Assemblages of surface-active arthropods in pristine and disturbed savannah

by

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Submitted in fulfilment of the academic requirements for the degree of Master of Science in Biological Sciences in the School of Life Sciences University of KwaZulu-Natal Pietermaritzburg

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SUMMARY

Savannahs are structurally complex ecosystems rich in biodiversity, and the conversion of savannahs into human-modified landscapes poses a significant risk to organisms with limited dispersal abilities. Surface-active arthropods have limited dispersal abilities and are sensitive to changes in their environment; as a result, they are restricted to specific habitats with the resources that they need. Surface-active arthropods are essential in ecosystem processes, such as playing a direct or indirect role in water infiltration into the soil and its storage, decomposition of plant and animal matter, nutrient cycling, humification and biological pest control. Many landscapes of natural vegetation in South Africa have been transformed into croplands, residential and commercial areas. In Mpumalanga province, croplands (including fruit plantations) dominate the landscape where savannah vegetation occurred previously. This study investigated the influences of disturbance (transformed savannah vs pristine savannah) and season on the diversity of four groups of surface-active arthropods (ants, beetles, millipedes and spiders) in the savannah biome in Mpumalanga province. The objectives of the study were to determine 1) whether flightless arthropod assemblages differ between disturbed and pristine savannah, and 2) whether functional guilds of flightless arthropod assemblages differ between summer and winter. Field sampling using pitfall traps was done to collect the surface-active arthropods in pristine and disturbed savannah during summer and winter. All samples were sorted into morphospecies and identified into family or genus where possible and then assigned into functional guilds. Functional guilds were allocated based on the feeding habits of the surface-active arthropods, resulting in three distinct functional guilds (detritivores, herbivores and carnivores) being identified. Surface-active arthropods with diverse feeding habits were lumped to form a fourth functional guild, the “diverse functional guild”. I found significant differences in the species composition of ants, beetles and spiders between disturbed and pristine savannahs. The species richness and abundance of ants was significantly greater in the disturbed than pristine savannah, while beetles and spiders had similar species richness and abundance between the two habitat types. The number of unique species of the surface-active arthropods in the disturbed savannah were two times more than those in the pristine savannah. The species richness and composition of all functional guilds of the surface-active arthropods differed between summer and winter, with greater species richness in summer than in winter. Herbivorous and carnivorous arthropods had significantly higher abundance in summer than in winter, while the abundance of detritivores and the “diverse functional guild” was similar between the two seasons. This study shows that different vegetation types support different compositions of surface-active arthropods and that there may be a positive relationship between vegetation structure and the assemblages of surface-active arthropods in the savannah. Furthermore, the study highlights a potentially positive relationship between the assemblages of herbivorous and carnivorous arthropods. I recommend that it may be essential to consider both disturbed and pristine habitat types in the conservation of surface-active arthropods, especially in South Africa where most of the land is outside of formal conservation areas. This assertion is supported by the greater number of unique species of surface-active arthropods found in the disturbed than in the pristine savannah. My study provides relevant baseline information because little is known about the assemblages of surface-active arthropods in savannah landscapes dominated by croplands. Furthermore, my study gives some insight on how the assemblages of surface-active arthropods may respond to disturbance in the savannah.

PREFACE

The fieldwork described in this dissertation was carried out in the Barberton Nature Reserve and the outskirts of Mbombela City, Mpumalanga province, South Africa, under the supervision of Dr Zivanai Tsvuura, Dr Inam Yekwayo and Prof. Tarombera Mwabvu.

This study represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others, it is duly acknowledged in the text.

[redacted]

Signed by: Dr Zivanai Tsvuura (supervisor)
Date: 26 October 2021

DECLARATION 1: PLAGIARISM

I, Risuna Wain Mavasa, 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.

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information unless specifically acknowledged as being sourced from other persons.

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a) their words have been re-written, but the general information attributed to them has been referenced.

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(v) where I have used material for which publications followed, I have indicated in detail my role in the work.

(vi) this dissertation is primarily a collection of material prepared by myself with an intention to publish as journal articles.

(vii) this dissertation does not contain text, graphics or tables copied and pasted from the internet, unless specifically acknowledged, and the source being detailed in the dissertation and the references sections.

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DECLARATION 2: PUBLICATIONS

Chapter 2

Mavasa, R., Yekwayo, I., Mwabvu, T., Tsvuura, Z. Assemblages of ants, beetles and spiders in a disturbed and pristine savannah in South Africa. Submitted to African Entomology.

Author contributions: IY, TM and ZT conceived the study. IY, TM and RM designed the study and conducted the study. RM and IY analysed the data. RM wrote the original draft. All authors contributed to reviewing and editing the manuscript.

Chapter 3

Mavasa, R., Yekwayo, I., Mwabvu, T., Tsvuura, Z. Effect of season on the functional guilds of surface-active arthropods in the savannah, Mpumalanga province. (in preparation)

Author contributions: IY, TM and ZT conceived the study. IY, TM and RM designed the study and conducted the study. RM and IY analysed the data. RM wrote the original draft. All authors contributed to reviewing and editing the manuscript.

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Psalms 126:3 (New Living Translation)

DEDICATION

This work is dedicated to Ukahle Mavasa and Andziso Mavasa. May this work serve as an inspiration to you, and may you know always that you can achieve anything that you set your mind to.

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ABBREVIATIONS AND ANNOTATIONS USED

OMC	Outskirts of Mbombela City
BNR	Barberton Nature Reserve
χ^2	Chi-square
df	Degrees of freedom
Error df	Error degrees of freedom
P	Probability

CHAPTER 1

1. GENERAL INTRODUCTION

1.1. Background

The savannah biome can be described as an area that is covered largely by a grass matrix and woody plants that are distributed sparsely (Bond, 2008; Wakeling et al., 2012; Hutley and Setterfield, 2018). Moreover, the savannah is a structurally complex ecosystem and rich in biodiversity, allowing it to support a variety of life forms (Botha et al., 2016; Hutley and Setterfield, 2018). The savannah biome is found in all tropical parts of the world and shares several grass species across different continents (Nix, 1983; Solbrig et al., 1996). For example, *Cymbopogon citratus* occurs in Africa, India and South America, while *Themeda triandra* is shared amongst Africa, India and Australia (Cole, 1987; Solbrig et al., 1996).

In Southern Africa, the savannah biome is a dominant vegetation type, covering over 45% of the total area (Mucina and Rutherford, 2010). The savannah biome in South Africa occurs in the northern and eastern parts of the country and covers more than 33% of South Africa (Sankaran et al., 2005; Mucina and Rutherford, 2010). The altitude of the savannah biome in South Africa ranges from sea level to 2000 m above sea level (Wakeling et al., 2012). Altitude is an important component of the savannah and all vegetation types because it influences the occurrence of vegetation types by confining temperature and rainfall regimes to a specific range in a particular area (Wakeling et al., 2012; Reisch and Rosbakh, 2021; Stanbrook et al., 2021; Zhang et al., 2021). For example, areas at high altitudes experience lower temperatures and high incidences of frost compared with areas at low altitudes, which experience warmer temperatures and low incidences of frost (Mucina and Rutherford, 2010).

The savannah biome in South Africa can be classified into three types based on the proportions of woody vegetation and the grassy matrix. Where the woody vegetation is dense, the savanna is referred to as woodland savannah (Vasconcelos et al., 2009). Where the canopy of woody plants is very close in height to the grassy matrix, the savannah is referred to as shrubveld savannah (Bredenkamp, 1987; Ribeiro et al., 2019). Where the woody vegetation does not form a distinct layer, usually with no clear distinction between small trees and shrubs, the savannah is referred to as bushveld savannah (Mucina and Rutherford, 2010). The present study was conducted in a Legogote Sour Bushveld savannah, with elements of the Barberton Serpentine Sourveld (Mucina and Rutherford, 2010).

In South Africa, the savannah biome is characterized by the austral summer and winter seasons (ARC–ISCW, 2019). The biome receives about 235 to 1 000 mm of rain each year, with most of the rain occurring during the summer season (Mucina and Rutherford, 2010; ARC–ISCW, 2019). The high rainfall in the summer, coupled with high temperatures, favours the growth, development and productivity of plants in the savannah (Hutley and Setterfield, 2018; Mishra and Young, 2020). The high productivity of plants in summer generates a wealth of mesofilters and resources for organisms, including arthropods, which are essential in many ecosystem processes (Crous et al., 2013; Vaca-Sánchez et al., 2021). Arthropods play a critical role as ecosystem engineers in several environments. These arthropods are involved in ecosystem services such as nutrient cycling (Sagi and Hawlena, 2021), control of alien invasive plants (Shoba and Olckers, 2010), and serve also as a food source for other animals (Kolkert et al., 2021). Dung beetles, for example, store mammal faecal matter underground for nesting and feeding, and therefore, aid in nutrient cycling and cleaning of the environment (Hanski and Cambefort, 2014).

The savanna biome in South Africa is under threat currently due to anthropogenic activities such as expansion of agricultural activities and urbanisation. The conservation of the savannah biome in South Africa occurs mainly in formal conservation areas such as nature and game reserves (Bond and Archibald, 2003). Although South Africa has plenty of nature reserves, the majority of the savannah biome and other natural vegetation occurs outside of these formal conservation areas, where the savannah vegetation is converted to croplands, industrial areas, and residential developments to support the growing human population (Mucina and Rutherford, 2010; Yekwayo and Mwabvu, 2019). The conversion of landscapes of natural vegetation into croplands, industrial areas and residential developments poses a significant risk to arthropods with limited dispersal abilities (Mauda et al., 2018; Eisenhauer et al., 2019; Seibold et al., 2019).

Surface-active arthropods have limited dispersal abilities and are sensitive to changes in their environment; as a result, they are restricted to specific habitats that have the resources they need (Gaigher and Samways, 2010; Samways et al., 2010; Magoba and Samways, 2012; Hlongwane et al., 2019). The sensitivity of these arthropods to changes in their environment can be used to identify facets of the environment that are responsible for changes in their assemblages (e.g., Purdon et al., 2019; Seibold et al., 2019; Foster et al., 2021). In addition, changes in the assemblage of surface-active arthropods can be associated with changes in their local environment because of their dispersal limitations (see Yekwayo et al., 2018; Ferrenberg et al., 2019). As such, changes in the species composition of surface-active arthropods present a potentially effective and essential monitoring tool. The changes can be used to measure rapid environmental change as a result of anthropogenic disturbance (see Narimanov et al., 2021; Rahman et al., 2021) or to measure changes that are associated with changes in season (as reported by de Oliveira et al., 2021).

1.2. Aims and objectives

Many landscapes of natural vegetation in South Africa have been transformed into croplands, residential and commercial areas (Botha et al., 2015; Jewitt et al., 2015; Hlongwane et al., 2019; Hyvärinen et al., 2019). In Mpumalanga province, croplands, in the form of subtropical fruit plantations, dominate the landscape where savannah vegetation previously occurred. This study investigated the influence of disturbance (transformed savannah vs less transformed or pristine savannah) and season on the diversity of four groups of surface-active arthropods (that is, ants, beetles, millipedes and spiders) at sites in the savannah biome of Mpumalanga province. The objectives of the study were to determine whether or not 1) surface-active arthropod assemblages differ between disturbed and pristine savannah, and 2) assemblages of functional guilds of surface-active arthropods differ between summer and winter seasons. The study may be relevant for providing baseline information because little is known about surface-active arthropod assemblages in savannah landscapes that are dominated by various anthropogenic disturbances in Mpumalanga province, South Africa. In addition, data obtained from this study will contribute towards producing a checklist of surface-active arthropods occurring in pristine and transformed habitat types within the savannah biome in the Mpumalanga province.

1.3. Structure of the thesis

This thesis is made up of a General Introduction (Chapter 1), two research papers (Chapter 2 and 3), and a General Conclusion (Chapter 4). The two research papers were written as stand-alone chapters with the purpose of publication in particular journals. As a result, some repetition in the methods was inevitable. These chapters were formatted accordingly.

Chapter 1 (this chapter) provides context to the study by providing the background of the study, aims, objectives and structure of the thesis. In **Chapter 2**, the focus of the study is on the composition of surface-active arthropods in a pristine and anthropogenically transformed (disturbed) savannah. Here I compared the species richness, the abundance of species and species composition of ants, beetles, millipedes and spiders between pristine and disturbed savannah in Mpumalanga province, South Africa.

In **Chapter 3**, the focus of the study is on effect of season on four functional guilds of surface-active arthropods in the savannah, Mpumalanga province, South Africa. I compared the abundance of species, and species composition and species richness of functional guilds of surface-active arthropods between summer and winter in the Barberton Nature Reserve.

Chapter 4 provides a conclusion to the thesis by summing up important findings of the study from the two research papers and making concluding remarks about the implications of the results of this study for the conservation of surface-active arthropods. Additionally, the limitations of the study were also discussed in this chapter.

1.4. References

ARC-ISCW, 2019. Water and climate data (unpublished). In: Agricultural Research Council (ARC) Institute for Soil Climate and Water (ISCW) (Ed.). Agro Climatology Division, Stellenbosch, South Africa.

Bond, W.J., 2008. What limits trees in C4 grasslands and savannas? Annual Review of Ecology, Evolution and Systematics 39, 641–659.

Bond, W.J., Archibald, S., 2003. Confronting complexity: fire policy choices in South African savanna parks. International Journal of Wildland Fire 12, 381–389.

Botha, M., Siebert, S., Van den Berg, J., Maliba, B., Ellis, S., 2015. Plant and arthropod diversity patterns of maize agro-ecosystems in two grassy biomes of South Africa. Biodiversity and Conservation 24, 1797–1824.

Botha, M., Siebert, S.J., Van den Berg, J., 2016. Do arthropod assemblages fit the grassland and savanna biomes of South Africa? South African Journal of Science 112, 1–10.

Bredenkamp, G., 1987. An overview of the major plant communities of the Manyeleti Game Reserve Gazankulu, South Africa. Coenoses 2, 75–84.

Cole, M.M., 1987. The savannas. Progress in Physical Geography 11, 334–355.

Crous, C.J., Samways, M.J., Pryke, J.S., 2013. Exploring the mesofilter as a novel operational scale in conservation planning. Journal of Applied Ecology 50, 205–214.

de-Oliveira, C., Pereira, de Oliveira, C., Martins, Specht, A., Frizzas, M.R., 2021. Seasonality and distribution of Coleoptera families (Arthropoda, Insecta) in the cerrado of central Brazil. Revista Brasileira de Entomologia 65, e20210025. https://doi.org/10.1590/1806-9665-RBENT-2021-0025

Eisenhauer, N., Bonn, A., Guerra, C.A., 2019. Recognizing the quiet extinction of invertebrates. Nature Communications 10, 50. https://doi.org/10.1038/s41467-018-07916-1

Ferrenberg, S., Wickey, P., Coop, J.D., 2019. Ground-dwelling arthropod community responses to recent and repeated wildfires in conifer forests of northern New Mexico, USA. Forests 10, 667. https://doi.org/10.3390/f10080667

Foster, J.G., Gervan, C.A., Coghill, M.G., Fraser, L.H., 2021. Are arthropod communities in grassland ecosystems affected by the abundance of an invasive plant? Oecologia 196, 1–12.

Gaigher, R., Samways, M., 2010. Surface-active arthropods in organic vineyards, integrated vineyards and natural habitat in the Cape Floristic Region. Journal of Insect Conservation 14, 595–605.

Hanski, I., Cambefort, Y. (eds.), 2014. Dung Beetle Ecology. Princeton University Press, Princeton.

Hlongwane, Z.T., Mwabvu, T., Munyai, T.C., Tsvuura, Z., 2019. Epigaeic ant diversity and distribution in the Sandstone Sourveld in KwaZulu-Natal, South Africa. African Journal of Ecology 57, 382–393.

Hutley, L.B., Setterfield, S.A., 2018. Savanna. In: Fath, B. (Ed.), Encyclopedia of Ecology, 2nd ed. Elsevier BV, Oxford

Hyvärinen, O., Timm-Hoffman, M., Reynolds, C., 2019. Vegetation dynamics in the face of a major land-use change: a 30-year case study from semi-arid South Africa. African Journal of Range and Forage Science 36, 141–150.

Jewitt, D., Goodman, P.S., Erasmus, B.F., O'Connor, T.G., Witkowski, E.T., 2015. Systematic land-cover change in KwaZulu-Natal, South Africa: implications for biodiversity. South African Journal of Science, 111, 1–9. http://dx.doi.org/10.17159/SAJS.2015/20150019

Kolkert, H.L., Smith, R., Rader, R., Reid, N., 2021. Prey removal in cotton crops next to woodland reveals periodic diurnal and nocturnal invertebrate predation gradients from the crop edge by birds and bats. Scientific Reports 11, 5256. https://doi.org/10.1038/s41598-021-84633-8

Magoba, R.N., Samways, M.J., 2012. Comparative footprint of alien, agricultural and restored vegetation on surface-active arthropods. Biological Invasions 14, 165–177.

Mauda, E.V., Joseph, G.S., Seymour, C.L., Munyai, T.C., Foord, S.H., 2018. Changes in land use alter ant diversity, assemblage composition and dominant functional groups in African savannas. Biodiversity Conservation 27, 947–965.

Mishra, N.B., Young, K.R., 2020. Savannas and grasslands. In: Wang Y (ed.), Terrestrial Ecosystems and Biodiversity, 1st ed. CRC Press, Boca Raton.

Mucina, L., Rutherford, M.C. (eds.), 2010. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Narimanov, N., Kempel, A., van Kleunen, M., Entling, M.H., 2021. Unexpected sensitivity of the highly invasive spider *Mermessus trilobatus* to soil disturbance in grasslands. Biological Invasions 23, 1–6. https://doi.org/10.1007/s10530-020-02348-9

Nix, H.A., 1983. Climate of tropical savannas. In: Bourliere F (ed), Ecosystems of the World, 13th ed. Elsevier, Amsterdam.

Purdon, J., Parr, C.L., Somers, M.J., 2019. Grazing by large savanna herbivores indirectly alters ant diversity and promotes resource monopolisation. PeerJ 7, e6226. https://doi.org/10.7717/peerj.6226

Rahman, A.U., Jones, H.P., Hosler, S.C., Geddes, S., Nelson, M., Barber, N.A., 2021. Disturbance-induced trophic niche shifts in ground beetles (Coleoptera: Carabidae) in restored grasslands. Environmental Entomology, 50, 1075–1087. https://doi.org/10.1093/ee/nvab065

Reisch, C., Rosbakh, S., 2021. Patterns of genetic variation in European plant species depend on altitude. Diversity and Distributions 27, 157–163.

Ribeiro, N., Ruecker, G., Govender, N., Macandza, V., Pais, A., Machava, D., Chauque, A., Lisboa, S.N., Bandeira, R., 2019. The influence of fire frequency on the structure and botanical composition of savanna ecosystems. Ecology and Evolution 9, 8253–8264.

Sagi, N., Hawlena, D., 2021. Arthropods as the Engine of Nutrient Cycling in Arid Ecosystems. Insects 12, 726. https://doi.org/10.3390/insects12080726

Samways, M.J., McGeoch, M.A., New, T.R., 2010. Insect conservation: a handbook of approaches and methods. Oxford University Press, Oxford.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., 2005. Determinants of woody cover in African savannas. Nature 438, 846–849.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674.

Shoba, Z., Olckers, T., 2010. Reassessment of the biology and host range of *Acanthoscelides macrophthalmus* (Chrysomelidae: Bruchinae), a seed-feeding beetle released for the biological control of *Leucaena leucocephala* in South Africa. African Entomology 18, 1–10.

Solbrig, O.T., Medina, E., Silva, J.F., 1996. Determinants of tropical savannas. In: Solbrig O.T., Medina E., Silva J.F. (eds). Biodiversity and Savanna Ecosystem Processes: A Global Perspective. Springer, Berlin. https://doi.org/10.1007/978-3-642-78969-4_2

Stanbrook, R., Wheater, C.P., Harris, W.E., Jones, M., 2021. Habitat type and altitude work in tandem to drive the community structure of dung beetles in Afromontane forest. Journal of Insect Conservation 25, 159–173.

Vaca-Sánchez, M.S., Maldonado-López, Y., González-Rodríguez, A., Oyama, K., Fernandes, G.W., Fagundes, M., López-Barbosa, E.C., Aguilar-Peralta, J.S., Cuevas-Reyes, P., 2021. Canopy arthropod diversity associated with *Quercus laurina*: importance of an oak species diversity gradient on abundance, species richness and guild composition. Journal of Insect Conservation. https://doi.org/10.1007/s10841-021-00352-5

Vasconcelos, H.L., Pacheco, R., Silva, R.C., Vasconcelos, P.B., Lopes, C.T., Costa, A.N., Bruna, E.M., 2009. Dynamics of the leaf-litter arthropod fauna following fire in a neotropical woodland savanna. PLoS One 4, e7762. https://doi.org/10.1371/journal.pone.0007762

Wakeling, J.L., Cramer, M.D., Bond, W.J., 2012. The savanna-grassland ‘treeline’: why don’t savanna trees occur in upland grasslands? Journal of Ecology 100, 381–391.

Yekwayo, I., Mwabvu, T., 2019. Diversity and composition of flightless arthropods on rock outcrops and adjacent vegetation in the savannah, Mpumalanga province, South Africa. African Journal of Ecology. https://doi.org/10.1111/aje.12617

Yekwayo, I., Pryke, J.S., Gaigher, R., Samways, M.J., 2018. Only multi-taxon studies show the full range of arthropod responses to fire. PLoS One 13, e0195414. https://doi.org/10.1371/journal.pone.0195414

Zhang, Y., Ai, J., Sun, Q., Li, Z., Hou, L., Song, L., Tang, G., Li, L., Shao, G., 2021. Soil organic carbon and total nitrogen stocks as affected by vegetation types and altitude across the mountainous regions in the Yunnan province, south-western China. Catena 196, 104872. https://doi.org/10.1016/j.catena.2020.104872

CHAPTER 2

2. Composition of surface-active arthropods in pristine and disturbed savannah

Abstract

Savannah vegetation is a structurally complex ecosystem consisting of a diverse community of plants such as grasses, shrubs and trees and animals such as arthropods. Surface-active arthropods form a significant component of the total arthropods described to date and are essential in many ecosystem processes that help maintain life on Earth for all organisms, including humans. The anthropogenic conversion of natural landscapes into cropland, residential and industrial areas has a negative impact on surface-active arthropods that have limited dispersal abilities and narrow habitat preference. This study was conducted to investigate the effect of disturbance on assemblages of four groups of surface-active arthropods (ants, beetles, millipedes and spiders) in pristine and disturbed savannah in Mpumalanga province, South Africa. Two habitats, disturbed and undisturbed savannahs, with 15 sites each, were selected for the study. The disturbed savannah was a fallow land close to ongoing industrial and residential developments, while the pristine savannah was a protected area with little human interference. Pitfall traps were used to sample the surface-active arthropods. All the samples collected were sorted into family and morphospecies and then identified to genus where possible. The species richness, abundance, and composition of the surface-active arthropods were analysed in R using generalised linear mixed models and linear mixed models. In addition, indicator species analysis of the disturbed and pristine savannahs was also conducted in R to determine which surface-active arthropods were strongly associated with a particular habitat. We found that species richness and abundance of ants was higher in disturbed than in pristine savannah. In contrast, species richness and abundance of beetles and spiders were similar in disturbed and pristine savannahs. Moreover, the species composition of ants, beetles, and spiders was different between disturbed and pristine savannahs. The disturbed savannah had two times more unique indicator species of the surface-active arthropods than the pristine savannah. Results from our study highlight the role of anthropogenic disturbance in negatively driving assemblages of surface-active arthropods in natural landscapes. I show that it may be important to consider disturbed and pristine habitat types in conservation because different habitats support different assemblages of surface-active arthropods.

Keywords: Arthropods, assemblages, disturbance, savannah

2.1. Introduction

The savannah is one of the most diverse biomes on Earth (Hutley and Setterfield, 2018). Savannah is primarily characterised by a layer of grasses interrupted by sparsely distributed woody vegetation (Wakeling et al., 2012; Lehmann et al., 2014). The woody plants of the savannah biome have open canopies, which allow direct sunlight to filter through to the understorey vegetation (Mucina and Rutherford, 2010). The structure of the savannah biome allows several biological activities to occur both in the canopy and understorey vegetation (Simioni et al., 2003). For example, arthropods, which play an integral part in several ecosystems, are active in the canopy and understorey vegetation (Simioni et al., 2003; Marquart et al., 2020).

The positive effects of arthropods help maintain biological activities in an ecosystem (Menta and Remelli, 2020). For example, surface-active arthropods are involved either directly or indirectly in water supply, nutrient cycling, primary production, soil formation and climate regulation (Lavelle et al., 2006). Moreover, some surface-active arthropods, such as mites, springtails, millipedes, many larval and adult insects, play a significant role as indicators of soil function and quality (Stork and Eggleton, 1992; Paoletti, 1999; Lavelle et al., 2006). These functions are essential in maintaining life on Earth for all organisms, including humans.

Surface-active arthropods form a significantly high component of the total arthropod species that have been described to date (Stork, 2018; Eisenhauer et al., 2019; Seibold et al., 2019). These arthropods have limited dispersal abilities (Lavelle et al., 2006) and are sensitive to changes in the environment (Yekwayo and Mwabvu, 2019). The limited dispersal ability, coupled with a high sensitivity to changes in the environment, make surface-active arthropods vulnerable to disturbance (Kwon et al., 2013; Eisenhauer et al., 2019). Common forms of ecological disturbance that are known to influence the distribution of surface-active arthropods include unsustainable fire regimes, the introduction of invasive alien plant and animal species, global climate change and land-use change (Vergnes et al., 2014; Høye and Culler, 2018; Eisenhauer et al., 2019; Menta and Remelli, 2020).

Substantial evidence indicates that the increase in the severity and frequency of fires in natural ecosystems has a negative impact on surface-active arthropods (Kwon et al., 2013; Puga et al., 2017; Yekwayo et al., 2018). The changes in natural fire regimes have been linked with pressure imposed by global climate change (Koltz et al., 2018). Fires affect surface-active arthropod biomass through direct mortality and the modification of understorey characteristics (Parr et al., 2004; Kwon et al., 2013). Furthermore, fires affect the dispersal and colonisation rates of surface-active arthropods (Koltz et al., 2018; Yekwayo et al., 2018). For example, Ferrenberg et al. (2019) found that the quality of decaying matter, understorey litter, coarse wood debris, tree basal area, amount of exposed rock and the amount of bare ground had significant effects on the community structure of surface-active arthropods in conifer forests that had variable fire regimes in northern New Mexico. The type of fire regime in an ecosystem affects all these understorey characteristics strongly, thus, indicating that disturbance by fire has an important influence on the community structure of surface-active arthropods.

The introduction of alien invasive plants has far more effects on surface-active arthropod community structure than the intensification of agricultural activities (Magoba and Samways, 2012). The limited dispersal abilities, coupled with host specificity, make certain arthropods, particularly herbivores, vulnerable to changes in vegetation structure (McIntyre et al., 2001; Kwon et al., 2013). Alien invasive plants often homogenise vegetation structure, leaving the area unsuitable for arthropod species that feed only on natural vegetation (Magoba and Samways, 2012). The results of homogenising vegetation structure by an introduction of alien invasive plants could lead to local extinction of certain surface-active arthropods, particularly herbivores. For example, Proches et al. (2008) found that herbivorous arthropods were less abundant and less diverse on alien plants than on native vegetation in the Western Cape, South Africa.

Over the years, there has been an increase in the general loss of arthropod biodiversity due to a rise in the demand for land (Hendrickx et al., 2007; Høye and Culler, 2018; Eisenhauer et al., 2019). Clearing of natural vegetation for farming, urban development and residential areas are some of the significant land-use practices threatening arthropod biodiversity currently (Vergnes et al., 2014; Eisenhauer et al., 2019). For example, in Germany, Seibold et al. (2019) observed over nine years, an overall decline in the gamma diversity and biomass of arthropods due to increasing intensification of land use and growing demand for land. Furthermore, in a southern African savannah, Mauda et al. (2018) observed significantly lower species diversity of ants in croplands and villages than in rangelands that are distant from homes.

Savannahs are structurally complex ecosystems that are rich in arthropod biodiversity (Hlongwane et al., 2019; Yekwayo and Mwabvu, 2019). Conversion of savannahs into croplands (Mauda et al., 2018) and residential areas (Yekwayo and Mwabvu, 2019) poses a significant risk to arthropods with limited dispersal abilities. Disturbance through residential and other infrastructural developments results in fragmentation, isolation of habitats and a reduction in habitat size, making it unsuitable for specialised arthropod groups (Kwon et al., 2013).

Despite the dominance of arthropods, the response of several groups of arthropods in pristine and disturbed environments is not yet fully understood (Hlongwane et al., 2019; Seibold et al., 2019; Yekwayo and Mwabvu, 2019). In addition, there are not enough baseline data and long-term data that will enable monitoring of arthropods and enable engagements in well-informed conservation efforts (Mauda et al., 2018; Seibold et al., 2019; Yekwayo and Mwabvu, 2019). To gather baseline data and to understand the effects of disturbance on several groups of arthropods, I investigated the effects of disturbance on surface-active arthropod assemblages in pristine and disturbed savannah in Mpumalanga province, South Africa. The pristine location selected for the study had more structurally complex vegetation and diverse topography than the disturbed location. Therefore, I expected the pristine location to have a higher species diversity of surface-active arthropods than the disturbed location.

2.2. Materials and methods

2.2.1. Study sites

The study was conducted at two locations, the first approximately 9.15 km from the city centre (measured using Google Maps, 2020) on the outskirts of Mbombela City (OMC) (25º23′44.5"S, 30º57′18.4"E) and the second at Barberton Nature Reserve (BNR) (25º36′17.5"S, 30º58′10.7"E), both in the lowveld of Mpumalanga province of South Africa (Fig. 2.1). At each location, 15 sites were selected. Sites at the OMC were categorised as disturbed, and sites at BNR were categorised as pristine. The pristine sites were in a protected area with little human interference. Barberton Nature Reserve covers about 27 541 ha of land (Mpumalanga Tourism and Parks Agency, 2019). The disturbed sites were on fallow land (864.2 ha) (measured using Daft Logic, 2020) that is approximately 1 km (measured using Google Maps, 2020) from ongoing residential (Msholozi township) and industrial developments (Rocky Drift).

The selected study sites have an elevation ranging from 613 to 827 m above sea level, occur in a moderate rainfall area, and experience wet summers and dry winters with a mean annual rainfall between 600 and 700 mm (Mucina and Rutherford, 2010; ARC-ISCW, 2019). In summer, temperatures range from 13 − 40ºC in Barberton and 14 − 43ºC in Mbombela (ARC-ISCW, 2019). Winter temperatures range from 2 − 35ºC in Barberton and -9 − 35ºC in Mbombela (ARC-ISCW, 2019). Barberton and Mbombela are located in the north-eastern part of South Africa, which falls within the savannah biome (Mucina and Rutherford, 2010).

The geology of the area is composed mainly of the Kaapvaal Craton, a very stable rock of the ancient continental crust (Poujol et al., 2003). Barberton Nature Reserve is part of the Barberton Makhonjwa Mountains UNESCO World Heritage Site (Shah et al., 2018; Oosthuizen, 2020), and falls within the Barberton Centre of Plant Endemism (Williamson and Balkwill, 2015; Oosthuizen, 2020). The area includes outcrops of serpentine rocks of the Barberton Greenstone Belt and surrounding non-serpentine areas (Mucina and Rutherford, 2010; Williamson and Balkwill, 2015). Soils derived from the outcrops of the serpentine rocks are known to contain low levels of calcium to magnesium ratio, low overall nutrient content compared with surrounding non-serpentine soils, high nickel and chromium toxicity and low water retention capacity (Roberts and Proctor, 1992; Williamson and Balkwill, 2006). The Barberton Centre of Plant Endemism has rich floral diversity (Mucina and Rutherford, 2010; Williamson and Balkwill, 2015). The area supports over 2 176 plant species recorded to date, 80 of which are endemics (Oosthuizen, 2020).

The vegetation in BNR can be described as sour bushveld of the savannah biome (Mucina and Rutherford, 2010). Some of the woody plant species observed at BNR are *Grewia occidentalis* (Malvaceae), *Olea europaea* subsp. *africana* (Oleaceae), *Ruttya ovata* (Acanthaceae), *Vachellia nilotica* (Fabaceae), *Diospyros* sp. (Ebenaceae), *Euclea* sp. (Ebenaceae) and *Ximenia* sp. (Olacaceae). The grass layer is composed mostly of *Heteropogon contortus* (Poaceae), *Panicum maximum* (Poaceae) and *Hyparrhenia hirta* (Poaceae). The OMC area is dominated mainly by bushveld savannah with patches of shrubveld savannah (Mucina and Rutherford, 2010). The grasses, *Aristida* sp., *Hyparrhenia* sp. and *Cymbopogon* sp., among others, characterise the grass layer, while the woody layer is dominated by *Vachellia tortilis* (Fabaceae) in the OMC area. *Sclerocarya birrea* (Anacardiaceae), which is native to the area, and two invasive alien plant species, *Psidium guajava* (Myrtaceae) and *Lantana camara* (Verbenaceae), were observed also in the disturbed sites.

2.2.2. Data collection procedure

The study was conducted in austral summer (December 2018 – February 2019) when the activity of flightless arthropods was high. Several studies have indicated that the activity and abundance of flightless arthropods are affected significantly by changes in temperature such that they are more active in summer than in winter (Niemelä et al., 1992; Botes et al., 2006; Barahona-Segovia et al., 2019; Suheriyanto et al., 2019). Therefore, sampling flightless arthropods in summer increases the chances of making observations that are representative of these taxa in the disturbed and pristine savannah.

The unbaited pitfall trapping method was used because pitfalls are quick to install and sample continually, requiring periodic emptying only and, therefore, are a cost-effective method (Leather, 2005; Samways et al., 2010). Furthermore, the pitfall trapping method allows large numbers of surface-active arthropods to be caught with minimal effort compared to other methods such as suction sampling and foliage bagging (Leather, 2005). A pitfall trap in this study was an open-top cylindrical plastic jar of 6 cm diameter and 13.5 cm depth. Pitfall traps were quarter filled with 50% ethylene glycol and inserted into the soil with the rim of the jar level with the soil surface. The flushing of the rim with the soil was done so that there was no vertical barrier encountered by the surface-active arthropods. The disturbed and pristine locations had 15 replicate sites each, with sites at each location being at a distance of at least 300 m apart to avoid pseudo-replication. Each site was a 10 m x 10 m plot with six pitfall traps installed in each corner for a sum of 24 traps per site.

At each site, traps were set and emptied after six days. The procedure was carried out continually without rest between the sampling efforts for four times during the sampling period. After emptying each trap, contents from all the pitfall traps were washed with tap water to remove ethylene glycol, after which the samples were preserved in absolute alcohol. Contents of all the 24 pitfall traps in each site were amalgamated to form one sample. The amalgamation of pitfall trap contents from each site was done to reduce digging-in effects (Samways et al., 2010) and remove catch differences resulting from the spatial arrangement of each pitfall trap in each site (Brennan et al., 2005; Leather, 2005). Arthropods were then sorted into morpho-species and later identified to family and genus where possible.

2.2.3. Data analysis

Species richness, abundance, and composition of ants, beetles, and spiders were determined in R (R Core Team, 2021) using generalised linear mixed models (GLMMs) and linear mixed models (LMMs). Millipedes were excluded from the species richness, abundance, and composition analyses due to a low number of species (11 morphospecies). The package *lme4* (Bates et al., 2015) was used to fit GLMMs and LMMs, while the package *multcomp* (Hothorn et al., 2008) was used to generate post hoc results of the GLMMs and LMMs. Two independent variables, the status of savannah habitat (disturbed and pristine) and the elevation of sites, were included in the GLMMs and LMMs, where the status of the savannah (disturbed and pristine) was used as a fixed factor, while the elevation of sites was used as a random factor.

Tests for normality of the data were carried out using the Shapiro-Wilk test and visually by looking at quantile-quantile plots. Generalised linear mixed models were used when analysing the species abundance of ants, beetles and spiders because these data were not normally distributed. Poisson distribution was used when analysing the species abundance of spiders. However, the species abundance of ants and beetles was over-dispersed; as such, the negative binomial distribution was used. Linear mixed models were used when analysing the species richness of ants, beetles, and spiders because these data were normally distributed.

Species composition was determined using the manyglm function in the package *mvabund* (Wang et al., 2012). Negative binomial distribution was used for the generalised linear models (GLMs) to determine the species composition of ants, beetles and spiders. Two variables (status of the savannah and total abundance of each species per habitat type) were used in the GLMs.

The indicator species analysis included all four taxa (ants, beetles, millipedes, and spiders). The indicator species analysis of the two habitats (disturbed and pristine savannah) was also conducted in R using the function multipatt found in the *indicspecies* package (De Caceres and Legendre, 2009). Multipatt groups species according to their association with a particular site. Only species that are significantly associated with specific habitat types ($p < 0.05$) were listed in the results of the multilevel pattern analysis.

2.3. Results

2.3.1. Species richness, abundance and composition of ants

In total, 308 741 specimens from five subfamilies and 15 genera with 138 morphospecies of ants were identified in this study. Subfamilies with the highest species richness were Myrmicinae (74 morphospecies), followed by Formicinae (38 morphospecies). Dolichoderinae and Dorylinae had the lowest species richness, with one morphospecies each. The most abundant subfamily was Formicinae (250 199 specimens), followed by Myrmicinae (51 928 specimens). A single morphospecies belonging to the genus *Camponotus* contributed 240 790 individuals to the total number of Formicinae specimens, with 240 789 individuals in the disturbed and one individual in the pristine savannah. The least abundant subfamilies were Dolichoderinae with one individual and Ponerinae with 1 811 individuals.

Species richness and abundance of ants were significantly higher in disturbed than in pristine savannah (Table 2.1; Figs 2.2a, 2.3a). There were significant differences in the composition of ants between disturbed and pristine savannah (Table 2.1).

2.3.2. Species richness, abundance and composition of beetles

A total of 5 013 specimens belonging to 23 families with 186 morphospecies of beetles were collected in this study. The family with the highest species richness was Scarabaeidae (56 morphospecies), followed by Chrysomelidae (32 morphospecies), Carabidae (20 morphospecies) and Curculionidae (20 morphospecies). Anthicidae, Cantharidae, Coccinellidae, Discolomatidae, Elmidae, Erotylidae and Trogidae had the lowest species richness with a single morphospecies each. The most abundant family was the Scarabaeidae (2 150 specimens), followed by Carabidae (564 specimens) and Elateridae (478 specimens). Coccinellidae and Elmidae were the least abundant families, with a single specimen each.

Species richness and abundance of beetles was similar between disturbed and pristine savannah (Table 2.1; Figs 2.2b, 2.3b). The species composition of beetles in disturbed and pristine savannahs was significantly different (Table 2.1).

2.3.3. Species richness, abundance and composition of spiders

A total of 8 847 specimens of spiders belonging to 32 families with 302 morphospecies were collected and identified. The families with the highest species richness of spiders was Salticidae (77 morphospecies), followed by Gnaphosidae and Lycosidae with 28 morphospecies each. Tetragnathidae, Selenopidae, Scytodidae, Miturgidae, Agelenidae, Microstigmatidae, Segestriidae, Prodidomidae, and Hahniidae had the lowest species richness with a single morphospecies each. The most abundant family was Zodariidae (2 872 specimens), followed by Gnaphosidae (1 685 specimens) and Salticidae (1 518 specimens). Tetragnathidae, Selenopidae, Scytodidae, Miturgidae and Agelenidae were the least abundant families with a single specimen each.

Species richness and abundance of spiders were similar in disturbed and pristine savannah (Table 2.1; Figs 2.2c, 2.3c). However, there was a significant difference in the composition of spiders collected from disturbed and pristine savannah (Table 2.1).

2.3.4. Species richness and abundance of millipedes

In total, 248 specimens belonging to eight families with 11 morphospecies of millipedes were collected. The Harpagophoridae, Odontopygidae, and Spirostreptidae had the highest species richness, with two morphospecies each. Arthrosphaeridae, Nemasomatidae, Polydesmidae, Procyliosomatidae, and Sphaerotheriidae had the lowest species richness with a single morphospecies each. The most abundant families were the Harpagophoridae (102 specimens), followed by the Spirostreptidae (43 specimens). The least abundant families were the Nemasomatidae (one specimen) and the Sphaerotheriidae (ten specimens).

2.3.5. Indicator species analysis

Multilevel pattern analysis of morphospecies found no shared indicator species between disturbed and pristine savannah (Tables 2.2 and 2.3). In total, 100 indicator species were identified out of 637 morphospecies from four taxa (ants, beetles, millipedes and spiders). Sixty-eight indicator species were significantly associated with disturbed savannah (Table 2.2), while 32 were indicator species of the pristine savannah (Table 2.3).

2.4. Discussion

2.4.1. Species richness and abundance

I expected the species richness of ants, beetles and spiders to be greater in pristine than in disturbed savannah. However, I found that the species richness of ants in disturbed savannah was significantly greater than in pristine savannah. Moreover, the species richness of beetles and spiders was similar between disturbed and pristine savannahs. The pristine savannah was in a protected area with little human interference, while the disturbed savannah was fallow land close to ongoing residential and industrial development. As such, conditions in the pristine savannah were more stable than in disturbed savannah where there was a high human population, which disturbed the vegetation through anthropogenic activities (cultivation, plant harvesting, overgrazing by livestock, etc) and therefore disturbed environmental conditions and microhabitats for the surface-active arthropods. Pristine savannahs are more structurally complex and provide a more diverse community of plants and microhabitats for arthropods than the disturbed savannahs (Alves Da Mata and Tidon, 2013; de Visser et al., 2015); as such, results from this study were not expected.

The species richness of the ants, beetles and spiders can be explained in terms of the intermediate disturbance hypothesis, which suggests that species richness will increase if the disturbance is not significant enough to remove all the species in a particular site, but significant enough to allow *r* and *K*-selected species to coexist (Grime, 1973; Horn, 1975; Connell, 1978). If disturbance results in the loss of species, perhaps through extirpation, species adapted to disturbance (disturbance specialists) may colonise the newly disturbed site rapidly (King and Tschinkel, 2008). Greater colonisation by disturbance specialist species results in species turnover but no difference in the species richness of the area before and after disturbance (Swart et al., 2019). In my study, the disturbed habitat type may have undergone intermediate disturbance. This assertion is supported by the high number of unique species (two times more) in the disturbed than pristine savannah (Table 2.1; 2.3). However, this is not a gradient study, and the assertion is solely based on the putative occurrence of type of magnitude of the disturbance in the disturbed savannah.

I also found that ants may be more responsive to disturbance than beetles and spiders. This was shown by greater species richness and abundance of ants in disturbed than pristine savannahs. My results are supported by observations of Savitha et al. (2008), who found greater species richness and abundance of ants in disturbed (city parks and suburbs with dry forests and a few orchards) than less disturbed sites (natural dry thorny and deciduous forests on the outskirts of the city) in Bangalore, India. The extremely high abundance (> 240 000 individuals) of a single morphospecies belonging to the genus *Camponotus* in the disturbed savannah compared to the pristine savannah (one individual) highlights the role of human-induced disturbance in driving the assemblage composition of surface-active arthropods. The large number of individuals of a single ant species in disturbed versus pristine savannah is supported by experimental evidence indicating that human-induced activities drive species invasions and ecological change (King and Tschinkel, 2008). In a large-scale experiment of ecological invasion by ants in the state of Florida, USA, King and Tschinkel (2008) found that *Solenopsis invicta* (fire ants), a disturbance specialist, reduced the abundance and diversity of native ants in forest habitats after the human-induced disturbance had occurred. However, in the absence of human-induced disturbance, the fire ants could not invade the forests and affect the abundance of native ants negatively (King and Tschinkel, 2008). In addition, Berman et al. (2013) found that the invasion of *Anoplolepis gracilipes* (yellow crazy ants) and *Wasmannia auropunctata* (electric ants) in the main island of the New Caledonian archipelago is facilitated by disturbance.

I found similar species richness and abundance of spiders in disturbed and pristine savannahs. Similarly, Moorhead and Philpott (2013) examined spider communities in vacant lots, community gardens, and fragments of natural forests in the United States, and found no significant differences in the species richness of spiders among the three habitats. The observed similarity of species richness and abundance of spiders in the present study is not unusual because several studies found similarities in species richness and abundance of spiders between disturbed and undisturbed habitats (Copley and Winchester, 2010; Stenchly et al., 2012; Melliger et al., 2018). The similarity in species richness and abundance of spiders in pristine and disturbed savannah may have resulted from species turnover. My study revealed that the overall species richness and abundance of spiders might not provide enough information on the effect of disturbance. However, investigating the species richness and abundance of a few families or focusing on functional group response may provide more information about the impact of disturbance on surface-active arthropods. This is borne out in Switzerland by Narimanov et al. (2021), who found that the invasive *Mermessus trilobatus* (Linyphiidae) is more sensitive to soil disturbance in grasslands than native species of spiders. Furthermore, Narimanov et al. (2021) found that the abundance of *Oedothorax apicatus* (Linyphiidae) increases after superficial soil tillage has occurred. These studies suggest that it is possible to determine the effects of disturbance on species richness and abundance of spiders using singleton groups.

There were similar abundances and species richness of beetles between disturbed and pristine savannahs. Unlike this study which investigated the overall taxa of beetles in disturbed and pristine savannah, much of the research on beetle assemblages has focused on ground beetles (Carabidae) and dung beetles (Scarabaeidae) (Hanski and Cambefort, 2014; Gallé et al., 2018; Correa et al., 2019; Rahman et al., 2021), and not much is available on overall species richness and abundance of beetles. As such, it is challenging to make comparisons with these studies because of the differences in the levels of resolution, which differ from that of the present study. The present study included 23 families of beetles, which is many more taxa than in many other studies of the composition of beetles. For example, Rahman et al. (2021), who investigated the effect of disturbance on the trophic niche of six species of ground beetles in 20 tallgrass prairies, found that the response of ground beetles to disturbance varies. In particular, Rahman et al. (2021) argued that morphological traits and microhabitat preferences are important and affect how ground beetles respond to disturbance. The results from the present study suggest that overall species richness and abundance of beetles may not be an appropriate indicator of disturbance, which is most likely because of species turnover at the disturbed sites. However, reducing the taxa, for example, focusing on one or two families (Carabidae or Scarabaeidae), could provide more information on the possible changes in species richness and abundance resulting from habitat disturbance.

2.4.2. Species composition

I found that the species composition of ants, beetles, and spiders differed between the disturbed and pristine savannah. Moreover, the multilevel pattern analysis of morphospecies in the present study found that the disturbed savannah had 68% unique species compared with

32% in the pristine savannah. These results are consistent with the observations of Yekwayo and Mwabvu (2019), who reported dissimilarities in species composition of surface-active arthropods, with a greater number of unique species in disturbed than in pristine savannah. According to the intermediate disturbance hypothesis, moderate levels of disturbance create an environment where competitively superior species can coexist with those that are competitively inferior, resulting in high species richness (Grime, 1973; Horn, 1975; Connell, 1978; Osman, 2015). As such, the high number of indicator species in the disturbed savannah that were observed in this study may have been due to moderate levels of disturbance.

In my study, the disturbed and pristine savannah did not have any shared indicator species. The lack of shared indicator species can be explained by differences between the vegetation of disturbed and pristine savannahs. The relationship between vegetation characteristics or type of vegetation and surface-active arthropods is well documented, and several studies have reported that species composition of surface-active arthropods varies with vegetation type or structure (Whitmore et al., 2002; Copley and Winchester, 2010; Moorhead and Philpott, 2013; Hlongwane et al., 2019; Rahman et al., 2021). For example, Hlongwane et al. (2019) found that the diversity of ants in the sandstone sourveld of KwaZulu-Natal is influenced by the type of vegetation. Moreover, other studies reported also that different vegetation types support different compositions of surface-active arthropods (Mauda et al.,2018; Leonard et al., 2021; Hoffmann et al., 2021). The present study highlights further the role that disturbance plays in altering the assemblage composition of surface-active arthropods. My study shows that changes in vegetation structure, as a result of human-induced disturbance, result in significant changes in the species composition of surface-active arthropods.

Other factors that affect the species composition of surface-active arthropods include the size of the regional species pool, dispersal distance, ability to disperse, competition with other species of surface-active arthropods, facilitation by related species, predation, resource availability and environmental heterogeneity (Brown et al., 2007; Arribas et al., 2021; Woodcock et al., 2021). Human-induced disturbance affects these factors by altering habitat structure and reducing the biomass of vegetation and surface-active arthropods in a habitat (King and Tschinkel, 2008; Swart et al., 2019. The different composition of surface-active arthropods observed in the present study between disturbed and pristine savannah illustrate further that human-induced disturbance drives the species composition and assemblages of surface-active arthropods in natural habitats.

2.5. Conclusion

Human-induced disturbance affects the assemblages of surface-active arthropods in various ways. My study demonstrates that disturbance, because of anthropogenic activity, results in significant changes in the species composition of surface-active arthropods, which can be related to changes in vegetation structure. In addition, I show that biodiversity parameters such as species richness and abundance may not be appropriate indicators of disturbance because of species turnover in disturbed habitats. I show that certain species of surface-active arthropods, the disturbance specialists, become highly abundant in habitats where there is human-induced disturbance. However, in the absence of human-induced disturbance, the disturbance specialists occur in low abundances.

Furthermore, the present study shows that ants may be more sensitive to disturbance at a community level than beetles and spiders, indicating that different arthropod groups respond differently to disturbance. The present study shows that disturbed and pristine savannahs have unique species composition of surface-active arthropods. As such, it is essential to consider all habitat types when making efforts to conserve the biodiversity of surface-active arthropods, particularly because a greater percentage of semi-natural habitats in South Africa occur outside protected areas.

2.6. References

Alves Da Mata, R., Tidon, R., 2013. The relative roles of habitat heterogeneity and disturbance in drosophilid assemblages (Diptera, Drosophilidae) in the Cerrado. Insect Conservation and Diversity 6, 663–670.

ARC-ISCW, 2019. Water and climate data (unpublished). In: Agricultural Research Council (ARC) Institute for Soil Climate and Water (ISCW) (Ed.). Agro climatology division, Stellenbosch.

Arribas, P., Andújar, C., Salces-Castellano, A., Emerson, B.C., Vogler, A.P., 2021. The limited spatial scale of dispersal in soil arthropods revealed with whole-community haplotype-level metabarcoding. Molecular Ecology 30, 48–61.

Barahona-Segovia, R.M., Crespin, S.J., Grez, A.A., Veloso, C., 2019. Anthropogenic thermal gradient in managed landscapes determines physiological performance and explains the edge-biased distribution of ectothermic arthropods. Forest Ecology and Management 440, 147–157.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67, 1–48.

Berman, M., Andersen, A.N., Ibanez, T., 2013. Invasive ants as back-seat drivers of native ant diversity decline in New Caledonia. Biological Invasions 15, 2311–2331.

Botes, A., McGeoch, M., Robertson, H., Van Niekerk, A., Davids H., Chown, S., 2006. Ants, altitude and change in the northern Cape Floristic Region. Journal of Biogeography 33, 71–90.

Brennan, K.E., Majer, J.D., Moir, M.L., 2005. Refining sampling protocols for inventorying invertebrate biodiversity: influence of drift–fence length and pitfall trap diameter on spiders. Journal of Arachnology 33, 681–702.

Brown, R.L., Jacobs, L.A., Peet, R.K., 2007. Species richness: small scale, eLS. John Wiley and Sons, Chichester.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Copley, C.R., Winchester, N.N., 2010. Effect of disturbance and distance from a riparian corridor on spiders in a temperate rainforest. Canadian Journal of Forest Research 40, 904–916.

Correa, C.M., Braga, R.F., Louzada, J., Menéndez, R., 2019. Dung beetle diversity and functions suggest no major impacts of cattle grazing in the Brazilian Pantanal wetlands. Ecological Entomology 44, 524–33

Daft-Logic, 2020. Google Maps Area Calculator Tool. Daft-Logic. Available from: https://www.daftlogic.com/projects-google-maps-area-calculator-tool.htm#. (accessed 23 February 2020)

De Caceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574.

de Visser, S.N., Freymann, B.P., Foster, R.F., Nkwabi, A.K., Metzger, K.L., Harvey, A.W., Sinclair, A.R.E., 2015. Serengeti IV: sustaining biodiversity in a coupled human-natural system. In: Anthony, R.E.S., Kristine, L.M., Simon, A.R.M., John, M.F. (Eds.), 10th ed. Invertebrates of the Serengeti: Disturbance Effects on Arthropod Diversity and Abundance. University of Chicago Press, Chicago.

Eisenhauer, N., Bonn, A., Guerra, C.A., 2019. Recognising the quiet extinction of invertebrates. Nature Communications 10, 50. https://doi.org/10.1038/s41467-018-07916-1

Ferrenberg, S., Wickey, P., Coop, J.D., 2019. Ground-dwelling arthropod community responses to recent and repeated wildfires in conifer forests of northern New Mexico, USA. Forests 10, 667. https://doi.org/10.3390/f10080667

Gallé, R., Császár, P., Makra, T., Gallé-Szpisjak, N., Ladányi, Z., Torma, A., Ingle, K., Szilassi, P., 2018. Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites. Landscape Ecology 33, 1435–1446.

Google Maps, 2020. Distance Measurement. Google. Available from: https://www.google.co.za/maps/@-5.4774137,30.9593232,13z/data=!4m2!6m1!1s1rZCw3GV6WECFZ51o8KZbASHQUliZutGr?hl=en. (accessed 03 April 2020)

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344–347.

Hanski, I., Cambefort, Y., 2014. Dung Beetle Ecology. Princeton University Press, Princeton.

Hendrickx, F., Maelfait, J.P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology 44, 340–351.

Hlongwane, Z.T., Mwabvu, T., Munyai, T.C., Tsvuura, Z., 2019. Epigaeic ant diversity and distribution in the Sandstone Sourveld in KwaZulu-Natal, South Africa. African Journal of Ecology 57, 382–393.

Hoffmann, H., Peter, F., Herrmann, J.D., Donath, T.W., Diekötter, T., 2021. Benefits of wildflower areas as overwintering habitats for ground-dwelling arthropods depend on landscape structural complexity. Agriculture, Ecosystems and Environment 314, 107421. https://doi.org/10.1016/j.agee.2021.107421

Horn, H.S., 1975. Markovian properties of forest succession. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Belknap Press, Cambridge.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical Journal 50, 346–363.

Høye, T.T., Culler, L.E., 2018. Tundra arthropods provide key insights into ecological responses to environmental change. Polar Biology 41, 1523–1529.

Hutley, L.B., Setterfield, S.A., 2018. Savanna. In: Fath, B. (Ed.), Encyclopedia of Ecology, 2nd ed. Elsevier BV, Oxford.

King, J.R., Tschinkel, W.R., 2008. Experimental evidence that human impacts drive fire ant invasions and ecological change. Proceedings of the National Academy of Sciences USA 105, 20339–20343.

Koltz, A.M., Burkle, L.A., Pressler, Y., Dell, J.E., Vidal, M.C., Richards, L.A., Murphy, S.M., 2018. Global change and the importance of fire for the ecology and evolution of insects. Current Opinion in Insect Science 29, 110–116.

Kwon, T.-S., Park, Y.K., Lim, J.-H., Ryou, S.H., Lee, C.M., 2013. Change of arthropod abundance in burned forests: Different patterns according to functional guilds. Journal of Asia-Pacific Entomology 16, 321–328.

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

Leather, S.R., 2005. Pitfall trapping in ecological studies. In: Lawton, J.H., Likens, G.E. (Eds.), Insect Sampling in Forest Ecosystems. Blackwell Publishing, Oxford, pp. 37–57.

Lehmann, C.E., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J., 2014. Savanna vegetation-fire-climate relationships differ among continents. Science 343, 548–552.

Leonard, E.E., Mast, A. M., Hawkins, C.P., Kettenring, K.M., 2021. Arthropod assemblages in invasive and native vegetation of Great Salt Lake wetlands. Wetlands 41. https://doi.org/10.1007/s13157-021-01446-1

Magoba, R.N., Samways, M.J., 2012. Comparative footprint of alien, agricultural and restored vegetation on surface-active arthropods. Biological Invasions 14, 165–177.

Marquart, A., Geissler, K., Heblach, J., Lobas, C., Münch, E., Blaum, N., 2020. Individual shrubs, large scale grass cover and seasonal rainfall explain invertebrate-derived macropore density in a semi-arid Namibian savanna. Journal of Arid Environments 176, https://doi.org/10.1016/j.jaridenv.2020.104101

Mauda, E.V., Joseph, G.S., Seymour, C.L., Munyai, T.C., Foord, S.H., 2018. Changes in land use alter ant diversity, assemblage composition and dominant functional groups in African savannas. Biodiversity Conservation 27, 947–965.

McIntyre, N.E., Rango, J., Fagan, W.F., Faeth, S.H., 2001. Ground arthropod community structure in a heterogeneous urban environment. Landscape and Urban Planning 52, 257–274.

Melliger, R.L., Braschler, B., Rusterholz, H.-P., Baur, B., 2018. Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. PLoS One 13, p.e0199245. https://doi.org/10.1371/journal.pone.0199245

Menta, C., Remelli, S., 2020. Soil health and arthropods: from complex system to worthwhile investigation. Insects 11, 54. https://doi.org/10.3390/insects11010054

Moorhead, L.C., Philpott, S.M., 2013. Richness and composition of spiders in urban green spaces in Toledo, Ohio. Journal of Arachnology 41, 356–363.

Mpumalanga Tourism and Parks Agency, 2019. Barberton Nature Reserve. Pii Digital. Available from: http://www.mpumalanga.com/our-provincial-parks/barberton-nature-reserve. (accessed 23 February 2020)

Mucina, L., Rutherford, M.C. (eds.), 2010. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Narimanov, N., Kempel, A., van Kleunen, M., Entling, M.H., 2021. Unexpected sensitivity of the highly invasive spider *Mermessus trilobatus* to soil disturbance in grasslands. Biological Invasions 23. https://doi.org/10.1007/s10530-020-02348-9

Niemelä, J., Spence, J.R., Spence, D.H., 1992. Habitat associations and seasonal activity of ground beetles (Coleoptera, Carabidae) in central Alberta. Canadian Entomologist 124, 521–540.

Oosthuizen, N., 2020. Mountainlands Nature Reserve. Creative Africa Media, South Africa. Available from: https://www.mountainlands.co.za/plantlife/ (accessed 23 February 2020).

Osman, R., 2015. The intermediate disturbance hypothesis. In: B. Fath (ed.), Encyclopedia of Ecology. Elsevier B.V., Amsterdam. https://doi.org/10.1016/B978-0-12-409548-9.09480-X

Paoletti, M.G., 1999. Using bioindicators based on biodiversity to assess landscape sustainability. In: Paoletti, M.G., (ed.), Invertebrate Biodiversity as Bioindicators of Sustainable Landscapes. Elsevier, Amsterdam. https://doi.org/10.1016/B978-0-444-50019-9.50004-2

Parr, C.L., Robertson, H.G., Biggs, H.C., Chown, S.L., 2004. Response of African savanna ants to long-term fire regimes. Journal of Applied Ecology 41, 630–642.

Poujol, M., Robb, L., Anhaeusser, C., Gericke, B., 2003. A review of the geochronological constraints on the evolution of the Kaapvaal Craton, South Africa. Precambrian Research 127, 181–213.

Proches, S., Wilson, J.R., Richardson, D.M., Chown, S.L., 2008. Herbivores, but not other insects, are scarce on alien plants. Austral Ecology 33, 691–700.

Puga, J.R.L., Abrantes, N.J.C., de Oliveira, M.J.S., Vieira, D.C.S., Faria, S.R., Gonçalves, F., Keizer, J.J., 2017. Long-term impacts of post-fire mulching on ground-dwelling arthropod communities in a eucalypt plantation. Land Degradation and Development 28, 1156–1162.

R Core Team, 2021. R: A Language and Environment for Statistical Computing, version 4.0.5 ed. R Foundation for Statistical Computing, Vienna.

Rahman, A.U., Jones, H.P., Hosler, S.C., Geddes, S., Nelson, M., Barber, N.A., 2021. Disturbance-induced trophic niche shifts in ground beetles (Coleoptera: Carabidae) in restored grasslands. Environmental Entomology, nvab065. https://doi.org/10.1093/ee/nvab065

Roberts, B., Proctor, J., (eds) 1992. The ecology of areas with serpentinised rocks: a world view. Kluwer Academic Publishers, Amsterdam.

Samways, M.J., McGeoch, M.A., New, T.R., 2010. Insect Conservation: A Handbook of Approaches and Methods. Oxford University Press, New York.

Savitha, S., Barve, N., Davidar, P., 2008. Response of ants to disturbance gradients in and around Bangalore, India. Tropical Ecology 49, 235–243.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674.

Shah, T., Burrows, J., Darbyshire, I., 2018. A new species of Ochna (Ochnaceae) from the Barberton mountains of Mpumalanga, South Africa. Phytotaxa 374, 241–248.

Simioni, G., Gignoux, J., Le Roux, X., 2003. Tree layer spatial structure can affect savanna production and water budget: results of a 3-D model. Ecology 84, 1879–1894.

Stenchly, K., Clough, Y., Tscharntke, T., 2012. Spider species richness in cocoa agroforestry systems, comparing vertical strata, local management and distance to forest. Agriculture, Ecosystems and Environment 149, 189–194.

Stork, N.E., 2018. How many species of insects and other terrestrial arthropods are there on Earth? Annual Review of Entomology 63, 31–45.

Stork N. E., Eggleton P., 1992. Invertebrates as determinants and indicators of soil quality. American Journal of Alternative Agriculture 7, 38–47.

Suheriyanto, D., Soemarno, S., Yanuwiadi, B., Leksono, A.S., Prasetiyo, D.H., Permana, S.R., 2019. Effects of season on abundance and diversity of soil arthropods in Mangli coffee plantation Kediri Regency, East Java, Indonesia. International Journal of Engineering and Technology 8, 131–135.

Swart, R.C., Pryke, J.S., Roets, F., 2019. The intermediate disturbance hypothesis explains arthropod beta-diversity responses to roads that cut through natural forests. Biological Conservation 236, 243–251.

Vergnes, A., Pellissier, V., Lemperiere, G., Rollard, C., Clergeau, P., 2014. Urban densification causes the decline of ground-dwelling arthropods. Biodiversity and Conservation 23, 1859–1877.

Wakeling, J.L., Cramer, M.D., Bond, W.J., 2012. The savanna-grassland 'treeline': why don't savanna trees occur in upland grasslands? Journal of Ecology 100, 381–391.

Wang, Y., Naumann, U., Wright, S., Warton, D., 2012. mvabund: an R package for model-based analysis of multivariate data. Methods in Ecology and Evolution 3, 471–474

Whitmore, C., Slotow, R., Crouch, T.E., Dippenaar-Schoeman, A.S., 2002. Diversity of spiders (Araneae) in a savanna reserve, Northern Province, South Africa. The Journal of Arachnology 30, 344–356.

Williamson, S., Balkwill, K., 2006. Factors determining levels of threat to serpentine endemics. South African Journal of Botany 72, 619–626.

Williamson, S., Balkwill, K., 2015. Plant census and floristic analysis of selected serpentine outcrops of the Barberton Greenstone Belt, Mpumalanga, South Africa. South African Journal of Botany 97, 133–142.

Woodcock, B., Pywell, R., Macgregor, N., Edwards, M., Redhead, J., Ridding, L., Batáry, P., Czerwiński, M., Duffield, S., 2021. Historical, local and landscape factors determine the success of grassland restoration for arthropods. Agriculture, Ecosystems and Environment 308, 107271, https://doi.org/10.1016/j.agee.2020.107271

Yekwayo, I., Mwabvu, T., 2019. Diversity and composition of flightless arthropods on rock outcrops and adjacent vegetation in the savannah, Mpumalanga province, South Africa. African Journal of Ecology 57, 3, 443–447.

Yekwayo, I., Pryke, J.S., Gaigher, R., Samways, M.J., 2018. Only multi-taxon studies show the full range of arthropod responses to fire. PLoS One 13, e0195414. https://doi.org/10.1371/journal.pone.0195414

2.7. Tables

Table 2.1. Species richness, abundance and composition of ants, beetles, and spiders collected from disturbed and pristine savannah. Significant p-values are shown in bold.

	Ants			**Beetles**			**Spiders**		
	χ2	df	p	χ2	df	p	χ2	df	p
Species richness	34.855	1	**<0.001**	0.596	1	0.440	3.328	1	0.068
Species abundance	17.049	1	**0.036**	0.004	1	0.951	3.823	1	0.051
	Deviance	Error df	p	Deviance	Error df	p	Deviance	Error df	p
Species composition	484.5	28	**<0.001**	579.9	28	**<0.001**	981.2	28	**<0.001**

Table 2.2. Multilevel pattern analysis of morphospecies associated with disturbed savannah. Data are arranged in descending order of taxon and morphospecies.

Taxon	**Morphospecies**	**Association value**	**p-value**
Formicidae	*Bothroponera* sp.1	0.683	0.008
	Camponotus sp.1	0.730	0.002
	Camponotus sp.2	0.816	0.008
	Camponotus sp.3	0.577	0.044
	Camponotus sp.4	0.677	0.017
	Camponotus sp.5	0.714	0.035
	Camponotus sp.6	0.931	0.001
	Camponotus sp.7	0.854	0.001
	Crematogaster sp.1	0.813	0.014
	Crematogaster sp.2	0.905	0.001
	Formicinae 4	0.759	0.002
	Formicinae 9	0.599	0.046
	Lepisiota sp.1	0.928	0.001
	Monomorium sp.1	0.988	0.001
	Myrmicinae 1	0.730	0.004
	Myrmicinae 2	0.577	0.044
	Myrmicinae 3	0.858	0.001
	Myrmicinae 4	0.632	0.014
	Myrmicinae 5	0.632	0.022
	Myrmicinae 6	0.577	0.040
	Myrmicinae 7	0.766	0.020
	Myrmicinae 8	0.730	0.001
	Pheidole sp.1	0.944	0.001
	Pheidole sp.2	0.779	0.028
	Ponerinae 1	0.632	0.021
	Ponerinae 2	0.730	0.003
	Ponerinae 3	0.731	0.030
	Ponerinae 4	0.893	0.001
	Ponerinae 5	0.648	0.044
	Tetramorium sp.1	0.923	0.001

	Tetramorium sp.2	0.847	0.001
Coleoptera	Carabidae 1	0.632	0.017
	Carabidae 2	0.730	0.003
	Carabidae 3	0.730	0.002
	Carabidae 4	0.683	0.008
	Carabidae 5	0.844	0.001
	Carabidae 6	0.853	0.001
	Curculionidae 1	0.927	0.001
	Elateridae 1	0.876	0.001
	Scarabaeidae 1	0.627	0.048
	Scarabaeidae 2	0.732	0.013
	Staphylinidae 1	0.730	0.002
	Tenebrionidae 1	0.632	0.014
	Tenebrionidae 2	0.816	0.001
	Tenebrionidae 3	0.829	0.001
	Tenebrionidae 4	0.877	0.001
Diplopoda	Odontopigidae 1	0.683	0.032
Araneae	Araneae 1	0.577	0.037
	Araneae 2	0.577	0.045
	Gnaphosidae 1	0.632	0.016
	Gnaphosidae 2	0.730	0.003
	Gnaphosidae 3	0.577	0.050
	Gnaphosidae 4	0.775	0.002
	Gnaphosidae 5	0.800	0.001
	Hahniidae 1	0.577	0.045
	Lycosidae 1	0.809	0.002
	Lycosidae 2	0.842	0.001
	Lycosidae 3	0.931	0.001
	Oxyopidae 1	0.856	0.001
	Oxyopidae 2	0.632	0.016
	Philodromidae 1	0.775	0.002
	Salticidae 1	0.775	0.001
	Spider 1	0.658	0.014

	Theridiidae 1	0.683	0.010
	Zodariidae 1	0.968	0.001
	Zodariidae 2	0.757	0.018
	Zodariidae 3	0.996	0.001
	Zodariidae 4	0.927	0.001

Table 2.3. Multilevel pattern analysis of morphospecies associated with pristine savannah. Data are arranged in descending order of taxon and morphospecies.

Taxon	**Morphospecies**	**Association value**	**p-value**
Formicidae	*Camponotus* sp.8	0.931	0.001
	Camponotus sp.9	0.577	0.049
	Odontomachus sp.1	0.886	0.001
	Tetramorium sp.3	0.718	0.009
Coleoptera	Anobiidae 1	0.749	0.016
	Chrysomelidae 1	0.830	0.012
	Chrysomelidae 2	0.777	0.033
	Scarabaeidae 3	0.632	0.016
	Scarabaeidae 4	0.632	0.019
	Scarabaeidae 5	0.632	0.024
	Scarabaeidae 6	0.632	0.018
	Scarabaeidae 7	0.874	0.001
	Scarabaeidae 8	0.818	0.046
	Scarabaeidae 9	0.577	0.037
	Scarabaeidae 10	0.577	0.039
	Scarabaeidae 11	0.683	0.006
	Tenebrionidae 5	0.837	0.002
Diplopoda	Harpagophoridae 1	0.722	0.012
	Procyliosomatidae 1	0.577	0.042
Araneae	*Caponia* sp.1	0.790	0.027
	Ctenidae 1	0.632	0.019
	Gnaphosidae 5	0.776	0.023
	Gnaphosidae 6	0.577	0.046
	Lycosidae 4	0.612	0.040
	Lycosidae 5	0.768	0.005
	Nemesiidae 1	0.711	0.005
	Nemesiidae 2	0.627	0.030
	Salticidae 2	0.577	0.042
	Salticidae 3	0.628	0.042
	Salticidae 4	0.577	0.046

	Spider 2	0.810	0.001
	Zodariidae 5	0.683	0.016

2.8. Figures

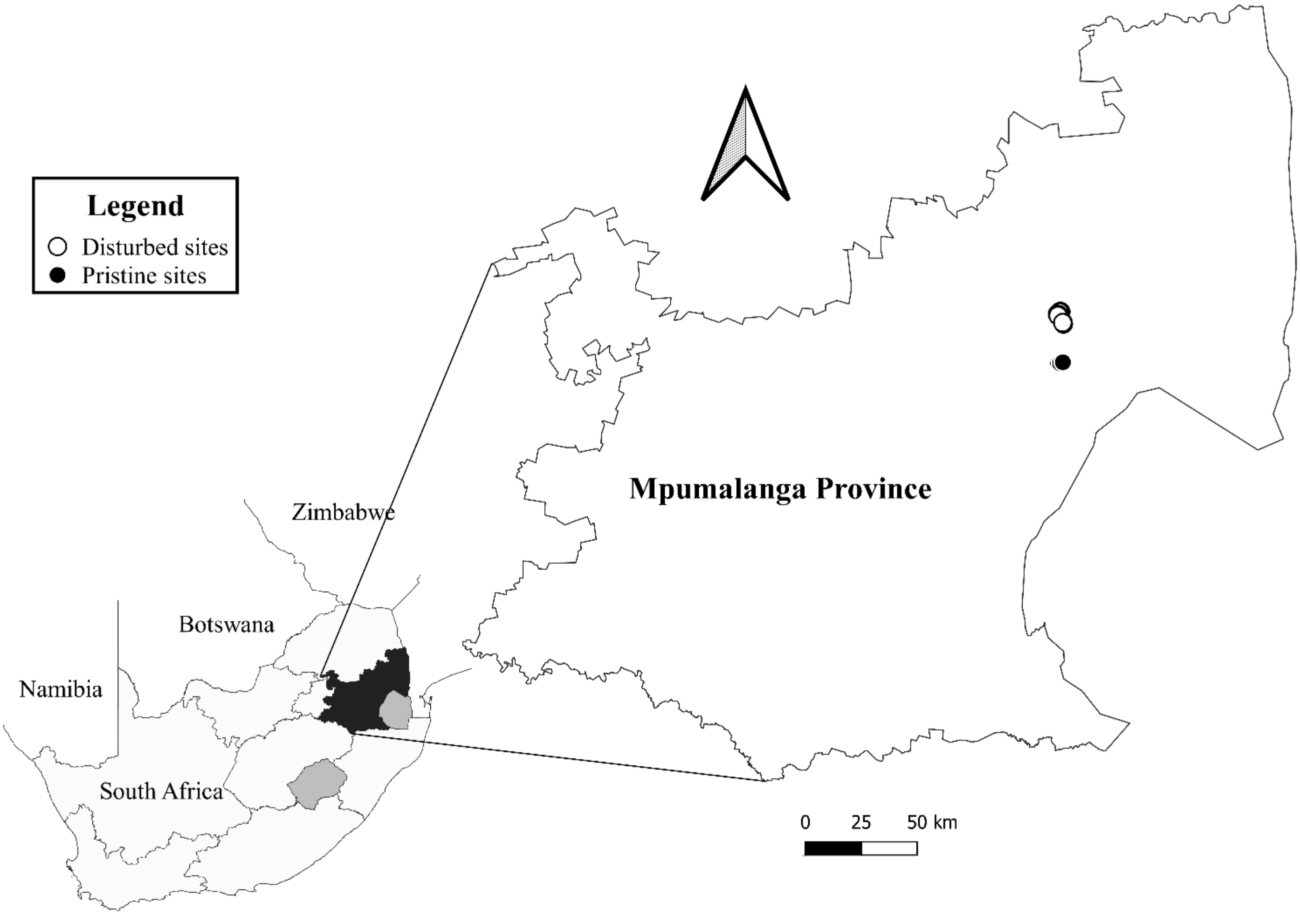

Fig. 2.1. Location of the study sites in Barberton Nature Reserve (pristine sites) and the outskirts of Mbombela City (disturbed sites) in Mpumalanga province of South Africa.

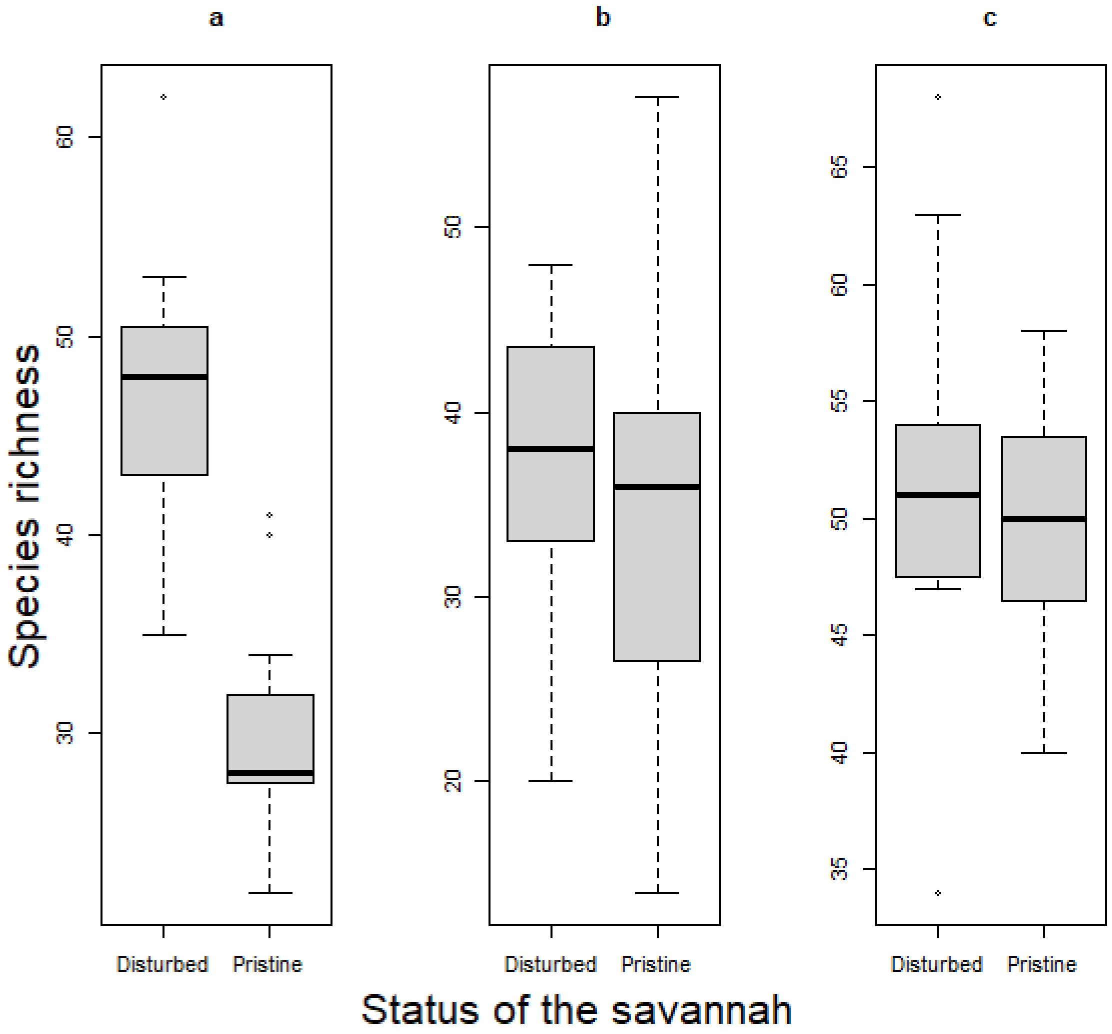

Fig. 2.2. Species richness of (**a**) ants, (**b**) beetles, and (**c**) spiders in pristine and disturbed savannah. There were significant differences (**<0.001**) in the species richness of ants between disturbed and pristine savannah (**a**). Species richness of beetles and spiders was similar between disturbed and pristine savannah (**b** and **c**). Boxplots indicate medians (black horizontal lines) with 25th and 75th percentiles (whiskers), quartiles (interquartile range box and the median) and outliers (asterisks).

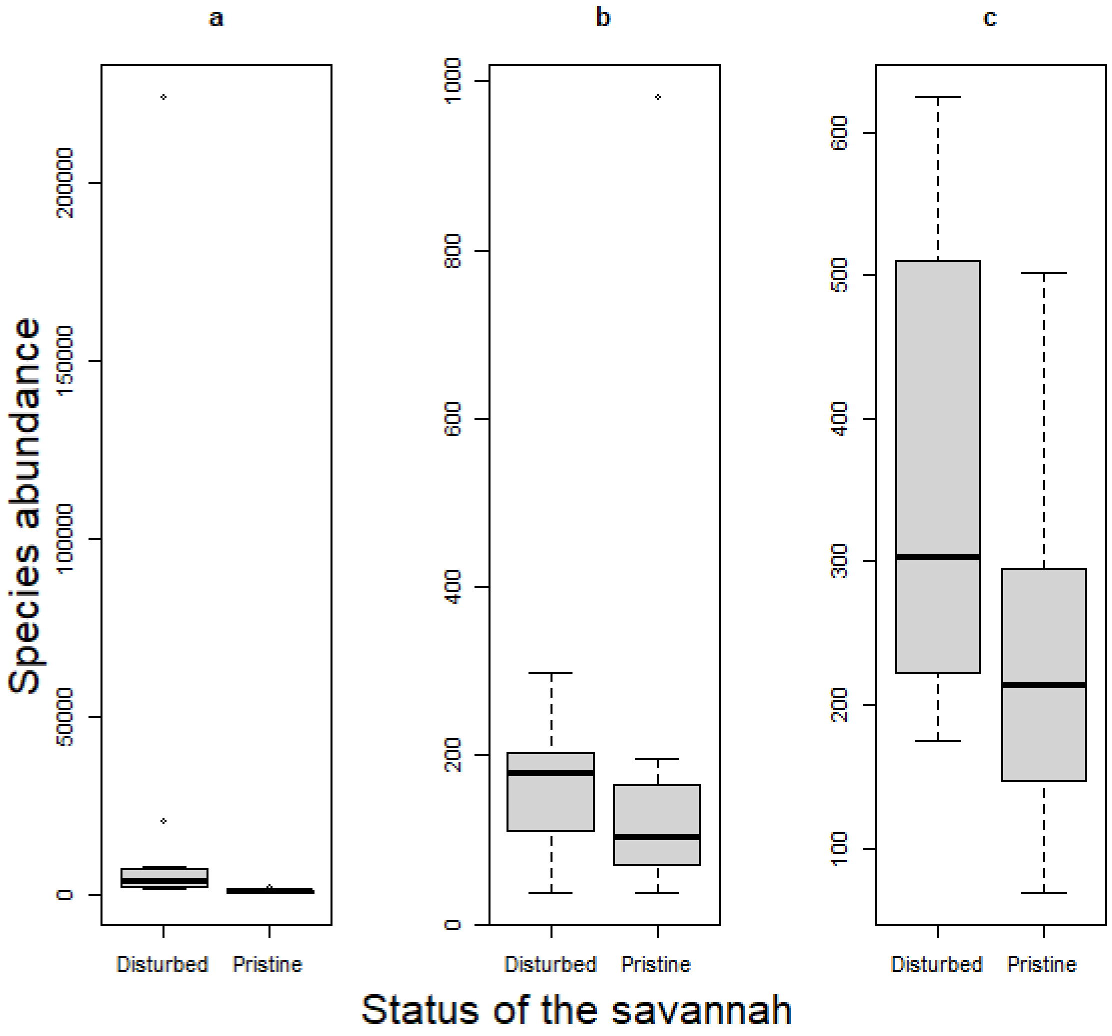

Fig. 2.3. Species abundance of (**a**) ants, (**b**) beetles, and (**c**) spiders in pristine and disturbed savannah. There were significant differences (**0.036**) in the species abundance of ants between disturbed and pristine savannah (**a**). Species abundance of beetles and spiders was similar in pristine and disturbed savannah (**b** and **c**). Boxplots indicate medians (black horizontal lines) with 25th and 75th percentiles (whiskers), quartiles (interquartile range box and the median) and outliers (asterisks).

CHAPTER 3

3. Effect of season on the functional guilds of surface-active arthropods in the savannah, Mpumalanga province

Abstract

Surface-active arthropods have limited dispersal abilities and are sensitive to changes in their environment. Their sensitivity allows for the identification of aspects of environmental change that are responsible for changes in the assemblages of these arthropods. Limited dispersal abilities allow for changes in the populations of the surface-active arthropods to be linked reliably to changes in their local environment. This study was conducted to investigate the effect of season on the assemblages of functional guilds of four groups of surface-active arthropods (ants, beetles, millipedes, and spiders). Ten study sites were selected, where sampling was carried out during the wet season (December 2018 – February 2019) and then repeated at the same sites in the dry season (June 2019 – August 2019), in a savannah of Mpumalanga province, South Africa. Pitfall trapping was used to sample the surface-active arthropods, which were sorted and identified to family and genus where possible, and then allocated to functional guilds. Functional guilds of the surface-active arthropods were categorised based on their feeding habits into detritivores, herbivores and carnivores. Surface-active arthropods that have diverse feeding habits were assigned to a functional guild called the “diverse functional guild”. There was a greater species richness of all functional guilds in summer (wet season) than in winter (dry season). The abundances of herbivorous and carnivorous arthropods were higher in summer than in winter, while the abundances of detritivores and the diverse functional guild were similar between summer and winter. In addition, the species composition of all the functional guilds was significantly different between summer and winter. These findings highlight a potentially positive relationship between the assemblages of herbivorous and carnivorous surface-active arthropods in the savannah, which may be driven by differences in both species richness and the abundance of these functional guilds. Moreover, the present study shows that winter and summer have different species compositions of functional guilds of surface-active arthropods in the savannah. This study shows that changes in temperature that are associated with changes in season may not be significant in driving assemblages of surface-active arthropods during summer and winter in the savannah, which suggests that seasonal changes in temperature affects surface-active arthropods minimally. I argue that other factors, for example, vegetation characteristics that are shaped by season and life history characteristics of the surface-active arthropods, play a primary role in driving assemblages of the functional guilds of surface-active arthropods in the savannah.

Keywords: Arthropods, functional guilds, savannah, season.

3.1. Introduction

Arthropods are the most abundant and diverse group of animals on earth (Stork, 2018), and their diversity and abundance of allow them to drive several vital ecological processes (Pizzolotto et al., 2018; Menta and Remelli, 2020). For example, arthropods have direct and indirect involvement in infiltration and storage of water in the soil, decomposition of dead plant and animal tissues, nutrient cycling, humification, and pest control through biological interactions (Lavelle et al., 2006; Menta and Remelli, 2020). These ecological processes result from arthropods exploiting resources in an ecosystem (McIntyre et al., 2001; Høye and Culler, 2018).

There are two concepts (functional guild and functional group) that help strengthen our understanding of how organisms share and exploit resources to drive ecological processes in an ecosystem (Blondel, 2003). The functional guild concept focuses on the competitive relationships within groups of species, whilst the functional group concept focuses on ecological processes and functions of species in an ecosystem (Fox and Brown, 1995; Blondel, 2003). The two concepts group individuals based on the exploitation of resources and ecological processes or function regardless of the phylogenetic relationships of species (Wilson, 1999).

The type of resources that are shared and exploited similarly define functional guilds (Brussaard, 1998). For example, locusts and leaf-cutter ants use plant foliage and can be placed within the same guild regardless of how they process the resource. Locusts consume leaves directly as food (Shrestha et al., 2021), whilst leaf-cutter ants use the leaves to cultivate a Lepiotaceae fungus, which is food for the ants (Khadempour et al., 2021). The two taxa (locusts and leaf-cutter ants) are in the same guild because they compete for the same resource (leaves) even though they process the resource differently.

On the other hand, functional groups are defined by the ecological process or function and do not consider competition for resources (Fox and Brown, 1995; Wilson, 1999; Blondel, 2003). Some arthropods (for example, bees and butterflies) pollinate plants but do not compete for the same resources. Bees are primary pollinators of fruit crops (Elzay and Baum, 2021), whilst butterflies are primary pollinators of several vegetables and herbs (Andersson et al., 2002). In this example, bees and butterflies can be in one functional group because they perform the same ecological function of pollination, although they do not compete for the same resource.

The use of these functional guilds and groups depends largely on the questions that are being addressed. The present study uses the functional guild approach because it is easy to demonstrate sharing and competition for resources in animal taxa. For example, in arthropods, exploitation of resources by members of the same guild can be demonstrated by using morphological traits that are fundamental for resource acquisition (Wilson, 1999; Blondel, 2003; Cardoso et al., 2011). The arrangement of mouthparts (such as, biting and chewing) is one of the morphological traits used to demonstrate resource sharing in arthropods. The functional guild approach is a starting point for understanding how organisms adapted to a particular set of resources interact with their environment and with each other, making functional guilds fundamental units of any ecosystem (Wilson, 1999; Blondel, 2003).

This study focuses on four groups of surface-active arthropods (that is, ants, beetles, millipedes, and spiders) because they have limited dispersal abilities and are sensitive to changes in their environment (Yekwayo et al., 2018; Mwabvu and Yekwayo, 2020). Therefore, changes in their populations can be linked reliably to changes in their local environment. The sensitivity of surface-active arthropods to modifications in their environment allows for the application of biological knowledge to identify aspects of environmental change responsible for changes in the composition or diversity of these arthropods.

The interaction of these surface-active arthropods with their environment is influenced by the availability of resources (Wolda, 1978; Pinheiro et al., 2002) and climatic conditions in their ecosystem (Logan et al., 1976; Klok and Harrison, 2013; Barahona-Segovia et al., 2019; Tembe and Mukaratirwa, 2020). For example, the seasonality of weather patterns can affect the emergence, growth, dispersal, and reproduction of surface-active arthropods (Pinheiro et al., 2002; Bowie et al., 2014). In southern Africa, millipedes in the Order Spirostreptida are active during the spring – summer months and stay in burrows during the winter period when the climatic conditions are inhospitable (Dangerfield and Telford, 1991; Dangerfield et al., 1992; Minelli, 2011).

In the savannah biome, environmental conditions vary depending on the season (Mucina and Rutherford, 2010; Hutley and Setterfield, 2018). The wet season occurs in summer when temperatures are warm to hot (Lehmann et al., 2014; Hutley and Setterfield, 2018). The dry season is in winter when temperatures are cooler than in summer but relatively warmer than in other biomes such as thicket, grasslands or forests (Mucina and Rutherford, 2010; Lehmann et al., 2014). These seasonal patterns of temperature and precipitation in the savannah modify the physical environment, which causes variation in the availability of resources for plants and animals (Pinheiro et al., 2002; Hutley and Setterfield, 2018). Plants in the savannah biome are more productive in the wet season than in the dry season because the high rainfall and warm temperatures favour their growth (Govender et al., 2006; Beckage et al., 2019). During the wet season, the increased productivity of plants in the savannah increases the availability of resources for surface-active arthropods in lower trophic levels such as detritivores and herbivores (Kwon et al., 2013). As such, the increase in resources may result in the increase in population densities of these arthropods. Moreover, the increased plant productivity has indirect positive effects on carnivorous arthropods because of the increases in prey abundance.

The adaptations of guild members to changing climatic conditions in the savannah depend largely on the physiology and life histories of species (Wolda, 1988; Pinheiro et al., 2002). The mechanisms may include mode of overwintering, rate of development of immature life stages, adult longevity, and the number of broods that guild members produce per year (Pinheiro et al., 2002; Suheriyanto et al., 2019). For example, several species of surface-active arthropods have a period of suspended development when food is scarce and when climatic conditions (such as photoperiod, humidity and precipitation) are inhospitable (Lees, 2016; Saunders, 2020). Thus, surface-active arthropods save energy by reducing their metabolic activity, allowing them to go through seasons with harsh climatic conditions (Kipyatkov, 2001). In the savannah, several spider families, including the Linyphiidae, Araneidae, Lycosidae, Thomisidae and Salticidae, reproduce during the wet season when climatic conditions are favourable to their development and hibernate as eggs or as spiderlings in different instars during the dry season (Schaefer, 1977). These mechanisms create variability in the composition of surface-active arthropods during the wet and dry seasons.

Another major factor contributing to variability in the composition of surface-active arthropods in different seasons is temperature (Logan et al., 1976; Klok and Harrison, 2013). Arthropods are ectothermic and are active within specific temperature ranges depending on the species (Klok and Harrison, 2013). Not only does temperature affect the metabolism of arthropods, but it also influences their daily and seasonal cycles and physiology (Briere et al., 1999). For example, the survival of the forest-dwelling wood ant (*Formica aquilonia*) during diapause is dependant largely on overwintering temperatures (Sorvari et al., 2011). High overwintering temperatures increase metabolic costs by increasing the rate at which the ants consume energy reserves (Sorvari et al., 2011). Lower overwintering temperatures ensure that the ants can go through winter without depleting the body fat content necessary for survival (Sorvari et al., 2011; Berman and Zhigulskaya, 2012). Moreover, leaf beetles (Chrysomelidae) and ground beetles (Carabidae) find shelter under debris, rocks and leaf litter where they overwinter to escape the cold and harsh climatic conditions that come with the dry season (Björkman and Eklund, 2006; Gallé et al., 2018; Pizzolotto et al., 2018; Hoffmann et al., 2021).

Availability of resources and variation in temperature are among significant factors that influence the activity of surface-active arthropods (Pinheiro et al., 2002; Suheriyanto et al., 2019). Other factors that may affect the activity of surface-active arthropods include soil moisture and vegetation structure, rate of parasitism, rate of predation and the number of pathogens present in the environment (Briere et al., 1999; Pinheiro et al., 2002; Silveira et al., 2010; Bowie et al., 2014). These factors differ during the wet and dry seasons (Pinheiro et al., 2002; Tembe and Mukaratirwa, 2020). The seasonality of these factors can affect how arthropods are distributed in their ecosystem and how abundant these arthropods are during a particular season. For example, *Gonimbrasia belina*, a species of emperor moth native to low-lying areas in the savannah of southern Africa, is active in a larval form (mopane worm) during summer months and burrows into the ground where it overwinters as a pupa during the dry season (Klok and Chown, 1999; Stack et al., 2003). Burrowing assists *G. belina* in escaping pathogens, predators and hiding from different fly and parasitic wasp species (Gaston et al., 1997; Frears et al., 1999; Klok and Chown, 1999).

Factors that influence the activity of surface-active arthropods in different seasons are complex and interconnected (Pinheiro et al., 2002; Anjos et al., 2016; Tembe and Mukaratirwa, 2020), making it difficult to separate and test these factors independently. Several studies have investigated the effect of season on arthropod activity and abundance (Pinheiro et al., 2002; Suheriyanto et al., 2019; Marquart et al., 2020; Hoffmann et al., 2021). However, not much work has been carried out on how different seasons affect functional guilds of arthropods. Therefore, more research is needed to deepen our understanding of the impact that climatic and environmental variables have on the activity and spatiotemporal distribution of functional guilds of arthropods. This study investigated the effect of season on the species richness, abundance of species and species composition of functional guilds of four groups of surface-active arthropods (ants, beetles, millipedes, and spiders) in the savannah biome of the Mpumalanga province, South Africa.

3.2. Materials and Methods

3.2.1. Study sites

The study was conducted in Barberton Nature Reserve in the lowveld of Mpumalanga province of South Africa (Fig. 3.1). Ten study sites, at least 300 m apart, were selected randomly in the 27 541-ha nature reserve. These study sites have an elevation ranging from 693 – 788 m above sea level. Barberton Nature Reserve (BNR) occurs in an area that experiences moderate rainfall (600 – 700 mm), wet summer (December – February) and dry winter (June – August) periods (Mucina and Rutherford, 2010; ARC–ISCW, 2019). In summer, temperatures in Barberton range from 13 − 40ºC, while in winter, they range from 2 − 35ºC (ARC–ISCW, 2019).

The Kaapvaal Craton, one of the oldest and most intensely studied Archean rocks in the world, is the primary underlying rock of the Barberton area (Poujol et al., 2003). The Barberton Nature Reserve is part of the Barberton Makhonjwa Mountains UNESCO World Heritage Site, which contains 40% of the Barberton Greenstone Belt (Shah et al., 2018; Oosthuizen, 2020), and falls within the Barberton Centre of Plant Endemism where 80 of the 2 200 plant species are endemic (Williamson and Balkwill, 2015; Oosthuizen, 2020). The area includes outcrops of serpentine rocks of the Barberton Greenstone Belt and surrounding non-serpentine areas (Mucina and Rutherford, 2010; Williamson and Balkwill, 2015). Soils derived from the serpentine rock outcrops are characterised by low calcium to magnesium ratio, low overall nutrient content compared with surrounding non-serpentine soils, high nickel and chromium toxicity and low water retention capacity (Roberts and Proctor, 1992; Williamson and Balkwill, 2006).

The vegetation in BNR can be described as Legogote Sour Bushveld, with elements of the Barberton Serpentine Sourveld (Mucina and Rutherford, 2010). Some of the woody plant species that I observed at BNR include *Grewia occidentalis* L. (Malvaceae), *Olea europaea* subsp. *africana* Mill. (Oleaceae), *Ruttya ovata* Harv. (Acanthaceae), *Vachellia nilotica* (L.) P. Hurter & Mabb (Fabaceae), *Diospyros* spp. (Ebenaceae), *Euclea* spp. (Ebenaceae) and *Ximenia* spp. (Olacaceae). The grass layer was composed mainly of *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult., *Panicum maximum* Jacq., and *Hyparrhenia hirta* (L.) Stapf.

3.2.2. Data collection procedure

The study was conducted during the wet (December 2018 – February 2019) and dry seasons (June 2019 – August 2019). The pitfall trapping method (Samways et al., 2010) was used because pitfalls are quick to install and sample continually, requiring periodic emptying only and thus cost-effective (Leather, 2005; Samways et al., 2010). Moreover, the pitfall traps allow large numbers of surface-active arthropods to be caught with minimal effort (Leather, 2005). Pitfall traps in this study were open-top cylindrical plastic jars of 6 cm in diameter and 13.5 cm in depth.

Pitfall traps were quarter filled with 50% ethylene glycol and inserted into the soil with the rim of the jar level with the soil surface to ensure that the surface-active arthropods do not encounter a vertical barrier before potentially falling into the trap. Each site was a 10 x 10 m plot with six pitfall traps installed at each corner, giving a sum of 24 traps per site. The pitfall traps installed at each corner were approximately 2 m apart in a 3 x 2 grid pattern.

At each site, traps were set and emptied after six days (sampling time). The procedure was carried out four times at each site during each of the sampling periods (wet and dry seasons). There was no rest between each sampling time and the next, pitfall trapping was conducted continually. After emptying each trap, contents from the pitfall traps were washed with tap water to remove ethylene glycol, after which the samples were preserved in absolute alcohol. Contents of all the 24 pitfall traps from each site were amalgamated to form one sample, which reduces digging-in effects (Samways et al., 2010) and also removes catch differences resulting from the spatial arrangement of pitfall traps in each site.

Arthropods were sorted into morpho-species and later identified into family or genus where possible and then assigned into functional guilds. The method of resource acquisition by the surface-active arthropods was used to allocate the surface-active arthropods into different functional guilds. The functional guilds to which the surface-active arthropods were assigned included carnivores, detritivores and herbivores. In addition, because all the surface-active arthropods were identified to either family or genus, it was not feasible to allocate guilds to some morpho-species that belonged to taxonomic units (that is, family or genus) that have diverse modes of resource acquisition. As such, I erected a fourth functional guild, the "diverse functional guild", which had arthropods that have diverse diets.

3.2.3. Data analysis

Samples from the four sampling intervals during each season of sampling were pooled for each site before analysis to obtain a more precise estimate of the assemblage indices. Species abundance and richness of carnivores, herbivores, detritivores, and diverse functional guilds of arthropods were determined in R (R Core Team, 2021) using the generalised linear mixed models (GLMMs) and linear mixed models (LMMs). The *lme4* package (Bates et al., 2015) was used for the GLMMs and LMMs. The Shapiro-Wilk test and quantile-quantile plots were used to test for the normality of the data. The data on species richness and abundance of carnivores, detritivores, and herbivores were not normally distributed; as such, GLMMs with a Poisson distribution were used. Season was used as a fixed factor, and site was used as a random factor in the species richness and abundance models of carnivores, herbivores, and detritivores. Data sets of species richness and abundance of diverse functional guilds were normally distributed. As such, LMMs were used to determine species richness and abundance of diverse functional guilds and in both the models (species richness and abundance); season was used as a fixed factor while elevation was a random factor. The log-link function was used for the GLMMs with Poisson distribution, and the identity link function was used for the LMMs.

The *mvabund* package (Wang et al., 2012) was used to determine the species composition of carnivores, herbivores, detritivores, and diverse functional guilds. The *mvabund* package contains functions for analysing ecological multivariate data. The function manyglm found in the *mvabund* package was used to fit generalised linear models (GLMs) with negative binomial distribution to determine the species composition of carnivores, herbivores, detritivores, and diverse functional guilds. The log-link function was used for the GLMs with the negative binomial distribution. Season was used as a fixed factor, and the total abundance of arthropods by species in each site per season was used as a random factor. The distribution specified for each dependent variable investigated is the one that provided the best goodness of fit model.

3.3. Results

3.3.1. Species richness, abundance and composition of carnivores

A total of 9 983 carnivores belonging to spiders, beetles, and ants from 36 families with 320 morpho-species were recorded in the study. Spiders (262 morpho-species) had the highest species richness, followed by beetles (30 morpho-species), while ants (28 morpho-species) had the lowest species richness. Ants (6 082 specimens) were the most abundant taxon, followed by spiders (3460 specimens), while beetles (441 specimens) were the least abundant. There was a significant difference in species richness, abundance, and composition of carnivores between summer and winter, with higher species richness and abundance in summer than in winter (Table 3.1; Figs 3.2a and 3.3a).

3.3.2. Species richness, abundance and composition of detritivores

In total, 5 071 detritivores belonging to ants, beetles, and millipedes from 11 families with 71 morpho-species were collected. Beetles (55 morpho-species) had the highest species richness, while ants and millipedes had the lowest species richness with eight morpho-species each. The most abundant taxon was ants (3 588 specimens), followed by beetles (1 381 specimens), and the least abundant were millipedes (102 specimens). The species richness and composition of detritivores differed significantly between summer and winter; however, the species abundance was similar (Table 3.1; Fig. 3.3b). Species richness of detritivores was higher in summer than in winter (Fig. 3.2b).

3.3.3. Species richness, abundance and composition of herbivores

A total of 389 specimens of herbivores belonging to six families with 47 morpho-species of beetles were collected in this study. Chrysomelidae (21 morpho-species) and Curculionidae (14 morpho-species) had the highest species richness. Families with the lowest species richness were Meloidae (two morpho-species), followed by Mordellidae (three morpho-species), Buprestidae (three morpho-species), and Elateridae (four morpho-species). Chrysomelidae (236 specimens) and Curculionidae (54 specimens) were the most abundant families, while Meloidae (three specimens) and Mordellidae (13 specimens) were the least abundant. Species richness, abundance, and composition of herbivores were significantly different between summer and winter, with higher species richness and abundance in summer than in winter (Table 3.1; Figs 3.2c and 3.3c).

3.3.4. Species richness, abundance and composition of diverse functional guilds

In total, 7 121 specimens belonging to ants and beetles from nine families with 87 morpho-species were allocated to the diverse functional guilds. The Formicidae (59 morpho-species) and Tenebrionidae (12 morpho-species) had the highest species richness, while the Silvanidae, Anthribidae, Discolomatidae, and Lampyridae had the lowest species richness with one morpho-species each. The Formicidae (6 935 specimens) and Tenebrionidae (136 specimens) were the most abundant families. The least abundant families were the Anthribidae (one specimen), followed by the Lampyridae and Melandryidae, with two specimens each.

There were significant differences in the species richness and composition of diverse functional guilds between summer and winter, with higher species richness in summer than in winter (Table 3.1; Fig. 3.2d). Species abundance of the diverse functional guilds was similar between summer and winter (Table 3.1; Fig. 3.3d).

3.4. Discussion

The present study found that the species richness and composition of all the functional guilds of arthropods differed between summer and winter, with high species richness in summer. These results may be explained by the resource-ratio hypothesis, which suggests that species with low resource requirements will outcompete other species when the resources are limited, resulting in a reduction of the number of species in a community (Tilman, 1985). During winter in the savannah, plants become less productive than in summer (Hutley and Setterfield, 2018), which reduces resources available to arthropods at lower trophic levels, such as herbivores (Pinheiro et al., 2002; Anjos et al., 2016; de Oliveira et al., 2021). The reduction of the abundance of arthropods at lower trophic levels due to a reduction in their resources may have a negative effect on other arthropods such as carnivores. These bottom-up effects of plants on arthropod communities have been shown to influence assemblages of arthropods positively (for example, Sobek et al., 2009; Haddad et al., 2011; de Araújo, 2013). In particular, Forkner and Hunter (2000) found that the bottom-up effects of plants on arthropods have a positive relationship with arthropod assemblages in vegetation dominated by oak trees in Whitehall Forest, United States. Moreover, Vaca-Sánchez et al. (2021) found that canopy arthropods are more diverse and abundant in diverse *Quercus* forests (which provide greater resources, niches, and microenvironments for the arthropods) than in less diverse *Quercus* forests; suggesting that the availability of resources is a significant factor in shaping the assemblages of functional guilds of arthropods.

Additionally, the results from the present study may be explained partly by the life history strategies that arthropods use to cope with changing climatic conditions that are associated with changes in seasons. For example, some species of arthropods have a period of suspended development when climatic conditions are inhospitable (Sorvari et al., 2011; Berman and Zhigulskaya, 2012; Saunders, 2020). Furthermore, some arthropods overwinter as different instars when environmental conditions are unfavourable (Schaefer, 1977; Lees, 2016). In particular, *Pardosa agrestis* (Lycosidae) and *Pardosa hortensis* (Lycosidae) reach high densities and reproduce in the spring – summer months, with their spiderlings overwintering as different instars during the dry season (autumn – winter) (Kiss and Samu, 2002). Moreover, Jaskuła and Soszyńska-Ma (2011) noted that the activity of ground beetles in central and northern Europe decreases towards the end of autumn, is lowest in the middle of winter, and increases in spring. These life-history characteristics could contribute to fluctuations in species richness, the abundance of species and species composition of arthropods in different seasons. In the present study, I sampled the surface-active arthropods in one summer and one winter. Therefore, the results of this study should be interpreted with caution due to the lack of replication of the seasons.

The fluctuation of arthropod assemblages associated with changes in seasons has been well studied (for example, Pinheiro et al., 2002; Silveira et al., 2012; Anjos et al., 2016; Tembe and Mukaratirwa, 2020; de Oliveira et al., 2021). However, most research has focused on a few functional guilds without studying the response of arthropod functional guilds to season at a community level. Moreover, there are potential problems associated with definitions in the field of functional ecology. For example, some consider a functional guild to be a group of organisms with similar growth, reproductive and metabolic characteristics, and perform the same ecological function (for example, Bongers and Bongers, 1998; Ferris et al., 2001), while some use the method of resource acquisition to categorise organisms into functional guilds (for example, Blondel, 2003; Melliger et al., 2018). In particular, Cardoso et al. (2011) categorised spiders into different guilds, including sensing, sheet, space, orb-web weavers, ambush, and ground hunters; while Schmitz and Suttle (2001) used mechanistic details about the effects of each species on the food web, resulting in functional guilds made up of "sit-and-wait", "sit-and-pursue" and "actively-hunting" spiders.

I found a higher abundance of herbivores and carnivores in summer than in winter. The fluctuation in the abundance of herbivorous and carnivorous arthropods between seasons may be related to the fluctuation in resources associated with the changes in seasons (Bowie et al., 2014; de Oliveira et al., 2021). The savannah has an austral summer when plants are productive and resources become abundant for herbivores, while the winter occurs in the dry season when plants are not as productive as in summer and resources are less abundant (Mucina and Rutherford, 2010; Hutley and Setterfield, 2018). The higher abundance of herbivorous arthropods in summer than in winter in this study may be supported by some previous experimental evidence, which indicates that vegetation has profound effects on the assemblages of arthropods at lower trophic levels. For example, Ebeling et al. (2018) found that vegetation-associated arthropods (such as herbivores) respond more strongly to changes in vegetation than other arthropod functional guilds at the Jena biodiversity experimental plots in Germany. As such, I argue that in the present study, the changes in the abundance of herbivorous arthropods between summer and winter are associated strongly with changes in vegetation that are linked to changes in season.

Detritivores and arthropods with diverse feeding habits ("diverse functional guild") had similar abundances in winter and summer. I suspect that the similarities in the abundance of detritivorous arthropods may have been due to little fluctuations in their resources, as suggested by the resource-ratio hypothesis (Tilman, 1985). Detritivorous arthropods feed on detritus (for example, bodies or fragments of bodies of dead organisms and faecal material) which is available throughout the year under different environmental conditions (Davidson and Groner, 2021; Sagi and Hawlena, 2021), and therefore, the resources were not a limiting factor for the detritivorous arthropods because they were available throughout the two sampling periods (summer and winter). Similarities in the "diverse functional guild" may have been due to the lumping of some taxa to form one functional guild. For example, the inclusion of flexible feeders in the guild, which can change the mode of resource acquisition (predation or scavenging) depending on the availability of food, which is also influenced by season (Marquart et al., 2020). These flexible feeders may essentially respond like detritivores because just like detritivorous arthropods, the flexible feeders may not be limited by the availability of food.

Moreover, the similarities in the abundance of species coupled with differences in species composition of detritivorous arthropods and the "diverse functional guild" may have been driven by seasonal shifts in the abundance of constituent groups. As environmental conditions change because of changes in season, some arthropods might decrease in abundance in summer while others decrease in abundance during winter, resulting in a seasonal niche differentiation with the overall effect being neutral for their abundance of species (Pinheiro et al., 2002). For example, within the guild of detritivorous arthropods in the present study, the Spirostreptidae, Harpagophoridae and Odontopygidae were recorded in summer only, while the *Pheidole* spp. doubled in abundance during winter. The change in the abundance of the Spirostreptidae, Harpagophoridae and Odontopygidae may have been influenced by soil moisture (Dangerfield et al., 1992; Minelli, 2011; Joly et al., 2021) associated with variation in rainfall between the dry and wet season (ARC–ISCW, 2019). The greater abundance of the *Pheidole* spp. in summer than in winter may have been due to variation in their colony sizes associated with variation in their brood sizes in different seasons (Murdock and Tschinkel, 2015). In particular, Shukla and Rastogi (2012) found that the colony sizes of *Pheidole* spp. was significantly greater in winter than in summer and was positively associated with brood size, in their study in India.

Changes in seasons are often coupled with significant changes in temperature (Elsen et al., 2021). However, the area where sites for the present study were located had little variation in temperature during summer and winter (ARC–ISCW, 2019). As such, the present study is pointing towards the significance of other environmental factors, for example, vegetation characteristics that are shaped by changes in season (Hutley and Setterfield, 2018), variation in soil moisture (Dangerfield and Telford, 1991), and variation in photoperiod (Saunders, 2020) during different seasons. These environmental factors may be responsible for the observed variations in the species richness, the abundance of species, and species composition of some functional guilds of surface-active arthropods between winter and summer. In particular, short-day length, which characterises the end of summer and beginning of autumn triggers diapause in arthropods such as mosquitoes (Peffers et al., 2021), suggesting that arthropod assemblages could be affected by other environmental factors that are associated with changes in season, even when resources are not limited.

Moreover, the idea that photoperiod may have significant effects on arthropods is supported by some previous experimental evidence. For example, Lone et al. (2011) found that *Camponotus paria* (Formicidae), develops faster from larval to adult stage under long days in an experimental trial with varying photo-phases in Bangalore, India. Therefore, *C. paria* is likely to reach greater abundances in summer when days are longer because of long-day lengths, which favour their faster development, which will likely affect guild composition positively. As such, I argue that variation in photoperiod because of change in seasons, combined with other environmental factors, excluding temperature variation, could have played a significant role in the variation of assemblages of the functional guilds of surface-active arthropods between summer and winter in this study.

3.5. Conclusion

In this study, I demonstrate that the factors affecting the changes in abundance, species richness, and species composition of assemblages of functional guilds of surface-active arthropods during summer and winter in the savannah are complex and interconnected and may be explained by multiple hypotheses. The present study highlights a potential link between the assemblages of herbivorous and carnivorous functional guilds of arthropods in the savannah, which is supported by several studies in other ecosystems (for example, Haddad et al., 2011; Ebeling et al., 2018; Koricheva and Hayes, 2018; Vaca-Sánchez et al., 2021). I show that changes in season are associated with changes in the species richness, abundance of species and species composition of some surface-active arthropod functional guilds in the savannah. In addition, this study suggests that temperature might not play a significant role in the fluctuation of the assemblages of functional guilds of surface-active arthropods during summer and winter. As such, other environmental factors that are associated with changes in seasons may be the significant driving forces of the fluctuation of assemblages of the functional guilds of surface-active arthropods in the savannah. However, results from the present study should be interpreted with caution due to the lack of replication of seasons.

3.6. References

Andersson, S., Nilsson, L.A., Groth, I., Bergström, G., 2002. Floral scents in butterfly-pollinated plants: possible convergence in chemical composition. Botanical Journal of the Linnean Society 140, 129–153.

Anjos, D., Alves-Silva, E., Ribeiro, S.P., 2016. Do fire and seasonality affect the establishment and colonisation of litter arthropods? Journal of Insect Conservation 20, 653–661.

ARC–ISCW, 2019. Water and climate data (unpublished). In: Agricultural Research Council (ARC) Institute for Soil Climate and Water (ISCW) (Ed.). Agro-climatology division, Stellenbosch, South Africa.

Barahona-Segovia, R.M., Crespin, S.J., Grez, A.A., Veloso, C., 2019. Anthropogenic thermal gradient in managed landscapes determines physiological performance and explains the edge-biased distribution of ectothermic arthropods. Forest Ecology and Management 440, 147–157.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67, 1–48.

Beckage, B., Bucini, G., Gross, L.J., Platt, W.J., Higgins, S.I., Fowler, N.L., Slocum, M.G., Farrior, C., 2019. Water Limitation, Fire, and Savanna Persistence. In: Savanna Woody Plants and Large Herbivores (eds P.F. Scogings and M. Sankaran). John Wiley and Sons, New Jersey.

Berman, D., Zhigulskaya, Z., 2012. Preadaptation of *Formica aquilonia* and *Formica lugubris* ants (Hymenoptera, Formicidae) to low wintering temperatures in Northeast Asia. Entomological Review 92, 487–496.

Björkman, C., Eklund, K., 2006. Factors affecting willow leaf beetles (*Phratora vulgatissima*) when selecting overwintering sites. Agricultural and Forest Entomology 8, 97–112.

Blondel, J., 2003. Guilds or functional groups: does it matter? Oikos 100, 223–231.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Applied Soil Ecology 10, 239–251.

Bowie, M., Klimaszewski, J., Vink, C., Hodge, S., Wratten, S., 2014. Effect of boundary type and season on predatory arthropods associated with field margins on New Zealand farmland. New Zealand Journal of Zoology 41, 268–284.

Briere, J.F., Pracros, P., Le Roux, A.Y., Pierre, J.S, 1999. A novel rate model of temperature-dependent development for arthropods. Environmental Entomology 28, 22–29.

Brussaard, L., 1998. Soil fauna, guilds, functional groups and ecosystem processes. Applied Soil Ecology 9, 123–135.

Cardoso, P., Pekár, S., Jocqué, R., Coddington, J.A., 2011. Global patterns of guild composition and functional diversity of spiders. PLoS One 6, e21710. https://doi.org/10.1371/journal.pone.0021710

Dangerfield, J.M., Milner, A.E., Matthews, R., 1992. Seasonal activity patterns and behaviour of juliform millipedes in south-eastern Botswana. Journal of Tropical Ecology 8, 451–464.

Dangerfield, J.M., Telford, S.R., 1991. Seasonal activity patterns of Julid millipedes in Zimbabwe. Journal of Tropical Ecology 7, 281–285.

Davidson, B., Groner, E., 2021. An arthropod community beyond the dry limit of plant life. Journal of Arid Land 13, 629–638.

de Araújo, W.S., 2013. Different relationships between galling and non-galling herbivore richness and plant species richness: a meta-analysis. Arthropod-Plant Interactions 7, 373–377.

de Oliveira, C.P., de Oliveira, C.M, Specht, A., Frizzas, M.R., 2021. Seasonality and distribution of Coleoptera families (Arthropoda, Insecta) in the Cerrado of Central Brazil. Revista Brasileira de Entomologia 65. https://doi.org/10.1590/1806-9665-RBENT-2021-0025

Ebeling, A., Hines, J., Hertzog, L.R., Lange, M., Meyer, S.T., Simons, N.K., Weisser, W.W., 2018. Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. Basic and Applied Ecology 26, 50–63.

Elsen, P.R., Farwell, L.S., Pidgeon, A.M., Radeloff, V.C., 2021. Contrasting seasonal patterns of relative temperature and thermal heterogeneity and their influence on breeding and winter bird richness patterns across the conterminous United States. Ecography 44, 953–965.

Elzay, S.D., Baum, K.A., 2021. Landscape characteristics predict body sizes in wild bees: implications for pollination services and foraging range. Journal of Insect Conservation 25, 243–253.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Applied Soil Ecology 18, 13–29.

Forkner, R.E., Hunter, M.D., 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. Ecology 81, 1588–1600.

Fox, B.J., Brown, J.H., 1995. Reaffirming the validity of the assembly rule for functional groups or guilds: a reply to Wilson. Oikos 73, 125–132.

Frears, S.L., Chown, S.L., Webb, P.I., 1999. Temperature dependence of feeding behaviour in the mopane worm (Lepidoptera). Journal of Thermal Biology 24, 241–244.

Gallé, R., Császár, P., Makra, T., Gallé-Szpisjak, N., Ladányi, Z., Torma, A., Ingle, K., Szilassi, P., 2018. Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites. Landscape Ecology 33, 1435–1446.

Gaston, K.J., Chown, S., Styles, C., 1997. Changing size and changing enemies: the case of the mopane worm. Acta Oecologica 18, 21–26.

Govender, N., Trollope, W.S., Van Wilgen, B.W., 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. Journal of Applied Ecology 43, 748–758.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Tilman, D., 2011. Plant diversity and the stability of food webs. Ecology Letters 14, 42–46.

Hoffmann, H., Peter, F., Herrmann, J.D., Donath, T.W., Diekötter, T., 2021. Benefits of wildflower areas as overwintering habitats for ground-dwelling arthropods depend on landscape structural complexity. Agriculture, Ecosystems and Environment 314, 107421. https://doi.org/10.1016/j.agee.2021.107421

Høye, T.T., Culler, L.E., 2018. Tundra arthropods provide key insights into ecological responses to environmental change. Polar Biology 41, 1523–1529.

Hutley, L.B., Setterfield, S.A., 2018. Savanna. In: Fath, B. (Ed.), Encyclopedia of Ecology, 2nd ed. Elsevier BV, Oxford, pp. 623–633.

Jaskuła, R., Soszyńska-Maj, A., 2011. What do we know about winter active ground beetles (Coleoptera, Carabidae) in central and northern Europe? Zoo Keys, 517–532.

Joly, F.X., McAvoy, E., Subke, J.A., 2021. Synergistic interactions between detritivores disappear under reduced rainfall. Ecology 102, e03299. https://doi.org/10.1002/ecy.3299

Khadempour, L., Kyle, J.E., Webb-Robertson, B.-J.M., Nicora, C.D., Smith, F.B., Smith, R.D., Lipton, M.S., Currie, C.R., Baker, E.S., Burnum-Johnson, K.E., 2021. From plants to ants: Fungal modification of leaf lipids for nutrition and communication in the leaf-cutter ant fungal garden ecosystem. mSystems 6, e01307–20

Kipyatkov, V.E., 2001. Seasonal life cycles and the forms of dormancy in ants (Hymenoptera: Formicoidea). Acta Societatis Zoologicae Bohemicae 65, 211–238.

Kiss, B., Samu, F., 2002. Comparison of autumn and winter development of two wolf spider species (Pardosa, Lycosidae, Araneae) having different life-history patterns. Journal of Arachnology 30, 409–415.

Klok, C., Chown, S., 1999. Assessing the benefits of aggregation: thermal biology and water relations of anomalous emperor moth caterpillars. Functional Ecology 13, 417–427.

Klok, C.J., Harrison, J.F., 2013. The temperature size rule in arthropods: independent of macro-environmental variables but size-dependent. Integrative and Comparative Biology 53, 557–570.

Koricheva, J., Hayes, D., 2018. The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. Functional Ecology 32, 1704–1717.

Kwon, T.-S., Park, Y.K., Lim, J.-H., Ryou, S.H., Lee, C.M., 2013. Change of arthropod abundance in burned forests: Different patterns according to functional guilds. Journal of Asia-Pacific Entomology 16, 321–328.

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

Leather, S.R., 2005. Pitfall trapping in ecological studies. In: Lawton, J.H., Likens, G.E. (Eds.), Insect Sampling in Forest Ecosystems. Blackwell Publishing, Oxford. pp. 37–57.

Lees, A.D., 2016. The Physiology of Diapause in Arthropods. Cambridge University Press, Cambridge.

Lehmann, C.E., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J., 2014. Savanna vegetation-fire-climate relationships differ among continents. Science 343, 548–552.

Logan, J., Wollkind, D., Hoyt, S., Tanigoshi, L., 1976. An analytic model for description of temperature-dependent rate phenomena in arthropods. Environmental Entomology 5, 1133–1140.

Lone, S.R., Ilangovan, V., Murugan, M., Sharma, V.K., 2011. Short- and long-day responses in the pre-adult developmental duration of two species of Camponotus ants. Chronobiology International 28, 163–169.

Marquart, A., Geissler, K., Heblach, J., Lobas, C., Münch, E., Blaum, N., 2020. Individual shrubs, large scale grass cover and seasonal rainfall explain invertebrate-derived macropore density in a semi-arid Namibian savanna. Journal of Arid Environments 176, 104101. https://doi.org/10.1016/j.jaridenv.2020.104101

McIntyre, N.E., Rango, J., Fagan, W.F., Faeth, S.H., 2001. Ground arthropod community structure in a heterogeneous urban environment. Landscape and Urban Planning 52, 257–274.

Melliger, R.L., Braschler, B., Rusterholz, H.P., Baur, B., 2018. Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. PLoS One 13, e0199245 https://doi.org/10.1371/journal.pone.0199245

Menta, C., Remelli, S., 2020. Soil health and arthropods: from complex system to worthwhile investigation. Insects 11, 54. https://doi.org/10.3390/insects11010054

Minelli, A., (ed) 2011. The Myriapoda: treatise on zoology-anatomy, taxonomy, biology. Brill Publishers, Leiden.

Mucina, L., Rutherford, M.C., (eds) 2010. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Murdock, T., Tschinkel, W., 2015. The life history and seasonal cycle of the ant, *Pheidole morrisi* Forel, as revealed by wax casting. Insectes Sociaux 62, 265–280.

Mwabvu, T., Yekwayo, I., 2020. A checklist of ants (Formicidae), spiders (Araneae) and millipedes (Spirostreptida) of the savannah in Mpumalanga province, South Africa. African Journal of Ecology 58, 138–144

Oosthuizen, N., 2020. Mountainlands Nature Reserve. Creative Africa Media, South Africa. Available from: https://www.mountainlands.co.za/plantlife/ (accessed 23 February 2020)

Peffers, C.S., Pomeroy, L.W., Meuti, M.E., 2021. Critical photoperiod and its potential to predict mosquito distributions and control medically important pests. Journal of Medical Entomology 58, 1610–1618.

Pinheiro, F., Diniz, I., Coelho, D., Bandeira, M., 2002. Seasonal pattern of insect abundance in the Brazilian cerrado. Austral Ecology 27, 132–136.

Pizzolotto, R., Mazzei, A., Bonacci, T., Scalercio, S., Iannotta, N., Brandmayr, P., 2018. Ground beetles in Mediterranean olive agroecosystems: Their significance and functional role as bioindicators (Coleoptera, Carabidae). PLoS One 13, e0194551. https://doi.org/10.1371/journal.pone.0194551

Poujol, M., Robb, L., Anhaeusser, C., Gericke, B., 2003. A review of the geochronological constraints on the evolution of the Kaapvaal Craton, South Africa. Precambrian Research 127, 181–213.

R Core Team, 2021. R: A Language and Environment for Statistical Computing, version 4.0.5 ed. R Foundation for Statistical Computing, Vienna

Roberts, B., Proctor, J., (eds) 1992. The ecology of areas with serpentinised rocks: a world view. Kluwer Academic Publishers, Amsterdam.

Sagi, N., Hawlena, D., 2021. Arthropods as the engine of nutrient cycling in arid ecosystems. Insects 12, 726. https://doi.org/10.3390/insects12080726

Samways, M.J., McGeoch, M.A., New, T.R., 2010. Insect conservation: a handbook of approaches and methods. Oxford University Press, New York, United States.

Saunders, D.S., 2020. Dormancy, diapause, and the role of the circadian system in insect photoperiodism. Annual Review of Entomology 65, 373–389.

Schaefer, M., 1977. Winter ecology of spiders (Araneida). Zeitschrift für Angewandte Entomologie 83, 113–134.

Schmitz, O.J., Suttle, K.B., 2001. Effects of top predator species on direct and indirect interactions in a food web. Ecology 82, 2072–2081.

Shah, T., Burrows, J., Darbyshire, I., 2018. A new species of Ochna (Ochnaceae) from the Barberton Mountains of Mpumalanga, South Africa. Phytotaxa 374, 241–248.

Shrestha, S., Thakur, G., Gautam, J., Acharya, N., Pandey, M., Shrestha, J., 2021. Desert locust and its management in Nepal: a review. Journal of Agriculture and Natural Resources 4, 1–28.

Shukla, R., Rastogi, N., 2012. Seasonal variation in the population structure of the dimorphic ant, *Pheidole* spp. (Hymenoptera: Formicidae) colonies. Journal of Experimental Zoology, India 15, 227–231.

Silveira, J.M., Barlow, J., Andrade, R.B., Mestre, L.A., Lacau, S., Cochrane, M.A., 2012. Responses of leaf-litter ant communities to tropical forest wildfires vary with season. Journal of Tropical Ecology 28, 515–518.

Silveira, J.M., Barlow, J., Louzada, J., Moutinho, P., 2010. Factors affecting the abundance of leaf-litter arthropods in unburned and thrice-burned seasonally-dry Amazonian forests. PLoS One 5, e12877. https://doi.org/10.1371/journal.pone.0012877

Sobek, S., Scherber, C., Steffan-Dewenter, I., Tscharntke, T., 2009. Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. Oecologia 160, 279–288.

Sorvari, J., Haatanen, M.K., Vesterlund, S.R., 2011. Combined effects of overwintering temperature and habitat degradation on the survival of boreal wood ant. Journal of Insect Conservation 15, 727–731.

Stack, J., Dorward, A., Gondo, T., Frost, P., Taylor, F., Kurebgaseka, N., 2003. Mopane worm utilisation and rural livelihoods in southern Africa. In: International Conference on Rural Livelihoods, Forests and Biodiversity, Bonn, Germany. pp. 19–23.

Stork, N.E., 2018. How many species of insects and other terrestrial arthropods are there on earth? Annual Review of Entomology 63, 31–45.

Suheriyanto, D., Soemarno, S., Yanuwiadi, B., Leksono, A.S., Prasetiyo, D.H., Permana, S.R., 2019. Effects of season on abundance and diversity of soil arthropods in Mangli Coffee Plantation Kediri Regency, East Java, Indonesia. International Journal of Engineering and Technology 8, 131–135.

Tembe, D., Mukaratirwa, S., 2020. Forensic entomology research and application in southern Africa: A scoping review. South African Journal of Science 116, 1–8.

Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist 125, 827–852.

Vaca-Sánchez, M.S., Maldonado-López, Y., González-Rodríguez, A., Oyama, K., Fernandes, G.W., Fagundes, M., López-Barbosa, E.C., Aguilar-Peralta, J.S., Cuevas-Reyes, P., 2021. Canopy arthropod diversity associated with *Quercus laurina*: importance of an oak species diversity gradient on abundance, species richness and guild composition. Journal of Insect Conservation. https://doi.org/10.1007/s10841-021-00352-5

Wang, Y., Naumann, U., Wright, S., Warton, D., 2012. mvabund: an R package for model-based analysis of multivariate data. Methods in Ecology and Evolution 3, 471–474.

Williamson, S., Balkwill, K., 2006. Factors determining levels of threat to serpentine endemics. South African Journal of Botany 72, 619–626.

Williamson, S., Balkwill, K., 2015. Plant census and floristic analysis of selected serpentine outcrops of the Barberton Greenstone Belt, Mpumalanga, South Africa. South African Journal of Botany 97, 133–142.

Wilson, J.B., 1999. Guilds, functional types and ecological groups. Oikos 86, 507–522.

Wolda, H., 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. The Journal of Animal Ecology 47, 369–381.

Wolda, H., 1988. Insect seasonality: why? Annual Review of Ecology and Systematics 19, 1–18.

Yekwayo, I., Pryke, J.S., Gaigher, R., Samways, M.J., 2018. Only multi-taxon studies show the full range of arthropod responses to fire. PLoS One 13, e0195414. https://doi.org/10.1371/journal.pone.0195414

3.7. Tables

Table 3.1. Species richness, abundance, and composition of arthropod groups categorised as carnivores, detritivores, herbivores, and diverse functional guild in summer and winter in the savannah at Barberton Nature Reserve. Significant p-values are shown in bold.

	Carnivores			**Detritivores**			**Herbivores**			**Diverse functional guild**		
	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
Species richness	28.819	1	**<0.001**	27.966	1	**<0.001**	34.529	1	**<0.001**	6.852	1	**0.009**
Species abundance	25.614	1	**<0.001**	0.031	1	0.861	33.652	1	**<0.001**	0.819	1	0.366
	Deviance	Error df	*P*	Deviance	Error df	*P*	Deviance	Error df	*P*	Deviance	Error df	*P*
Species composition	994.5	18	**<0.001**	327.8	18	**<0.001**	99.05	18	**<0.001**	463	18	**<0.001**

3.8. Figures

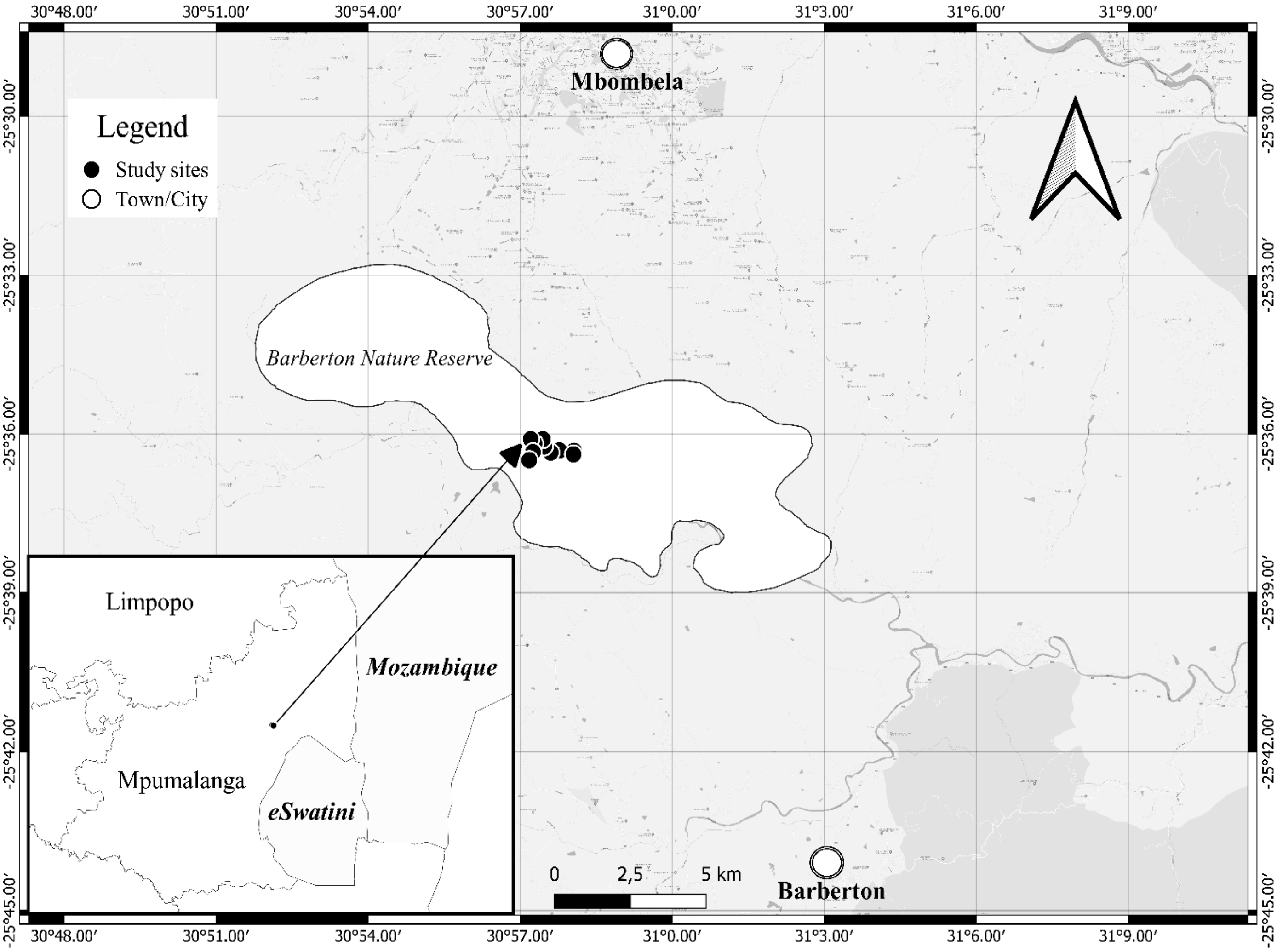

Fig. 3.1. Location of the study sites in Barberton Nature Reserve in Mpumalanga province of South Africa.

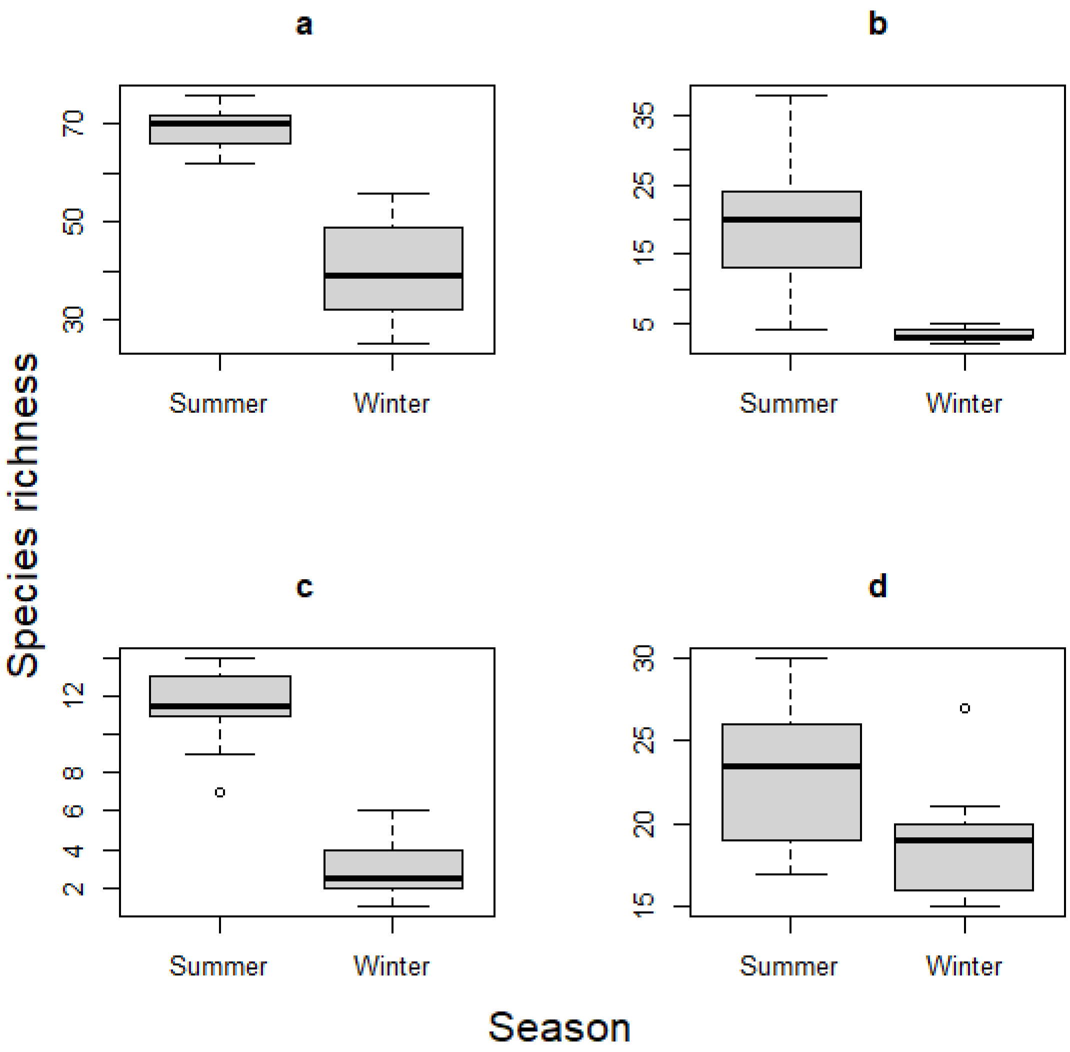

Fig. 3.2. Species richness of **a)** carnivores, **b)** detritivores, **c)** herbivores and **d)** diverse functional guild of arthropods in summer and winter in the savannah. There were significant differences in species richness of carnivores (< 0.001), detritivores (< 0.001), herbivores (< 0.001) and diverse functional guilds (0.009) of surface-active arthropods between summer and winter (**a, b, c** and **d**). Boxplots indicate medians (black horizontal lines) with 25th and 75th percentiles (whiskers), quartiles (interquartile range box and the median) and outliers (circles).

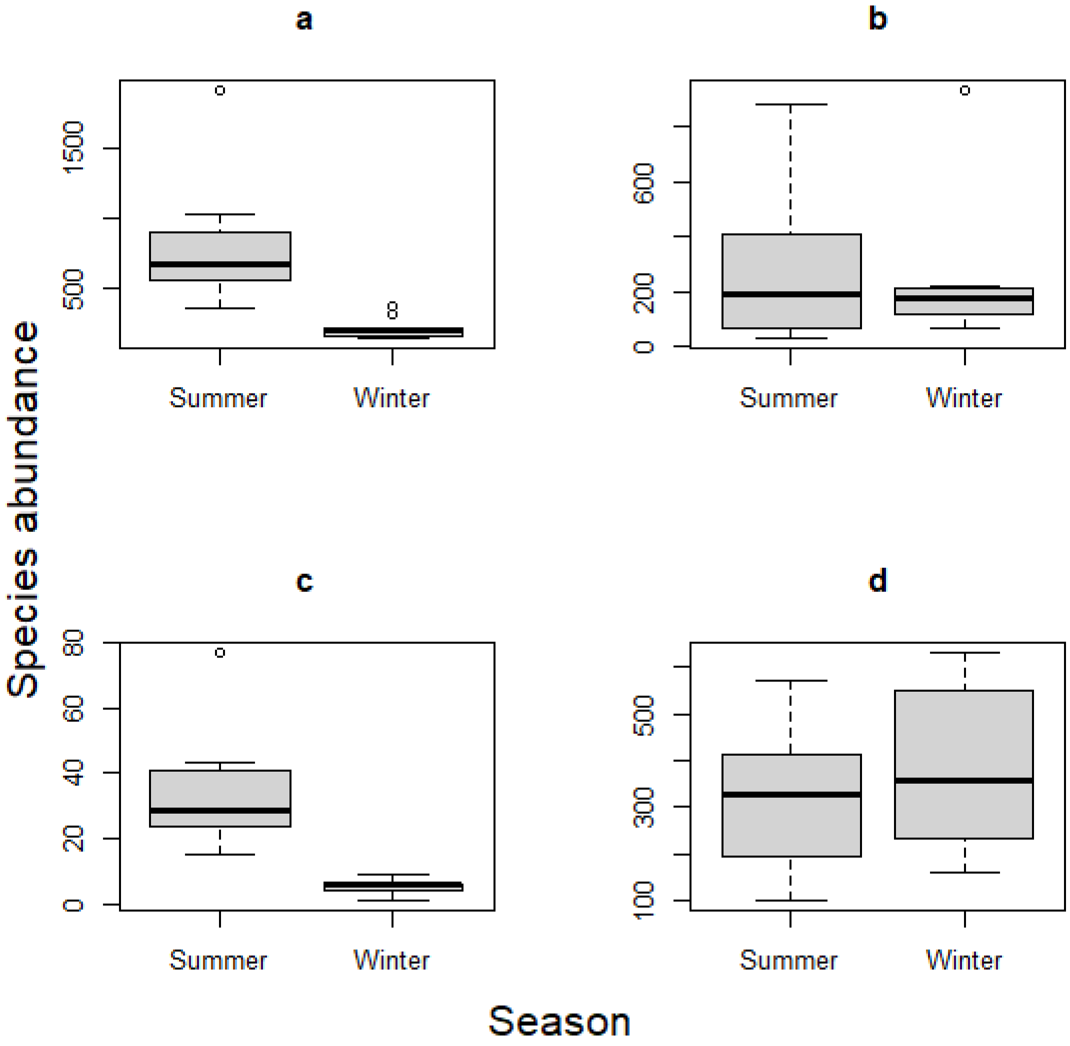

Fig. 3.3. Species abundance of **a)** carnivores, **b)** detritivores, **c)** herbivores and **d)** diverse functional guild of arthropods in summer and winter in the savannah. There were significant differences in the species abundance of carnivores (<0.001) and herbivores (<0.001) between winter and summer (**a** and **c**). Species abundance of detritivores and diverse functional guilds of surface-active arthropods were similar between summer and winter (**b** and **d**). Boxplots indicate medians (black horizontal lines) with 25th and 75th percentiles (whiskers), quartiles (interquartile range box and the median) and outliers (circles).

CHAPTER 4

4. GENERAL CONCLUSION

4.1. Revisiting the aims and hypotheses of the study

This study had two aims that I dealt with in the two research papers. The aim of the first research paper (Chapter 2) was to compare the assemblages of surface-active arthropods (ants, beetles, millipedes and spiders) between pristine and disturbed savannah. The pristine savannah was a natural landscape or protected area with little human interference; while the disturbed savannah was a fallow land (> 15 years) close to an industrial area, croplands and ongoing residential development. As such, I expected the pristine area to have greater species richness and abundance of species, as well as more unique species of surface-active arthropods than the disturbed savannah.

In the second research paper (Chapter 3), I compared the assemblages of functional guilds of surface-active arthropods between the wet (summer) and the dry (winter) seasons. The South African savannah is characterised by an austral summer and winter (Mucina and Rutherford, 2010), with most of the rain occurring during the summer months (Mucina and Rutherford, 2010; ARC–ISCW, 2019). As such, I expected the functional guilds of the surface-active arthropods to have greater species richness and abundance in summer when plants are more productive leading to a greater abundance of resources for the surface-active arthropods than in winter when climatic conditions are inhospitable to some groups of arthropods (see Lees, 2016), and resources are limiting. During winter, some arthropods hibernate or aestivate (see Kipyatkov, 2001; Saunders, 2020; Peffers et al., 2021). For example, in southern Africa, millipedes are inactive in the dry season, they burrow in the ground to avoid the harsh climatic conditions that are associated with changes in season (Dangerfield et al., 1992).

4.2. Summary of the main findings discussed in Chapter 2

In comparing the assemblages of surface-active arthropods between the disturbed and pristine savannah, I found a significant difference in the species composition of all the surface-active arthropods between the disturbed and pristine savannah. In addition, the disturbed savannah had twice the number of indicator species than the pristine savannah. These results demonstrate that different habitat types may support different assemblages of surface-active arthropods, an idea that is supported strongly by several studies (e.g., Mauda et al., 2018; Melliger et al., 2018; Yekwayo and Mwabvu, 2019; Foster et al., 2021; Leonard et al., 2021; Vaca-Sánchez et al., 2021).

Furthermore, I found significant differences in the species richness and the abundance of ants, whilst the species richness and abundance of beetles and spiders were similar between disturbed and pristine savannahs. I argue that ants may be more responsive to disturbance than beetles and spiders because of their greater species richness and abundance between the disturbed and pristine savannahs. The greater species richness and abundance of ants between disturbed and pristine savannah is supported by Savitha et al. (2008) in their study in India.

However, the greater sensitivity of ants to disturbance compared to beetles and spiders does not imply that beetles and spiders are resilient or unaffected by disturbance. When I looked at all the assemblage indices collectively, I found a significant difference in species composition of all taxa but similarities in species richness and abundance of beetles and spiders between the disturbed and pristine savannah. The significant differences in their species composition suggest that disturbance altered negatively the composition of beetles and spiders in the savannah. I argue that the similarities in the species richness and abundance of beetles and spiders between these habitat types may have been due to species turnover at the disturbed sites. This idea of species turnover of surface-active arthropods in disturbed habitats is supported by Swart et al. (2019), who found that there is a replacement of species of arthropods by different species of surface-active arthropods at sites associated with anthropogenic disturbance, for example, edges of the roads and hiking trails, in an Afrotemperate forest complex, South Africa.

4.3. Summary of the main findings discussed in Chapter 3

When I compared the functional guilds of surface-active arthropods between summer and winter, I found that all the functional guilds of the surface-active arthropods had different species compositions between summer and winter. I found greater species richness of all the functional guilds of the surface-active arthropods in summer than in winter. In addition, the abundance of species of carnivorous and herbivorous surface-active arthropods was greater in summer than in winter; whilst that of the “diverse functional guild” and detritivorous surface-active arthropods was similar between summer and winter.

The species richness of all the functional guilds of the surface-active arthropods can be explained by the resource-ratio hypothesis (Tilman, 1985), which suggests that species with lower resource requirements will outcompete species with higher resource requirements when resources become limited. The similarities in the abundance of species between summer and winter of the “diverse functional guild” may have been due to the lumping of some arthropods into one functional guild. Moreover, the similarities in the abundance of detritivores between summer and winter may have been due to little fluctuation or changes in the availability of resources (for example, mesofilters and food sources) between seasons. Additionally, the similarities in the abundance of detritivorous arthropods may have been due to seasonal shifts in the abundance of constituent groups, resulting in a seasonal niche differentiation (Pinheiro et al., 2002), with the overall effect being neutral for their abundance of species. In this study, there were no significant changes in temperature of the selected study sites between summer and winter. As such, I argue that other environmental variables may be responsible for changes in the assemblage of the functional guilds of the surface-active arthropods in summer and winter. For example, variation in vegetation characteristics that are shaped by changes in season (Hutley and Setterfield, 2018), variation in soil moisture (Dangerfield and Telford, 1991), and variation of photoperiod (Saunders, 2020) between summer and winter may affect the assemblages of surface-active arthropods. In particular, short day length induces diapause in the ant *Lepisiota semenovi* (Formicidae), indicating that variation in photoperiod associated with a change in season can cause changes in the activity of some arthropods.

4.4. Limitations of the study

In this study, I compared assemblages of surface-active arthropods at a community level, which may not be ideal for studying the effects of disturbance on surface-active arthropods because of species turnover at disturbed sites. Majority of the studies in ecology focus on a single group or taxon of arthropods, such as ants (see Hlongwane et al., 2019 and Muluvhahothe et al., 2021) or beetles (see Correa et al., 2019 and Rahman et al., 2021). In addition, surface-active arthropods were identified to family and genus where possible. As such, it was challenging to observe taxon-specific responses of the surface-active arthropods to disturbance. Moreover, vegetation variables (e.g., herbaceous plant height, grass biomass, plant density) were used in exploratory data analysis but did not explain patterns of arthropod abundance, species composition and species richness, which may have been due to variation in responses by each individual species, and so were excluded from the confirmatory data analysis presented in the thesis. In chapter 3, the study focused on the effect of season on functional guilds of surface-active arthropods. However, there was no replication of seasons. This study was done in a single summer and winter season due to time constraints. Therefore, the results of this study that are discussed in Chapter 3 should be interpreted with caution.

4.5. Conclusion and recommendations

My study showed that disturbed and pristine savannah vegetation types support different compositions of surface-active arthropods. In addition, the different composition of the functional guilds of surface-active arthropods between summer and winter in the savannah can be linked to changes in vegetation characteristics that are associated with changes in season. As such, I recommend that it may be essential to consider all habitat types for the conservation of surface-active arthropods, especially in South Africa where the majority of the land falls outside of the formal conservation areas (Yekwayo et al., 2016; Mauda et al., 2018). The large number of unique species that I recorded in the disturbed savannah supports this assertion. Furthermore, it may be essential to involve communities in conservation initiatives because community participation is an effective measure in biodiversity conservation (Zhang et al., 2020) and has the potential to improve the lives of people living within such communities (Nzama, 2009). This can be achieved in several ways, including the creation of “multispecies livelihoods” (Thomsen and Thomsen, 2021) to promote biodiversity conservation in South Africa. The fact that previous studies focused on singleton arthropod groups suggests that there is a knowledge gap with respect to the collective response of different arthropod groups in a single ecosystem. As such, more studies conducted at a community level are required to deepen our understanding on the collective response of different arthropod groups within ecosystems.

4.6. References

ARC–ISCW, 2019. Water and climate data (unpublished). In: Agricultural Research Council (ARC) Institute for Soil Climate and Water (ISCW) (Ed.). Agro-climatology division, Stellenbosch.

Correa, C.M., Braga, R.F., Louzada, J., Menéndez, R., 2019. Dung beetle diversity and functions suggest no major impacts of cattle grazing in the Brazilian Pantanal wetlands. Ecological Entomology 44, 524–533.

Dangerfield, J.M., Milner, A.E., Matthews, R., 1992. Seasonal activity patterns and behaviour of juliform millipedes in south-eastern Botswana. Journal of Tropical Ecology, 451–464.

Dangerfield, J.M., Telford, S.R., 1991. Seasonal activity patterns of Julid millipedes in Zimbabwe. Journal of Tropical Ecology 7, 281–285.

Foster, J.G., Gervan, C.A., Coghill, M.G., Fraser, L.H., 2021. Are arthropod communities in grassland ecosystems affected by the abundance of an invasive plant? Oecologia 196. https://doi.org/10.1007/s00442-020-04833-3

Hlongwane, Z.T., Mwabvu, T., Munyai, T.C., Tsvuura, Z., 2019. Epigaeic ant diversity and distribution in the Sandstone Sourveld in KwaZulu-Natal, South Africa. African Journal of Ecology 57, 382–393.

Hutley, L.B., Setterfield, S.A., 2018. Savanna. In: Fath, B. (Ed.), Encyclopedia of Ecology, 2nd ed. Elsevier BV, Oxford, pp. 623–633.

Kipyatkov, V.E., 2001. Seasonal life cycles and the forms of dormancy in ants (Hymenoptera: Formicoidea). Acta Societatis Zoologicae Bohemicae 65, 211–238.

Lees, A.D., 2016. The physiology of diapause in arthropods. Cambridge University Press, Oxford.

Leonard, E.E., Mast, A.M., Hawkins, C.P., Kettenring, K.M., 2021. Arthropod assemblages in invasive and native vegetation of Great Salt Lake wetlands. Wetlands 41, 1–17.

Mauda, E.V., Joseph, G.S., Seymour, C.L., Munyai, T.C., Foord, S.H., 2018. Changes in land use alter ant diversity, assemblage composition and dominant functional groups in African savannas. Biodiversity Conservation 27, 947–965.

Melliger, R., Braschler, B., Rusterholz, H., Baur, B., 2018. Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. PLoS One 13. https://doi.org/10.1371/journal.pone.0199245

Mucina, L., Rutherford, M.C., (eds) 2010. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Muluvhahothe, M.M., Joseph, G.S., Seymour, C.L., Munyai, T.C., Foord, S.H., 2021. Repeated surveying over 6 years reveals that fine-scale habitat variables are key to tropical mountain ant assemblage composition and functional diversity. Scientific Reports 11, 1–10. https://doi.org/10.1038/s41598-020-80077-8

Nzama, A., 2009. The nexus between sustainable livelihoods and ecological management of the world heritage sites: lessons from iSimangaliso World Heritage Park, South Africa. Inkanyiso: Journal of Humanities and Social Sciences 1, 34–42.

Peffers, C.S., Pomeroy, L.W., Meuti, M.E., 2021. Critical photoperiod and its potential to predict mosquito distributions and control medically important pests. Journal of Medical Entomology 58, 1610–1618.

Pinheiro, F., Diniz, I., Coelho, D., Bandeira, M., 2002. Seasonal pattern of insect abundance in the Brazilian cerrado. Austral Ecology 27, 132–136.

Rahman, A.U., Jones, H.P., Hosler, S.C., Geddes, S., Nelson, M., Barber, N.A., 2021. Disturbance-induced trophic niche shifts in ground beetles (Coleoptera: Carabidae) in restored grasslands. Environmental Entomology 50, 1075–1087. https://doi.org/10.1093/ee/nvab065

Saunders, D.S., 2020. Dormancy, diapause, and the role of the circadian system in insect photoperiodism. Annual Review of Entomology 65, 373–389.

Savitha, S., Barve, N., Davidar, P., 2008. Response of ants to disturbance gradients in and around Bangalore, India. Tropical Ecology 49, 235–243.

Swart, R.C., Pryke, J.S., Roets, F., 2019. The intermediate disturbance hypothesis explains arthropod beta-diversity responses to roads that cut through natural forests. Biological Conservation 236, 243–251.

Thomsen, B., Thomsen, J., 2021. Multispecies livelihoods: partnering for sustainable development and biodiversity conservation. In: Leal Filho, W., Marisa Azul, A., Brandli, L., Lange Salvia, A., Wall, T. (Eds.), Partnerships for the Goals. Springer International Publishing, New York

Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist 125, 827–852.

Vaca-Sánchez, M.S., Maldonado-López, Y., González-Rodríguez, A., Oyama, K., Fernandes, G.W., Fagundes, M., López-Barbosa, E.C., Aguilar-Peralta, J.S., Cuevas-Reyes, P., 2021. Canopy arthropod diversity associated with *Quercus laurina*: importance of an oak species diversity gradient on abundance, species richness and guild composition. Journal of Insect Conservation. https://doi.org/10.1007/s10841-021-00352-5

Yekwayo, I., Mwabvu, T., 2019. Diversity and composition of flightless arthropods on rock outcrops and adjacent vegetation in the savannah, Mpumalanga province, South Africa. African Journal of Ecology 57, 443–447. https://doi.org/10.1111/aje.12617

Yekwayo, I., Pryke, J.S., Roets, F., Samways, M.J., 2016. Surrounding vegetation matters for arthropods of small, natural patches of indigenous forest. Insect Conservation and Diversity 9, 224–235.

Zhang, Y., Xiao, X., Cao, R., Zheng, C., Guo, Y., Gong, W., Wei, Z., 2020. How important is community participation to eco-environmental conservation in protected areas? From the perspective of predicting locals' pro-environmental behaviours. Science of The Total Environment 739, 139889. https://doi.org/10.1016/j.scitotenv.2020.139889