation in Pietermaritzburg, KwaZulu-Natal. Among the four groups of arthropods selected in the present study, ants were the most abundant group, followed by beetles. This is a common pattern in most epigeic arthropod studies as beetles and ants comprise about 50% and 40% of all insect species, respectively (Stork 1990).

The abundance of ground-dwelling arthropods differed among vegetation types and sites. The abundance of ants showed contrasting patterns between sites. At Springside, the abundance of ants was greater in intact grassland than in forest and alien-invaded grassland habitats, whereas in Tanglewood ants were most abundant in alien-invaded grassland than in the other habitats. This contrast may be due to that in Springside, the disturbance to the grassland was characterized by a plantation of a single woody plant species, *Pinus patula*, whereas in Tanglewood the alien-invaded grassland consisted of a variety of alien-invasive shrubs, including *Lantana camara*, *Solanam nigrum*, *Tithonia diversifolia*, and *Diplocycle pumatus*. The woody invader plants can portray the

greatest impact on arthropod communities than shrub and herbaceous invaders as shown by the poor species richness and diversity of arthropods under habitats invaded by *A. mearnsii* and *A. longifolia* than habitats invaded by *L. lantana* and *S. mauritianum* in Pietermaritzburg, KwaZulu-Natal (Samways et al. 1996). Moreover, the high abundance of ants in invaded grasslands of Tanglewood may be further explained by the 'intermediate disturbance hypothesis' which suggests that the species abundance and diversity become greater in less or moderately disturbed ecosystems (Bongers et al. 2009). Findings at Tanglewood concur with that of Niba and Mafereka (2015), who reported a high abundance of ants in mixed alien plant habitats than in pristine habitats in Luchaba Nature Reserve, Eastern Cape. However, even though ants were in higher abundance in alien-invaded grassland at Tanglewood, the results also show that the diversity and evenness of ants in invaded grassland were lower than that of intact grassland.

Invasive plants can influence the diversity of arthropods by causing one species to be in greater abundance while reducing the abundance of other species. Such effects can lead to local extinctions of the affected species, while promoting the proliferation of the invasive plant species(Swart et al. 2019, Mavasa et al. 2023). The results here show that invasive alien plants can decrease the occurrence of other arthropod species. These results illustrate how habitat forms of plant species can affect ground-dwelling arthropods. The high abundance of one species of arthropods might deceive policymakers into thinking that alien plants have no effect or support more species than intact native vegetation.

Among ground-dwelling arthropods, spiders are one of the highly diverse groups of predatory arthropods globally (Cardoso et al. 2011). They can be used as bioindicators of habitat quality and environmental changes due to their sensitivity to changes in habitat structure (Dippenaar-Schoeman et al. 2015). Invasive alien plants may affect the abundance and species composition of

spiders by altering vegetation structure and soil properties, which severely threatens habitat quality. The current study showed that invasive alien plants significantly negatively affected the species richness and diversity of spiders. In both sites, the intact grassland was the most abundant, species-rich, and diverse habitat for spiders compared to alien-invaded grassland. This result concurs with other studies that have been conducted on a similar subject in South Africa (e.g. Mgobozi et al. 2008, Magoba et al. 2015). In particular, Mgobozi et al. (2008) reported a lower species diversity and richness of spiders in sites that were invaded by *Chromolaena odorata*. Whereas, Theron et al. (2020) reported that natural vegetation can support the high species diversity and richness of spiders. Mgobozi et al. (2008) further found that the effect of invasive alien plants on arthropods could be reversible with the removal of alien plants, for they recorded an increase in spider abundance in previously infested sites cleared of alien plants.

In a variety of studies, Orthopterans are reported to be sensitive to habitat change (Fartmann et al. 2012, Dvořák et al. 2022), yet in this study, the Orthopterans showed non-significant response among the three habitats and between sites. However, most diversity and evenness of Orthopterans were reported in the alien-invaded grassland. Palmer et al. (2004) mentioned that intact habitats do not always reach high abundance and species richness due to less habitat variation. However, each group of ground-dwelling arthropods will present a certain pattern depending on the intensity and period of disturbance.

The high abundance of *Pheidole* sp.02 (*megacephala* gp.) in all vegetation types followed by *Curculionidae* sp.01 mostly in the forest habitat, suggest that these species could be used as good bioindicators from disturbances that are associated with alien invasive plants. Both *Pheidole* sp.02 (*megacephala* gp.) and *Curculionidae* sp.01. as the most dominant morphospecies in this study, contributed most to the dissimilarity between vegetation types. Studies investigating arthropods

as bioindicators have reported ants and beetles as some of the good bioindicators in an ecosystem (e.g. Work et al. 2008, Hoffmann 2010, Tiede et al. 2017, Carvalho et al. 2020, Zina et al. 2021).

5.2   Species richness and abundance of ground-dwelling arthropods between seasons

Ground-dwelling arthropods are linked to primary productivity and precipitation, as precipitation regulates and limits the physiology of arthropods while primary productivity serves as a source of food and shelter for arthropods (Barahona-Segovia et al. 2019, Uhey et al. 2020). Precipitation plays an important role in plant growth, influencing the species composition of arthropod communities. Arthropods increase in species richness and abundance in warmer and moist climates and decrease in arid climates to avoid the risk of desiccation from dry and high temperatures. In that way, temperature and precipitation may be the limiting factors for ground-dwelling arthropod communities (Supriya et al. 2019). A variety of studies have reported that high soil moisture content is positively correlated to plant growth, and this may result in a high abundance and richness of arthropods due to plant resources availability (Sanders et al. 2003, Dalerum et al. 2017, Uhey et al. 2020, Fischer et al. 2022).

Part of this study assessed the response of ground-dwelling arthropods in wet and dry seasons, which was undertaken to determine the impacts of seasonal change on the abundance and species richness of ground-dwelling arthropods. The results showed that seasonal change may impact species richness and abundance of ground-dwelling arthropods. However, the impact varies between groups of arthropods. While species richness and abundance of Orthopterans and spiders showed no significant difference between seasons, species richness of beetles and ants was higher in the wet than in the dry season. These results are partially similar to those of Mavasa et al. (2022) where similarly the species richness of beetles was greater in the wet season but contrarily, in

Mavasa et al. (2022), the species richness and abundance of ants showed no significant difference between seasons.

The greater species richness and abundance of ants and beetles in the wet season can be explained by the 'resource-ratio hypothesis'. The resource-ratio hypothesis states that species that can thrive through limited resources will out-compete other species in the community when the resources are limited, reducing the number of species in a community (Tilman 1985). In the dry season, the resources are limited and theprimary productivity is lower than in the wet season. Therefore, there is limited food and shelter for arthropods which results in reduced abundance. The pitfall trap is one of the most used methods to survey the community diversity and species composition of ground-dwelling arthropods worldwide (Hohbein and Conway 2018, Saji et al. 2021, Sial et al. 2022). However, the number of arthropods that are trapped in pitfall traps can be influenced by factors such as seasonal change (Saji et al. 2021). In dry and cold season ground-dwelling arthropods are less active because of low energy levels which is caused by too low temperatures. Therefore, the low abundance of ants and beetles in the dry season than in the wet season could also result from having fewer active individuals in the dry season.

The consistency in species richness and abundance of Orthopterans and spiders in the wet and dry seasons may be explained by that climate change has altered the normalities of seasonality and weather patterns. The organisms are exposed to the extremes of each season, such as the heavy rains and drought in wet and dry seasons, respectively (Held and Soden 2006). It may be difficult for arthropods of small body sizes to sustain their survival against the intensifying weather extremes. In the dry season, arthropods are susceptible to desiccation owing to their small body size and high surface-to-area volume ratio (Hadley 1984). In the wet season, arthropods can be easily washed-out during periods of floods. These two weather extremes may cause a reduction in

the abundance of arthropods. The non-significance results of Orthopterans and spiders between seasons might be because fewer individuals were present.

The overall response of arthropods to seasons showed that seasonality was inconsistent among species richness, abundance, and species composition of ground-dwelling arthropods of different taxa (ants, beetles, Orthopterans, and spiders). The variation in the presence and absence of certain species in a particular season was expected, as species have different seasonal and locality preferences (Tembe and Mukaratirwa 2020). In the present study, ants were the most abundant, with high species diversity each season. This is a common phenomenon in ground-dwelling surveys, as ants are the most ubiquitous taxa in terrestrial ecosystems (Stork 2018).

5.3   Species composition of ground-dwelling arthropods in response to soil characteristics

A variety of biotic and abiotic factors, such as the type of vegetation and soil properties can influence ground-dwelling arthropod communities. For example, Pan et al. (2018) showed that soil variables were as good as vegetation structure in predicting the community structure of ground-dwelling arthropods. Soil properties such as soil pH, amounts of total nitrogen and phosphorus, electrical conductivity, and soil water content all affect vegetation and the community of ground-dwelling arthropods. Moreover, vegetation produces litter which affects soil geochemistry. Therefore, soil properties will change with changing vegetation structure (Pan et al. 2018).

The results of vegetation type and soil properties showed that soil properties such as soil pH, total nitrogen, and phosphorus affected the distribution and composition of ground-dwelling arthropods between habitat types. From the present study, ants and spiders were mostly found in the intact grassland, and their species composition was correlated to the soil pH, K, and soil bulk density.

These results match the findings by Gilgado et al. (2022) where soil pH affected the species composition of ants, beetles, and centipedes when these parameters were compared at different levels of elevation. However, this contrast with Pan et al. (2018), where soil pH was invariable in influencing the species composition of ground-dwelling arthropods. These results may imply that it is not adequate to conclude the species composition of ground-dwelling arthropods based on one soil characteristic. Other factors, such as soil temperature, may be more important in influencing the composition of ground-dwelling arthropods. Also, soil texture and soil moisture content can affect arthropods when arthropods move to areas with optimum moisture content during dry and cold seasons, and these may change arthropod species composition rather than soil characteristics per se (Mackay et al. 1986, Shapiro et al. 2000, Alekseev et al. 2006).

Soil texture which was presented as clay content also affected the distribution of arthropods in association with other soil properties such as organic carbon and total nitrogen. The results showed that Orthopterans showed a stronger association with the alien-invaded grassland than other groups. The soil variables which correlated with the species distribution of arthropods in alien-invaded habitat were clay content, organic carbon, and N. Finely textured soils are reported as favorable for ground-dwelling arthropods. This is because of their nutrient availability and water-holding ability (Li et al. 2013, Pan et al. 2015). Organic carbon mostly explains the variation in species composition of decomposers and herbivorous arthropods (Gilgado et al. 2022). The positive correlation between organic carbon and Orthopterans might be explained by that most Orthopterans are herbivores.

Chapter Six: Conclusion and Recommendations

6.1 Overall remarks and hypotheses

The overall results show that intact grassland was the most species-rich and diverse habitat for ground-dwelling arthropods followed by the forest, while degraded grassland was the least. The implications of these results suggest that invasive alien plants pose more negative than positive impacts on the abundance and composition of ground-dwelling arthropods. Although alien-invaded grassland had a high abundance of a few species of Orthopterans, the reduction of species and diversity in invaded grasslands was obvious and the importance of having a balance in species groups of ground-dwelling arthropods cannot be ignored, as different species play a different role in an ecosystem.

For most groups of ground-dwelling arthropods, the findings supported the hypothesis that alien plant-invaded grassland will have the least abundance and low species richness of ground-dwelling arthropods than the intact grassland and forest habitats. An exception was the abundance of Orthopterans, which was greater in alien-invaded grassland than in native vegetation. The greater abundance and species diversity of ants, spiders, and beetles in the natural vegetation of the KwaZulu-Natal Sandstone Sourveld showed that there is hope and a greater need for conserving the little that is left of the remnants of KZNSS from the above-ground fauna perspective.

I found that seasonality has a major impact on determining the abundance of ground-dwelling arthropods. However, it can be concluded that under the umbrella of seasonality, there are underlying factors that affect the abundance and species composition of ground-dwelling arthropods, such as temperature, a high percentage of litter cover during the winter season, and the change in soil texture between dry and wet seasons. All these factors are interconnected to each other and could pose similar or contrasting impacts on ground-dwelling arthropods. Therefore,

future studies could consider looking at each concept and its effect on ground-dwelling arthropods and then grouping factors that show similar patterns rather than considering one factor (i.e. seasonality) at a time.

The results showed that not all soil characteristics are important in determining the species composition and distribution of ground-dwelling arthropods and that each group of ground-dwelling arthropods responds differently to various soil characteristics. Other soil characteristics had a stronger correlation to the distribution of arthropods than others. However, this study showed that it is essential to consider soil characteristics when studying the community diversity of arthropods, as soil physiochemistry varies among sites.

6.2 Conservation and management recommendations

Drawing from the overall result of this study, alien invasive plants did reduce the abundance and species composition of ground-dwelling arthropods. However, knowing the several effects of alien invasive species as outlined by (Spyreas et al. 2010, Litt et al. 2014, Kato-Noguchi 2020), it is recommended that the management and the KZNSS reserve conservancy team should consider eradicating the invasive alien plants, especially the species-poor pine plantation in the Springside Nature Reserve, which particularly compromised the abundance and diversity of Orthopterans groups. After eradication, it is important to consider rehabilitation of the patches of KZNSS by planting native grasses and shrubs before alien pioneer species encroach on the vulnerable land. Moreover, the protection of the KZNSS is not only of intrinsic value but also supports the livelihoods of humans through subsistence farming of crops and livestock, such as cattle. Protection of uncultivated natural vegetation such as remnants of KZNSS can increase farmland biodiversity (Ekroos et al. 2016) and improves arthropod ecosystem services (Isaacs et al. 2009).

Patches of natural vegetation can act as refuge sites for arthropods during a period of disturbance or unfavourable conditions within an ecosystem (Theron et al. 2020).

The present study only considered the community composition of ground-dwelling arthropods. Future research, however, must consider studies on volant and vegetation canopy arthropods as well, as sub-terranean arthropods are part of a bigger community in an ecosystem and are interdependent on other organisms and vice versa. For example, while ground-dwelling arthropods are prey to most aerial and other animals in the grassland such as birds, they also depend on vegetation canopy arthropods such as bugs and gnats as food sources.

The study also noted a knowledge gap on the possible impacts on ground-dwelling arthropods by vegetation management implications, particularly on private and/or municipality-protected reserves. Vegetation management can either benefit or harm arthropods and other grassland organisms. For example, some grassland beetles such as carabids occurred in high abundance in intensively managed grasslands of Castor Hanglands National Nature Reserve (Rushton et al. 1990, Mavasa et al. 2023), whereas 63% of 243 sampled arthropods species occurred in high abundance in restored grasslands than in intensively managed grassland of cantons of Zurich (Albrecht et al. 2010). It would be interesting to investigate the management systems that landowners practice on the remnants of KZNSS and to assess how these management systems could impact the density and species composition of arthropods. Also, mismanagement of vegetation can promote the establishment of invasive alien plants. The current study observed some detrimental impacts of invasive alien plants on some groups of ground-dwelling arthropods, such as the reduction of ants in a grassland invaded by *Pinus patula* and the low species richness and diversity of spiders in alien invaded grassland. Therefore, I recommend future research that will investigate the impacts of vegetation management on arthropods in the patches of KZNSS,

not only ground-dwelling arthropods but also the vegetation canopy arthropods, as they could be affected by the cutting or grazed grasslands.

6.3   Limitations of the study

Pitfall trapping is one of the most frequently used methods for sampling ground-dwelling arthropods. This method has proved to be the most simple, cost-effective, and efficient sampling technique for ground-dwelling arthropods (Saji et al. 2021, Sial et al. 2022). However, as with any other sampling method, pitfall trapping has some limitations that might affect the sampling effort of arthropods. For example, the distance between the traps, the size of the trap opening, and the frequency at which traps are monitored. In the present study, we used only the pitfall trap method to sample the ground-dwelling arthropods. Although it was the most effective for sampling ants and beetles, we noted that orthopteran sampling might have been limited by using one sampling method. This might be because Orthopterans are jumping animals. It is suspected that some individuals of Orthopterans might have escaped the trap by jumping pass the mouth of the trap. Therefore, I recommend that future studies use more than one sampling method to accommodate all targeted groups of arthropods. Among the recommended methods this include active searching methods, like sweep netting, bush beating, leaf litter sifting and quadrant searches. Also, various passive sampling methods, including malaise traps. In addition, the sampling time is a crucial factor as arthropod activity changes with microclimatic changes. In the present study the five days sampling time might have limited the overall species turnover and diversity. It is recommended that the sampling time is spread across the season.Furthermore, some of the traps were lost due to both human and large vertebrate, for example monkeys curiosity, and they were removed from the sampling point. In addition, some traps were sand/water filled in days of high rainfall. Therefore,

the study recommends increasing the monitoring frequency of traps, especially on days when high

rainfall is predicted.

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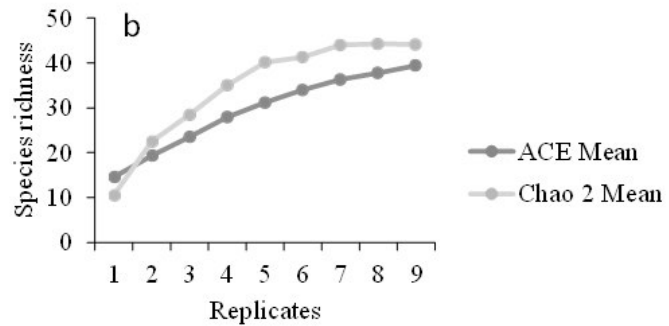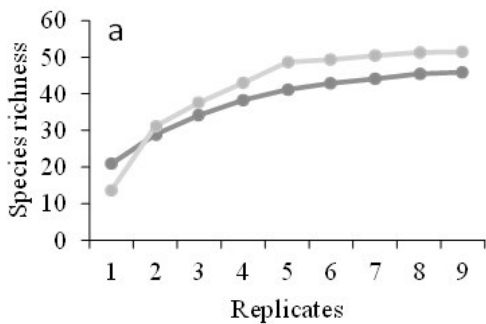
Supplementary Information

Figure S1. Species accumulation curve for sampling effort of ants at (a) Springside and (b) Tanglewood, based on Abundance-based Coverage Estimator and Chao 2 estimator.

Figure S2. Species accumulation curve for sampling effort of beetles at (a) Springside and (b) Tanglewood, based on Abundance-based Coverage Estimator and Chao 2 estimator.

Figure S3. Species accumulation curve for sampling effort of Orthopterans at (a) Springside and (b) Tanglewood, based on Abundance-based Coverage Estimator and Chao 2 estimator.
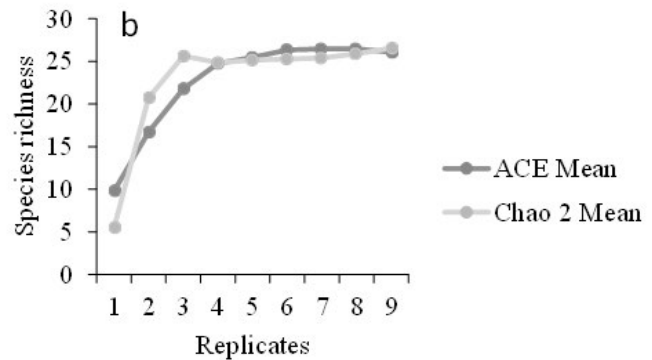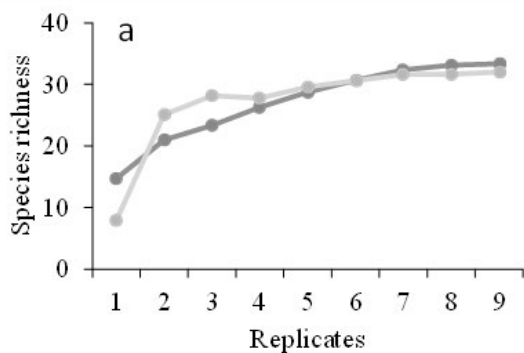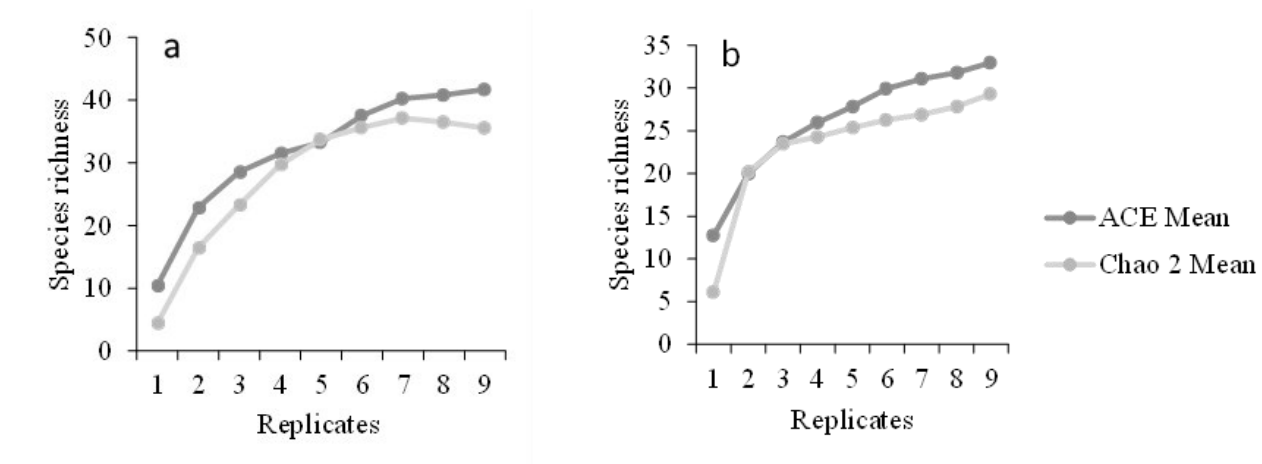

Figure S4. Species accumulation curve for sampling effort of spiders at (a) Springside and (b) Tanglewood, based on Abundance-based Coverage Estimator and Chao 2 estimator.
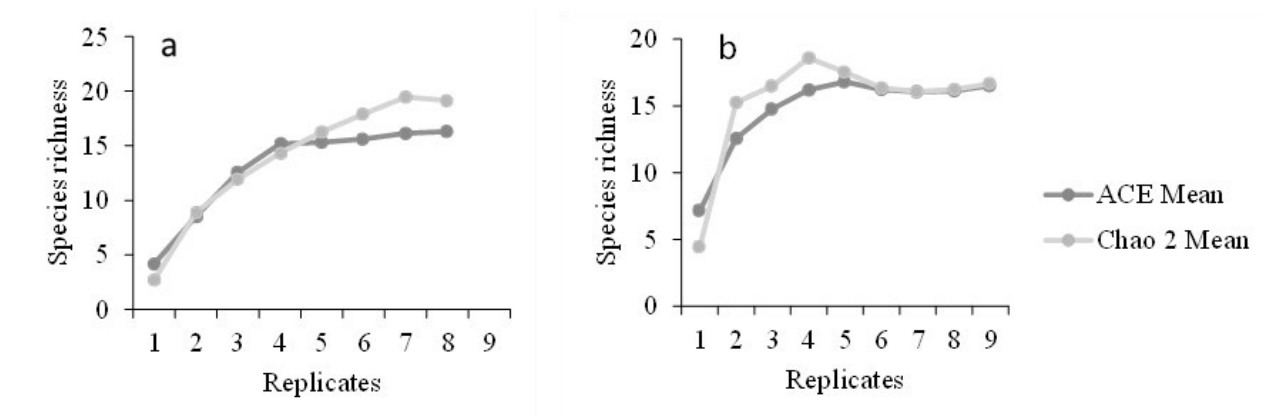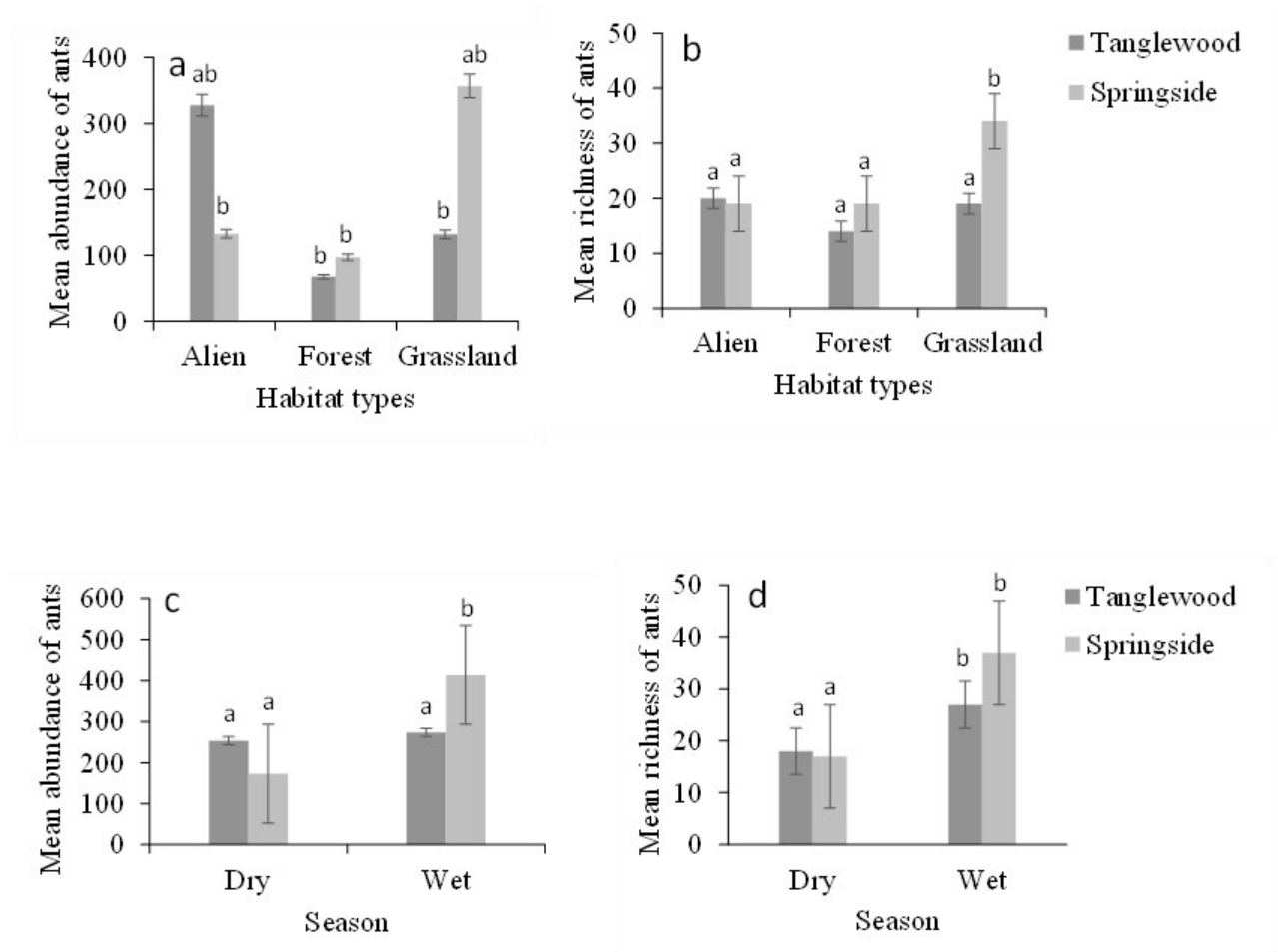
Figure S5. Mean (±SE) (a, c) abundance and (b, d) richness of ground-dwelling ants sampled in three habitats in dry and wet seasons of Springside and Tanglewood.

Figure S6. Mean (±SE) (a,c) abundance and (b,d) richness of ground-dwelling beetles sampled in three habitats in dry and wet seasons of Springside and Tanglewood.

Figure S7. Mean (±SE) (a,c) abundance and (b,d) richness of ground-dwelling Orthopterans sampled in three habitats in dry and wet seasons of Springside and Tanglewood.

Figure S8. Mean (±SE) (a,c) abundance and (b,d) richness of ground-dwelling spiders sampled in three habitats in dry and wet seasons of Springside and Tanglewood.
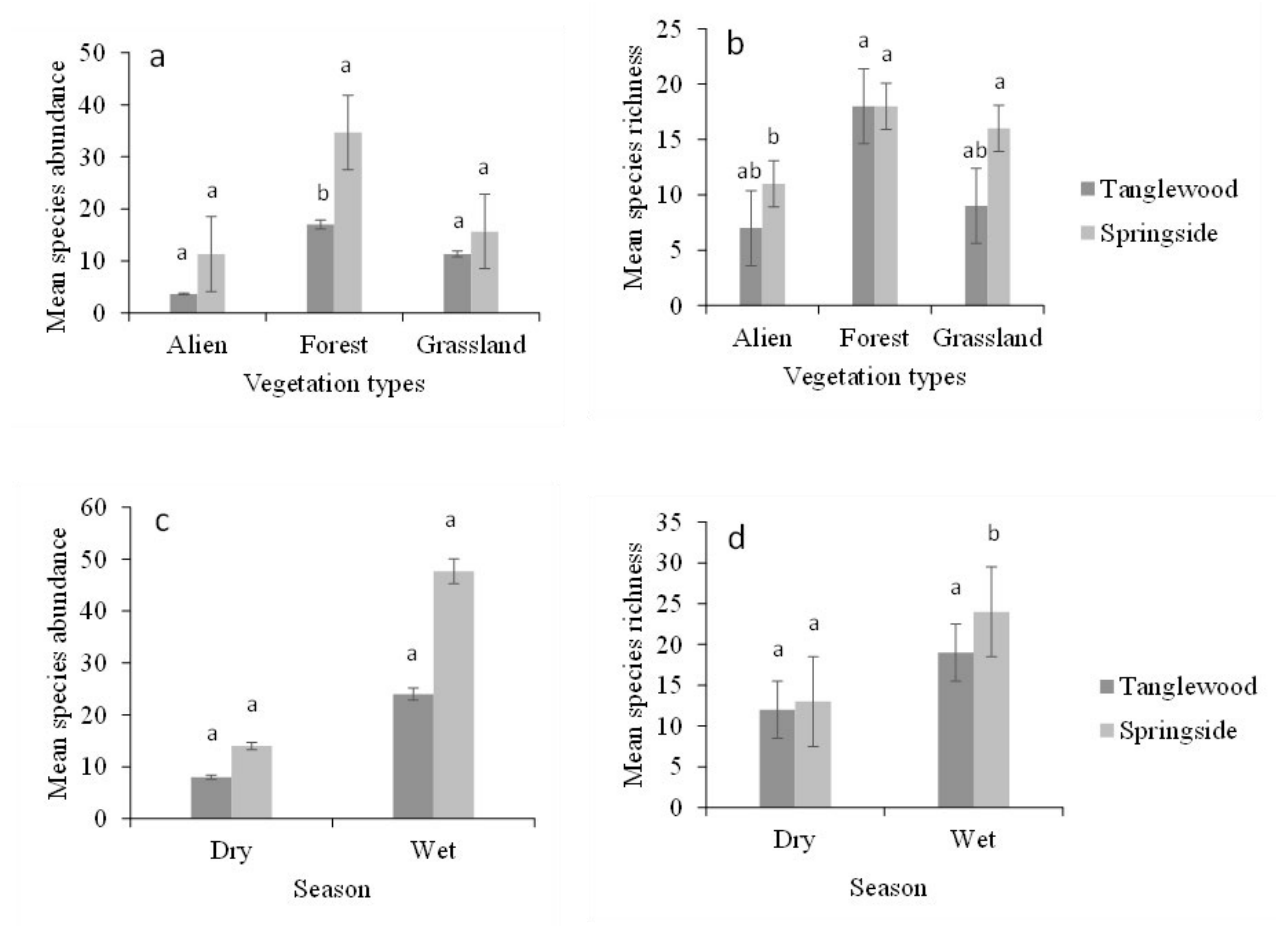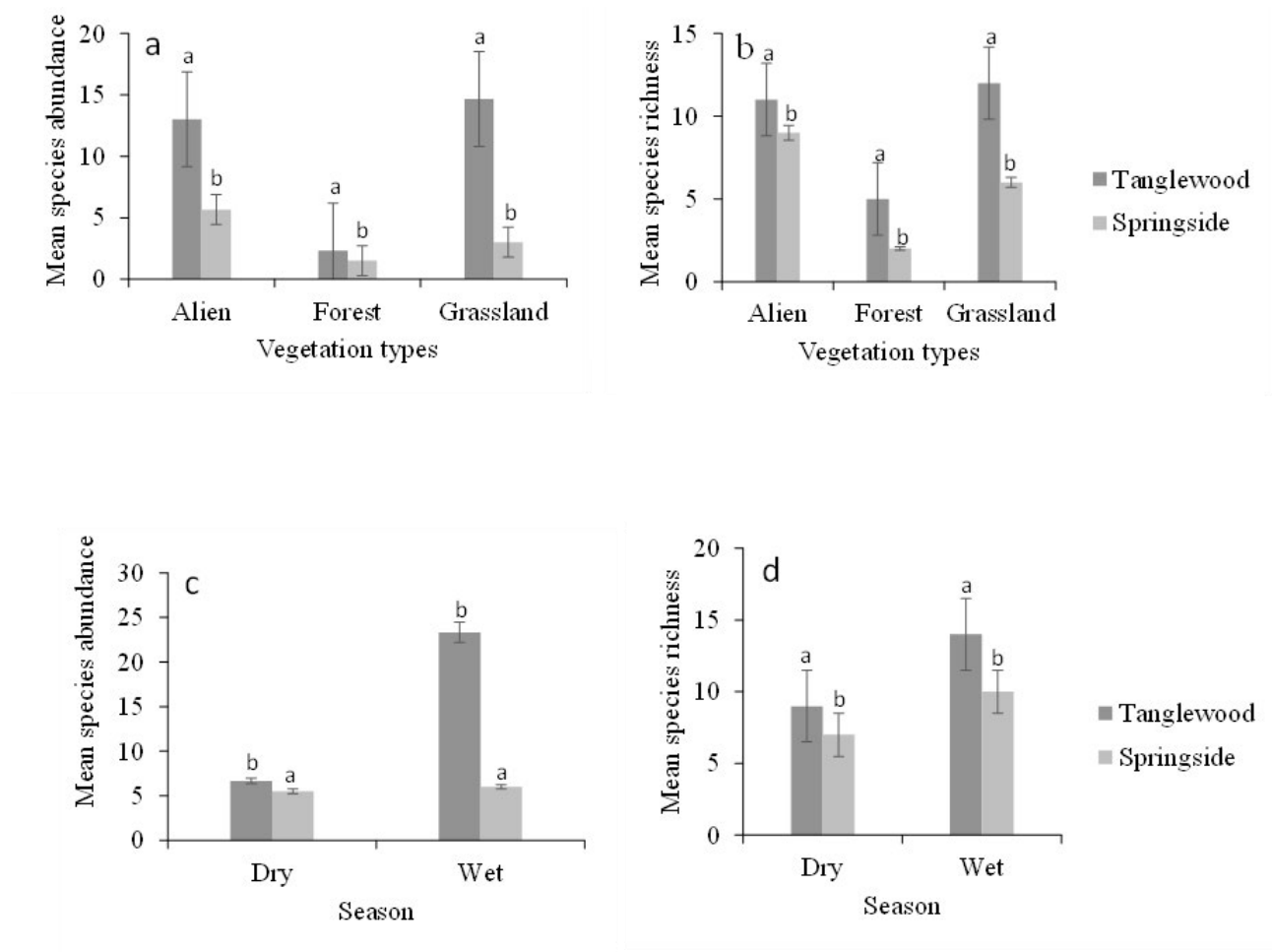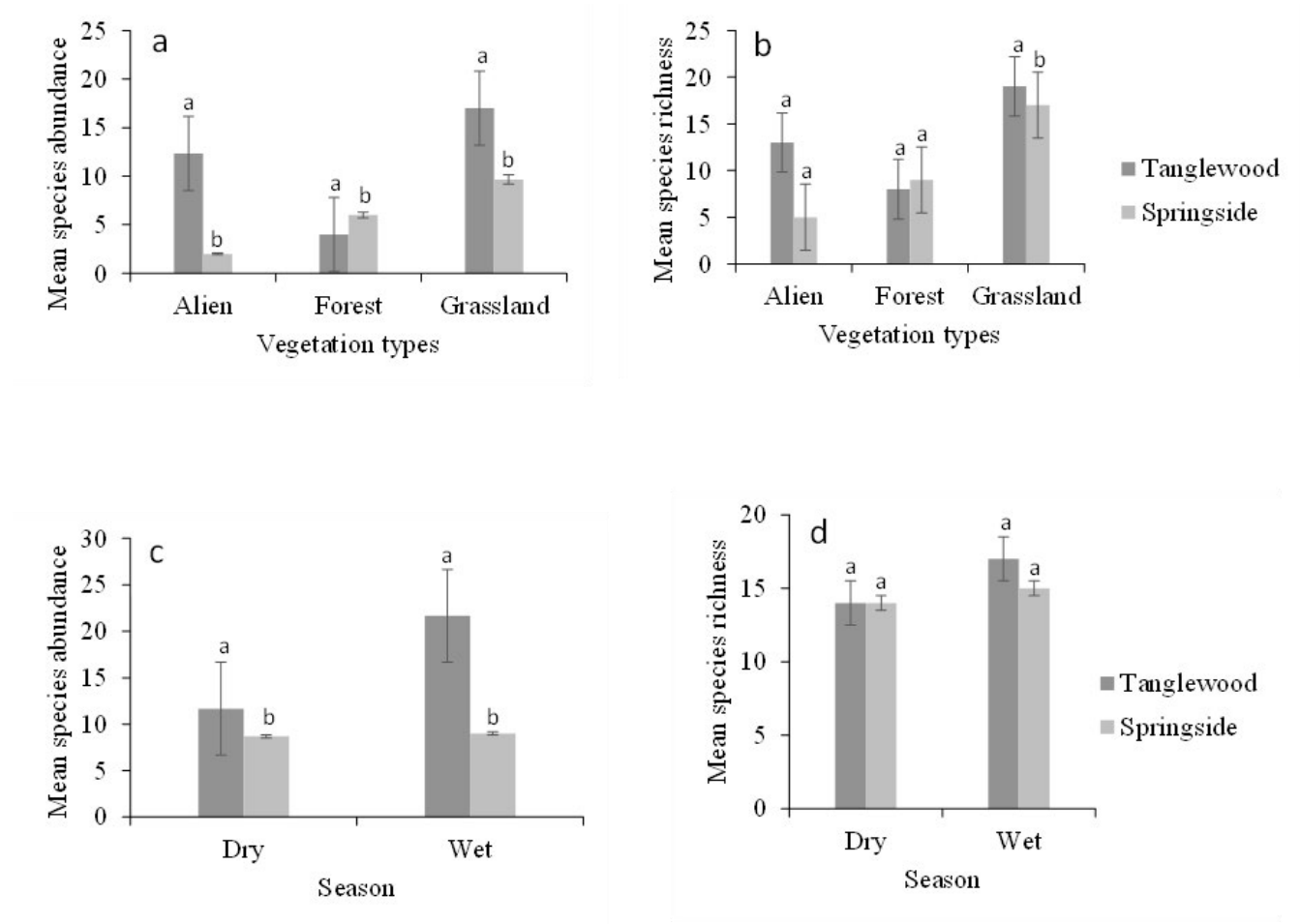
Table S1. SIMPER analysis indicating the contribution of ants morphospecies to average dissimilarity among habitat types in Springside and Tanglewood.

		Springside NR		
Habitat types	Average dissimilarity %	Species	Species contribution %	Cumulative contribution %
Alien vs Forest	88.2	*Pheidole* sp.02 (*megacephala* gp.)	45.8	45.8
		Tetramorium sp.01(*squaminode* gp.)	13.7	59.5
		Anoplolepsis cf *custodiens*	10.0	69.4
Alien vs Grassland	57.3	*Pheidole* sp.02 (*megacephala* gp.)	44.5	44.5
		Pheidole sp.01	11.7	56.2
		Pheidole sp.04	9.0	65.2
Forest vs Grassland	92	*Pheidole* sp.02 (*megacephala* gp.)	49.3	49.3
		Pheidole sp.01	8.5	57.8
		Pheidole sp.04	6.0	63.7

		Tanglewood NR		
Habitat types	Average dissimilarity %	Species	Species contribution %	Cumulative contribution %
Alien vs Forest	68.2	*Pheidole* sp.02 (*megacephala* gp.)	70.2	70.2
		Leptogenys ?*schwabi*	5.6	75.9
		Myrmicaria sp.01	5.3	81.1
Alien vs Grassland	51.8	*Pheidole* sp.02 (*megacephala* gp.)	53.5	53.5
		Myrmicaria sp.01	14.8	68.3
		Nylanderia sp.01	5.3	73.6
Forest vs Grassland	69.4	*Pheidole* sp.02 (*megacephala* gp.)	39.8	39.8
		Myrmicaria sp.01	16.7	56.5
		Leptogenys ?*schwabi*	10.7	67.2

Table S2. SIMPER analysis indicating the contribution of beetles morphospecies to average dissimilarity among habitat types in Springside and Tanglewood.

		Springside NR		
Habitat types	Average dissimilarity %	Species	Species contribution %	Cumulative contribution %
Alien vs Forest	89.3	*Nitidulidae* sp.01	14.7	14.7
		Cicindelidae sp.01	11.2	25.9
		Tenebrionidae sp.04	10.8	36.7
Alien vs Grass	90.9	*Curculionidae* sp.01	21.7	21.7
		Scarabaeidae sp.03	11.4	33.2
		Hydrophilidae sp.01	7.5	40.6
Forest vs Grass	80.2	*Nitidulidae* sp.01	14.9	14.9
		Cicindelidae sp.01	10.5	25.3
		Tenebrionidae sp.04	10.3	35.6

		Tanglewood NR		
Habitat types	Average dissimilarity %	Species	Species contribution %	Cumulative contribution %
Alien vs Forest	90.6	*Nitidulidae* sp.01	17.7	17.7
		Scarabaeidae sp.07	9.4	27.1
		Carabidae sp.02	7.6	34.7
Alien vs Grass	98.9	*Curculionidae* sp.01	35.2	35.2
		Scarabaeidae sp.03	17.9	53.1
		Hydrophilidae sp.02	9	62.1
Forest vs Grass	88.7	*Curculionidae* sp.01	19.8	19.8
		Nitidulidae sp.01	14.9	34.7
		Curculionidae sp.03	8.2	42.9

Table S3. SIMPER analysis indicating the contribution of Orthopteran morphospecies to average dissimilarity among habitat types in Springside and Tanglewood.

		Springside NR		
Habitat types	Average dissimilarity %	Species	Species contribution %	Cumulative contribution %
Alien vs Forest	77.8	*Cophogryllus* sp.02	21.1	21.1
		Tetrigidae sp.01	13.7	34.8
		Acrididae sp.01	11.1	46
Alien vs Grass	90.4	*Cophogryllus* sp.02	24.1	24.1
		Anostostomatidae sp.01	11.4	35.5
		Tetrigidae sp.01	10.6	46.1
Forest vs Grass	100	*Cophogryllus* sp.02	25.9	25.9
		Anostostomatidae sp.01	21.8	47.7
		Acrididae sp.01	18.8	66.4

		Tanglewood NR		
Habitat types	Average dissimilarity %	Species	Species contribution %	Cumulative contribution %
Alien vs Forest	93.8	*Gryllidae* sp.07	30.5	30.5
		Gryllidea sp.05	14.8	45.2
		Gryllidae sp.06	11.2	56.4
Alien vs Grass	90.2	*Gryllidae* sp.07	19.6	19.6
		Cophogryllus sp.03	17.04	36.6
		Gryllidea sp.05	10.03	46.7
Forest vs Grass	91.9	*Cophogryllus* sp.03	23.9	23.9
		Gryllidae sp.08	13.7	37.6
		Acrididae sp.01	10.9	48.5

Table S4. SIMPER analysis indicating the contribution of spiders morphospecies to average dissimilarity among habitat types in Springside and Tanglewood.

		Springside NR		
Habitat types	Average dissimilarity %	Species	Species contribution %	Cumulative contribution %
Alien vs Forest	92.6	*Pholcidae* sp.01	30	30
		Sicariidae sp.01	10	40
		Zodariidae sp.01	9	49
Alien vs Grass	90.3	*Hermacha bicolor*	14.8	14.8
		Clubiona sp.01	14.5	29.3
		Clubiona sp.02	9.9	39.2
Forest vs Grass	86.8	*Pholcidae* sp.01	16.2	16.2
		Clubiona sp.01	11.1	27.4
		Hermacha bicolor	9.4	36.8

		Tanglewood NR		
Habitat types	Average dissimilarity %	Species	Species contribution %	Cumulative contribution %
Alien vs Forest	84.2	*Echinax* sp.01	19.6	19.6
		Lycosidae sp.08	14.1	33.8
		Lycosidae sp.07	12.1	45.9
Alien vs Grass	79.6	*Lycosidae* sp.05	13.8	13.8
		Echinax sp.01	9.6	23.3
		Hermacha bicolor	9.1	32.5
Forest vs Grass	85.5	*Lycosidae* sp.05	17.4	17.4
		Pholcidae sp.01	10.5	27.8
		Hermacha bicolor	10.2	38

Table S5. The codes and morphospecies of ground-dwelling arthropods at Springside and

Tanglewood.

Species group	Morphospecies	Code
Ants	*Anochectus* sp.01	An01
	Anoplolepsis cf *custodiens*	Ancu
	Bothroponera sp.01	Bot01
	Bothroponera sp.02	Bo02
	Camponotus sp.01 (*cintellus* gp.)	Ca01c
	Camponotus sp.02 (*maculatus* gp.)	Ca02m
	Camponotus sp.03	Ca03
	Camponotus sp.03 (*etiolipes* gp.)	Ca03e
	Camponotus sp.04	Ca04
	Crematogaster sp.01	Cr01
	Crematogaster sp.02	Cr02
	Crematogaster sp.03 (*rufigina* gp.)	Cr03r
	Hypoponera sp.01	Hyp01
	Lepisiota sp.01 (*capensis* gp.)	Le01c
	Lepisiota sp.02 (*spinosior* gp.)	Le02s
	Lepisiota sp.03 (*capensis* gp.)	Le03c
	Lepisiota sp.04	Le04
	Lepisiota sp.04 (*capensis* gp.)	Le04c
	Leptogenys ?*schwabi*	Le?sc
	Leptogenys cf *intermedia*	Lein
	Mesoponera sp.01	Mes01
	Mesoponera sp.02	Mes02
	Monomorium sp.01 (*monomorium* gp.)	Mo01m
	Monomorium sp.02 (*Monomorium* gp.)	Mo02m
	Monomorium sp.04 (*monomorium* gp.)	Mo04m
	Myrmicaria sp.01	Myr01
	Nylanderia sp.01	Ny01
	Nylanderia sp.02	Ny02
	Ophthalmopone sp.01	Op01
	Parasyscia sp.01	Pa01
	Pheidole sp.01	Ph01
	Pheidole sp.02 (*megacephala* gp.)	Ph02m
	Pheidole sp.03	Ph03
	Pheidole sp.04	Ph04
	Pheidole sp.05	Ph05
	Pheidole sp.06	Ph06
	Plectroctena sp.01	Pl01

	Plectroctena sp.02	Ple02
	Polyrhachis sp.01	Po01
	Solenopsis sp.01	So01
	Solenopsis sp.02	So02
	Solenopsis sp.03	So03
	Tetramorium notiale	Teno
	Tetramorium ? *notiale*	Te?no
	Tetramorium cf. *setigerum*	Tese
	Tetramorium sp.01 (*squaminode* gp.)	Te01s
	Tetramorium sp.02	Te02
	Tetramorium sp.03 (*simillimum* gp.)	Te03s
	Tetramorium sp.04 (*sericeiventre* gp.)	Te04s
	Tetramorium sp.05	Te05
	Tetramorium sp.06	Te06
	Tetramorium sp.07	Te07
	Tetramorium sp.10 (*similimum* gp.)	Te10s
	Tetramorium sp.11	Te11
	Tetramorium sp.12	Te12
	Tetramorium sp.13	Te13
Beetles	*Bolboceratidae* sp.01	Bo01
	Carabidae sp.01	Ca01
	Carabidae sp.02	Ca02
	Carabus nemoralis	Cane
	Cerapterus laceratus	Cela
	Chrysomelidae sp.01	Ch01
	Cicindelidae sp.01	Ci01
	Cicindelidae sp.02	Ci02
	Curculionidae sp.01	Cu01
	Curculionidae sp.02	Cu02
	Curculionidae sp.03	Cu03
	Curculionidae sp.04	Cu04
	Elateridae sp.01	El01
	Hydrophilidae sp.01	Hyd01
	Limnichidae sp.01	Li01
	Meloidae sp.01	Mel01
	Nitidulidae sp.01	Ni01
	Nitidulidae sp.02	Ni02
	Proagoderua sp.01	Pr01
	Scarabaeidae sp.01	Sc01
	Scarabaeidae sp.02	Sc02
	Scarabaeidae sp.03	Sc03

	Scarabaeidae sp.04	Sc04
	Scarabaeidae sp.05	Sc05
	Scarabaeidae sp.06	Sc06
	Scarabaeidae sp.07	Sc07
	Sisyphus sp.01	Sis01
	Staphylinidae sp.01	Sta01
	Tenebrionidae sp.01	Te01
	Tenebrionidae sp.02	Te02
	Tenebrionidae sp.03	Te03
	Tenebrionidae sp.04	Te04
	Thermophilum sp.01	Th01
	Trogidae sp.01	Tr01
Orthopteran	*Acanthogryllus* sp.01	Aca01
	Acrididae sp.01	Ac01
	Anostostomatidae sp.01	Ans01
	Anostostomatidae sp.02	Ans02
	Cedariniasp sp.01	Ce01
	Cophogryllus sp.01	Co01
	Cophogryllus sp.02	Co02
	Cophogryllus sp.03	Cop03
	Gryllacrididae sp.01	Gra01
	Gryllidae sp.01	Gr01
	Gryllidae sp.02	Gr02
	Gryllidae sp.03	Gr03
	Gryllidae sp.04	Gr04
	Gryllidea sp.05	Gr05
	Gryllidae sp.06	Gr06
	Gryllidae sp.07	Gr07
	Gryllidae sp.08	Gr08
	Gryllidae sp.09	Gr09
	Onosandrus sp.01	On01
	Platygrllus sp.01	Pla01
	Rhaphidophoridae sp.01	Rh01
	Schistocerca sp.01	Sch01
	Stenopelmatidae sp.01	Ste01
	Tetrigidae sp.01	Tet01
Spiders	*Caponia chelifera*	Cach
	Clubiona sp.01	Cl01
	Clubiona sp.02	Cl02
	Clubiona sp.03	Cl03
	Corinnidae sp.01	Cor01

Corinnidae sp.02	Cor02
Ctenolophus sp.01	Ct01
Cybaeidae sp.01	Cy01
Echinax sp.01	Ec01
Gnaphosidae sp.01	Gn01
Hermacha bicolor	Hebi
Hermacha crudeni	Hecr
Homostola sp.01	Ho01
Linyphiidae sp.01	Li01
Lycosidae sp.01	Ly01
Lycosidae sp.02	Ly02
Lycosidae sp.03	Ly03
Lycosidae sp.04	Ly04
Lycosidae sp.06	Ly06
Lycosidae sp.07	Ly07
Lycosidae sp.08	Ly08
Lycosidae sp.05	Ly05
Mashimo sp.01	Ma01
Mysmenidae sp.01	Mys01
Pholcidae sp.01	Pho01
Pholcidae sp.02	Pho02
Runcinia affinis	Ruaf
Salticidae sp.01	Sa01
Salticidae sp.02	Sa02
Sicariidae sp.01	Sic01
Zodariidae sp.01	Zo01