# The impact of land-use change on arthropod diversity along an arid elevational gradient

**by**

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**Submitted in fulfilment of the academic requirements of**
**Master of Science**

in Ecological Science

School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg

South Africa

January 2022

# PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Biology, School Life Sciences, College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The research was financially supported by National Research Foundation (NRF).

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

[redacted]

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# DECLARATION OF PLAGIARISM

I, S'phesihle Mkhungo declare that:

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

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Please note that chapter two and chapter three of this thesis were written as standalone papers and therefore some repetition was unavoidable.

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# ABSTRACT

Land-use change is a major threat to global biodiversity. The rapid growth of the human population has resulted in increased landscape modifications and habitat loss. The impact includes reduced species diversity, ecosystem instability, altered species interactions and altered food webs. Land-use has increased drastically in mountainous areas, mainly through agriculture and human settlements. Mountains support approximately one-third of the terrestrial diversity and host half of the global biodiversity hotspots. The high variation in habitat structure and microclimates, within short distances allows mountains to support high species diversity. This study aimed to investigate the impact of increasing land-use change, elevation, and season on selected arthropod diversity, and community composition along the Western Soutpansberg mountain range in Limpopo province of South Africa. The objectives of the study were to determine spider and ant diversity patterns along the mountain. Secondly, to determine the role of land-use, elevation, and season in structuring the diversity of both taxa. Lastly, to compare the composition of spider and ant assemblages across the various sites and identify indicator species for monitoring land-use change in the study area.

A standardized pitfall trap survey was used to sample ants and spiders along an elevational transect that stretches across the southern and northern aspects of the mountain. The elevational transect (800 m a. s. l – 1700 m a. s. l) was made up of 18 sites, some of which have undergone human transformation mainly through agriculture and settlements. Sampling took place during the dry season (September 2019) and wet season (January 2020). Generalized linear mixed models with Poisson error distributions were used to determine the impact of land-use, elevation, season on spider and ant species richness and activity. Community composition was analyzed using NMDS (non-metric multidimensional scaling), PERMANOVA and ANOSIM analyses.

Land-use had a positive effect on spider and ant diversity as the transformed sites had significantly higher species richness and activity for both taxa, particularly the agricultural sites and human settlement. However, species evenness was significantly lower in the transformed sites and higher in the natural sites. Species richness and activities for both taxa were highest at the low elevations. Spider diversity was higher in the dry season, but ants peaked in the wet season. Spider and ant assemblages were highly distinct between the land-use types and elevations. Ant assemblages remained similar between the seasons, while spider composition was slightly different across the two seasons. Spider and ant assemblages in the transformed sites were highly uneven which indicates a large disproportion in the number of individuals within the species found in transformed sites. It also indicates high species dominance, which is driven by the disturbance-tolerant species.

One spider species, *Copa flavoplumosa*, was identified as an indicator species for the *Eucalyptus* plantations. All land-use types had an ant indicator species, which was either *Monomorium damarense* and/or *Lepisiota* sp.02 (*spinosior* gp.). High species dominance displayed by spider and ant assemblages in the modified habitats might have adverse effects on native and endemic communities. Because dominant and disturbance-tolerant species are likely to increase if more natural land is converted. This study was the first to investigate the impact of land-use changes at the Soutpansberg mountain range. The results indicate that land-use change had a positive effect on arthropod species richness and activity. However, species evenness was negatively affected. Although the land-use changes at Soutpansberg can increase the diversity of certain species, the potential to sustain the populations over the long term is unknown. Therefore, further assessments and monitoring of diversity in the region is recommended to understand the long-term impact of land-use and for informed decision making and strategy in conservation efforts.

# ACKNOWLEDGEMENTS

I would like to express my deep and sincere gratitude to my supervisor Dr. Caswell Munyai for this opportunity. Your support and guidance were invaluable throughout the project. I will forever cherish your wise words, impeccable work ethic, attitude, and drive for success. Thank you for caring not only for my academic success but also for my social and mental wellbeing. I would also like to thank my co-supervisor, Prof. Stefan Foord. His insightful and important input for this dissertation is highly appreciated. Thank you for your involvement in fieldwork and assistance with statistical analysis.

Special thanks to the Ant lab, you guys made the whole process easier. Your support and brilliant ideas are very much appreciated; Sbongiseni Xolo, Nokubonga Thabethe, Snenhlahla Mntambo, Thandeka Mahlobo, Fanele Hlabisa, Lindiwe Khoza, and Concialia Mukanga you all were helpful. I am deeply thankful to the University of Venda team of Lorraine, Ratshi, Consol for their assistance with fieldwork.

I am grateful to my family for their love and support throughout. Thank you for understanding why I had to spend so much time away from home and for encouraging me to persevere. Thank you to my friends, Anele Khowa, Gcinumuzi Zungu, Fanele Zulu, Sfiso Zungu for your assistance with washing and sorting pitfall traps.

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# CHAPTER 1: General introduction and overview

## 1.1 Land-use change impact

The transformation of natural habitats for anthropogenic uses has increased drastically in recent decades. The rapid growth of the human population is the primary source of the upsurge in land-use practices (Chengsutdha et al., 2016). Inevitably, the increased conversion of natural land has translated into large-scale biodiversity loss and extinctions globally (Tilman, 1998; Prieto-Benítez and Méndez, 2011; Schuldt and Staab, 2015). Industrial and agricultural expansions coupled with a higher demand for natural resources such as water, fuel, and food have placed terrestrial ecosystems under tremendous pressure (Maitima et al., 2009). A large portion of the natural landscape has been lost or altered through anthropogenic disturbances (Attwood et al., 2008). Over the past 300 years, humans have also had a significant impact on the Earth's natural resources (Beniston, 2001). In that period between 30 and 50% of the Earth's land surface has been converted mostly into human settlements and agricultural systems (Beniston, 2001; Mauda et al., 2018). Also, greenhouse gas emissions have increased so much that it has resulted in global climate change (Stavi and Lal, 2013). The fixed nitrogen production by humans is now more than twice as much as the natural sources combined (Walker et al., 2019).

Indeed, many biologists have agreed that the world is currently undergoing the sixth mass extinction as a result of human activities (Raven and Wagner, 2021). The decline of pristine spaces and landscapes is rapid and results in many species losing their habitat. Land-use practices such as agriculture, urbanization, deforestation, livestock ranching, and mining are the main reasons for habitat loss and degradation (Prieto-Benítez and Méndez, 2011, Yeo et al., 2011). Agriculture is one of the most common and important land-use practices. Research shows that pastures and croplands now make up one-third of the global land surface (Maitima et al., 2009; Taylor and Rising, 2021). In Europe alone, 34% of the terrestrial area is used for crop production (Reidsma et al., 2006). In Africa, the population is expected to rise fourfold by the year 2100 (Gerland et al., 2014), and considering that the African population is the most malnourished, the rapid expansion and intensification of agricultural practices is expected to continue (Joseph et al., 2018; Mauda et al., 2018).

Commercial farming and food production has increased massively to keep pace with the growing population (Fróna et al., 2019). The expansion of agricultural systems can be detrimental to local biodiversity and also the surrounding ecosystems (Reidsma et al., 2006). Habitat loss, reduced spatial heterogeneity and the use of fertilizers and pesticides are the main sources of biodiversity loss in agro-ecosystems (McKinney, 2008; Geiger et al., 2010; Bernadou et al., 2013). Previous studies have shown the negative effects of agricultural practices on various taxa. For instance, Geiger et al. (2010) found that agricultural intensification reduced bird, wild plant, and carabid species in eight European countries, with the application of fungicides and insecticides the main drivers of the decline in biodiversity. In Sub-Saharan Africa, the extensive growth of agriculture was associated with reduced mammal, bird, and plant diversity (Perrings and Halkos, 2015).

Urbanization is also one of the leading forces behind the transformation of natural ecosystems (Otoshi et al., 2015). Approximately 43% of the Earth's land surface has been taken up and degraded by humans (Tilman, 1998; Prieto-Benítez and Méndez, 2011). Urbanization is also linked to the increase of invasive alien species (Bharti et al., 2016; Santana Marques et al., 2020). In addition, urbanization reduces biodiversity and the capacity of certain species to provide critical ecosystem services due to habitat destruction and fragmentation (Sanford et al., 2009; Quintas-Soriano et al., 2016). A comprehensive review of the impact of urbanization revealed that areas with high levels of urbanization and development had decreased species richness for mammals, reptiles, amphibians, invertebrates, and plants (McKinney, 2008). In a global meta-analysis, Fenoglio et al. (2020) also found that arthropod richness and abundance were low in urbanized landscapes.

The high demand for land for human settlements and agriculture has also caused the rate of deforestation to increase significantly (Pabst et al., 2013). Forests, woodlands, and grasslands are declining at an alarming rate worldwide (Ojima et al., 1994; Laurance, 2010). The increased clearing of tropical forests is even more concerning, given their high biodiversity and endemism. Between 2000 and 2010 alone, more than 7 million ha of forests were lost (Soh et al., 2019). Even though different taxa respond differently to clearing, forest and vegetation clearing tend to negatively impact biodiversity (e.g., Pandit et al., 2007; Barlow et al., 2016; Symes et al., 2018). As a result of habitat simplification, altered resource availability and temperature, and reduced niche availability (Attwood et al., 2008).

Important ecosystem processes such as carbon sequestration, soil attributes, water relations, and nutrient pathways can be affected by changes in land-use and land cover (Becker et al., 2007; Polasky et al., 2011). Land-use changes can also disturb food webs at a range of trophic levels (Joseph et al., 2018), leading to interruption or even loss of ecosystem functions and ecosystem instability (Polasky et al., 2011; Joseph et al., 2018). The capacity of ecosystems to provide resources such as food, water, wood, and air quality for human livelihoods also declines due to extensive land-use (Laureto et al., 2015). Terrestrial land has lost approximately

10% of its potential to provide “direct benefits” due to the intensive use of natural resources and land (Prieto-Benítez and Méndez, 2011).

Drastic changes in habitat structure can also lead to the entry of foreign and invasive species and the disappearance of some indigenous species (Ojima et al., 1994). When natural ecosystems are disturbed, invasions by exotic or invasive species become more probable (Hierro et al., 2006; Kotanen, 2004). A large number of exotic species have been directly and indirectly introduced into new ecosystems through habitat disturbance resulting in native species being depleted and replaced, thereby significantly changing the population and community dynamics (Tilman, 1998; Zakkak et al., 2014). Therefore, land-use changes have caused a substantial shift in composition, distribution, and range of many species across various ecosystems as landscapes have become increasingly fragmented and degraded (Tilman, 1998). Ultimately the integrity and status of most ecosystems have been negatively affected by these land transformations (Quintas-Soriano, 2016).

## 1.2 Land-use impact in mountainous regions

Mountains have unique landforms and features that make them one of the most complex ecological systems in the world. They support a large and unique portion of the Earth's terrestrial biodiversity (Körner and Ohsawa, 2005). In fact, most hotspots for endemic species (Dirnböck and Rabitsch, 2011) and protected areas (Körner, 2004; Kollmair et al., 2005) are located in mountainous regions. Many human societies also depend on mountains for survival and sustainability (Chakraborty, 2019). Approximately 50% of the human population is directly or indirectly dependent on mountain catchment water (Körner, 2004). Mountains also influence marine systems and atmospheric circulation patterns to create complex climatic patterns (Hoorn et al., 2013), influencing the climate at both the regional and global scales (Perrigo et al., 2020).

Habitat diversity, varying exposure due to slopes, compressed climatic zones and the climate-topography interaction makes mountain communities extremely diverse with high endemism (Ruggiero and Hawkins, 2008; Perrigo et al., 2020). The high variability in environmental conditions over relatively short distances creates substantial landscape and habitat heterogeneity (Bernadou et al., 2013; Elsen et al., 2018). It also makes mountains powerful tools for ecological research (Bishop et al., 2014; Munyai and Foord, 2015). Therefore, biodiversity patterns that usually occur at large scales can be studied easily along elevational gradients (Bernadou et al., 2013). Studies have yielded various patterns of diversity for multiple taxa along elevational gradients. The most common of these are the mid-elevation peak (Sanders, 2002; Kluge et al., 2006; Munyai and Foord, 2012) and declining species richness with elevation (Rahbek, 2005; Malsch et al., 2008; Le Cesne et al., 2015). Some studies have also found increasing richness with elevation (Sanders et al., 2003; Malumbres-Olarte et al., 2018).

Several hypotheses have been proposed to explain diversity patterns along elevational gradients. These include the thermal energy hypothesis, mid-domain effect, the area and elevation climatic model (Szewczyk and McCain, 2016). The thermal energy hypothesis is temperature-based, and it predicts that warmer temperatures allow for increased productivity and extended periods of foraging (Sanders et al., 2007; Jayatilaka et al., 2011). As elevation increases, the temperatures decrease, resulting in a monotonic decrease of diversity (Szewczyk and McCain, 2016). The mid-domain effect predicts that species richness will peak at mid-elevations because of geometric constraints affecting the distributional ranges of species (Colwell and Lees, 2000). The area hypothesis states that increased area results in higher species richness as larger areas support more populations, and area typically decreases with elevation in mountains (Rosenzweig, 1992). The elevation climate model proposes that diversity is driven by a combination of precipitation and temperature (Brown, 2001). According to the model, the warm and wet elevation bands will have the highest diversity of species (McCain, 2007). Furthermore, the local climate affects resource availability which also influences foraging strategies and periods (Marques et al., 2017).

Human populations are increasing rapidly in mountainous areas and anthropogenic impacts in the form of logging, agricultural expansions and human settlements have placed mountain ecosystems under threat (Beniston, 2001; Körner, 2004). According to Elsen et al. (2020), 57% of all mountains are under severe pressure from land-use changes. Stochastic extinctions are more likely to occur when mountain species are faced with restricted habitat areas and population declines (Elsen and Tingley, 2015). Additionally, habitat loss reduces the number of endemic species while it increases non-native and widely distributed species (Maeto and Sato, 2004). This is concerning given the high endemism mountains display.

Also, climate and land-use change have already caused range shifts in mountain species and these shifts may accelerate in the future due to climate change increasing with elevation (Elsen et al., 2018). Species are also likely to migrate to higher elevations to find more suitable temperatures due to global warming (Flores et al., 2018; Bishop et al., 2019). The predicted upward shift will inevitably reduce the geographical range and fundamental niches of species inhabiting high lands, leading to extinction (Dirnböck and Rabitsch, 2011). Furthermore, the ectotherm communities inhabiting high elevations will be at risk as rapid changes in thermal regimes will affect their ecological fitness and ecosystem functioning (Joseph et al., 2019).

### 1.3 The role of arthropods as indicators of ecosystem integrity

Arthropods are one of the most diverse and dominant organisms globally, which explains their presence and abundance in almost all terrestrial habitats (Barton et al., 2017, Mauda et al., 2018, Schwerdt et al., 2018). According to Lingbeek et al. (2017), arthropods comprise more than 90% of terrestrial biodiversity. They occupy all local spaces and consist of crucial functional groups at different trophic levels (Schaffers et al., 2008). Arthropods are important for ecosystem functioning and stability because of the essential roles they perform in an ecosystem (Schaffers et al., 2008; Yekwayo et al., 2016). These roles are critical for ecosystem health and sustainability and the livelihoods of human societies (Lingbeek et al., 2017). These roles include regulating, supporting, provisioning, and cultural services. Importantly, some of these services contribute massively towards primary production. Hence, the ecological and economical importance of arthropods is increasingly being appreciated (Mauda et al., 2018).

Arthropods have also been shown to be excellent bioindicators in various ecosystems. Bioindicators are taxa or functional groups that reflect the state of the environment (Schwerdt et al., 2018). Bioindicators are useful tools for detecting and monitoring environmental stress, or disturbances. They are particularly valuable in conservation planning, assessing the recovery of ecosystems after disturbances or monitoring the response of ecosystems to management decisions (Holt and Miller, 2011). Bioindicators are usually characterized by ubiquity, abundance and sensitivity to environmental disturbances or changes, and they also tend to be easy to sample and identify (Schwerdt et al., 2018). Two terrestrial groups, in particular, ants and spiders, are some of the most widely studied bioindicators (Beiroz et al., 2014; Schuldt and Staab, 2015). Furthermore, arthropods often have very short generation times compared to other species, making them highly responsive to environmental change (Angulo et al., 2016; Bishop et al., 2016; Buczkowski and Richmond, 2012).

Ants (Hymenoptera: Formicidae) are among the most abundant and diverse arthropod groups globally (Schofield et al., 2016). They are extremely dominant and occupy almost all terrestrial ecosystems (Flores et al., 2018). In the tropics alone, 50% of invertebrate abundance is estimated to be made up of ants (Schofield et al., 2016). They are regarded as ecosystem engineers because of the wide variety of ecosystem functions they perform (Maleque et al., 2009; Buczkowski and Richmond, 2012; Del Toro et al., 2012). For instance, they are involved in decomposition, pest control, soil aeration and soil mixing (Del Toro et al., 2012; Mauda et al., 2018). Ants also have influence over plant community composition and diversity, through seed dispersal, pollination, seed harvesting, and by influencing soil and nutrient processes (Frouz and Jilková, 2008; Kaspari et al., 2010; Lengyel et al., 2010; Rostás and Tautz, 2010). They also regulate herbivore abundance and drive top-down effects as predators (Flores et al., 2018). They are often used as biological control agents against pests (Wilby et al., 2006; Andersen, 2019).

Ants can also influence the assemblages of other invertebrates by altering and regulating the distribution of resources (Kaspari et al., 2011; Mauda et al., 2018). Without the services of ant species, the stability of most terrestrial ecosystems would be significantly impacted and would cause a domino effect that would likely end in substantial biodiversity loss. There is also considerable support for using ants as indicators of disturbance due to high abundance and sensitivity to environmental changes (Andersen et al., 2002; Flores et al., 2018). Thus, ants have been used as indicators in livestock grazing (Hoffman, 2000), range-land monitoring (Andersen and Majer, 2004), forest management (Maleque et al., 2009; Hethcoat et al., 2019), agricultural land-use (Philpott et al., 2006; Rubiana et al., 2015; Previati et al 2017), mine-site rehabilitation (Majer, 1983) and urbanization impact (Melliger et al., 2018).

Spiders are the most abundant predatory group in terrestrial environments (Barton et al., 2017; Joseph et al., 2018). They are one of the most diverse taxa on Earth, with a wide distribution (Hatley and Macmahon, 1980; Sanders and Platner, 2007; Hore and Unival, 2008; Zakkak et al., 2014). Spiders occupy important points in terrestrial food webs and the highest trophic levels among arthropods (Prieto-Benítez and Méndez, 2011; Samu et al., 2014). They also ensure that food webs maintain their stability, prevent trophic cascades and influence nutrient cycling (Bowden and Buddle, 2010; Dippenaar-Schoeman et al., 2011; Joseph et al., 2018). The varying nature of their predation tactics allows spiders to fill several important ecological niches (Samu et al., 2014). The presence of spiders can be beneficial for plant species since spiders often prey on insect herbivores (Sanders and Platner, 2007). Their predatory nature coupled with high diversity and ubiquity makes them pivotal for ecosystem functioning in natural and disturbed ecosystems (Foord et al., 2008; Mineo et al., 2010; Samu et al., 2014; Joseph et al., 2018).

Spiders act as biological control agents and can influence the diversity and composition of other arthropods, making them extremely valuable in agroecosystems and forests (Dippenaar-Schoeman et al., 2011; Prieto-Benítez and Méndez, 2011; Campuzano et al., 2019). Ecologically, spiders are regarded as good bioindicators for environmental change. They are sensitive to changes in vegetation, microclimate, litter depth and habitat structure (Hore and

Unival, 2008; Zakkak et al., 2014; Schwerdt et al., 2018), and therefore they respond rapidly to these changes. This sensitivity to changes is why spiders have been used in numerous ecosystems to assess habitat quality (Campuzano et al., 2019). The ability to disperse extensively and persist in different habitats also influences their use as model species (Maleque et al., 2009). Spiders are also relatively simple to sample, and they can also be easily identified (Foord et al., 2008; Maleque et al., 2009). Hence their use as bioindicators in agricultural (Downie et al., 1999; Woinarski et al., 2002; Kim et al., 2020), urbanization (Fraser and Frankie, 1986) and forest management (Maelfait and Hendrickx, 1997) studies.

Anthropogenic disturbances have caused a biodiversity crisis globally (Lingbeek et al., 2017), placing many ecosystems at the brink of collapse because of biodiversity loss. Arthropods are one of the most threatened animal groups. Any land-use changes that disturb the microclimate, resource availability, soil, vegetation, and competitive interactions can radically change arthropod communities (Bharti et al., 2016; Barton et al., 2017). In fact, insect biodiversity is declining much quicker than plants and vertebrates (Schaffers et al., 2008). Studies also show the negative impact of land-use change on arthropods. In Western Madagascar, Gray and Jongepier (2008) reported that arthropod diversity declined due to human disturbances in a deciduous forest reserve. While Hendrickx et al. (2007) assessed the response of arthropod diversity to land-use intensity in 24 agricultural landscapes in Europe and found that arthropod species richness decreased as land-use intensity increased. Additionally, Woinarski et al. (2002) compared ant and spider diversity between pastoral and military land-use and an undisturbed site in a tropical savanna in Australia. Ant and spider diversity was lower in the land-use sites compared to undisturbed sites (Woinarski et al., 2002).

Drastic changes in arthropod assemblages can result in unregulated invertebrate pest diversity and unbalanced food webs (Attwood et al., 2008; Joseph et al., 2018). Important ecosystem functions and services can be lost if there is a drastic change of arthropod diversity in an environment (Attwood et al., 2008). These events have far-reaching implications for biodiversity and primary production. Ultimately, the transformation in land-use results in changes in interspecies interactions in the composition and structure of arthropod communities since arthropods are extremely dependent on vegetation structure and diversity (Attwood et al., 2008). Changes in arthropod communities can also affect resource availability and use, disturbing the fundamental niches for many species.

### 1.4 Justification of the current study

One of the primary objectives of modern ecology is forecasting the response of biodiversity to global changes (Flores et al., 2018). The impact of land-use change is still poorly quantified in the African continent despite the apparent negative effect of land-use change and the fast rate at which it occurs, especially in African countries (Mauda et al., 2018). In South Africa, studies show a sharp decline of pristine spaces such as natural forests, bushvelds and grasslands in the last three decades (Hoffman, 2014; Siebert et al., 2021). While built-up environments have increased drastically as well. that the natural land is expected to be transformed to meet the needs of the growing human population, the knowledge gap on this topic is concerning. By identifying and understanding the extent to which land-use and other anthropogenic impacts have on biodiversity, we can obtain important information that could be useful for biodiversity conservation efforts (Angulo et al., 2016). Understanding the impact of disturbance on ecologically dominant taxa such as ants and spiders is important because these taxa often impact other biotas through complex cascading effects (Andersen, 2019).

Biologists maintain that long-term monitoring of elevational transects in mountainous areas can give insight into the mechanisms and processes behind natural diversity (Munyai and Foord, 2012). Understanding the drivers behind biodiversity patterns has long been the center of ecological research (Bishop et al., 2014). This allows for a better understanding of life on Earth and provides vital information for policy or decision-making in conservation (Bishop et al., 2014; Chiu et al., 2020). Furthermore, it is important to include multiple taxonomic groups when investigating the impact of environmental change on biodiversity because arthropod taxa have been shown to have variable responses to environmental disturbances (Lingbeek et al., 2017).

The Soutpansberg mountain range is a major centre of endemism for flora and fauna (Foord et al., 2008; Joseph et al., 2019). It is a high long-term priority for conservation due to its high levels of biological diversity (Foord et al., 2008). The Soutpansberg mountain is a core biodiversity area for the Vhembe Biosphere Reserve (Foord et al., 2008) and is listed as a national priority area for conservation (Joseph et al., 2019). It has the highest family and generic level plant diversity among centres of plant endemism in southern Africa (Symes et al., 2000; Foord et al., 2008; Munyai and Foord, 2012). The mountain range harbours 33% of the reptiles in South Africa, 75% of the avifauna in South Africa and 60% of South Africa's mammals (Munyai and Foord, 2012).

The Soutpansberg mountain is characterized by varied environmental conditions due to its orientation. There is high variability in its topography, climatic conditions and vegetation type over relatively short distances (Symes et al., 2000; Munyai and Foord, 2015). This variation has resulted in many endemic species inhabiting the mountain range. The east-northeast to west-southwest orientation results in the southern slope which is mesic with bushland, thicket, grassland and forest habitats while the north is arid and largely characterized by hot and open dry savannah (Munyai and Foord, 2015). In recent years, human encroachment along the Soutpansberg mountain range has increased immensely, resulting in many natural land transformations and land-use changes along the mountain. These transformations include agricultural systems, human settlements, and commercial forests and other plantations, leading to the clearing of native vegetation. There is a concern that the increased changes in land-use across the mountain range might endanger the high biodiversity and endemism of the area.

Therefore, the current study investigates the impact of land-use changes on the western Soutpansberg mountain using spiders and ants as model taxa. By assessing the overall diversity and its response to varying land-use types, elevations and seasonality along the gradient (Chapter 2). Chapter three of the study compares spider and ant community composition at different elevations, land-uses, and seasons and identifies the indictor taxa for both groups along the mountain.

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# CHAPTER 2: Impact of anthropogenic disturbances on arthropod diversity along an elevational gradient

## Abstract

Mountain ecosystems are focal points of some of the highest endemicity and biodiversity. However, anthropogenic impacts in the form of land-use have placed intense pressure on montane biodiversity. The conversion of natural land for anthropogenic uses can lead to ecosystem instability and biodiversity loss. The impact of land-use change remains poorly quantified in the African continent, which is also predicted to have massive landscape transformations in the future. The current study investigated the effect of land-use change, elevation and season on spider and ant activity and diversity along the western Soutpansberg mountains in Limpopo province, South Africa. A standardized survey using pitfall sampling was conducted across an elevational transect. The transect consists of 18 sites across the mountain, which included several land-use types including human settlements, cropland, bush encroached sites, cleared bush sites, *Eucalyptus* plantations and macadamia orchards. Spider diversity peaked in the human-modified habitats, particularly the cropland and macadamia orchards. Ant diversity was also higher in the transformed sites, with the bush cleared site and cropland recording the highest ant diversity. Spider species richness and activity were higher in the dry season, while ant species richness and activity were highest in the wet season. Both taxa displayed unevenness and dominance in the transformed sites, which may negatively affect ecosystem processes and functional diversity within the communities. Notably, the results show that the transformed sites recorded higher richness and activity overall than the untransformed sites, for both taxa. Indicating a positive impact of land-use on arthropod diversity. This is likely a result of an influx of disturbance-tolerant and opportunistic species into the transformed sites, as these sites displayed high levels of unevenness. Overall, land-use had more influence on arthropod diversity than elevation and season in Soutpansberg. Furthermore, ants were found to be more sensitive to land-use than spiders. Further studies on land-use impacts in the region are encouraged to detect long-term trends and impacts.

Keywords: Mountains, land-use change, diversity, elevation, arthropods, season

## Introduction

Mountainous regions harbor nearly a third of the terrestrial biodiversity, despite constituting less than 20% of the global land surface (Elsen et al., 2018). In this context, montane ecosystems account for a disproportional number of faunal and floral species for their extent, including threatened and rare species (Körner and Ohsawa, 2005; Elsen et al., 2018). As a result, many mountain ranges are considered biodiversity hotspots (Ruggiero and Hawkins, 2008; Munyai and Foord, 2012). Mountains can support and maintain high diversity due to great climate and landscape heterogeneity over short distances (Ruggiero and Hawkins, 2008; Bernadou et al., 2013), providing high variability in environmental conditions within compact spaces, creating a complex topography (Bernadou et al., 2013). Landscape heterogeneity also leads to high species turnover and extremely low extinction rates in mountainous areas (Hoorn et al., 2013; Steinbauer et al., 2016).

The biogeographical characteristics of mountains are also important for the isolation and migration of species, promoting speciation and ultimately diversity (Becker et al., 2007; Merckx et al., 2015). The formation and growth of mountain ranges can lead to landmasses being separated, isolating species (Hoorn et al., 2013; Elsen et al., 2018). Alternatively, it can lead to continents joining and facilitating migration in the process. For these reasons, mountain ecosystems also represent some of the highest endemicity on Earth (Hethcoat et al., 2019). The importance of mountains has been further emphasized by the re-emergence of mountain ecosystem studies in the last couple of decades (Szewczyk and McCain, 2016).

Mountains are one of the most diverse biotas globally but are also the most threatened by anthropogenic disturbances such as logging, agricultural expansions, and human settlements (Körner, 2004). Land-use changes have become a driving force for biodiversity in mountainous regions due to increased human encroachment. These land-uses have tremendously modified natural landscapes and altered ecosystems by changing the faunal and floral diversity and composition considerably (Ojima et al., 1994). Ecosystem provisioning and functioning have also been affected by changes in land-use, leading to the loss of important ecosystem services and processes (Joseph et al., 2018; Dalle Laste et al., 2019). The loss of ecosystem services and functioning is detrimental to plants, animals, and human well-being (Dalle Laste et al., 2019). Also, the constant change in species assemblages, richness, and composition due to anthropogenic disturbances is likely to reduce ecosystem stability over time drastically (Joseph et al., 2019). Land-use change is now considered the leading source of biodiversity loss in numerous ecosystems including mountains (Soh et al., 2019; Elsen et al., 2020).

The impact of land-use changes on biodiversity and ecosystems has been studied extensively (e.g., Cernusca et al., 1996; Reidsma et al., 2006; Maitima et al., 2009; Butler et al., 2010; Ghaffari et al., 2010; Pabst et al., 2013; Quintas-Soriano et al., 2016) and in recent decades, interest in land-use impact on mountain ecosystems and diversity has increased. Most studies have reported reduced diversity for various taxa. Peters et al. (2019) found that land-use changes in Mount Kilimanjaro decreased animal, plant, and soil microbial diversity especially in the arid low elevations of the mountain. In the central Alps of Italy, Niedrist et al. (2009) showed that ten different land-use types had significantly reduced plant diversity and that composition was also different between the habitats. Shahabuddin et al. (2021) also revealed that bird species decreased due to land-use changes in the Western Himalaya mountain range.

Due to the effects of anthropogenic disturbances on biodiversity, it is important to document the impacts of land-use change on the diversity of native communities. Specifically in mountain ecosystems since they support a significant portion of the global biodiversity and provide important resources and services for many human societies (Laureto et al., 2015). Understanding how arthropods respond to land-use change is crucial for biodiversity conservation and maintenance of some important ecological processes, because arthropods have important ecological roles in the environment. Arthropods perform important functions in terrestrial ecosystems as prey, predators, pollinators, decomposers (Pearson and Derr, 1986; Litt et al., 2014). They are also involved in maintaining soil structure, nutrient cycling, seed harvesting, and dispersal (Attwood et al., 2008). Additionally, arthropods have the ecological qualities to be excellent bioindicators of environmental changes. They are abundant, respond quickly to habitat stress and disturbances, and are relatively easy and cheap to sample (Schwerdt et al., 2018).

When assessing the impact of anthropogenic disturbances on biodiversity, one must focus on taxa and subsystems that may reveal the broader range of consequences and implications of those effects (Bestelmeyer and Wiens, 1996; Andersen, 2019). Moreover, understanding land-use effects are important for policy and decision-making on land management. Therefore, the current study assessed spider and ant species richness and activity patterns along an elevational gradient and varied land-use practices, across two seasons in the western Soutpansberg mountains. We also partitioned the relative contribution of elevation, land-use and seasonality in explaining the variation in spider and ant species richness and activity along the mountain.

## Methods and materials

*Study area*

The study was conducted across the Soutpansberg which is located in the Limpopo province of South Africa. The transect was set at 200 m elevational intervals on the south (mesic) and north (arid) side of the mountain. The altitudinal range is from 800 to 1700 m.a.s.l on both aspects of the mountain. The transect includes 18 sites with diverse habitat structures, which form the diverse landscape of the western Soutpansberg mountains. Four sites on the southern aspects are within the protected area of the Luvhondo Nature Reserve. The mountain range is a center of endemism and is well recognized for its highly diverse habitats (Figure 2.1, Table 2.1). However, some areas along the mountain have been transformed through land-use changes. These changes have seen an increase in agricultural activities, residential areas and alien invasive forests.

At low elevations there are rural human settlements and related infrastructure. Agriculture (crop and cattle farming) is the main economic activity in the region, with some large-scale commercial farms located on both aspects of the mountain. Bushlands, forests and shrublands make up most of the vegetation in Western Soutpansberg, and in some sites mechanical clearing has been used to remove invasive woody vegetation. The natural sites are named according to the elevation and slope/aspect e.g., 10N is 1000 m a. s. l on the northern aspect and 16S is 1600 m a. s. l on the southern aspect. The transformed sites are named after the land-uses of those sites e.g., CL is the cropland (farm) and VIL is the village/human settlement. The elevation and aspect of all the study sites are listed in Table 2.1.

The sites consist of distinct habitat types along the two slopes of the mountain range. In the southern aspect, habitat types include forests, thicket shrubland and alien invasive plantations. The lowest elevational site is a village (VIL), mainly human settlements (Fig 2.2k). It is followed by the cropland (CL), a potato farm (Fig 2.2h); both sites are at 800 m a. s. l. At 900 m a. s. l. there are two sites adjacent to each other, a bush encroached (BE) (Fig 2.2a) and cleared bush site (CBE) (Fig 2.2l) characterized by closed and open shrublands, respectively. The 1000 m a. s. l. site is mostly used for cattle grazing and consists of low thickets (Fig 2.2b). The mid-elevation sites on the southern aspect are made up of both natural and non-native forests, 1200 m a. s. l. (12SA) is a tall forest (Fig 2.2c) while 1200 m a. s. l. (12SB) is a short forest (Fig 2.2d). At 1400 m a. s. l. there are three sites, one natural/untransformed (14SA) and two transformed sites (a blue gum plantation and macadamia orchard). Site 14SA is mainly made up of open woodland (Fig 2.2e). The blue gum plantation (BP) is an abandoned *Eucalyptus* plantation (Fig 2.2i), and the macadamia orchard (MO) which is an orchard farm (Fig 2.2j). The highest site on the southern slope is 16S which is at 1600 m a. s. l and consists of a grassland (Fig 2.2f).

The northern aspect of the mountain is mainly characterized by woodland habitats. The lowest sites which occupy the 800 m a. s. l elevational band are 08NA and 08NB. Site 08NA comprises open and low woodlands (Fig 2.3a). While site 08NB is made up of a shrubland-thicket matrix and is easily distinguishable by red Kalahari sand found at the site (Fig 2.3e). The mid-elevation (1000 m a. s. l and 1200 m a. s. l) sites 10N (Fig 2.3b) and 12N (Fig2.3c) are dominated by rocky and short woodlands. Further up the elevational gradients on the northern aspect are sites 14NA and 14NB. Site 14NA is a semi-arid and sandy woodland (Fig 2.3d), while 14NB is a riverine forest (Fig 2.3f). The summit of the mountain, 1700 m a. s. l. (17N), is mostly a grassland (Fig 2.2g).

Table 2.1 Summary of 18 sites along the elevational gradient with their habitat types and aspects along the western Soutpansberg mountains

| Sites | Aspect | Elevation (m a. s. l) | Elevational zone | Transformation | Land-use type | Vegetation type |
|---|---|---|---|---|---|---|
| Village (VIL) | South | 800 | Low | Transformed | Human settlement | HS |
| Cropland (CL) | South | 800 | Low | Transformed | Cropland | CL |
| Bush encroachment (BE) | South | 900 | Low | Transformed | Bush encroachment | SMMT |
| Cleared bush encroachment (CBE) | South | 900 | Low | Transformed | Cleared bush encroachment | SMMT |
| 10S | South | 1000 | Low | Untransformed | Natural | SMMT |
| 12SA | South | 1200 | Mid | Untransformed | Natural | SF |
| 12SB | South | 1200 | Mid | Untransformed | Natural | SF |
| 14SA | South | 1400 | High | Untransformed | Natural | CMV |
| Blue gum plantation (BP) | South | 1400 | High | Transformed | *Eucalyptus* plantation | SBGF |
| Macadamia orchard (MO) | South | 1400 | High | Transformed | Macadamia orchard | O |
| 16S | South | 1600 | High | Untransformed | Natural | CMV |
| 17N | North | 1700 | High | Untransformed | Natural | LS |
| 14NB | North | 1400 | High | Untransformed | Natural | RF |
| 14NA | North | 1400 | High | Untransformed | Natural | LS |
| 12N | North | 1200 | Mid | Untransformed | Natural | LS |
| 10N | North | 1000 | Low | Untransformed | Natural | LS |
| 08NA | North | 800 | Low | Untransformed | Natural | ANB |
| 08NB | North | 800 | Low | Untransformed | Natural | ANB |

Vegetation type key: ANB: Arid Northern Bushveld, LS: Leached Sandveld, CMV: Cool Mistbelt Vegetation, SF: Soutpansberg Forest, SMMT: Soutpansberg Moist Mountain thicket, SBGF: Soutpansberg blue gum forest, CL: Cropland, O: Orchard, RF: Riverine forest, HS: Human settlement (Mostert et al., 2008).

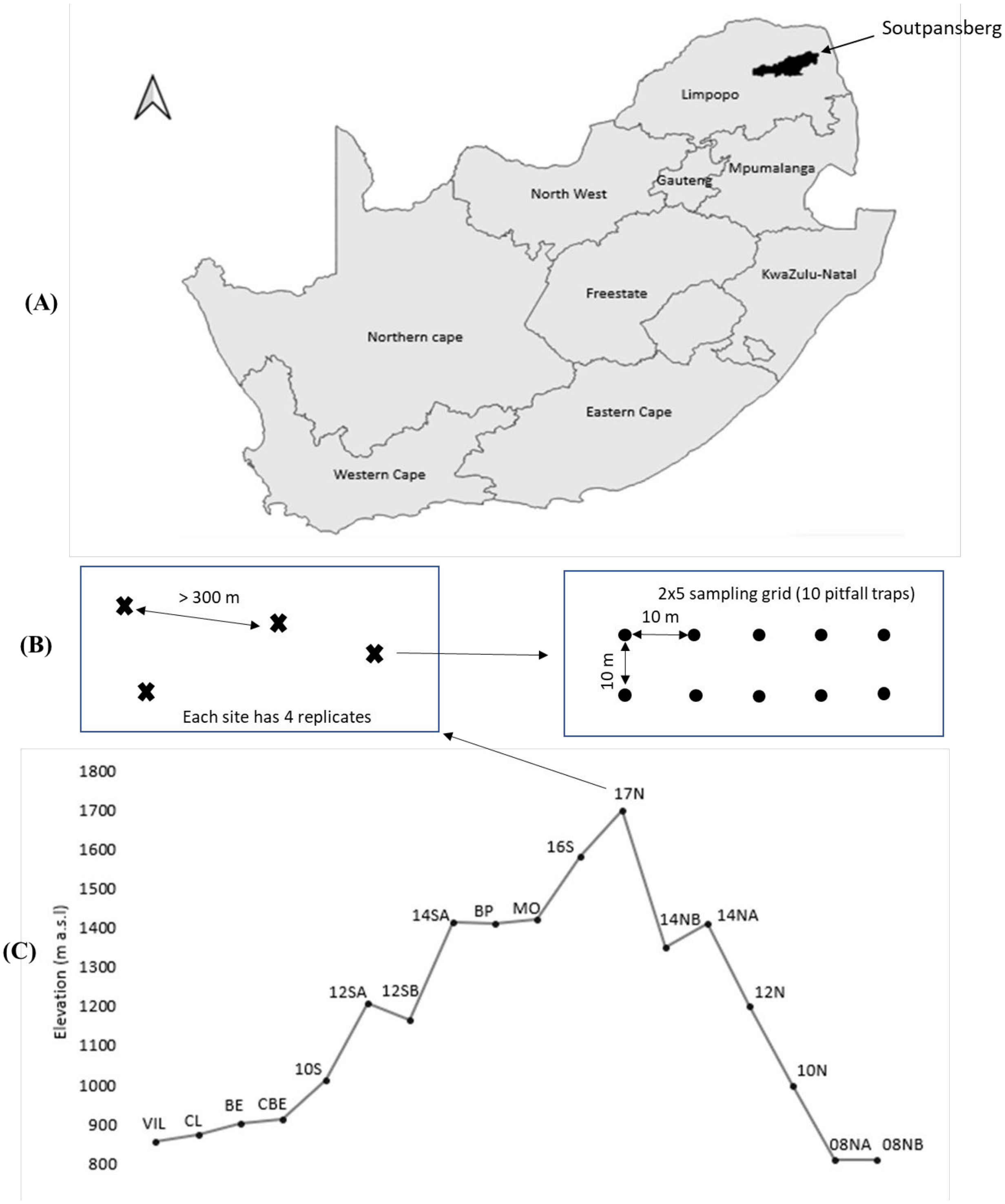

Figure 2.1: (A) location of the Soutpansberg mountains in South Africa, (B) representation of 72 replicates and the 10 laid pitfall traps (720 pitfall traps in total), (C) a sketch showing the 18 sampled sites across the elevational gradient.

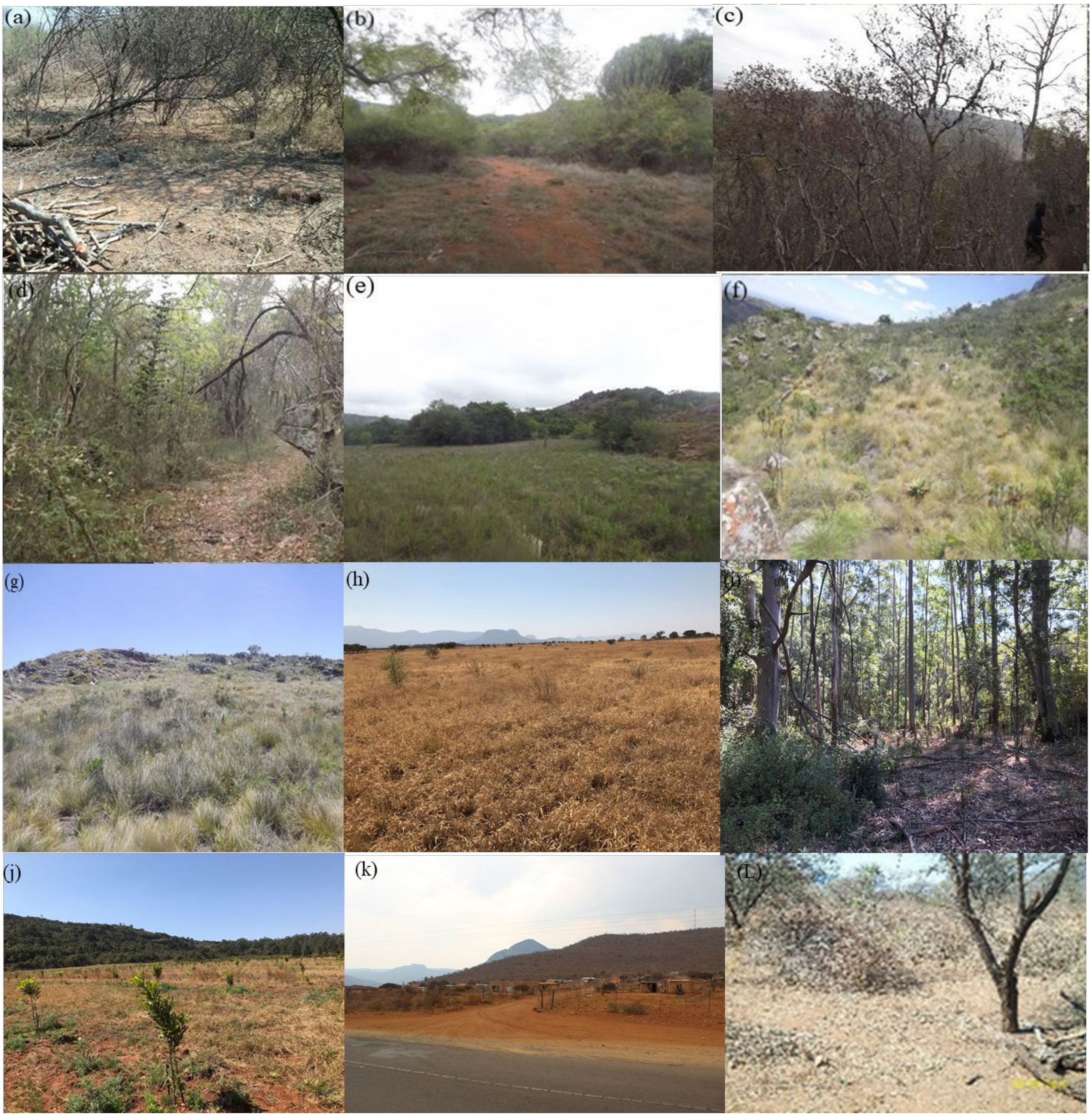

Figure 2.2: Habitat types on the southern aspect of the mountain: (a) BE (Closed Shrubland), (b) 10S (Low Thicket), (c) 12SA (Tall forest), (d) 12SB (Short forest), (e) 14SA (Open woodland), (f) 16S, (g) 17N (Grassland-herbland), (h) CL (Cropland), (i) BP (Blue gum plantation), (j) MO (Macadamia orchard), (k) VIL (Human settlement) and (l) CBE (Cleared Bush Encroachment).

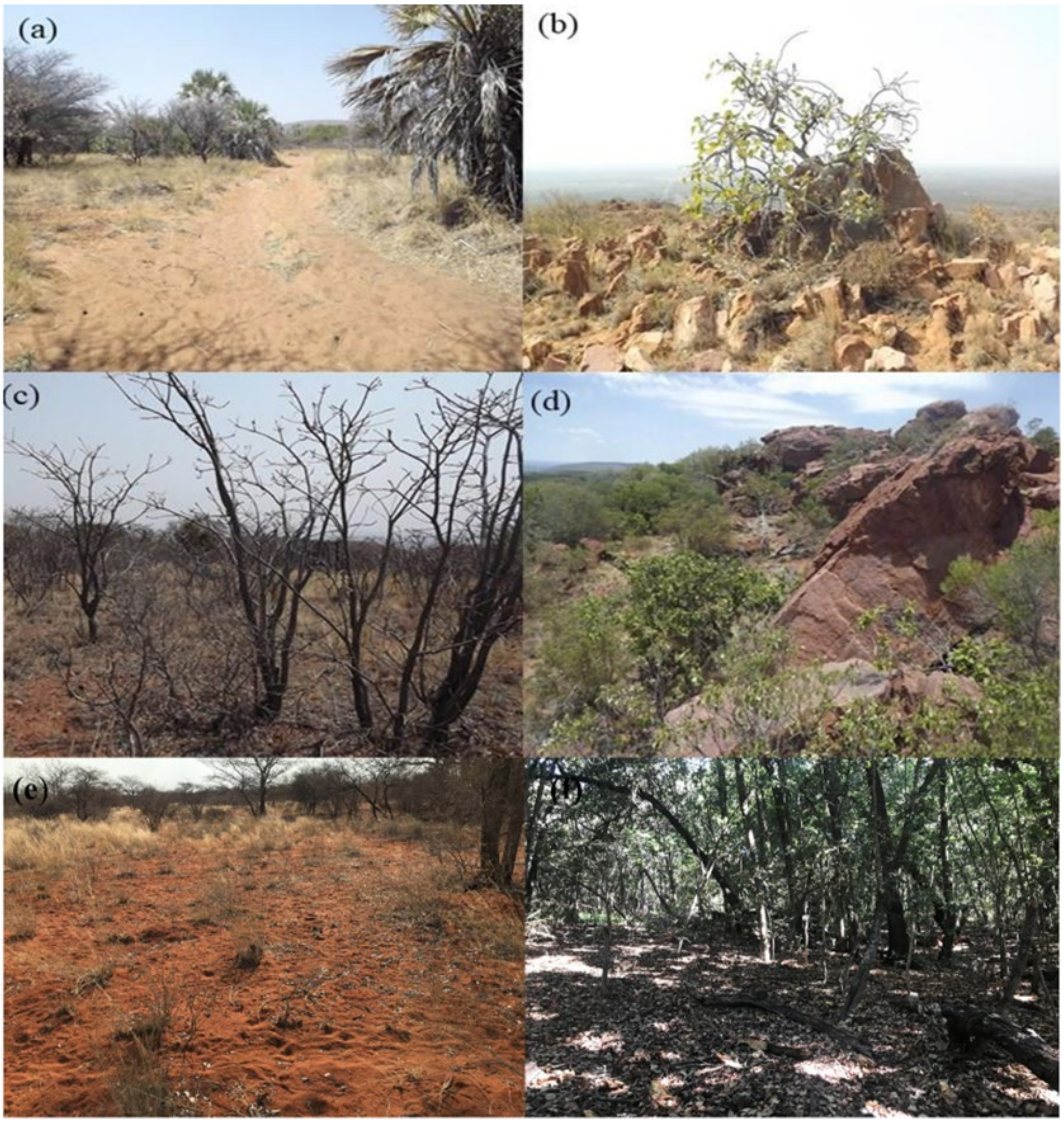

Figure 2.3: Habitat types on the northern aspect of the transect: (a) 08NA (woodland), (b) 10N (woodland), (c) 12N (woodland), (d) 14NA (woodland), (e) 08NB (woodland), (f) 14NB (Riverine forest).

### *Ant and Spider Sampling*

The transect is made up of 18 sites at approximately 200 m elevational distances, with some sites occupying the same elevational band (e.g. 12SA and 12SB). Each site had four replicates that were at least more than 300 m apart. Each replicate had 10 pitfall traps which were placed 10 m apart in a 2 x 5 sampling grid (Figure 2.1). Pitfall traps were made up of small plastic containers with a diameter of 62 mm. The pitfall traps were left open for five days during September 2019 (dry-hot season) and January 2020 (wet-hot season). The pitfall traps contained a 50% propylene glycol solution, which does not attract or repel ants and spiders (Munyai and Foord, 2012). The pitfall traps were washed in the laboratory where the ants and spiders were separated from the other invertebrates and then stored in 70% alcohol. Prof. A.S. Dippennar-Schoeman identified the spiders at the Agricultural Research Council (ARC). Spider specimens were identified to species level where possible, otherwise to genus and then morphospecies. The ants were identified to species level and some to genus level, then morphospecies using Fisher and Bolton (2016) and online databases; viz. AntWiki (http://www.antwiki.org/) and AntWeb (http://antweb.org/).

## Data Analysis

The iNext online program was used to analyse the sample coverage of all the sites on the transect for both taxa (Chao et al., 2016). Sample coverage measures the probability of occurrence of the species observed within a sample or site (Chao et al. 2016). Sample coverage of 0.90 and above indicates that sampling sufficiently represents spider and ant communities in the study sites (Chao et al. 2016). A sample coverage value of one indicates that sampling was complete. The species richness, activity, evenness and Simpson diversity index were modelled using R (R Development Core Team, 2020). In the current study, species activity refers to individuals per trap.

In order to assess how spider and richness and activity varied with land-use, season and elevation, Generalised Linear Mixed Effects Models (GLMM) with Poisson distributions were used. Species richness and activity were set as the response or dependent variables. Land-use types were set as fixed variables, with season and categories as random intercepts. The categories variable is a combination of the aspect and elevation of the sampled sites. Model was ran using lme4 library in R (Pinheiro and Bates, 2016). The data was pooled for all four replicates at each site.

## Results

### *Sample completeness*

The transect sites had a relatively low sample coverage for spiders (0.84±0.08) (Appendix C). The latter suggests that more species could have been found with further sampling. However, the sampling effort was sufficient for the ants as most sites had sample coverage close to one (0.99±0.002) (Appendix C).

### *Taxonomic results*

A total of 2 673 individual spiders were sampled, consisting of 198 species from 105 genera belonging to 40 families. The most abundant families were Ammoxenidae and Gnaphosidae (Appendix A). They comprised 28% and 23% of the total spider abundance, respectively. Family Gnaphosidea was also the most species rich with 45 species. The second most specious family was Salticidae, which consisted of 24 species (Appendix A). Families Entypesidae, Eresidae, Filistatidae, Hersilidae and Orsolobidae were the least diverse, as they all had just one individual per species (Appendix A). In terms of genera, *Ammoxenus* and *Asemesthes* (Gnaphosidae) were the most abundant with 28 % and 11% of the total abundance, respectively (Appendix A). The genus *Zelotes* (Gnaphosidae) was the most species rich of all the genera with nine species, followed by *Asemesthes* (Gnaphosidae) with eight species (Appendix A).

A total of 49 735 ant specimens from six subfamilies, 41 genera and 128 species were collected along the transect (Appendix B). Subfamily Myrimicinae consisted of 71% of the abundance and 54% of the species, while Formicinae accounted for 27% abundance and 28% species. Subfamily, Pseudomyrmicinae was the least abundant (2 specimens) and one species (Appendix B). The most abundant genera in the transect were *Pheidole* (30%) and *Monomorium* (23%), while *Tetramorium* had the most species (16%), followed by *Camponotus* and *Monomorium* (both 11%) (Appendix B). The least represented genera were *Acropyga* and *Strumigenys*, with only a single individual each. *Anoplolepis custodiens* (22%) and *Pheidole sp. 05* (*megacephala* gp.) (10%) were the most abundant species (Appendix B).

*Spider species richness, activity and evenness: Land-use, Elevation and Season*

The macadamia orchard, cropland and human settlement had significantly higher spider species richness (Table 2.2). The model shows that overall land-use explained only 18 % of the variation in spider richness (Table 2.4). With elevation, aspect and season only explaining 3 % of the variance in spider species richness (Table 2.4). The low elevation sites also recorded the highest spider richness on both aspects (Figure 2.4a). The general trend shows that spider richness was higher in the dry season (Figure 2.4a).

Spider activity was significantly higher at the macadamia orchard and cleared bush encroachment sites and according to the GLMM model, 63 % of the variation in spider activity was explained by land-use (Table 2.3; Table 2.4). While season, aspect and elevation only accounted for 22 % of the variation in spider activity (Table 2.4). Spider activity peaked in the low elevation zone for both aspects (Figure 2.4b). Overall, the dry season also had higher spider activity (Figure 2.4b).

Spider evenness was highest at sites 14NB and 12N, while the cleared bush encroachment and cropland recorded the lowest species evenness of all the sites (Figure 2.4c). Spider evenness was higher in dry season (Figure 2.4c).

*Ant species richness, activity and evenness: Land-use, Elevation and Season*

Ant species richness was highest in the cleared bush encroachment site, and significantly low in the blue gum plantation (Table 2.2). Ants were more sensitive to transformation, with land-use explaining 31 % of the variation in ant species richness (Table 2.4). Model shows that season, aspect and elevation explained 24 % of the variance in ant species richness (Table 2.4). Ant species richness peaked in the mid-elevation sites on the southern aspect and decreased with elevation on the northern slope (Figure 2.5a). Ant species richness was higher in the wet season (Figure 2.5a).

Ant activity was highest in the cropland and human settlement, while the blue gum plantation had significantly low ant activity (Table 2.3). Overall land-use explained 54 % of variation in ant activity while season, aspect and elevation explained only 45 % combined (Table 2.4). In the wet season ant activity also declined with elevation on the southern aspect and increased with increasing elevation on the northern aspect (Figure 2.5b). Ant activity was higher in the wet season (Figure 2.5b).

Ant species evenness was highest at sites 10N and 17N and the lowest evenness was at 14NB and the cropland (Figure 2.5c). The dry season had higher ant evenness (Figure 2.5c).

Table 2.2: Summary of Generalized Linear Mixed Model (GLMM) for ant and spider species richness along the Soutpansberg elevational gradient.

| | **Predictor variable** | **Estimate** | **Std. Error** | **z value** | **Pr(>\|z\|)** |
|---|---|---|---|---|---|
| **Spiders** | (Intercept) | 0.86 | 0.24 | 3.58 | < 0.0001 *** |
| | Cleared bush encroachment | 0.38 | 0.30 | 1.30 | 0.19 |
| | Cropland | 0.88 | 0.27 | 3.24 | < 0.0001 *** |
| | Eucalyptus plantation | 0.15 | 0.31 | 0.47 | 0.64 |
| | Human settlement | 0.58 | 0.29 | 1.97 | 0.05 |
| | Macadamia orchard | 1.17 | 0.26 | 4.44 | < 0.0001 *** |
| | Natural | 0.60 | 0.23 | 2.54 | 0.01 * |
| | **Predictor variable** | **Estimate** | **Std. Error** | **z value** | **Pr(>\|z\|)** |
| **Ants** | (Intercept) | 2.70 | 0.20 | 13.44 | P < 0.0001 *** |
| | Cleared bush encroachment | 0.23 | 0.12 | 1.93 | 0.05 |
| | Cropland | 0.18 | 0.12 | 1.47 | 0.14 |
| | Eucalyptus plantation | -0.94 | 0.24 | -3.98 | P < 0.0001 *** |
| | Human settlement | 0.09 | 0.13 | 0.75 | 0.45 |
| | Macadamia orchard | -0.36 | 0.22 | -1.63 | 0.10 |
| | Natural | -0.23 | 0.18 | -1.27 | 0.21 |

Table 2.3: Summary of Generalized Linear Mixed Model (GLMM) for spider and ant activity along the elevational gradient.

| | **Predictor variable** | **Estimate** | **Std. Error** | **z value** | **Pr(>\|z\|)** |
|---|---|---|---|---|---|
| **Spiders** | (Intercept) | 1.80 | 0.39 | 4.62 | < 0.0001 *** |
| | Cleared bush encroachment | 1.06 | 0.17 | 6.38 | < 0.0001 *** |
| | Cropland | 2.72 | 0.15 | 18.42 | < 0.0001 *** |
| | Eucalyptus plantation | -0.10 | 0.43 | -0.23 | 0.82 |
| | Human settlement | 0.67 | 0.17 | 3.75 | < 0.0001 *** |
| | Macadamia orchard | 1.52 | 0.40 | 3.77 | < 0.0001 *** |
| | Natural | 0.33 | 0.38 | 0.86 | 0.39 |
| | **Predictor variable** | **Estimate** | **Std. Error** | **z value** | **Pr(>\|z\|)** |
| **Ants** | (Intercept) | 5.23 | 0.50 | 10.44 | < 0.0001 *** |
| | Cleared bush encroachment | 0.47 | 0.03 | 15.20 | < 0.0001 *** |
| | Cropland | 2.22 | 0.03 | 85.94 | < 0.0001 *** |
| | Eucalyptus plantation | -1.44 | 0.39 | -3.65 | < 0.0001 *** |
| | Human settlement | 0.75 | 0.03 | 25.24 | < 0.0001 *** |
| | Macadamia orchard | 0.48 | 0.39 | 1.23 | 0.22 |
| | Natural | 0.03 | 0.39 | 0.08 | 0.94 |

Table 2.4: Variation partitioning for spider and ant species richness and activity based on the Generalized Linear Mixed Model (GLMM).

| Response variable | Taxa | Marginal | Conditional |
|---|---|---|---|
| Species richness | Spiders | 0.18 | 0.21 |
| | Ants | 0.31 | 0.55 |
| Activity | Spiders | 0.63 | 0.85 |
| | Ants | 0.54 | 0.99 |

Key: Marginal: Land-use type; Conditional: Land-use type, season, elevation and aspect

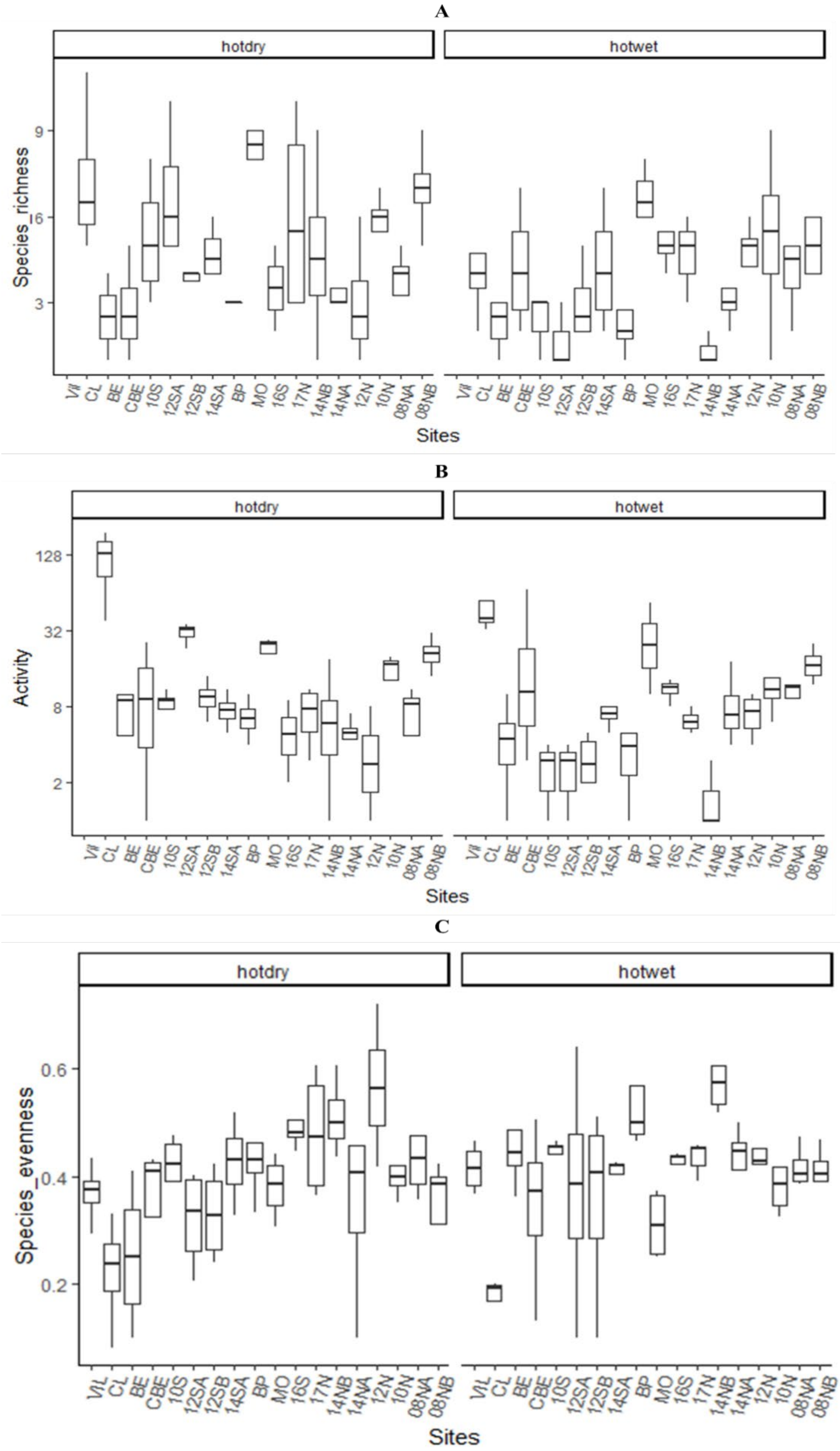

Figure 2.4: Spider species richness **(A)**, activity **(B)** and species evenness **(C)** across the Soutpansberg elevational transect in the dry (2019) and wet season (2020).

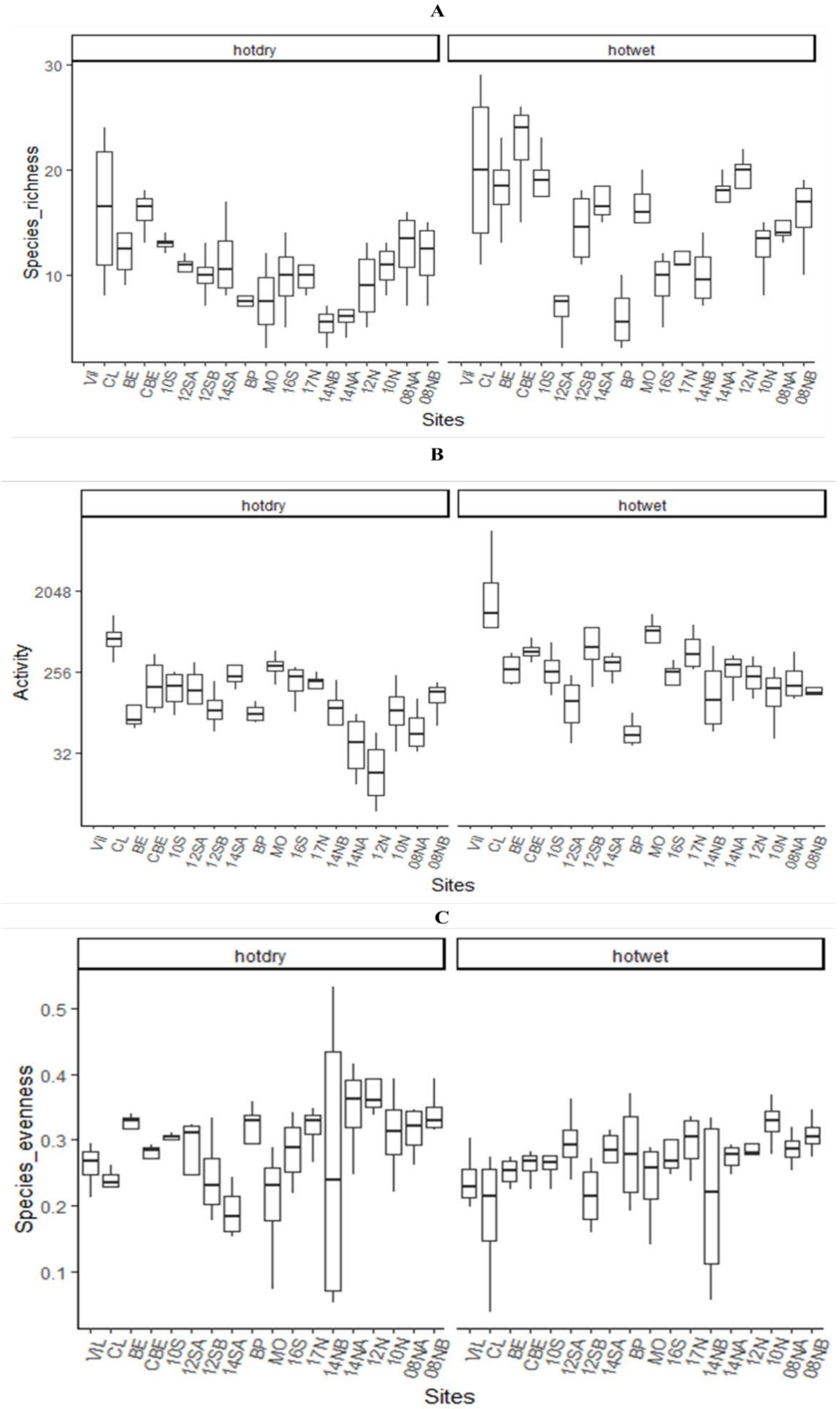

Figure 2.5: Ant species richness **(A)**, activity **(B)** and species evenness **(C)** across the Soutpansberg elevational transect in dry (2019) and wet season (2020).

## Discussion

### *Impact of land-use change*

Our results show that the different land-use practices in Soutpansberg had an impact on spider and ant diversity. Overall, the transformed sites had higher spider and ant diversity than the untransformed sites. Particularly the agricultural sites, human settlement, and mechanically bush cleared site. This was unexpected since agricultural management is regarded as one of the main drivers of the global insect decline (Wagner, 2020). Numerous studies have shown the negative impact of agriculture on arthropod diversity. For instance, Hendrickx et al. (2007) reported decreased arthropod species richness with increasing land-use intensity in 24 agricultural landscapes in seven temperate European countries. The arthropod taxa assessed included beetles, wild bees, and spiders (Hendrickx et al., 2007). In northeastern South Africa, Mauda et al. (2018) compared ant diversity between cropland, human settlement, and rangeland in open savanna. Ant species diversity was significantly lower at the cropland and human settlement (Mauda et al., 2018). Reduced habitat heterogeneity, alteration of prey communities, pesticides and the direct destruction of species communities are the main sources of reduced spider and ant diversity in agricultural ecosystems (Prieto-Benítez and Méndez, 2011; Apolinário et al., 2019; Dalle Laste et al., 2019).

However, low and moderate-intensity agro-ecosystems may promote arthropod richness and activity (Reidsma et al., 2006). The abundance of vegetation and pests in agro-ecosystems provides spiders and ants with shelter, food and other essential resources (Wielgoss et al., 2014). According to Bengtsson et al. (2005), organic agricultural systems, which are less intensively managed, tend to impact species richness and activity positively. Plants, birds, and insects show high abundance and richness in organic farming units (Bengtsson et al., 2005; Masoni et al., 2017). In contrast, over-simplified agro-ecosystems that are solely dependent on artificial inputs are not ecologically sustainable (Attwood et al., 2008). However, in this study the impact of agricultural land-use was positive on spider and ant richness and activity. Perhaps owing to the fact that the agricultural impacts in the current study are highly localized with natural landscapes still dominating the mountain range.

The village site also positively affected arthropod diversity, with spider and ant activity exceptionally high. The loss of habitat area and the replacement of native vegetation with infrastructure and/or non-native plants for landscaping are major impacts of human encroachment in natural environments (McKinney, 2008). These effects can drastically reduce local diversity and even lead to extinctions (Czech et al., 2000). However, the intensity of urbanization also influences the response of species (Melliger et al., 2018). At high intensities, urbanization almost always decreases species richness across multiple taxa. At low and intermediate levels of development, urbanization can increase species richness, especially in plants and invertebrates (McKinney, 2008). This may explain the high species richness and activity at the human settlements for both taxa. Magura et al. (2010) found that epigeic spider richness was significantly higher in urban and semi-urban sites compared to the native sites in Hungary. Another study compared ant diversity between a conserved forest and the surrounding residential areas and similarly, the residential sites had higher ant species richness than the forest sites (Lessard and Buddle, 2005).

Interestingly, both studies (Magura et al., 2010 and Lessard and Buddle, 2005) reported that the high diversity at disturbed sites was influenced by an increase in open-habitat and habitat generalist species. According to the habitat alteration hypothesis, changes in habitat structure due to anthropogenic disturbances increase open-habitat and habitat generalist species (Magura et al., 2004). The influx of these species from surrounding habitats leads to a decrease in native and habitat specialist species. Indeed, the high local species richness that some urban areas show tends to be at the cost of native species due to increased colonization by non-native and introduced species (McKinney, 2008; Elmqvist et al., 2016). Non-native species can have a detrimental impact on local ecosystem processes and services by exerting changes on food webs, resource availability, species interactions and competition (Kenis and Branco, 2010). Therefore, the high species richness and activity may result in unwanted aftereffects on the Soutpansberg ecosystems.

Arthropod diversity was also high at the bush cleared site, particularly the ant species. Studies show that vegetation cover and structure play an important role in the diversity and composition of spiders and ants (Hatley and Macmahon, 1980; Zakkak et al., 2014; Joseph et al., 2018; Nooten et al., 2019). The Soutpansberg bushvelds have already been categorized as “vulnerable” due to the rise of land-use changes in the area (Mucina and Rutherford, 2006; Munyati and Kabanda, 2009). It is widely accepted that reducing vegetation cover and complexity is one of the main reasons for decreased arthropod diversity in disturbed habitats (Bestelmeyer and Wiens, 1996; Nakamura et al., 2007; Meloni et al., 2020). Therefore, the increased clearing of vegetation raises concerns. Furthermore, the long term impacts of clearing vegetation on arthropod diversity along the mountain is unclear, despite the high diversity in cleared sites. However, reduced vegetation structure can also increase spider and ant diversity through increased micro-climate and habitat favorability for certain species (Bestelmeyer and Wiens, 1996). Hence, the same disturbance can either be advantageous or detrimental if it increases or decreases habitat favorability. For instance, arid-adapted species are likely to respond positively to clearing compared to shade-adapted species (Andersen, 2019). While bush encroachment is likely to decrease the richness and abundance of open habitat species (Zakkak et al., 2014).

In some cases, disturbances can increase the spatial heterogeneity of an area, which tends to promote species richness for many taxa (Ruggiero and Hawkins, 2008**;** Bernadou et al., 2013). According to Andersen (2019), some ant species prefer open habitats, meaning they are likely to respond positively to habitat disturbances (Munyai and Foord, 2012; Andersen, 2019). In Australia, such ant species mostly include hot-climate specialists, dominant Dolichoderinae, generalised Myrmicinae and opportunist functional groups (Andersen, 2019). A preference for open areas has also been shown for spiders. In a study on a mountain in Canada, Koponen (1987) showed that spider diversity was highest in open habitats and lowest at the forest sites. Muff et al. (2009) assessed spider assemblages between an alpine pasture and forest and found that spider species preferred an open-area habitat to a forested one. Interestingly, the intermediate areas produced a positive ecotone effect, by providing a combination of both habitats which benefited more species than either habitat (Muff et al., 2009).

Therefore, the intermediate disturbance hypothesis may explain the increased arthropod diversity in the disturbed sites. According to this hypothesis, local species diversity is maximized or increased significantly at intermediate levels of disturbance or stress (Connell, 1978). If the disturbance is not intense and frequent enough to remove all local species but enough to allow the entry of habitat generalists, disturbance-tolerant, and edge specialists, species richness will increase (Townsend et al., 1997; Swart et al., 2019). Therefore, the magnitude and type of habitat disturbance is an important factor, as it influences the response of species communities to land-use changes (Frishkoff et al., 2019). It is also important to note that much of the study area is still untransformed in the current study, and this has also influenced the response of arthropod communities. At low disturbance levels, dominant species are likely to drive other species out and the area also becomes encroached. Whereas at highly disturbed ecosystems, both early and late-successional species are at risk of extinction (Townsend et al., 1997).

Furthermore, the land-use practices at Soutpansberg are likely facilitating the entry and colonization of these sites by disturbance-tolerant species. Therefore, it is likely that transformed sites with high diversity are mostly dominated by non-native and disturbance-tolerant species capable of replacing native species at high rates. Previous studies have also used the intermediate hypothesis to explain the response of arthropod diversity to anthropogenic disturbances (Vonshak and Gordon, 2015; Tajthi et al., 2017; Swart et al., 2019). The high biodiversity and landscape complexity of Soutpansberg may also be alleviating the impact of the habitat disturbances occurring across the mountain since most of the transformed area is surrounded by the natural landscapes. Therefore, the observed diversity at the transformed sites may be a result of species filtering from the relatively pristine surrounding landscapes. Despite the significantly higher species richness and activity in the transformed sites, species evenness was extremely low in these sites for both taxa, particularly the cropland and cleared sites. This indicates that a few species dominate these sites, which further demonstrates that the disturbance in the area is increasing the proportional abundance of disturbance-tolerant species.

Ant species richness and activity were the lowest in the *Eucalyptus* plantations. The impact of *Eucalyptus* plantations on faunal diversity varies with taxa, age of plantation, and environmental context (Wolf and DiTomaso, 2017; Garcia and Clusella-Trullas, 2017). Despite this, *Eucalyptus* and other invasive plants are widely regarded as detrimental to arthropod biodiversity (Ashman and Watchorn, 2019). The low ant diversity at the *Eucalyptus* plantation in the current study may be a result of the closed canopy at the site, which reduces light availability and temperature, both of which influence ant diversity and distribution. Furthermore, the plantations in the study had highly specialized microhabitats with structurally poor ground vegetation and abundant leaf litter, which suggests that only specialized species can persist in those conditions. Similarly, Zahn et al. (2009) reported that ground arthropods diversity was lowest in the *Eucalyptus* plantation compared to other land-uses in Portugal. Also, in a recent study in the midlands of the KwaZulu-Natal province, Munyai et al. (2021) also reported low ant species richness in a *Eucalyptus* plantation compared to grassland and forest sites. *Eucalyptus* plants can alter the soil attributes, light and water availability and some studies have shown the negative relationship between invertebrate diversity and these plantations (Ratsirarson et al., 2002; da Silva et al., 2008).

Spider and ant evenness was lower in the transformed sites, which was indicated by species dominance. Dominance can play a crucial role in species diversity and community dynamics (Kimbro and Grosholz, 2006; Kwon et al., 2014). For instance, the presence of dominant species can alter species interactions and ecosystem process (Hillebrand et al., 2008). Also, the distribution of functional groups or traits within a community is influenced by the dominance distribution of species (Hillebrand et al., 2008). Furthermore, changes to traits within a community due to dominance can also negatively affect community stability, by reducing the resistance and resilience of a community to disturbances and invasions (Beiroz et al., 2014). Which indicates that the transformed sites are increasing the likelihood of ecosystem instability in the study area. Unstable ecosystems are not sustainable for species as extinctions become more frequent (Cleland, 2011). Evenly distributed communities are likely to make an ecosystem more resilient to stress and disturbances as the risk of losing an essential function or service is much lower (Hillebrand et al., 2008). Furthermore, communities with even species distributions tend to be more productive due to better exploitation of resource-based niches (Norberg et al. 2001; Genung et al., 2020). The most even arthropod communities were found in the sites with the least human interference and contact, including sites 10N, 12N, 14NA, 14NB. This suggests that land-use changes in the Soutpansberg region are creating unstable habitats, with a few species displaying dominance.

*Impact of elevation and seasonality*

Spider species richness and activity was higher in the low elevation sites for both aspects. Lower elevations tend to have more geographic area and higher primary productivity (Lawton et al., 1987), which may have influenced the pattern. Elevational bands with larger areas tend to have higher species diversity (Terborgh 1973; Rosenzweig 1992). Increased areas are likely to have more habitats available, which increases the chances of having species from neighboring habitats (Sanders, 2002). Also, larger areas have higher species richness owing to lower extinction rates. Furthermore, high species richness and activity at lower elevations has been reported in various other studies investigating the impact of altitude on ant diversity (Sanders, 2002, Bishop et al., 2014).

Contrastingly, ant species richness and activity were higher at mid elevational sites, the native tall forest and arid woodland. Similarly, previous studies on ant communities on the same transect reported a mid-elevation peak on the northern aspect and higher ant richness at the lower elevations on the southern aspect (Munyai and Foord, 2012; Munyai and Foord, 2015). The mid elevation peak is a commonly reported pattern for ant diversity studies along elevational gradients (Samson et al., 1997; Warne, 2013; Smith et al., 2014). The mid-domain effect and elevational climate models explain the mid-elevation peak in montane species (Szewczyk and McCain, 2016). The mid-domain effect states that species tend to overlap at the centre of a constrained domain in terms of distributional ranges, therefore, creating an abundance of species in the central parts of the domain (Colwell and Lees, 2000, McCain, 2009). The climate model explains the mid-elevation peak due to water and temperature restrictions at the base and summit of the mountain, respectively (Szewczyk and McCain, 2016). The high elevations displayed low arthropod diversity as expected. Higher elevations tend to have less geographical area which limits the number of biological populations and consequently the species diversity (Szewczyk & McCain, 2016). Furthermore, high elevation habitats are characterized by high fluctuations in temperatures and other environmental variables which means that only species that are highly adapted for those conditions can survive in those sites (Oyen et al., 2016)

Although the impact of seasonality on spider and ant diversity was minimal, both taxa showed interesting and varying seasonal patterns, which is predictable since both taxa are ectotherms (Barghusen et al., 1997; Entling et al., 2010; Pincebourde and Suppo, 2016; Fontanilla et al., 2019). By selecting specific times to be active during the day or even year, spiders and ants can consequently show different seasonal diversity patterns (Jayatilaka et al., 2011). Spider species richness and activity was higher in the dry season. Previous studies have shown that seasonality can greatly influence spider diversity. For instance, Campuzano et al. (2020) reported the lowest species richness in the dry season for spiders in a tropical mountain. In a Brazilian savanna, Mineo et al. (2010) also found that spider richness and abundance were highest in the wet season due to severe dry seasons.

The high spider diversity during the dry season (September to October, which in spring in the region) may be a result of increased activity and foraging by male spiders in search of females, which subsequently increases the probability of being trapped (Marques et al., 2017; Li and Jackson, 1996; Pearson and Derr, 1986). Ant species richness and activity were higher in the wet season. This is common in ant communities and similar studies of ants where seasonality was explored as a potential predictor for ant diversity and composition (Parr et al., 2004; Bishop et al.2014, Munyai and Foord, 2015). Ant species are most abundant and active during the summer rainfall periods (Munyai and Foord, 2015). These periods allow for longer foraging and has higher water availability (Szewczyk and McCain, 2016). Longer periods of foraging result in increased activity and a higher probability of being captured during sampling.

Overall, the results show that habitat transformations can positively impact on arthropod diversity and the response of both taxa to land-use practices supports the intermediate disturbance hypothesis. Interestingly, ants appear to be more sensitive to land-use change than spiders. Spiders seem less sensitive and respond more positively to land-use, particularly the cleared bush sites where bare ground is higher. Although the land-use change at Soutpansberg seems suitable for arthropod colonization, the potential to sustain populations over the long term is unknown. Therefore, further assessments and monitoring of diversity in the region are required to understand the long-term impact of land-use changes.

### *Conclusions*

The findings in this study contrast our assumptions and the majority of literature on the impacts of anthropogenic disturbances. Land-use practices generally decrease species diversity, primarily through habitat loss, fragmentation, and the reduction of ground cover (Maeto and Sato, 2004; Frishkoff et al., 2019). The results suggest that the transformed sites consist mostly of disturbance-tolerant species which are often habitat generalist species. However, the current chapter does not offer enough proof for this proposition. Furthermore, the proportion of habitat generalists species was not analyzed as there is not enough known about the biology of local species, as illustrated by the morphospecies in the species lists in the appendix (Appendix A and B). In the next chapter, the identities and composition of species in the transformed sites and natural sites are compared.

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# CHAPTER 3: The response of species composition of local assemblages to a gradient of land-use and elevation in Soutpansberg, Limpopo.

## Abstract

One of the most important goals in modern ecology is understanding and predicting the impact of global change and its drivers on ecological communities. Which involves understanding how ecological communities are assembled and distributed. The response of spider and ant communities were compared by land-use, elevation and season in western Soutpansberg mountains, and species that can be used as indicators for monitoring land-use in the area were identified. Standardized sampling using pitfall traps were used to sample ants and spiders in 18 sites across the elevational gradient in the dry and wet seasons. Majority of the sampled sites are relatively natural while others have undergone transformations through land-use changes including agriculture, human settlements and alien plantations. Spider and ant community composition was highly distinct between the transformed and untransformed sites, and between the elevational zones. Ant communities remained similar between the seasons while spider assemblages differed slightly from the dry to wet season. Two ant species, *Monomorium damarense* and *Lepisiota* sp.02 (*spinosior* gp.), were highly linked to the transformed sites while a spider species, *Copa flavoplumosa* was an indicator for the *Eucalyptus* plantations. Spider assemblages at Soutpansberg are influenced mainly by habitat structure while ant communities are mostly shaped by season. Spiders are highly sensitive to the spatial factors since they provide shelter and prey. While ants were are more responsive to microclimate, since they are a generally thermophilic taxon. Overall land-use had the most influence on spider and ant composition.

Keywords: land-use change, mountains, ants, spider, activity, composition, indicator species

## Introduction

Community composition, which refers to the identity and contribution of all the different species that make up a community as defined in Billhermer et al. (2001) and Downing (2005), is one of the most common and robust measures of biodiversity in ecology (Lamont, 1995). The composition of species assemblages can reflect the basic features of the environment or landscape because certain species only occupy certain environments (Lawler, 1993; Philippi, 1998). For that reason, studying community composition is particularly useful for comparing biodiversity and ecosystem dynamics between two or more regions (Hore and Unival, 2008; Zeller et al., 2017). Important ecological phenomena such as species interactions, habitat use, competition, population, and community dynamics can be analyzed using community composition and assembly (Rajaniemi et al., 2009; Timm and McGarigal, 2013; Aggemyr et al., 2018).

Understanding how ecological communities are assembled and distributed is a central theme in community ecology. It entails knowledge and understanding of processes that shape the identity and abundance of species within the communities. These processes can be characterized as either biotic or abiotic factors, and their influence on community structure is strong at both the local scale and landscape scale (Weibull and Östman, 2003; Schaffers et al., 2008). There is a set of hierarchical biotic and abiotic filters that species must overcome to survive in any given habitat (Schofield et al., 2016). Biotic and abiotic processes can therefore enhance habitat suitability and trait similarities that shape the composition of species communities (Srinivasan et al., 2019). Subsequently, any changes in community composition and structure at any given area over a period can be used to track and characterise environmental changes or disturbances (Carreño-Rocabado et al., 2012). This is essential for identifying and prioritizing areas for conservation actions (Timm and McGarigal, 2013; Angulo et al., 2016). This is particularly useful when considering the impact of anthropogenic activities which is now more evident and concerning than at any other time in human history on earth.

Humans are now the driving force behind global biodiversity loss. Larger human populations have resulted in increased land-uses such as urbanization and agriculture (Newbold, 2018). Unlike other environmental disturbances such as fire, drought, and flooding, land-use change led to more permanent biodiversity loss (Cleland et al. 2011; Prieto-Benítez and Méndez, 2011). The loss of populations and biodiversity due to human activities is the main threat of the Anthropocene (Wagner et al., 2021). Furthermore, land-use changes have resulted in modified and fragmented habitats (Lowe et al., 2018), and the loss of certain ecosystem services and functions (Patterson and Atmar, 2000; Polasky et al., 2011). Studies estimate that in the 19th and 20th centuries terrestrial ecological assemblages experienced a rapid decrease in species richness and abundance (Newbold et al., 2015). By 2005, it is estimated that ecological assemblages had been reduced by 13.6 % (Newbold, 2018). Such changes in community assemblages can deteriorate trophic systems and interspecies interactions (Cernusca et al., 1996; Lowe et al., 2018; Carrick and Forsythe, 2020). This can disturb the balance of an ecosystem (Joseph et al., 2018). Hence there is a growing need to maintain the ecological stability and integrity of natural and transformed ecosystems, and to do so, biological communities must be evaluated (Philpott et al., 2006; Beiroz et al., 2014). Studies show that anthropogenic activities are increasingly modifying ecological assemblages. Due to land-use changes, significant shifts in community composition and diversity have been observed in numerous taxa. For instance, major land-use impacts have been shown in plant (O'Connor, 2005), mammal (McCarthy et al., 2021), arthropod (McIntyre et al., 2001) and bird (Boren et al., 1999) communities.

The impact of land-use changes on arthropods in particular needs more focus and scrutiny as research shows that invertebrate species are declining rapidly worldwide (Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020). Also, habitat changes resulting from land-use are the leading cause of the decline in arthropod abundance and diversity globally. Therefore, the conservation of arthropods threatened by land-use is a timely and pressing issue (McIntyre et al., 2001; Wagner et al., 2021). Furthermore, arthropods perform important ecological roles, so their decline can have catastrophic effects on ecosystem functioning and stability (Attwood et al., 2008; Philpott et al., 2014). They are essential for decomposition, pollination, food web dynamics, nutrient cycling and redistribution (Pearson and Derr, 1986; Barton et al., 2017). Arthropods are highly abundant, allowing for large sample sizes and higher statistical power (Fontanilla et al., 2019). Compared to less abundant and large animals, arthropods are easier and cheaper to sample/capture (Hendrickx et al., 2007; Lingbeek et al., 2017). Arthropods also have the capacity to respond quickly to the rapid pace of land-use change because of short generation times and sensitivity to habitat changes (McIntyre et al., 2001; Yekwayo et al., 2016). However, there are also disadvantages to using arthropods in such studies such as the general difficulty of identification and a lack of knowledge on the biology of certain groups.

Ants form an exceptionally diverse, ubiquitous and abundant group and make up a large portion of the animal biomass (Fontanilla et al., 2019). They are regarded as ecosystem engineers due to their ability to influence resource availability (Drummond and Choate, 2011; Kaspari et al., 2011). Ants also have substantial influence over the structure of invertebrate assemblages, seed dispersal and soil formation (Folgarait, 1998, Del Toro et al., 2012, Flores et al., 2018). As model taxa, their response to disturbance is informative and useful for conservation and ecosystem management (Hoffman, 2000; Hethcoat et al., 2019). Spiders are often the most abundant and diverse predatory animal group in any given terrestrial habitat. They play important roles in both natural and transformed ecosystems by structuring arthropod communities and regulating pest populations (Sunderland and Samu, 2000; Wu et al., 2009; Barton et al., 2017). Spiders are highly responsive to changes in habitat and vegetation structure (Cobbold and MacMahon, 2012; Zakkak et al., 2014; Schwerdt et al., 2018).

Seasonality is an important factor in ecology as it can regulate and maintain the diversity of ecological communities (Weeks and Holtzer, 2000). It can also affect habitat complexity, food and resource availability (Mineo et al., 2010). These factors are essential for animal diversity because animal activity is heavily dependent on them, and this means seasonal variations can influence biodiversity measures (Liu et al., 2013). Therefore, it is crucial to account for seasonality when examining biodiversity (Mineo et al., 2010).

In the current study, we compare ant and spider community composition between different land-use types across the Soutpansberg mountain range, which is recognised as a center of endemism located in the north-eastern part of South Africa (Van Wyk and Smith, 2001; Mostert et al., 2008). The study also investigates the impact of elevation and season in shaping ant and spider community structure. Indicator species associated with the different land-use types, elevational zones, and aspects were also identified.

## Methods and Materials

### *Study area*

The study was conducted across the Soutpansberg which is located in the Limpopo province of South Africa. The transect was set at 200 m elevational intervals on the south (mesic) and north (arid) side of the mountain. The altitudinal range is from 800 to 1700 m.a.s.l on both aspects of the mountain. The transect includes 18 sites with diverse habitat structures, which form the diverse landscape of the western Soutpansberg mountains. Four sites on the southern aspects are within the protected area of the Luvhondo Nature Reserve. The mountain range is a center of endemism and is well recognized for its highly diverse habitats (Figure 2.1, Table 2.1). However, some areas along the mountain have been transformed through land-use changes. These changes have seen an increase in agricultural activities, residential areas and alien invasive forests.

At low elevations there are rural human settlements and related infrastructure. Agriculture (crop and cattle farming) is the main economic activity in the region, with some large-scale commercial farms located on both aspects of the mountain. Bushlands, forests and shrublands make up most of the vegetation in Western Soutpansberg, and in some sites mechanical clearing has been used to remove invasive woody vegetation. The natural sites are named according to the elevation and slope/aspect e.g., 10N is 1000 m a. s. l on the northern aspect and 16S is 1600 m a. s. l on the southern aspect. The transformed sites are named after the land-uses of those sites e.g., CL is the cropland (farm) and VIL is the village/human settlement. The elevation and aspect of all the study sites are listed in Table 2.1.

The sites consist of distinct habitat types along the two slopes of the mountain range. In the southern aspect, habitat types include forests, thicket shrubland and alien invasive plantations. The lowest elevational site is a village (VIL), mainly human settlements (Fig 2.2k). It is followed by the cropland (CL), a potato farm (Fig 2.2h); both sites are at 800 m a. s. l. At 900 m a. s. l. there are two sites adjacent to each other, a bush encroached (BE) (Fig 2.2a) and cleared bush site (CBE) (Fig 2.2l) characterized by closed and open shrublands, respectively. The 1000 m a. s. l. site is mostly used for cattle grazing and consists of low thickets (Fig 2.2b). The mid-elevation sites on the southern aspect are made up of both natural and non-native forests, 1200 m a. s. l. (12SA) is a tall forest (Fig 2.2c) while 1200 m a. s. l. (12SB) is a short forest (Fig 2.2d). At 1400 m a. s. l. there are three sites, one natural/untransformed (14SA) and two transformed sites (a blue gum plantation and macadamia orchard). Site 14SA is mainly made up of open woodland (Fig 2.2e). The blue gum plantation (BP) is an abandoned *Eucalyptus* plantation (Fig 2.2i), and the macadamia orchard (MO) which is an orchard farm (Fig 2.2j). The highest site on the southern slope is 16S which is at 1600 m a. s. l and consists of a grassland (Fig 2.2f).

The northern aspect of the mountain is mainly characterized by woodland habitats. The lowest sites which occupy the 800 m a. s. l elevational band are 08NA and 08NB. Site 08NA comprises open and low woodlands (Fig 2.3a). While site 08NB is made up of a shrubland-thicket matrix and is easily distinguishable by red Kalahari sand found at the site (Fig 2.3e). The mid-elevation (1000 m a. s. l and 1200 m a. s. l) sites 10N (Fig 2.3b) and 12N (Fig2.3c) are dominated by rocky and short woodlands. Further up the elevational gradients on the northern aspect are sites 14NA and 14NB. Site 14NA is a semi-arid and sandy woodland (Fig 2.3d), while 14NB is a riverine forest (Fig 2.3f). The summit of the mountain, 1700 m a. s. l. (17N), is mostly a grassland (Fig 2.2g).

*Ant and Spider Sampling*

The transect is made up of 18 sites at approximately 200 m elevational distances, with some sites occupying the same elevational band (e.g. 12SA and 12SB). Each site had four replicates that were at least more than 300 m apart. Each replicate had 10 pitfall traps which were placed 10 m apart in a 2 x 5 sampling grid (Figure 2.1). Pitfall traps were made up of small plastic containers with a diameter of 62 mm. The pitfall traps were left open for five days during September 2019 (dry-hot season) and January 2020 (wet-hot season). The pitfall traps contained a 50% propylene glycol solution, which does not attract or repel ants and spiders (Munyai and Foord, 2012). The pitfall traps were washed in the laboratory where the ants and spiders were separated from the other invertebrates and then stored in 70% alcohol. Prof. A.S. Dippennar-Schoeman identified the spiders at the Agricultural Research Council (ARC). Spider specimens were identified to species level where possible, otherwise to genus and then morphospecies. The ants were identified to species level and some to genus level, then morphospecies using Fisher and Bolton (2016) and online databases; viz. AntWiki (http://www.antwiki.org/) and AntWeb (http://antweb.org/).

### Data analysis

Data analysis was carried out using R, and the data was pooled for all four replicates at each site (R Core Team, 2020).The spider and ant data sets were analysed independently. In order to graphically visualise and compare spider and ant community composition by elevation, season, and land-use type across the transect, non-metric multidimensional scaling (NMDS) analyses was used. The NMDS distance matrix was calculated using the Bray-Curtis distance matrix with two dimensions and rank dissimilarity, and it was performed under 999 permutations. In the NMDS, the closer the points/sites are the more similar they are in terms of composition. Furthermore, a permutational multivariate analysis of variance (PERMANOVA) was carried out to test whether there is a difference in the spider and ant composition between the land-uses, elevations and seasons. The PERMANOVA was performed on Bray-Curtis similarity matrix of spider and ant activity data, and it was performed under 999 permutations.

An analysis of similarity (ANOSIM) in R Statistical Environment (R Core Team, 2020) was used to examine the similarity of spider and ant assemblages within the different land-uses, elevations, and seasons. The ANOSIM generates a Global R statistic that can be used to quantify the similarity of the assemblages. An R value closer to “1” suggests dissimilarity between the assemblages while an R value closer to “0” suggests similarity in the assemblages.

From the ANOSIM test, groups with R > 0.75 are highly different; groups whereby 0.5 < R < 0.75 are different; groups with 0.25 < R < 0.5 are different with some overlap; groups whereby 0.1 < R < 0.25 are different with high overlap or similar with some differences and groups where R < 0.1 are highly similar.

The indicator Value method (IndVal) was used to determine the characteristic species of each land-use type, elevational zone and aspect. The IndVal analysis basically computes the fidelity and specificity of a species to a particular habitat type (Dufrêne and Legendre, 1997). In the current study, an indicator value above 70% shows that a species is both highly specific and has high fidelity to that particular site. A species with an indicator value between 50 % and 70% was considered to be a detector species (McGeoch et al., 2002).

## Results

### *Spider and ant species composition*

The NMDS and PERMANOVA results show that both spider and ant community composition differed significantly between the land-use types (Figure 3.1, Table 3.1). The different elevational zones (low, mid, high) also had distinct assemblages for both taxa (Figure 3.1, Table 3.1). The seasonality effect on spider assemblages was minimal; the community assemblages did not change substantially between seasons (Figure 3.2.a, Table 3.1). Ant composition also remained similar between the dry and wet seasons (Figure 3.1.b, Table 3.1). Spider community composition was highly distinct between the two aspects, while ant composition was less distinct between the aspects indicating that ant species were shared between the aspects (Figure 3.3.b, Table 3.1). PERMOVA also revealed that land-use had the largest impact on spider and ant communities, followed by elevation and then season (Table 3.1). The ANOSIM test further showed that spider and ant assemblages were highly similar between elevations and seasons, indicating a substantial overlap in species (Table 3.2). The overlap or sharing of species was less frequent between land-use types (Table 3.2).

Altogether the transformed sites had highly dominant species compared to the untransformed sites for both taxa. For spiders, *Ammoxenus psammodromus* made up 48 % of the spiders found in the transformed sites (Appendix A). While *Anoplolepis cf. custodiens* accounted for 37.6 % of the ants (Appendix B). In contrast, the most abundant ant species in the untransformed sites, *Pheidole* sp.03 (*megacephala* gp.), only made up 15.8 % of the ants (Appendix B). A spider species, *Asemesthes ceresicola,* made up 15.9 % of the total spider abundance in untransformed sites (Appendix A).

### *Indicator species for the land-uses, elevational zones and aspects*

Only the blue gum plantation had a spider indicator species, *Copa flavoplumosa* (Table 3.3). Contrary to spiders, five sites had ant species as indicator species along the transect (Table 3.4). The human settlement, cropland, bush encroachment, cleared bush encroachment and macadamia orchard had an indicator species. All these sites had either *Monomorium damarense* or *Lepisiota* sp.02 (*spinosior* gp) as indicators or both (Table 3.4).

The low elevations had one spider detector species in *Diores auricular* (Table 3.5). Three spider indicator species, *Palpimanus squamata*, *Theuma purcelli* and *Palpimanus* sp. were found in the mid elevational zone with *Palpimanus squamata* having the highest specificity and fidelity to mid elevation sites (Table 3.5). The higher elevations did not have a spider indicator or detector species (Table 3.5).

*Monomorium damarense* was strongly associated with the low elevation zone (Table 3.6). While *Tetramorium* sp.07 (*weitzeckeri* gp.) was also an indicator for the mid elevational zone, there were also five ant detector species in this zone (Table 3.6). The higher elevation sites recorded only two ant detector species with *Tetramorium* sp.14 (*sereiceventre* gp.) and *Camponotus* sp.23 (Table 3.6).

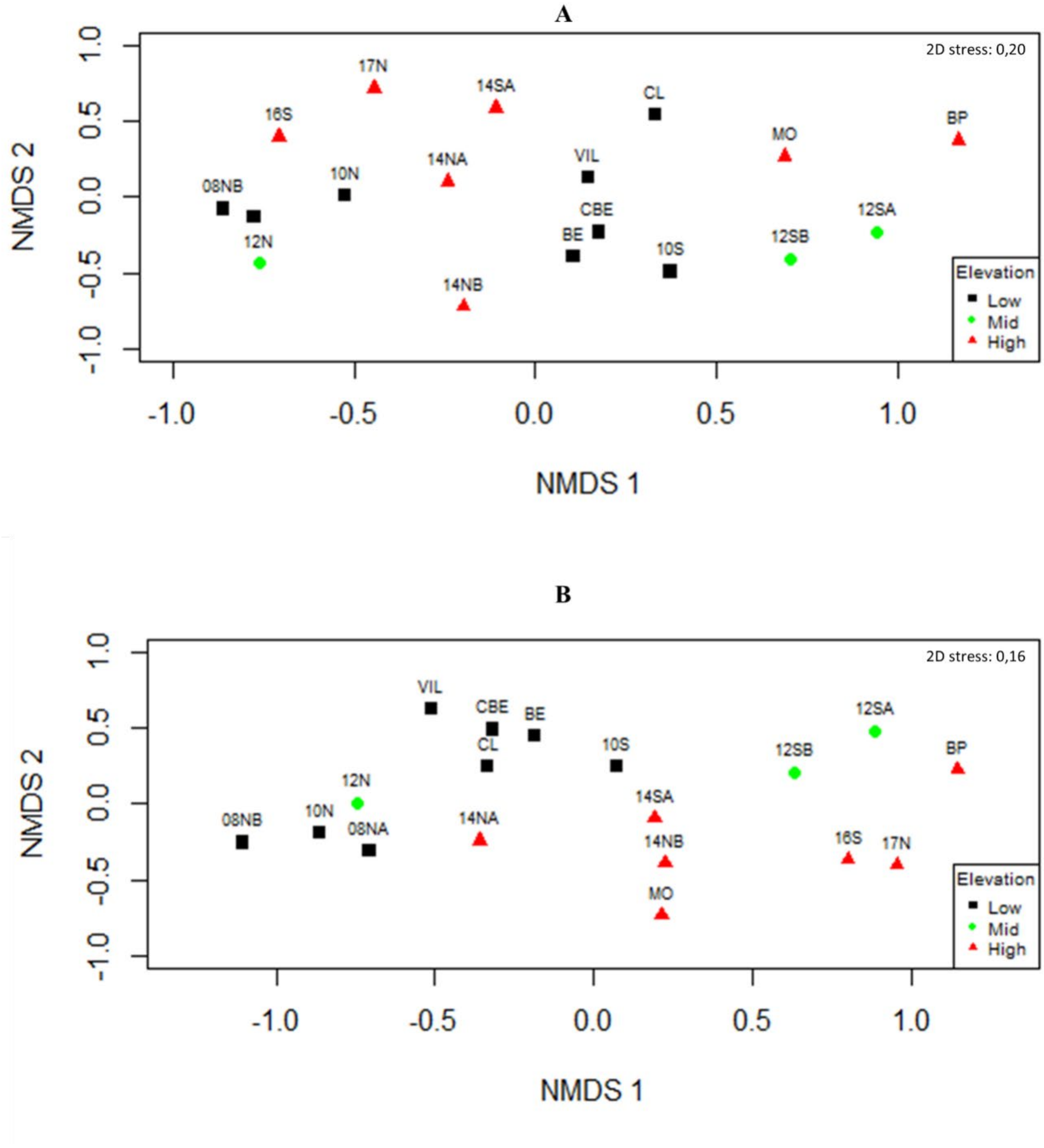

Figure 3.1: Non-metric Multi-Dimensional Scaling (NMDS) plots of spider **(A)** and ant **(B)** communities along the Soutpansberg elevational transect. Activity data was used for the ordination with sites were grouped by the elevational zones (low, mid, high) they occupy. VIL: Village, CL: Cropland, CBE: Cleared Bush Encroachment, BE: Bush Encroachment, 10S: 1000 m a. s. l on the southern aspect; 12SA: first site at 1200 m a. s. l on the southern aspect; 12SB: second site at 1200 m a. s. l on the southern aspect; 14SA: first site at 1400 m a. s. l on the southern aspect; BP: Blue gum Plantation, MO: Macadamia Orchard; 16S: 1600 m a. s. l on the southern aspect; 17N: 1700 m a. s. l. on the northern aspect; 14NA: first site at 1400 m

a. s. l on the northern aspect; 14NB: second site at 1400 m a. s. l on the northern aspect; 12N: 1200 m a. s. l on the northern aspect; 10N: 1000 m a. s. l on the northern aspect; 08NA: first site at 800 m a. s. l on the northern aspect; 08NB: second site at 800 m a. s. l on the northern aspect.

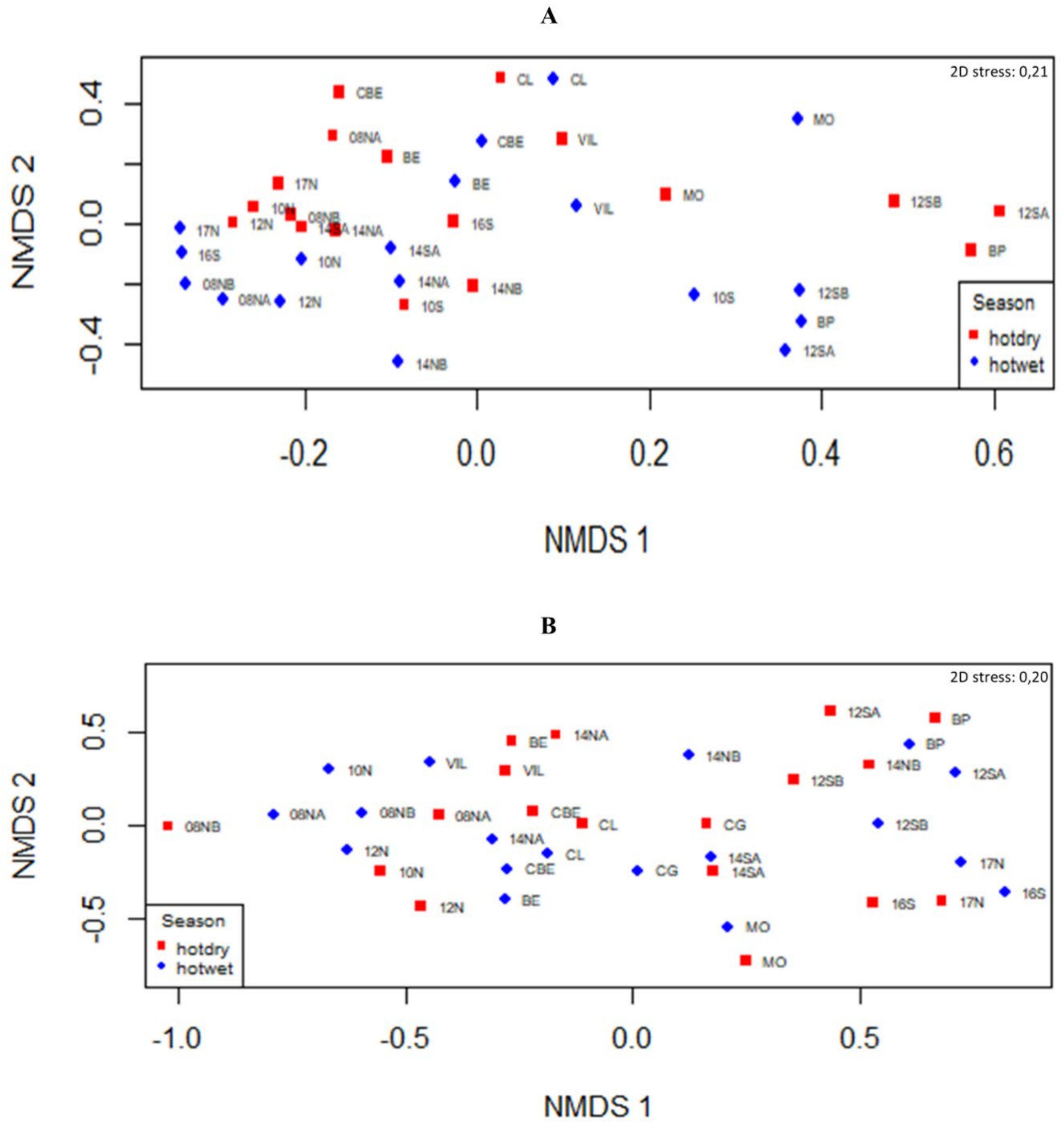

Figure 3.2: Non-metric multidimensional scaling (NMDS) plots of spider **(A)** and ant **(B)** community similarity across the transect between the dry and wet season. The plots were based on activity data and Bray-Curtis similarity was used on the two-dimensional plots. VIL:

Village, CL: Cropland, CBE: Cleared Bush Encroachment, BE: Bush Encroachment, 10S: 1000 m a. s. l on the southern aspect; 12SA: first site at 1200 m a. s. l on the southern aspect; 12SB: second site at 1200 m a. s. l on the southern aspect; 14SA: first site at 1400 m a. s. l on the southern aspect; BP: Blue gum Plantation, MO: Macadamia Orchard; 16S: 1600 m a. s. l on the southern aspect; 17N: 1700 m a. s. l. on the northern aspect; 14NA: first site at 1400 m a. s. l on the northern aspect; 14NB: second site at 1400 m a. s. l on the northern aspect; 12N: 1200 m a. s. l on the northern aspect; 10N: 1000 m a. s. l on the northern aspect; 08NA: first site at 800 m a. s. l on the northern aspect; 08NB: second site at 800 m a. s. l on the northern aspect.

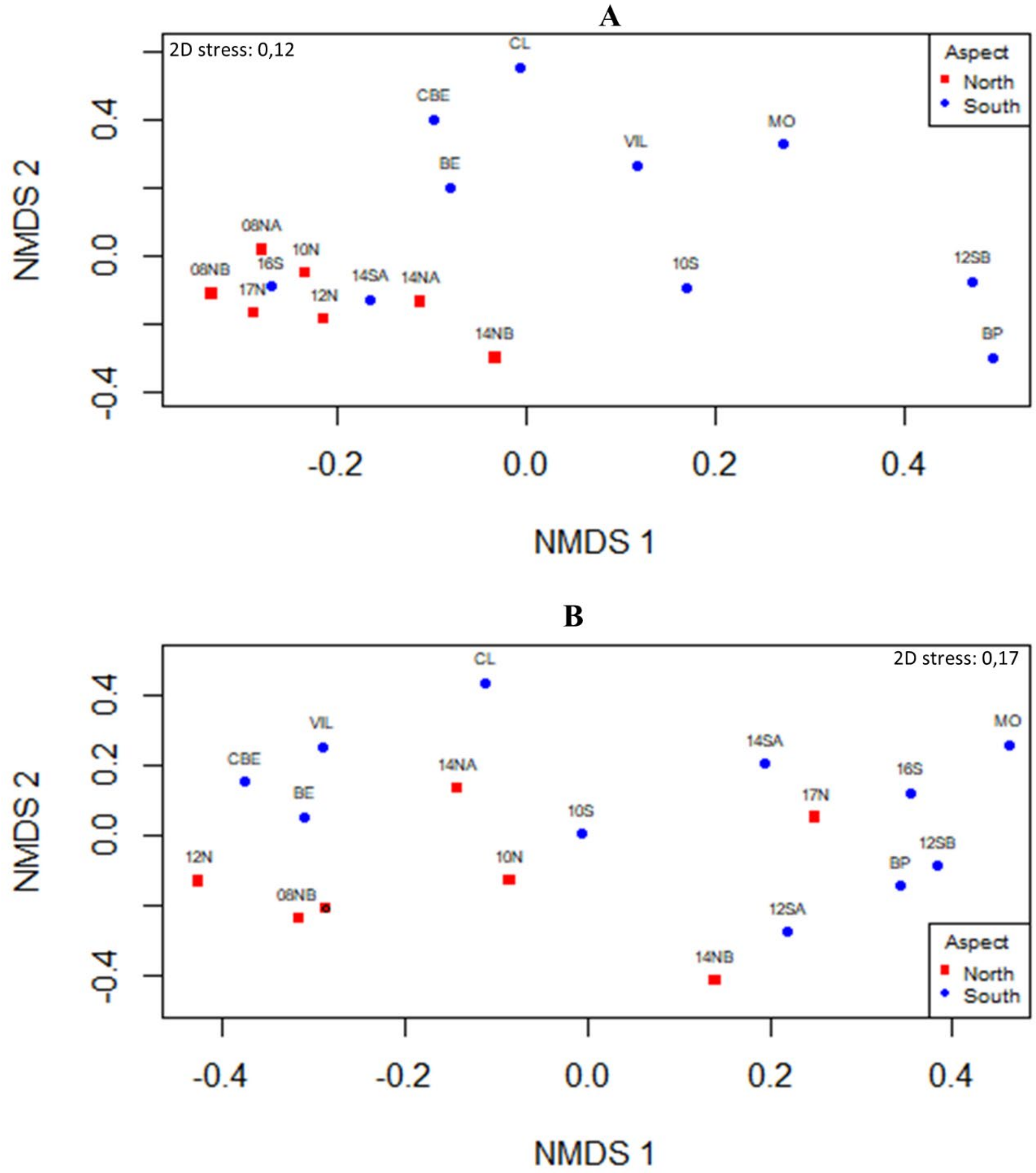

Figure 3.3: Non-metric multidimensional scaling (NMDS) plots of spider **(A)** and ant **(B)** community similarity across the transect between the southern and northern aspects of Soutpansberg. The plots were based on activity data and Bray-Curtis similarity was used on the two-dimensional plots. VIL: Village, CL: Cropland, CBE: Cleared Bush Encroachment, BE: Bush Encroachment, 10S: 1000 m a. s. l on the southern aspect; 12SA: first site at 1200 m a. s. l on the southern aspect; 12SB: second site at 1200 m a. s. l on the southern aspect; 14SA: first site at 1400 m a. s. l on the southern aspect; BP: Blue gum Plantation, MO: Macadamia Orchard; 16S: 1600 m a. s. l on the southern aspect; 17N: 1700 m a. s. l. on the northern aspect; 14NA: first site at 1400 m a. s. l on the northern aspect; 14NB: second site at 1400 m a. s. l on the northern aspect; 12N: 1200 m a. s. l on the northern aspect; 10N: 1000 m a. s. l on the northern aspect; 08NA: first site at 800 m a. s. l on the northern aspect; 08NB: second site at 800 m a. s. l on the northern aspect.

Table 3.1. PERMANOVA results based on Bray-Curtis dissimilarities using spider and ant activity data for species composition based in relation to land-use, elevation and season across the Soutpansberg elevational gradient.

| | | DF | SS | MS | Pseudo-F | $R^2$ | P |
|---|---|---|---|---|---|---|---|
| Land-use | Spiders | 6 | 2.50 | 0.42 | 1.35 | 0.42 | 0.01 |
| | Ants | 6 | 2.37 | 0.39 | 1.27 | 0.41 | 0.004 |
| Elevation | Spiders | 2 | 0.98 | 0.49 | 1.49 | 0.17 | 0.034 |
| | Ants | 2 | 1.12 | 0.56 | 1.80 | 0.19 | 0.01 |
| Season | Spiders | 1 | 0.97 | 0.97 | 2.60 | 0.07 | 0.001 |
| | Ants | 1 | 0.68 | 0.68 | 1.90 | 0.05 | 0.014 |
| Aspect | Spiders | 1 | 0.81 | 0.81 | 2.55 | 0.14 | 0.003 |
| | Ants | 1 | 0.67 | 0.67 | 2.10 | 0.12 | 0.014 |

Table 3.2: ANOSIM results based on Bray-Curtis dissimilarities using spider and ant activity data for species composition in relation to land-use, elevation and season across the Soutpansberg elevational gradient.

| | | R-Statistic | P-value |
|---|---|---|---|
| Land-use | Spiders | 0.41 | 0.01 |
| | Ants | 0.31 | 0.004 |
| Elevation | Spiders | 0.24 | 0.034 |
| | Ants | 0.33 | 0.01 |
| Season | Spiders | 0.21 | 0.001 |
| | Ants | 0.09 | 0.014 |
| Aspect | Spiders | 0.22 | 0.019 |
| | Ants | 0.18 | 0.042 |

Table 3. 3. Indicator values (IndVal) of spider species for the land-use type along the transects. Only species with significant indicator values are shown ($p < 0.05$).

| Land-use type | Species | Indicator value (%) | P-value |
|---|---|---|---|
| Blue gum plantation | *Copa flavoplumosa* | 98.8 | 0.0237 * |

Table 3. 4. Indicator values (IndVal) of ant species at the various land-use types in Soutpansberg. Only species with significant indicator values are shown ($p < 0.05$).

| Land-use type | Species | Indicator value (%) | P-value |
|---|---|---|---|
| Human settlement | *Monomorium damarense* | 94.4 | 0.0114 |
| Cropland | *Lepisiota* sp.02 (*spinosior* gp.) | 96.9 | 0.0422 |
| | *Monomorium damarense* | 94.4 | 0.0114 |
| Cleared bush encroachment | *Lepisiota* sp.02 (*spinosior* gp.) | 96.9 | 0.0436 |
| | *Monomorium damarense* | 94.4 | 0.0114 |
| Bush encroachment | *Monomorium damarense* | 94.4 | 0.0114 |
| Macadamia orchard | *Lepisiota* sp.02 (*spinosior gp.*) | 96.9 | 0.0444 |

Table 3. 5. Indicator values (IndVal) of spider species across the elevational zones (low, mid, high) of the transect. Only species with significant indicator values are shown (p < 0.05).

| Elevational zone | Species | Indicator value (%) | P-value |
|---|---|---|---|
| Low | *Diores auricular* | 60 | 0.0249 |
| Mid | *Palpimanus squamata* | 84.6 | 0.0035 |
| | *Theuma purcelli* | 75.6 | 0.0184 |
| | *Palpimanus sp.* | 70.7 | 0.0179 |
| | *Proevippa sp.* | 62.8 | 0.0088 |
| | *Proevippa fascicularis* | 60.7 | 0.0177 |
| | *Euryopis sp.* | 60.3 | 0.0184 |

Table 3. 6. Indicator values (IndVal) of ant species across the elevational zones (low, mid, high) of the Soutpansberg mountain. Only species with significant indicator values are shown (p < 0.05).

| Elevational zone | Species | Indicator value (%) | P-value |
|---|---|---|---|
| Low | *Monomorium damarense* | 90.1 | 0.0001 |
| | *Monomorium emeryi* | 51.4 | 0.0478 |
| Mid | *Tetramorium* sp.07 (*weitzeckeri.*gp) | 73.8 | 0.0078 |
| | *Hypoponera* sp.01 | 64.7 | 0.0367 |
| | *Plagiolepis* sp.02 | 60.2 | 0.0267 |
| | *Tetramorium* sp.12 (*squaminodis* gp.) | 57.5 | 0.0404 |
| | *Monomorium* sp.01 | 55.8 | 0.0325 |
| | *Carebara* sp.01 | 55.7 | 0.0202 |
| High | *Tetramorium* sp.14 (*sereiceventre.*gp.) | 52.7 | 0.0392 |
| | *Camponotu* sp.23 | 51.4 | 0.0330 |

## Discussion

### *Spider and ant community composition: Elevation, Season, and Land-use type*

Spider and ant species community composition was distinct between the three elevational zones (low, mid, and high). Elevation has already been shown to influence arthropod assemblages and diversity in Soutpansberg mountains. Similar to the current study, Munyai and Foord (2012) and Joseph et al. (2019) also reported that ant species composition varied between elevational zones in an earlier study on the same transect. While Malumbres-Olarte et al. (2018) also found that spider composition was significantly different between the elevational zones of the Udzungwa Mountains in Tanzania. The distinct ant and spider assemblages at different elevations can be attributed to difference in environmental conditions between elevational zones, which results in distinct communities (Janzen, 1967).

The low elevation zone had very distinct spider and ant assemblages. Species occupying low elevations often have narrow ecological niches, which limit their distribution and dispersal to the low elevations (McCain, 2009, Hua 2016), which explains why, in mountain ecology, low elevations tend to have highly distinct species assemblages (McCain, 2009, Hua, 2016). Also, species limited to low elevations tend to display niche conservatism, whereby they become specialized for those habitats over time, resulting in very distinct assemblages (Wiens et al., 2010). Mid-elevational zones tend to have less distinct species assemblages because of the overlap in the distributional ranges of species from the lower and higher elevational zones. This was the case for spider assemblages. However, the southern aspect of Soutpansberg is occupied by native forests at the mid-elevations and these forests have very distinct ant assemblages (Munyai and Foord, 2012). While the mid-elevations of the northern aspect is characterized by rocky soils and open woodlands which also have distinct ant assemblages because of the specific species adapted for those sites such as *Monomorium cf drapenum* and *Meranoplus cf glaber*.The high elevations also had distinct spider and ant communities, which was expected as the climatic conditions at high elevations are extremely variable. This often leads to species becoming specialized and adapted for those conditions to survive or persist in those habitats (McCain, 2009; Srinivasan et al., 2019; Dolson et al., 2020). Therefore, the communities at higher elevations are similar due to the limited group of species that are adapted to high elevations (Joseph et al., 2019).

Seasonality influences important abiotic factors, and these factors play a vital role in structuring spider assemblages. These factors include leaf litter, vegetation, and habitat structure. Vegetation and habitat structure strongly affect the diversity, distribution, and composition of spiders (Hore and Unival, 2008). Furthermore, vegetation provides shelter and resources for spiders, and so they respond rapidly to changes in vegetation (Zakkak et al., 2014). Litter also influences spider communities by providing prey, stable temperatures, high moisture levels and refuge from predation (Uetz, 1979). Hence different litter types are associated with varying assemblages of spiders. Therefore, seasonal changes were expected to have a greater influence on community composition, which is common in spider assemblages. In Mexico Campuzano et al. (2019) showed that spiders in a tropical mountain forest responded strongly to seasonal variations resulting in distinct assemblages between the dry and rainy seasons. Whitmore et al. (2002) also found strong seasonal patterns in spider composition in a savanna reserve in Limpopo, South Africa. Also, in the Cederberg Mountains Foord and Dippenaar-Schoeman (2016) reported that elevation and season interacted to influence spider diversity patterns.

By being active at specific times in the day or even time of the year, animals can inhabit different temporal niches and therefore reduce niche overlap (Otto and Svensson, 1982). The suitable periods of activity are mostly influenced by temperature and competition. Ants will avoid temperatures that restrict foraging activity by being active at specific times, if temperatures fall outside the critical thermal minima and maxima ($CT_{min}$ and $CT_{max}$) then foraging activity will be constrained (Jayatilaka et al., 2011). Foraging behaviour in spider is regulated by food or resource availability, studies show that spiders in prey-rich habitat will restrict their foraging activity and effort in order to reduce the risk of predation (Lubin and Henschel, 1996). Spiders are also able to change their predation rates depending on the availability of prey and will therefore consume prey according to the local abundance (Schmidt et al., 2012) Overall, these seasonal and daily activity patterns also allow these arthropods to avoid competitors and predators and exploit resources optimally.

Ant communities did not differ greatly between the two seasons. Ants are a generally thermophilic taxon (Kaspari and Weiser, 2000; Kaspari, 2001); therefore, seasonal variation is expected to cause a major shift in ant assemblages. Munyai and Foord (2012) showed that ant communities changed with the season on the same transect in Soutpansberg. However, some studies have also reported no changes in ant composition between seasons. For instance, Marques et al. (2017) investigated the impact of succession and seasonality on ant assemblages in a secondary tropical forest and found no changes in the composition of ant assemblages between the dry and wet seasons. In South Africa, Mauda et al. (2018) also reported that ant community composition did not respond to seasonality. Ant assemblages may remain similar across seasons due to their nests being mostly sedentary, limiting dispersal. This is likely the case in the current study. Furthermore, the climate in the Soutpansberg region is warm and arid which means that temperatures remain high in both the dry and wet seasons and because ants are more sensitive to temperatures it is plausible for ant communities to remain relatively unchanged during the different seasons.

Spider and ant assemblages were different between the natural sites and transformed sites. Important environmental factors such as habitat heterogeneity, vegetation structure and habitat openness are different between the natural and transformed sites. Therefore, differences in arthropod communities between the two were anticipated. Additionally, land-use practices such as agriculture and urbanization can lead to biotic homogenization whereby the similarity of local biotas increases taxonomically and functionally (Buczkowski and Richmond, 2012). Spiders and ants have already been shown to form distinct species assemblages in different land-use types. For instance, Rubiana et al. (2015) reported a significant difference in ant community structure between four land-use types (rubber plantations, forest, jungle rubber and oil palm plantations). While Rosa et al. (2018) found that spider communities differed between six land-use types including a native forest, *Eucalyptus* plantation and pastures. Habitat disturbances such as land-use change facilitates the addition and removal of certain species into a habitat, and resulting in new assemblages at those sites (Ojima et al., 1994).

Land-uses practices transform the natural environment resulting in more open, homogenous and fragmented habitats (Ojima et al., 1994, Maitima et al., 2009). Habitat openness is an important factor in this context, as it can influence the composition and diversity of most terrestrial communities. Habitat heterogeneity also affects local species assemblages. Studies show that composition and diversity between heterogeneous and homogeneous habitats differ considerably (Katayama et al., 2014; Samu et al., 2014; Melliger et al., 2018). In fact, when habitats become homogenous due to anthropogenic impacts, unique species are lost as habitat generalists species increase (Wilby et al., 2006). In Germany, Clough et al. (2005) found that landscape heterogeneity was one of the main predictors of spider richness in agricultural habitats. Therefore, it is logical that the transformed sites in the Soutpansberg area have different community assemblages because the transformations have resulted in changes to landscape heterogeneity.

Biotic and abiotic factors such as habitat structure, microclimate, resource availability and competition dynamics are critical for how ant and spider communities are structured (Maelfait and Hendrickx, 1997; Zakkak et al., 2014; Bharti et al., 2016). Any environmental disturbances or modifications that alter these factors will inevitably change ant (Andersen and

Majer, 2004; Andersen, 2019) and spider (Muff et al., 2009; Bowden and Buddle, 2010) communities in terms of composition and/or diversity. Therefore, depending on the taxa, severity and type of the disturbance or land-use in this context (Hoffman, 2000; McKinney, 2008; Andersen, 2019), diversity and composition may remain unchanged or change as in the case at Soutpansberg mountains. Also, highly mobile and widely distributed species tend to be more suited for disturbed habitats (Oliver and Morecroft, 2014; Andersen, 2019). This means changes in composition and diversity are always likely after habitat disturbances as disturbance tolerant species increase and specialists decrease.

### *Spider and ant indicator species for the land-use types, elevational zones and aspects*

None of the natural sites had indicator species for both taxa. Only one spider species was an indicator species of a land-use site, viz. *Copa flavoplumosa* was the indicator species for the blue gum plantations. Species of this genus have a high affinity for closed-canopy forests and moist savannas and mostly occur in leaf litter in various habitats (Haddad, 2013). This explains the association with the blue gum plantation as *Eucalyptus* plants shed leaves at high rates. Therefore, this species could be used as an indicator in these plantations.

Interestingly, several transformed sites had at least one ant indicator species for ants, with some shared between sites. These species were *Monomorium damarense* and *Lepisiota* sp.02 (*spinosior* gp.). Their strong affinity for the transformed sites in this study suggests that they could be used as indicator species for habitat disturbance in arid mountainous regions. It is important to note that these are habitat generalist species, which could indicate that the transformed sites are harbouring mostly habitat generalist species. Also, according to Andersen (2019) generalised ant groups are likely to persist in disturbed habitats. Munyai and Foord (2012) also found that the southern aspect of Soutpansberg shelters mostly habitat generalists, particularly at the low elevational bands, which happen to be experiencing most of the land-use and transformations. This further supports the notion that increased diversity in disturbed sites is often a result of disturbance tolerant species and habitat generalists taking over.

Several spider detector species were found along the elevational zones. Still, three indicator species (*Palpimanus* sp., *Theuma purcelli*, *Palpimanus squamata*) were found in the mid-elevation zone in the southern aspect. *Palpimanus squamata* displayed the most specificity and fidelity to mid elevation sites. Ant species *Monomorium damarense* and *Tetramorium* sp.07 (*weitzeckeri* gp.) displayed a high affinity to the low and mid elevational zones, respectively. They occurred mostly in the southern aspect. Similar to the land-use indicator species, ants of genus *Monomorium* tend to be habitat generalists, while those in genus

*Tetramorium* are largely opportunists (Andersen, 1997). Overall, our results show that the spiders are mostly influenced by habitat structure and ants mostly by temperature in western Soutpansberg mountains. We also found indicator species for some land-uses, with two ant species showing exceptionally high affinity for the transformed sites. Analysis of the spider and ant communities indicated uneven assemblages and species dominance for both taxa in transformed habitats. This supports the view that disturbances can lead to the dominance of certain species, such as opportunistic species and disturbance-tolerant species, and that dominant species can respond positively to disturbance (Parr, 2008).

Therefore, if land transformations continue in the region, it is plausible that dominant species will colonize more habitats in the area, negatively affecting endemic and native communities. According to Dirnböck and Rabitsch (2011) endemic species hotspots in the mountains are already expected to be the most affected by habitat loss. There should be broader concern if these land-use trends continue, because important ecosystem services and biodiversity could be lost in the long term. Furthermore, studies have shown that climate change can influence the geographical distribution of arthropods (Elsen et al., 2018). The combination of land-use and climate could have devastating impacts on biodiversity as ecosystem functioning is disturbed. Hence, land-use changes and biological communities along the Soutpansberg mountain range must continue to be monitored.

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# CHAPTER 4: CONCLUSION AND RECOMMENDATION FOR FURTHER RESEARCH

## 4.1 Introduction

The current greatest driver of biodiversity loss and ecosystem instability is land-use change with human settlements and agriculture being some of the most detrimental forms of anthropogenic pressure on biodiversity (Newbold, 2018). The impact of land-use change on biodiversity has been widely documented across a spectrum of ecosystems, plants, and animals. Studies show that land-use can negatively affect species diversity and human-wellbeing (Loreau et al., 2001; Hendrickx et al., 2007; García-Llamas et al., 2019). The latter has caused species loss, introduced alien invasive species, and disturbed food webs and ecosystem services. The upsurge in land-use change highly threatens mountain ecosystems. Mountains are important centres for ecological and cultural diversity (García-Llamas et al., 2019). Mountains display high variability in environmental conditions over short distances, resulting in highly diverse and endemic microhabitats.

Also affected by changes in land-use are arthropods. Arthropods are extremely abundant and diverse. They occupy almost all terrestrial ecosystems and play important roles in ecosystem functioning and services. Research indicates a considerable decline in arthropod diversity globally (Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020; van Klink et al., 2020). Long-term diversity monitoring and conservation efforts for insects are insignificant compared to other well-studied organisms such as terrestrial vertebrates, and this is especially true in Africa. The potential ecological and economic implications of declining arthropod diversity indicate a pressing need to accurately assess and monitor arthropod biodiversity amid land-use and climate change.

## 4.2 Revisiting the aims and objectives

The current study aimed at assessing the response of spider and ant richness and their activities to land-uses, elevation and season. The contribution of land-use, elevation and season in explaining the variation in spider and ant diversity were also determined. The results showed that spider and ant richness and activity were significantly higher in the transformed sites. However, species evenness was lower in the transformed sites. The mid-elevations had the highest ant diversity, and spider diversity was highest in the low elevations. Ant diversity peaked in the wet season, while spider diversity was higher in the dry season. The findings support the intermediate disturbance hypothesis since land-use in western Soutpansberg is still limited or confined to certain areas.

Spider and ant community composition was compared between the sites, elevations and seasons. Indicator species for the different land-use types were also identified. Spider and ant assemblages were significantly different between the land-uses, elevations. There were minimal changes in spider communities, while ants remained very similar between the two sampled seasons. There was one spider indicator species for the *Eucalyptus* plantations and two ant species were identified as indicators for the land-use sites. Collectively, spider and ant assemblages were highly uneven and displayed species dominance.

Overall, results showed that land transformation can increase arthropod richness and activity. The positive response of arthropods to land-use change may be due to an increase of wide-ranging species such as habitat generalists and not species with narrow distributional ranges (Katayama et al., 2014). The origin of those species was not probed in this study, therefore, they may be native or alien species. The species dominance and unevenness of arthropod communities in transformed sites might also indicate that land-use increases the colonization of disturbance-tolerant species in the region. Elevation and seasonality were also important factors for arthropod diversity; however, their impact has been masked or reduced by habitat changes and disturbances through land-use. The study also showed that some species have the potential to be indicators for some land-use practices.

### 4.3 Contributions of the study

The impact of land-use change on biodiversity has been researched extensively across a multitude of environments for various taxa. While many studies have investigated the impact of land-use change on diversity, very few have done so in mountainous regions in southern Africa. This study was the first to assess the impact of land-use changes on arthropod diversity and composition along the highly diverse elevational gradient in a centre of endemism. It is also the first to assess spider diversity and composition in the region. This study was also the first to use a multi-taxa approach for investigating land-use change across an elevational gradient with diverse land-use types and disturbance regimes. The findings of this study contribute to our understanding of ant and spider diversity patterns and show the need for continuous monitoring of land-use changes, especially in developing countries.

### 4.5 Challenges and future possibilities

The current study employed a standardized pitfall trap sampling method. This meant that only ground dwelling ants and spiders were sampled. Future studies should employ other sampling methods, perhaps sample both ground dwelling and arboreal species. It could also provide a broader and more precise picture of the diversity in any habitat. Investigation of the origin of the species that occupy the transect is also recommended as knowledge and understanding of the native and alien species could open up more interesting findings. Furthermore, analysis of climatic and edaphic attributes are recommended for future studies. These environmental variables play an important role in the diversity and composition of terrestrial communities. A trait-based approach to studying the effect of disturbances on the biodiversity of various ecosystems is also recommended. Functional diversity is fundamental for maintaining ecosystem services and functions (Laureto et al., 2015). Therefore, understanding how functional traits respond to the different land-uses can reveal more about habitat disturbance and associated impact on ecosystem functioning.

### 4.6 Final comments and summary of the conclusion

Mountain ecosystems are cradles of biodiversity and should be protected because of their importance for global biodiversity and ecosystem provision. Land-use change at the Soutpansberg is not as intensive as in other regions. However, the land transformations carried out thus far have already significantly affected arthropod diversity and composition across the mountain.

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# APPENDIX

Appendix A: Spider families and species collected over the study period at western Soutpansberg, Limpopo, South Africa. For some species, individuals were juveniles therefore they were counted as different species.

| Spider families and species | Transformed sites | Untransformed sites | Total |
|---|---|---|---|
| **Agelenidae** | **5** | **4** | **9** |
| *Benoitia ocellate* | 0 | 2 | 2 |
| *Benoitia* sp.2 | 0 | 2 | 2 |
| *Mistaria* sp. | 3 | 0 | 3 |
| *Mistaria* sp.1 | 1 | 0 | 1 |
| *Mistaria zuluana* | 1 | 0 | 1 |
| **Ammoxenidae** | **732** | **24** | **756** |
| *Ammoxenus psammodromus* | 731 | 9 | 740 |
| *Rastellus kariba* | 1 | 15 | 16 |
| **Anapidae** | **1** | **2** | **3** |
| *Crozetulus rhodesiensis* | 1 | 2 | 3 |
| **Araneidae** | **0** | **2** | **2** |
| *Lipocrea longissimi* | 0 | 1 | 1 |
| *Pararaneus* sp. | 0 | 1 | 1 |
| **Bemmeridae** | **2** | **0** | **2** |
| *Homostola pardalina* | 2 | 0 | 2 |
| **Caponiidae** | **0** | **3** | **3** |
| *Caponia chelifera* | 0 | 3 | 3 |
| **Clubionidae** | **0** | **1** | **1** |
| *Clubiona abbajensis* | 0 | 1 | 1 |
| **Corinnidae** | **20** | **26** | **46** |
| *Castianeira fulvipes* | 0 | 1 | 1 |
| *Copa flavoplumosa* | 18 | 21 | 39 |
| *Copa* sp. | 0 | 4 | 4 |
| *Corinnomma lawrencei* | 2 | 0 | 2 |
| **Ctenidae** | **6** | **16** | **22** |
| *Ctenus gulosus* | 6 | 10 | 16 |
| *Ctenus transvaalensis* | 0 | 6 | 6 |
| **Cyrtaucheniidae** | **9** | **27** | **36** |
| *Ancylotrypa* sp. | 3 | 3 | 6 |
| *Ancylotrypha nuda* | 0 | 21 | 21 |
| *Ancylotrypha* sp. | 6 | 2 | 8 |
| *Ancylotrypha* sp.2 | 0 | 1 | 1 |
| **Entypesidae** | **0** | **1** | **1** |
| *Hermacha mazoena* | 0 | 1 | 1 |
| **Eresidae** | **1** | **0** | **1** |
| *Dresserus colsoni* | 1 | 0 | 1 |
| **Filistatidae** | **0** | **1** | **1** |

| | | | |
|---|---|---|---|
| *Andoharano ansieae* | 0 | 1 | 1 |
| **Gnaphosidae** | **164** | **480** | **644** |
| *Aneplasa interrogationis* | 0 | 1 | 1 |
| *Asemesthes bilineatus* | 0 | 15 | 15 |
| *Asemesthes ceresicola* | 21 | 183 | 204 |
| *Asemesthes lineatus* | 0 | 36 | 36 |
| *Asemesthes numisma* | 0 | 1 | 1 |
| *Asemesthes pallidus* | 0 | 8 | 8 |
| *Asemesthes paynteri* | 2 | 0 | 2 |
| *Asemesthes* sp. | 13 | 30 | 43 |
| *Asemesthes* sp.1 | 0 | 1 | 1 |
| *Austrodomus scaber* | 2 | 0 | 2 |
| *Austrodomus* sp.1 | 0 | 1 | 1 |
| *Camillina arida* | 0 | 2 | 2 |
| *Camillina cordifera* | 4 | 1 | 5 |
| *Camillina* sp. | 0 | 2 | 2 |
| *Drassodes solitarius* | 3 | 2 | 5 |
| *Drassodes splendens* | 12 | 1 | 13 |
| *Drassodes stationis* | 2 | 4 | 6 |
| *Eleleis Limpopo* | 0 | 1 | 1 |
| *Ibala arcus* | 27 | 74 | 101 |
| *Ibala bilinearis* | 0 | 21 | 21 |
| *Ibala* sp. | 1 | 12 | 13 |
| *Leptodrassex* sp. | 0 | 1 | 1 |
| *Leptodrassex* sp.1 | 6 | 1 | 7 |
| *Megamyrmekion transvaalense* | 0 | 1 | 1 |
| *Micaria* sp. | 1 | 0 | 1 |
| *Nomisia* sp. | 0 | 1 | 1 |
| *Proevippa wanlessi* | 0 | 6 | 6 |
| *Theuma elucubata* | 0 | 1 | 1 |
| *Theuma foveolate* | 1 | 0 | 1 |
| *Theuma fusca* | 3 | 1 | 4 |
| *Theuma purcelli* | 0 | 2 | 2 |
| *Theuma* sp. | 4 | 4 | 8 |
| *Theuma* sp.1 | 0 | 4 | 4 |
| *Xerophaeus aurariarum* | 0 | 3 | 3 |
| *Xerophaeus bicavus* | 0 | 3 | 3 |
| *Xerophaeus* sp. | 0 | 4 | 4 |
| *Zelotes caldarius* | 0 | 3 | 3 |
| *Zelotes corrugatus* | 0 | 2 | 2 |
| *Zelotes fuligineus* | 0 | 6 | 6 |
| *Zelotes humilis* | 12 | 19 | 31 |
| *Zelotes sclateri* | 8 | 2 | 10 |
| *Zelotes scrutatus* | 2 | 6 | 8 |
| *Zelotes scutatus* | 0 | 1 | 1 |
| *Zelotes* sp. | 33 | 10 | 43 |

| | | | |
|---|---|---|---|
| *Zelotes tuckeri* | 7 | 3 | 10 |
| **Hersiliidae** | **0** | **1** | **1** |
| *Tyrotama soutpansbergensis* | 0 | 1 | 1 |
| **Idiopidae** | **0** | **2** | **2** |
| *Idiops castaneus* | 0 | 1 | 1 |
| *Idiops* sp. | 0 | 1 | 1 |
| **Linyphiidae** | **5** | **11** | **16** |
| *Agyneta habra* | 2 | 3 | 5 |
| *Meioneta natalensis* | 0 | 4 | 4 |
| *Pelecopsis janus* | 2 | 2 | 4 |
| *Pelecopsis* sp. | 1 | 2 | 3 |
| **Liocranidae** | **5** | **15** | **20** |
| *Rhaeboctesis exilis* | 1 | 7 | 8 |
| *Rhaeboctesis* sp. | 4 | 1 | 5 |
| *Rhaeboctesis trinotatus* | 0 | 7 | 7 |
| **Lycosidae** | **306** | **206** | **512** |
| *Allocosa excerta* | 1 | 0 | 1 |
| *Allocosa lawrencei* | 17 | 0 | 17 |
| *Allocosa* sp. | 19 | 11 | 30 |
| *Allocosa* sp.2 | 9 | 0 | 9 |
| *Arctosa* sp. | 1 | 5 | 6 |
| *Evippomma squamulatum* | 0 | 1 | 1 |
| *Hogna spenceri* | 1 | 0 | 1 |
| *Micaria* sp. | 1 | 0 | 1 |
| *Pardosa crassipalpis* | 167 | 0 | 167 |
| *Pardosa leipoldti* | 28 | 0 | 28 |
| *Pardosa* sp. | 36 | 26 | 62 |
| *Proevippa albiventris* | 0 | 4 | 4 |
| *Proevippa fascicularis* | 17 | 115 | 132 |
| *Proevippa* sp. | 6 | 20 | 26 |
| *Proevippa wanlessi* | 0 | 8 | 8 |
| *Ranops* sp. | 1 | 0 | 1 |
| *Trabea lawrencei* | 0 | 2 | 2 |
| *Trabea purcelli* | 0 | 9 | 9 |
| *Trabea* sp. | 2 | 5 | 7 |
| **Nemesiidae** | **2** | **4** | **6** |
| *Entypesa schoutendeni* | 0 | 1 | 1 |
| *Hermacha mazoena* | 2 | 3 | 5 |
| **Oecobiidae** | **0** | **2** | **2** |
| *Uroecobius ecribellatus* | 0 | 2 | 2 |
| **Oonopidae** | **1** | **4** | **5** |
| *Gamasomorpha humicola* | 1 | 2 | 3 |
| *Orchestina fannes* | 0 | 2 | 2 |
| Orsolopbidae | 0 | 1 | 1 |
| *Afrilobus* sp.1 | 0 | 1 | 1 |
| **Oxyopidae** | **13** | **7** | **20** |

| | | | |
|---|---|---|---|
| *Oxyopes bothai* | 2 | 2 | 4 |
| *Oxyopes dumonti* | 7 | 0 | 7 |
| *Oxyopes flavipalpis* | 0 | 1 | 1 |
| *Oxyopes jacksoni* | 2 | 1 | 3 |
| *Oxyopes* sp. | 2 | 3 | 5 |
| **Palpimanidae** | **0** | **11** | **11** |
| *Palpimanus* sp. | 0 | 3 | 3 |
| *Palpimanus squamata* | 0 | 8 | 8 |
| **Philodromidae** | **2** | **11** | **13** |
| *Hirriusa arenacea* | 0 | 4 | 4 |
| *Hirriusa* sp. | 0 | 2 | 2 |
| *Hirriusa variegata* | 0 | 2 | 2 |
| *Philodromus grosi* | 2 | 0 | 2 |
| *Philodromus* sp. | 0 | 2 | 2 |
| *Tibellus minor* | 0 | 1 | 1 |
| **Pholcidae** | **3** | **4** | **7** |
| *Quamtana lajuma* | 2 | 2 | 4 |
| *Quamtana* sp. | 1 | 2 | 3 |
| **Pisauridae** | **0** | **2** | **2** |
| *Cispius problematicus* | 0 | 2 | 2 |
| **Salticidae** | **116** | **170** | **286** |
| *Baryphas ahenus* | 0 | 1 | 1 |
| *Cyrba boveyi* | 0 | 1 | 1 |
| *Cyrba lineata* | 0 | 1 | 1 |
| *Evarcha* sp. | 1 | 5 | 6 |
| *Heliophanus* sp. | 1 | 0 | 1 |
| *Icius insolidus* | 1 | 10 | 11 |
| *Icius* sp. | 0 | 1 | 1 |
| *Langona bisecta* | 0 | 33 | 33 |
| *Langona hirsuta* | 6 | 29 | 35 |
| *Langona* sp.2 | 2 | 25 | 27 |
| *Langonella* sp.1 | 0 | 6 | 6 |
| *Menemerus* sp. | 1 | 0 | 1 |
| *Myrmarachne marshalli* | 1 | 0 | 1 |
| *Myrmarachne* sp. | 1 | 1 | 2 |
| *Pellenes bulawayoensis* | 1 | 0 | 1 |
| *Pellenes* sp. | 2 | 3 | 5 |
| *Pellenes tharinae* | 3 | 0 | 3 |
| *Phlegra procera* | 14 | 0 | 14 |
| *Pseudicius* sp. | 0 | 1 | 1 |
| *Stenaelurillus guttiger* | 69 | 51 | 120 |
| *Stenaelurillus nigricaudus* | 12 | 0 | 12 |
| *Thyene natalii* | 0 | 1 | 1 |
| *Thyenula* sp. | 1 | 1 | 2 |
| **Scytodidae** | **6** | **13** | **19** |
| *Scytodes clavata* | 2 | 2 | 4 |

| | | | |
|---|---|---|---|
| *Scytodes maritima* | 1 | 1 | 2 |
| *Scytodes quinqua* | 0 | 10 | 10 |
| *Scytodes* sp. | 3 | 0 | 3 |
| **Segestriidae** | **0** | **2** | **2** |
| *Ariadna bilineata* | 0 | 1 | 1 |
| *Ariadna* sp.1 | 0 | 1 | 1 |
| **Selenopidae** | **0** | **7** | **7** |
| *Anyphops* sp. | 0 | 1 | 1 |
| *Anyphops* sp.1 | 0 | 2 | 2 |
| *Selenops zuluanus* | 0 | 4 | 4 |
| **Sicariidae** | **3** | **3** | **6** |
| *Hexophthalma hahni* | 0 | 2 | 2 |
| *Loxosceles simillima* | 3 | 0 | 3 |
| *Sicarius hahnii* | 0 | 1 | 1 |
| **Sparassidae** | **0** | **12** | **12** |
| *Arandisa* sp. | 0 | 1 | 1 |
| *Olios brachycephalus* | 0 | 2 | 2 |
| *Olios chubbi* | 0 | 1 | 1 |
| *Olios correvoni* | 0 | 1 | 1 |
| *Olios* sp. | 0 | 5 | 5 |
| *Pseudomicrommata longipes* | 0 | 1 | 1 |
| *Zelotes humilis* | 0 | 1 | 1 |
| **Theraphosidae** | **1** | **8** | **9** |
| *Brachionopus pretoriae* | 0 | 3 | 3 |
| *Brachionopus* sp. | 0 | 4 | 4 |
| *Harpactirella flavipilosa* | 1 | 0 | 1 |
| *Harpactirella overdijki* | 0 | 1 | 1 |
| **Theridiidae** | **2** | **10** | **12** |
| *Euryopis* sp. | 0 | 6 | 6 |
| *Latrodectus renivulvatus* | 1 | 0 | 1 |
| *Phycosoma* sp. | 0 | 1 | 1 |
| *Ranops* sp. | 0 | 1 | 1 |
| *Theridion* sp. | 1 | 2 | 3 |
| **Thomisidae** | **5** | **3** | **8** |
| *Heriaeus* sp. | 1 | 0 | 1 |
| *Heriaeus peterwebbi* | 1 | 0 | 1 |
| *Heriaeus* sp. | 1 | 0 | 1 |
| *Ozyptila* sp. | 1 | 1 | 2 |
| *Pactates compactes* | 0 | 1 | 1 |
| *Stiphropus* sp. | 0 | 1 | 1 |
| *Xysticus natalensis* | 1 | 0 | 1 |
| **Trachelidae** | **1** | **3** | **4** |
| *Thysanina transversa* | 0 | 3 | 3 |
| *Trachelas* sp. | 1 | 0 | 1 |
| **Zodariidae** | **111** | **52** | **163** |
| *Australutica africana* | 4 | 2 | 6 |

| | | | |
|---|---|---|---|
| *Capheris crassimana* | 1 | 0 | 1 |
| *Capheris crassimanus* | 1 | 0 | 1 |
| *Cydrela schoemanae* | 0 | 7 | 7 |
| *Cydrela* sp. | 0 | 2 | 2 |
| *Cydrela* sp.1 | 0 | 1 | 1 |
| *Cyrioctea marken* | 0 | 2 | 2 |
| *Diores auricula* | 3 | 1 | 4 |
| *Diores auricular* | 27 | 1 | 28 |
| *Diores magicus* | 1 | 0 | 1 |
| *Diores* sp. | 17 | 9 | 26 |
| *Diores triarmatus* | 0 | 1 | 1 |
| *Heradida bicincta* | 0 | 7 | 7 |
| *Heradida* sp. | 2 | 0 | 2 |
| *Heradida* sp.1 | 5 | 2 | 7 |
| *Ibala arcus* | 1 | 0 | 1 |
| *Mastidiores* sp. | 1 | 2 | 3 |
| *Mastidiores* sp.1 | 13 | 3 | 16 |
| *Microdiores* sp. | 3 | 4 | 7 |
| *Ranops* sp.1 | 32 | 8 | 40 |
| **Total** | **1522** | **1151** | **2673** |

Appendix B: Ant subfamilies and species collected over the study period at western Soutpansberg, Limpopo, South Africa.

| Ant subfamilies and species | Transformed sites | Untransformed sites | Total |
|---|---|---|---|
| **Dolichoderinae** | **156** | **296** | **452** |
| *Tapinoma luteum* | 1 | 15 | 16 |
| *Tapinoma* sp.01 | 0 | 3 | 3 |
| *Technomyrmex pallipes* | 155 | 278 | 433 |
| **Dorylinae** | **20** | **59** | **79** |
| *Aenictus rotundatus* | 6 | 43 | 49 |
| *Dorylus helvolus* | 12 | 5 | 17 |
| *Parasyscia* sp.01 | 2 | 11 | 13 |
| **Formicinae** | **11697** | **1570** | **13267** |
| *Acropyga* sp.01 | 1 | 0 | 1 |
| *Anoplolepis cf. custodiens* | 10471 | 224 | 10695 |
| *Camponotus cf. niveosetosus* | 0 | 1 | 1 |
| *Camponotus cubangensis dofleini* | 0 | 2 | 2 |
| *Camponotus fulvopilosus* | 0 | 26 | 26 |
| *Camponotus mayri* | 3 | 0 | 3 |
| *Camponotus* sp.02 (*rufoglaucus* gp.) | 37 | 13 | 50 |
| *Camponotus* sp.03 (*niveosetosus* gp.) | 1 | 4 | 5 |
| *Camponotus* sp.03 *niveosetosus group* | 0 | 3 | 3 |
| *Camponotus* sp.04 (*etiolipes* gp.) | 0 | 2 | 2 |
| *Camponotus* sp.05 | 0 | 7 | 7 |
| *Camponotus* sp.06 (*maculatus* gp.) | 0 | 3 | 3 |
| *Camponotus* sp.07 (*empedocles* gp.) | 0 | 18 | 18 |
| *Camponotus* sp.08 (*mystaceus gp.*) | 0 | 2 | 2 |
| *Camponotus* sp.11 (*cinctellus* gp.) | 246 | 19 | 265 |
| *Camponotus* sp.12 (*cinctellus* gp.) | 30 | 0 | 30 |
| *Camponotus* sp.18 (*maculatus* gp.) | 110 | 73 | 183 |
| *Camponotus* sp.20 | 0 | 47 | 47 |
| *Camponotus* sp.20 (*niveosetosus* gp.) | 0 | 4 | 4 |
| *Camponotus* sp.23 | 32 | 42 | 74 |
| *Camponotus* sp.25 (*cinctellus* gp.) | 8 | 0 | 8 |
| *Lepisiota cf. longinoda* | 11 | 13 | 24 |
| *Lepisiota crinita* | 165 | 16 | 181 |
| *Lepisiota* sp.01 (*capensis* gp.) | 243 | 316 | 559 |
| *Lepisiota* sp.02 (*crinita* gp.) | 1 | 0 | 1 |
| *Lepisiota* sp.02 (*spinosior* gp.) | 35 | 14 | 49 |
| *Lepisiota* sp.03 (*crinita* gp.) | 71 | 1 | 72 |
| *Lepisiota* sp.08 (*capensis* gp.) | 2 | 48 | 50 |
| *Lepisiota* sp.10 (*capensis* gp.) | 4 | 1 | 5 |
| *Lepisiota* sp.12 (*spinosior* gp.) | 7 | 0 | 7 |
| *Plagiolepis* sp.01 | 1 | 0 | 1 |
| *Plagiolepis* sp.02 | 0 | 55 | 55 |
| *Plagiolepis* sp.03 | 4 | 15 | 19 |

|  |  |  |  |
|---|---|---|---|
| *Polyrhachis schistacea* | 24 | 14 | 38 |
| *Tapinolepis* sp.01 | 185 | 587 | 772 |
| *Tapinolepis* sp.02 | 5 | 0 | 5 |
| **Myrmicinae** | **15495** | **19858** | **35353** |
| *Cardiocondyla* sp.01 | 2 | 2 | 4 |
| *Cardiocondyla* sp.02 | 30 | 45 | 75 |
| *Carebara* sp.01 | 0 | 21 | 21 |
| *Cataulacus* sp.01 | 0 | 1 | 1 |
| *Cataulacus wissmannii* | 1 | 0 | 1 |
| *Crematogaster* sp.01 (*sphaerocrema* gp.) | 5 | 237 | 242 |
| *Crematogaster* sp.02 (*rufigena* gp.) | 0 | 25 | 25 |
| *Crematogaster* sp.03 (*rectinota* gp.) | 19 | 3 | 22 |
| *Crematogaster* sp.04 (*sphaerocrema* gp.) | 0 | 1 | 1 |
| *Crematogaster* sp.06 (*custanea complex*) | 2 | 13 | 15 |
| *Crematogaster* sp.07 | 301 | 0 | 301 |
| *Meranoplus perinqueyi* | 1 | 43 | 44 |
| *Meranoplus cf. glaber* | 0 | 21 | 21 |
| *Meranoplus magrettii* | 59 | 46 | 105 |
| *Messor* sp.01 | 30 | 0 | 30 |
| *Monomorium fastidium* | 2 | 106 | 108 |
| *Monomorium notulum* | 239 | 237 | 476 |
| *Monomorium albopilosum* | 2292 | 2362 | 4654 |
| *Monomorium cf. drapenum* | 10 | 512 | 522 |
| *Monomorium cf. junodi* | 2462 | 102 | 2564 |
| *Monomorium damarense* | 834 | 475 | 1309 |
| *Monomorium emeryi* | 311 | 24 | 335 |
| *Monomorium junodi* | 969 | 67 | 1036 |
| *Monomorium* 01*. notulum* | 0 | 22 | 22 |
| *Monomorium* sp.01 | 52 | 120 | 172 |
| *Monomorium* sp.07 | 0 | 10 | 10 |
| *Monomorium* sp.08 (*Monomorium* gp.) | 2 | 1 | 3 |
| *Monomorium* sp.10 (*salamonis* gp.) | 107 | 240 | 347 |
| *Monomorium* sp.12 (*Monomorium* gp.) | 0 | 1 | 1 |
| *Myrmicaria natalensis* | 547 | 787 | 1334 |
| *Ocymyrmex flaviventris* | 6 | 256 | 262 |
| *Ocymyrmex fortior* | 411 | 519 | 930 |
| *Ocymyrmex* sp.03 | 0 | 7 | 7 |
| *Pheidole* sp.01 (*megacephala* gp.) | 963 | 2600 | 3563 |
| *Pheidole* sp.02 (*liengmei* gp.) | 591 | 94 | 685 |
| *Pheidole* sp.03 (*megacephala* gp.) | 651 | 3484 | 4135 |
| *Pheidole* sp.05 (*megacephala* gp.) | 2064 | 2866 | 4930 |
| *Pheidole* sp.06 (*crassinoda* gp.) | 27 | 214 | 241 |
| *Pheidole* sp.06 (*crassinode* gp.) | 24 | 0 | 24 |
| *Pheidole* sp.07 | 92 | 496 | 588 |
| *Pheidole* sp.09 (*crassinoda* gp.) | 35 | 9 | 44 |
| *Pheidole* sp.10 (*megacephala* gp.) | 4 | 599 | 603 |

| | | | |
|---|---|---|---|
| *Pheidole* sp.13 | 256 | 16 | 272 |
| *Solenopsis* sp.01 | 3 | 99 | 102 |
| *Solenopsis* sp.02 | 8 | 103 | 111 |
| *Strumigenys pretoriae* | 0 | 1 | 1 |
| *Tapinolepis* sp.01 | 76 | 65 | 141 |
| *Tapinolepis* sp.02 | 19 | 0 | 19 |
| *Tetramorium baufra* | 7 | 293 | 300 |
| *Tetramorium 01. cf. setigerum* | 112 | 19 | 131 |
| *Tetramorium notiale* | 3 | 0 | 3 |
| *Tetramorium sepositum* | 5 | 88 | 93 |
| *Tetramorium setigerum* | 8 | 13 | 21 |
| *Tetramorium setuliferum* | 94 | 246 | 340 |
| *Tetramorium* sp.01 (*squaminode* gp.) | 54 | 131 | 185 |
| *Tetramorium* sp.04 (*gabonense* gp.) | 5 | 7 | 12 |
| *Tetramorium* sp.05 (*sereiceventre* gp.) | 830 | 0 | 830 |
| *Tetramorium* sp.07 (*weitzeckeri* gp.) | 21 | 363 | 384 |
| *Tetramorium* sp.08 (*similimum* gp.) | 32 | 23 | 55 |
| *Tetramorium* sp.08 (*simillimum* gp.) | 13 | 43 | 56 |
| *Tetramorium* sp.12 (*squaminodis* gp.) | 169 | 468 | 637 |
| *Tetramorium* sp.13 | 1 | 3 | 4 |
| *Tetramorium* sp.14 (*sereiceventre* gp.) | 52 | 720 | 772 |
| *Tetramorium* sp.16 (*sereiceventre* gp.) | 580 | 156 | 736 |
| *Tetramorium* sp.21 (*squaminode* gp.) | 0 | 18 | 18 |
| *Tetramorium* sp.23 (*solidum* gp.) | 1 | 1 | 2 |
| *Tetramorium* sp.24 (*transversinode* gp.) | 0 | 296 | 296 |
| *Tetramorium transversinode* | 1 | 18 | 19 |
| **Ponerinae** | **413** | **169** | **582** |
| *Anochectus cf. traegordhi* | 0 | 2 | 2 |
| *Anochetus* sp.01 | 2 | 1 | 3 |
| *Anochetus traegaordhi* | 0 | 1 | 1 |
| *Bothroponera* sp.01 | 4 | 0 | 4 |
| *Bothroponera* sp.02 | 21 | 84 | 105 |
| *Bothroponera strigulosa* | 23 | 31 | 54 |
| *Brachyponera* sp.01 | 321 | 0 | 321 |
| *Brachyponera* sp.02 | 2 | 0 | 2 |
| *Hypoponera* sp.01 | 1 | 3 | 4 |
| *Leptogenys intermedia* | 0 | 1 | 1 |
| *Leptogenys schwabi* | 0 | 1 | 1 |
| *Mesoponera caffraria* | 2 | 4 | 6 |
| *Odontomachus troglodytes* | 29 | 6 | 35 |
| *Ophthalmopone* sp.01 | 4 | 0 | 4 |
| *Platythyrea lamellosa* | 0 | 2 | 2 |
| *Platythyrea schultzei* | 0 | 3 | 3 |
| *Plectroctena* sp.01 | 3 | 13 | 16 |
| *Pseudoponera* sp.02 | 1 | 17 | 18 |
| **Pseudomyrmicinae** | **1** | **1** | **2** |

| | | | |
|---|---|---|---|
| *Tetraponera* sp.01 | 1 | 1 | 2 |

Appendix C: Land-use types for the sites and sample coverage for both taxa in all the Soutpansberg elevational transect sites.

| Site | Land-use type | Sample Coverage | |
|---|---|---|---|
| | | Spiders | Ants |
| VIL | Human settlement | 0.8991 | 0.9983 |
| CL | Cropland | 0.975 | 0.9997 |
| BE | Bush encroachment | 0.8196 | 0.9928 |
| CBE | Cleared bush encroachment | 0.9211 | 0.9966 |
| 10S | Natural | 0.767 | 0.9974 |
| 12SA | Natural | 0.9018 | 0.9977 |
| 12SB | Natural | 0.8011 | 0.9978 |
| 14SA | Natural | 0.7969 | 0.9969 |
| BP | Eucalyptus plantation | 0.7632 | 0.9881 |
| MO | Macadamia orchard | 0.9455 | 0.9988 |
| 16S | Natural | 0.7939 | 0.9972 |
| 17N | Natural | 0.7634 | 0.9974 |
| 14NA | Natural | 0.8021 | 0.9955 |
| 14NB | Natural | 0.6707 | 0.9953 |
| 12N | Natural | 0.7704 | 0.9925 |
| 10N | Natural | 0.8958 | 0.9974 |
| 08NA | Natural | 0.9031 | 0.9976 |
| 08NB | Natural | 0.9556 | 0.9974 |
| | | **0.8414** | **0.9963** |