# Response of arthropod biodiversity to native vegetation and monoculture plantations: Implications for conservation and management

By

**Thembekile A. Mthimunye**

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of

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School of Life Sciences
College of Agriculture, Engineering and Science
University of KwaZulu-Natal
Pietermaritzburg
Campus
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# PREFACE

This thesis is submitted to the School of Life Sciences, College of Agriculture, Engineering and Science, University of KwaZulu-Natal (UKZN), Pietermaritzburg, South Africa, for the degree of Master's in Entomology, under the supervision of Dr Caswell Munyai. The research was funded by the National Research Foundation (NRF).

This thesis has been prepared according to **Format 2** as outlined in the UKZN information for the guidance of examiners of Higher degrees, as a set of papers which are published, in press, submitted, or intended for submission.

As the candidate's supervisor, I have approved this thesis for submission.

[redacted]

Supervisor: Dr Caswell Munyai

Date 17 April 204

# ABSTRACT

Timber plantations are valuable to the global economy. They are inevitably forming part of future landscapes as they have become one of the main land use occupying the global land area. There is a growing interest and debate on their effect on biodiversity since they are non-native habitats with conservation potential. However, biodiversity response to timber plantations remains ambiguous, as previous studies have reported mixed findings. In addition, the factors that drive species' taxonomic responses to disturbance are not well-studied. Given that invertebrates, particularly arthropods, are the most abundant, the current study will investigate their response to timber plantations (at a global scale) and their diversity and drivers at a local scale (in the Midlands of KwaZulu-Natal). Particularly, the current study aimed to 1) systematically review published literature on arthropod diversity patterns in *Pinus* and *Eucalyptus* timber plantations versus natural vegetation globally, 2) compare the diversity and assemblage composition of different arthropod taxa in these plantations and a native forest in South Africa, 3) determine the environmental factors that drive such patterns, and 4) Assess the functional composition of arthropods in these habitats. To determine the response of arthropods to timber plantations globally, PRISMA guidelines were followed to systematically review the literature. One hundred and eleven studies from 30 countries were selected from the Web of Science, Google Scholar, and Scopus. The review highlighted that arthropod diversity declines with increased habitat simplicity, an attribute of most commercialised timber plantations of tree species outside their native ranges. To assess arthropod diversity at a local scale, ground-dwelling arthropods were collected using pitfall traps from *Pinus* and *Eucalyptus* plantations and a native forest in the Natal Midlands. Environmental data were recorded to test whether arthropods were driven by forest type, season, or microhabitat variables within those habitats. A total of 4 284 arthropod individuals were collected. Although different arthropod taxa had unique responses, the overall arthropod diversity was fairly similar across the three habitats. Habitat heterogeneity was higher in the native forest and correlated with the species richness of beetles and myriapods (centipedes and millipedes). Spider species richness was mainly driven by season, with most spider species collected during the dry-hot season. Ants were best predicted by habitat type as more species were collected in the native forest, although this was not statistically significant. The assemblage composition of beetle and spider communities significantly differed across the habitats, while ants and myriapods had similar communities. Functional redundancy was evident across the site, implying that declines in species richness in the plantations did not lead to a loss of ecosystem functions. This study shows that the generalisation of biodiversity response to timber plantations may be misleading. Rather, future studies should focus on the habitat-specific elements that drive species distribution in these disturbed ecosystems. In addition, it highlights the need to use complementary facets for biodiversity assessment, as taxonomic diversity may provide limited information on ecosystem functions if not combined with functional diversity.

# DECLARATIONS

## DECLARATION 1: PLAGIARISM

I, Thembekile A. Mthimunye declare that:

1. The research reported in this thesis is my original research, except where otherwise indicated.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs, or other information, unless specifically acknowledged as being sourced from other persons.
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   a. their words have been re-written but the general information attributed to them have been referenced, and
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# DECLARATION 2: PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis:

**PUBLICATION 1** (in preparation, Frontiers in Forests and Global Change)

**Arthropod diversity in timber plantations: A systematic review**

TA Mthimunye & Dr TC Munyai

*Author contributions:*

TAM and TCM conceived the manuscript. Data was collected and summarised by TAM. TAM led the writing of the manuscript.

**PUBLICATION 2** (in preparation, Forest Ecology and Management)

**What drives multiple arthropod communities in native forests and monoculture timber plantations?**

TA Mthimunye & Dr TC Munyai

*Author contributions:*

TAM and TCM conceived the manuscript. Data was collected by TAM and TCM. TAM led the writing of the manuscript.

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Thembekile Mthimunye

Date: January 2024

## DECLARATION 3: CONFERENCE PROCEEDINGS

Mthimunye T.A. & Munyai T.C. Local environmental drivers of arthropod diversity patterns in monoculture timber plantations. The Conservation Symposium 2023, Wild Coast Sun, Port Edward, 5 – 10 November 2023. Oral Presentation

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Mthimunye T.A. & Munyai T.C. Monoculture plantations may be a suitable habitat for some ground-dwelling arthropods. 11th Oppenheimer Research Conference 2023, Randjesfontein Cricket Pavilion, Midrand, 4 – 6 October 2023. Oral Presentation

Mthimunye T.A. & Munyai T.C. Are timber plantations ecological deserts for arthropod diversity? 23rd Congress of the Entomological Society of Southern Africa 2023, Stellenbosch University, 11 - 14 July 2023. Oral Presentation.

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'*You shall find favour and high esteem in the sight of God and men*' - Proverbs 3:4

# TABLE OF CONTENTS

## LIST OF FIGURES

# LIST OF TABLES

# CHAPTER 1: Introduction

## 1.1 Background of the study

Timber plantations dominate the global commercial forestry industry, making them an essential commodity for the economy worldwide. The commercial timber plantations generate about 34% of the world's timber, which is more than the amount generated from other timber sources such as old-growth forests (30%), managed and unmanaged second-growth forests, contributing 22% and 14%, respectively (Sedjo and Botkin, 1997). However, the demand for timber products will continue to increase as the human population grows (Hartley, 2002) causing more pressure on timber production. In South Africa, the forestry industry primarily grows three timber genera, namely, the pine (*Pinus*), bluegum (*Eucalyptus*) and the black wattle (*Acacia mearnsii*), each contributing 49%, 43% and 7% towards timber production in the country, respectively (Sedjo and Botkin, 1997).

Pine trees are native to the Northern hemisphere (Imanuddin *et al.*, 2020). Being the most diverse genus in the family Pinaceae, they consist of over 110 species globally (Imanuddin *et al.*, 2020). Pines were first introduced in the Southern Hemisphere between the 16th and the 17th century (Richardson, 2000; Simberloff *et al.*, 2010). In particular, the *P. pinaster* and the *P. pinea* were the first species introduced in South Africa in1685 for commercial reasons (Simberloff *et al.*, 2010). Their cultivation increased during the 1880s and peaked in the 1890s, owing to their invasion capacity (Richardson, 2000). South Africa is among the top three countries with large-scale plantations of non-indigenous tree species (Simberloff *et al.*, 2010). It has been cautioned that the tropical and subtropical regions will be more invaded by *P. caribaea, P. kesiya* and *P.oocarpa* in the near future (Richardson, 2000), and this will have certain implications on native biodiversity (McConnachie *et al.*, 2015; Cifuentes-Croquevielle *et al.*, 2020).

Similarly, to the pine trees, the silvicultural practice of the *Eucalyptus* contributes extensively to timber production. It is the second largest distributed timber tree genus globally, after the *Pinus* plantations (Keet and Richardson, 2022). It covers approximately 20 million ha of land worldwide (Keet and Richardson, 2022). This genus comprises over 700 species, making it the largest genus in the tribe Eucalypteae (Bayly, 2016; Hirsch *et al.*, 2020; Keet and Richardson, 2022). Most species naturally occur in Australia (Keet and Richardson, 2022). It was reported that over 200 species were introduced to South Africa by 2009 (Richardson *et al.*, 2003;

Bennett, 2010). The planting of *Eucalyptus* forests was due to their multiple benefits. They provide a constant supply of essential oils, charcoal products, and are also used in phytoremediation and ornamental plants (Keet and Richardson, 2022). However, they are primarily valued for their rapid regeneration, accelerating timber production while reducing timber harvesting from native forests (Majer and Recher, 1999).

The effect of timber plantations on biodiversity has been documented, reporting on contrasting responses from flora (Bremer and Farley, 2010; Calviño-Cancela *et al.*, 2012) and fauna (Barlow *et al.*, 2007). In addition, conservation strategies to reduce biodiversity loss in these ecosystems have been reported by Hartley (2002), who suggested that polyculture and planting of native trees is better than establishing monocultures of exotic trees. The latter study further suggested that site preparation techniques should resemble natural disturbances, with some individual trees left unharvested. There have been two major hypotheses between conservationists and industrial forest producers. The first hypothesis relates to the fact that timber plantations are expanding and will occupy a considerable proportion of the landscape in the future (Hartley, 2002). Secondly, timber plantations could contribute to biodiversity conservation (Hartley, 2002; Bremer and Farley, 2010). In contrast to the commonly accepted theory of timber plantations as biodiversity displacers, they are regarded as corridors for forest-adapted species, making them potential, alternative refuge sites (Norton, 1998; MacDonald, 2003; Samways *et al.*, 2010). They create a stable environment for the recolonisation of lower-order plants as tree interspacing opens bare ground for plant establishment (Bremer and Farley, 2010), which creates a more favourable ecosystem for animals to visit or reestablish populations (Hartley, 2002). Studies have reported that timber plantations can sustain populations of rare vertebrate species (Norton, 1998; Wilson and Watts, 1999), yet little is known about how they affect biodiversity at macro and micro scales and the factors that increase habitat suitability.

### The influence of habitat on arthropod communities

Arthropods are sensitive to habitat changes at landscape (Yekwayo *et al.*, 2016, 2017) and microhabitat scales (Gibbs and Stanton, 2001; Ober xand DeGroote, 2011; Philpott *et al.*, 2014). At a landscape scale, arthropod diversity is influenced by the surrounding vegetation, acting as source areas for populations (Garcia-Martinez *et al.*, 2017), while microhabitat factors such as moisture, temperature, light interception, and soil characteristics shape their presence and distribution at local scales (Cifuentes-Croquevielle *et al.*, 2020). Moisture (Kaspari and

Weiser, 2000) and temperature (Hernandez and Vaz-de-Mello, 2009) affect the activity and survival of terrestrial invertebrates, while soil acts as a habitat for terrestrial invertebrates while mediating nutrient transfer in the biosphere (Nsengimana, 2020; Wale and Yesuf, 2022).

The specified environmental conditions observed in habitats are often driven by plant diversity, vegetation structure (Cifuentes-Croquevielle *et al.*, 2020) and habitat complexity (Philpott *et al.*, 2014). Plant species diversity determines the quality and quantity of the leaf litter available to ground-dwelling arthropod communities (Villanueva-Lopez *et al.*, 2019; Cifuentes-Croquevielle *et al.*, 2020). Vegetation structure refers to the morphological and physical architecture of plants (Katherina *et al.*, 2018). This exacerbates the creation of a complex habitat structure for ground-dwelling arthropods as it creates leaf litter, logs and decaying organic matter which act as substrates for such arthropods. More complex environments improve the availability of resources and niches for arthropods (Leal *et al.*, 2016).

### Arthropods as drivers of ecosystem stability

Ecosystem functioning depends on species traits, which determine their resource use efficiency, and niche occupancy within that ecosystem (Cadotte *et al.*, 2011). Although species diversity provides a meaningful idea about ecosystem stability, it is considered more valuable when correlated with functional diversity (Bihn *et al.*, 2010; Cadotte *et al.*, 2011). Arthropods are responsible for maintaining ecosystem function as they aid in decomposition, nutrient recycling, and soil aeration (Maisto *et al.*, 2017; Wale and Yesuf, 2022). Consequently, they influence the ability of other organisms to obtain resources. Their movement between soil particles creates tunnels for other organisms to manoeuvre, forage or hide from predators. This further improves soil aeration and water infiltration for plant growth. Thus, arthropods sustain the ecological balance between organisms. However, with increasing habitat changes, evidence has shown that biodiversity loss diminishes ecological processes essential for supporting human-managed landscapes and the surrounding natural ecosystems (Chapin Iii *et al.*, 2000; Gaston, 2000; Petchey and Gaston, 2006).

### Arthropods as biological indicators of forest health

As commonly stated by ecologists, biological indicators should contain a subset of organisms or a surrogate species that inform us of the biodiversity patterns of a particular area (Bennett *et al.*, 2009). Although biological indicators do not represent all the flora and faunal diversity in a specific area, they provide an idea of the preserved ecosystem functions and environmental health (Bennett *et al.*, 2009). Arthropods are considered biological indicators and are used in ecological monitoring and assessment due to their sensitivity to environmental change (Maleque *et al.*, 2009; Camara *et al.*, 2012). Soil and leaf litter arthropods, in particular, are considered forest ecosystem engineers (Oxbrough *et al.*, 2012; Swart *et al.*, 2018) as they occupy the soil, leaf litter and understory vegetation (Katherina *et al.*, 2018; Swart *et al.*, 2018). They can alter leaf litter and soil characteristics, producing organic matter (Nsengimana, 2018), which supports other life forms in the soil. Their role in facilitating ecosystem function stems from their ecology as they interact with various organisms at different vegetation layers and above or below the soil surface. Therefore, their interaction with biodiversity may offer a reflection of the overall ecosystem interactions as they shape food webs and promote nutrient flow.

In addition, arthropods possess specific characteristics which make them unique for biological monitoring compared to other taxa. They are among the most abundant, diverse organisms with large biomass and density in terrestrial ecosystems (Bennett *et al.*, 2009; Nsengimana, 2018). They represent numerous trophic levels as a result of their high diversity (Nsengimana, 2018), and they have various dietary requirements at different developmental stages and classifications according to their ecosystem requirements (as generalists or specialists) (Wale and Yesuf, 2022). Additionally, arthropods have rapid regeneration rates, making them suitable for understanding environmental changes in a relatively short period (Nsengimana, 2018). Arthropods groups possess morphological characteristics and functional groups, enabling them to occupy diverse ecosystems and niches within ecosystems. Thus, measuring their changes at finer scales informs us about the habitat simplicity and disturbance intensity.

## 1.2 Justification of the study

Timber plantations have negatively affected biodiversity (Newbold *et al.*, 2015; Villanueva-Lopez *et al.*, 2019). This is of great concern as habitats increasingly become unavailable for species with specialised habitat requirements and diets. The loss of taxonomic and functional diversity of faunal communities decreases the ecosystem's resilience to threats and stability (Martello *et al.*, 2018; Cifuentes-Croquevielle *et al.*, 2020), eventually limiting its ability to provide essential ecosystem services (Eckert *et al.*, 2022b). Although timber plantations can survive in a wide range of environments (Sedjo, 1999), the loss of soil-dwelling and above-ground arthropods interferes with their functionality as an ecosystem (Bird *et al.*, 2004). The reduction of diverse arthropods will decrease decomposition rates and alter nutrient dynamics, reducing soil fertility and stability since soil aeration, moisture and infiltration will be negatively impacted (Bird *et al.*, 2004). The loss of above-ground arthropods may result in the loss of pollinators and seed dispersers.

Determining the diversity patterns and the specific environmental factors affecting arthropod communities is fundamental for understanding their persistence and the preservation of ecosystem functions they perform (Naeem and Wright, 2003; Cadotte *et al.*, 2011). The presence of diverse species is magnified by favourable environmental conditions, supporting healthy populations, and allowing for the coexistence of other species in the ecosystem (Flynn *et al.*, 2009). Forests are made up of different vegetation strata, resulting in diverse arthropod assemblages at different vegetation layers (Klunk *et al.*, 2018; Swart *et al.*, 2018). Therefore, factors that lead to environmental filtering above the soil surface are different from those found below or on the soil surface (Eckert *et al.*, 2022a). Therefore, it is essential to consider the specific drivers of arthropods at finer scales to draw robust conclusions on habitat suitability. This may advance sustainable production in timber plantations.

Although polyculture timber plantations are recommended for biodiversity conservation over monoculture timber plantations (Wang *et al.*, 2019; Damptey *et al.*, 2023), the latter seems favourable for yield output, as it increases the quality and quantity of timber produced (Liu *et al.*, 2018). Furthermore, converting from single-species monoculture to multiple species may take years, and forestry managers may be unprepared for such changes. Thus, more practical, evidence-based conservation measures are necessary for biodiversity improvement in the existing timber plantations. Habitat characteristics at various scales should be enhanced for invertebrate conservation to maintain their essential ecological functions.

### 1.2.1 Aim

The aim of this study was to assess patterns of arthropod diversity and assemblage composition in natural habitats and monoculture timber (*Eucalyptus* and *Pinus*) plantations at a global and local scale and determine the environmental drivers responsible for the observed difference.

### 1.2.2 Specific objectives

1. To conduct a global systematic review on arthropod diversity patterns and distributions in *Eucalyptus* and/or *Pinus* plantations and adjacent native vegetation across different ecozones (chapter 2).

2. To explore the role of adjacent habitats and how management strategies improve arthropod conservation (chapter 2).
3. To compare arthropod taxonomic diversity and assemblage composition between the native forest and timber plantations (*Pinus* also referred to as pine and *Eucalyptus* also referred to as bluegum) in the Natal Midlands (Chapter 3).
4. To determine what drives the diversity patterns of different arthropod groups and identify indicator species for the three forest types (Chapter 3).
5. Assess the functional composition of arthropods between the forest types and examine if functional redundancy is masked by taxonomic diversity (Chapter 3).

### 1.2.3 Hypotheses

It was hypothesized that monoculture timber plantations alter arthropod species diversity and their assemblage composition regardless of scale unless the plantations consist of a complex habitat structure enhanced by microhabitat factors. Gonzalez-Megias *et al.* (2007) detailed how spatial and temporal heterogeneity significantly affects arthropod communities. It was further hypothesised that natural vegetation (a natural forest) is more taxonomic and functionally diverse than monoculture timber plantations as they may contain more species with specialized ecosystem functions.

## 1.3 Dissertation outline

This dissertation is composed of four chapters:

Chapter one introduces the monoculture timber plantations, the contrasting views on how they affect biodiversity and the environmental variables that are likely to contribute to variation in biodiversity responses. It then reviewed the role of arthropods in ecosystem functioning and their use as bioindicators of sustainable forestry practices. The importance of this study is then justified and aims and objectives are specified.

Chapter two is a global systematic review that compares the response of arthropod diversity to monoculture timber plantations against natural ecosystems such as grasslands and forests. It considered published literature from different ecozones determine the effect of the macroclimate and to compare timber plantations in their native ranges and introduced regions.

Chapter three then compared arthropod taxonomic diversity and assemblage composition in monoculture timber plantations and a native forest at a local scale, i.e., the Natal Midlands in the KwaZulu-Natal province, South Africa. The microhabitat environmental variables that drive arthropod diversity were then assessed. Lastly, the indicator taxa associated with each forest type were identified, and functional diversity was investigated to determine the ecosystem stability of these plantations.

Chapter four provides concluding remarks for chapters two and three. Recommendations for future studies on forest arthropod biodiversity were further provided and the knowledge gaps were identified.

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# CHAPTER 2 : Arthropod diversity patterns in timber plantations: A systematic review

## Abstract

Timber plantations are inevitably forming part of future landscapes due to their economic value. Thus, research must be directed towards their ecological impact. Biodiversity response to timber plantations is ambiguous, although generalised. Therefore, a global systematic review was conducted on arthropod diversity patterns in *Pinus* and *Eucalyptus* monoculture plantations in reference to adjacent natural vegetation types. Literature search was conducted between February and July 2022 in Web of Science, Google Scholar, and Scopus. Data collection and synthesis followed a narrative approach. In total, 111 eligible studies from 30 countries, consisting of studies conducted between 1976 and 2022 were obtained. Most studies were conducted in the Neotropical region (n = 58), with the least studies carried out in the Indo-Malayan (n = 3) region. About 65% of the studies reported a decline in arthropod species richness in timber plantations. In comparison, 21% of the studies concluded that the plantations positively impacted species richness, while the remaining studies found no effect. Similarly, species abundance was negatively affected by the plantations in most studies (51%), with only 27% of the studies reporting a positive impact. Arthropod diversity declined in timber plantations sites that were established outside their native ranges. This supports the evidence of biodiversity loss in monoculture timber plantations, even among arthropods. The current review gives insights into the current knowledge of how arthropods respond to timber plantations within and outside their native ranges globally. Further research should use a more region-specific quantitative approach to gain insights into the local effects.

**Keywords:** Arthropod conservation, *Pinus*, *Eucalyptus*, plantation management, natural vegetation.

## 2.1 Introduction

Land-use change is a major threat to global biodiversity, especially in the Anthropocene (Meyfroidt *et al.*, 2010; Oliver and Morecroft, 2014). The intensively managed timber plantations are one of the leading causes of landscape transformation and degradation in the tropics (Hayes *et al.*, 2005). About one-third of the global land area contains natural forest (Aerts and Honnay, 2011), with 7% of that area being timber plantations (Feng *et al.*, 2023) which are increasing at an annual rate of 25000 km$^2$ (McFadden and Dirzo, 2018). In 2012, industrial forest plantations occupied an area of 533000 km$^2$ globally, and the countries that contributed the most were the United States of America (USA), Brazil, and China (Barua and Lehtonen, 2013). The expansion rate of forest timber plantations is expected to increase as the demand for timber continues to rise (Barua and Lehtonen, 2013) due to economic pressure.

Timber plantations are often deemed as 'biological deserts' due to their negative impact on overall biodiversity (Paquette and Messier, 2010). However, several studies have recognised timber plantations as potential hosts for biodiversity and, therefore, crucial for conservation (Alvey, 2006; Brockerhoff *et al.*, 2008; Braun *et al.*, 2017). Evidence has shown that they compensate for biodiversity loss caused by the deforestation of indigenous forests as these systems are created solely for timber harvesting, reducing harvesting in native forests (Lemenih and Teketay, 2004; Paquette and Messier, 2010). For this reason, more ecological enhancement should be directed towards timber species that are significantly important in the forestry industry and have a wide distribution globally, such as the *Pinus radiata* and the *Eucalyptus globulus* (Calviño-Cancela and Van Etten, 2018).

Although the *Pinus* and *Eucalyptus* timber plantations are among the most planted genera, they are at the centre of criticism due to their high-water demand (Williams, 2015), their invasive potential and displacement of biodiversity (Calviño-Cancela *et al.*, 2012; Calviño-Cancela and Van Etten, 2018; Piiroinen *et al.*, 2018). Recent studies have shown that *Eucalyptus* plantations may form part of suitable matrices between forests while creating a heterogeneous landscape to increase biodiversity at a larger scale (Van Schalkwyk *et al.*, 2021; Eckert *et al.*, 2022). Consequently, they contribute to high species diversity and turnover, regionally (Pirard *et al.*, 2016; Eckert *et al.*, 2022).

Multiple landscape attributes shape species richness, resulting in contradictory results from studies focusing on various biodiversity measures. Therefore, adopting an approach that maps biodiversity patterns at discrete levels, such as ecosystem diversity, species diversity, or genetic diversity is essential. To date, a considerable number of published articles have used species diversity as it is simple to quantify, define, and monitor (Nielsen *et al.*, 2014). In addition, it can be used as an indirect measure of ecosystem stability and functionality (Aerts and Honnay, 2011). This is because of some of its indices, for example, species richness, which provide some indication on functional compensation (García-Vega and Newbold, 2020). This implies that a single species can compensate for the loss of another species that performs the same ecosystem function (Aerts and Honnay, 2011). This is particularly true for invertebrates as they perform diverse ecological functions to maintain nearly every terrestrial ecosystem, including timber plantations (Sánchez Domínguez *et al.*, 2020).

Invertebrates have been regarded as good indicators of soil health (Cifuentes-Croquevielle *et al.*, 2020) and management regimes (Davis *et al.*, 2001; Langor and Spence, 2006; Maleque *et al.*, 2009) in forest ecosystems. However, the behaviour of a species, its habitat requirements and life history traits determine how a species responds to its environment (Aerts and Honnay, 2011). A considerable number of studies that documented the general response of biodiversity to timber plantations have prioritised vertebrates and plant communities (Hartley, 2002; Stephens and Wagner, 2007; McFadden and Dirzo, 2018), yet arthropods largely influence ecosystem health in timber plantation forests. Those that focused on arthropods are biased towards investigating insects as pests of timber plantations (Neumann and Marks, 1990; Paine *et al.*, 2010), although the effect of timber plantations on different arthropod groups remains ambiguous. This is because arthropods vary in their ability to disperse, reproduce, and recover following a disturbance. Therefore, the current review collectively summarises the diversity patterns of terrestrial arthropods globally in two commonly grown timber in genus, *Pinus,* and *Eucalyptus*. We assessed studies that dealt with arthropod species richness and abundance in *Pinus* and *Eucalyptus* plantations with reference to adjacent natural vegetation types, particularly indigenous primary forests, secondary forests, and grasslands. Our review answers explicitly the following questions:

1) What are the current global trends in studies investigating arthropod diversity and distribution in *Pinus and Eucalyptus* plantations?
2) How do arthropod species richness, abundance, and distribution respond to *Pinus* and *Eucalyptus* plantations?
3) What is the importance of various management strategies in timber plantations for arthropod conservation and the role of adjacent habitats?

## 2.2 Methods and materials

### *Search strategy*

Literature search was conducted on studies that compared arthropod taxonomic diversity in plantations and adjacent habitats characterised by natural vegetation types used as control sites. Peer review journal articles were obtained from the Web of Science (https://apps.webofknowledge.com), Google Scholar (https://scholar.google.co.za/) and

Scopus (https://www.scopus.com/). The search was conducted using specific search terms and Boolean operations. The search terms included 'arthropod*' AND ('plantation* OR planted forest* OR timber plantations OR production forest* OR exotic plantations') AND ('natural forest* OR indigenous forest* OR natural vegetation* OR grassland* OR pasture* OR land use*'). The same Boolean operations were repeated for each arthropod order in place of the general term 'arthropod'. The literature search was conducted between February 2022 and July 2022, firstly focusing on literature examining arthropods in *Eucalyptus* plantations, and then secondly, *Pinus* plantations. Therefore, relevant studies published after July 2022 were not considered. All the eligible studies were published between 1976 and 2023.

### *Data collection*

The journal articles that suited the search criteria were selected and screened. The titles and the abstracts of the selected papers were read to assess their relevance to the topic. To address the irregularity in the definitions of some search terms, timber plantations were defined as indigenous or exotic tree stands established by planting seeds or seedlings through the process of afforestation and deforestation for the production and harvesting of pulp and timber in a human-managed environment (Abbott *et al.*, 2003; Carnus *et al.*, 2006; Felton *et al.*, 2010). Natural vegetation is referred to as an ecosystem formed through biological processes or natural disturbances, as defined by Sprugel (1991). The full text of the relevant article was analysed to extract the key findings pertaining to arthropod diversity response once the article was regarded as relevant.

### *Inclusion and exclusion criteria*

Peer-reviewed research articles were based on the effects of timber plantations (*Pinus* and *Eucalyptus*) on arthropod taxonomic diversity. These had to suit the criteria listed in Table 2.1.

**Table 2.1.** Inclusion and exclusion criteria for the current study

| *Inclusion criteria* | *Exclusion criteria* |
|---|---|
| • Articles published only in English.<br>• Articles based on the collection of primary data. | • Books.<br>• Unpublished research reports. |
| • Articles that compared terrestrial arthropods inhabiting timber plantations with native vegetation types. | • Conference papers and presentations. |
| • Articles that clearly specified the plantation genus, with the plantation clearly classified as monoculture or mixed. | • Studies that reported on other taxonomic groups (such as other invertebrates, vertebrates, and plants) in conjunction with arthropods. |
| • Articles that specified where the study was conducted to determine whether the planted timber trees were native or non-native to the region. | |
| • Articles that reported on arthropod taxonomic diversity (species richness and abundance) between the habitats. | |
| • Study conducted on an adequate spatial scale and used sufficient methodology to collect arthropods. | |

*Data quality assessment*

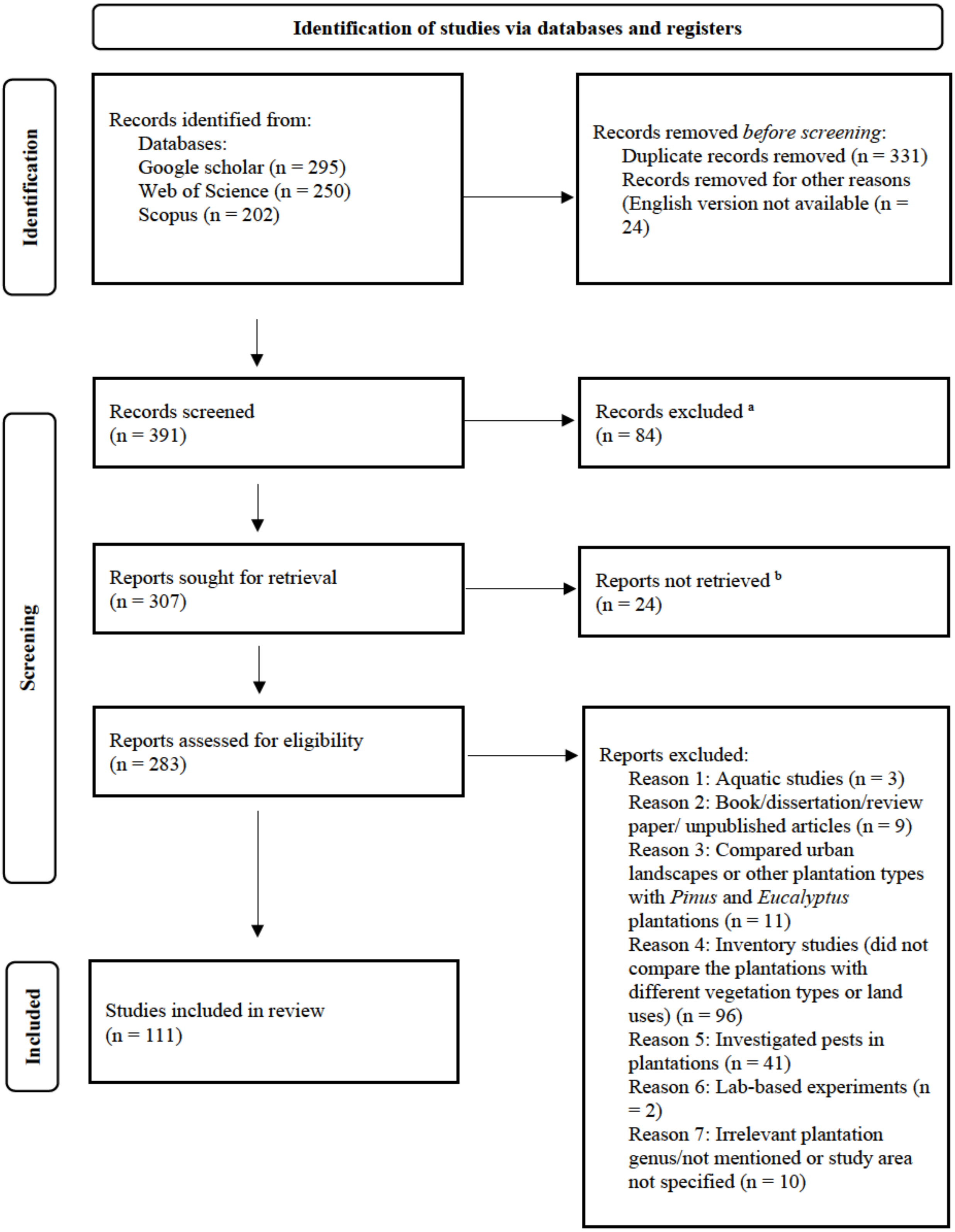
The selected articles were analysed to assess their quality for the current review article. It is crucial to note that various factors may influence the findings of different studies, affecting their reliability. Therefore, to overcome this, all the selected studies had to contain: 1) the genus of the plantation type clearly specified, 2) the region where the study was conducted to determine whether the planted timber trees were native or non-native to the region, 3) study conducted on an adequate spatial scale (plantations compared with habitats within the same terrestrial ecozone), 3) used sufficient methodology to collect arthropods, 4) compared the specified timber plantations with other vegetation types, 5) plantation clearly classified as monoculture or mixed and 6) arthropod taxonomic species richness and/or abundance patterns reported between the plantations and other natural vegetation types. Studies that reported on other taxonomic groups (such as other invertebrates, vertebrates, and plants) in conjunction with arthropods were not considered since the results on arthropods were inadequate and, therefore, arthropod species richness and abundant was not explicitly outlined.

### *Data extraction and synthesis*

A meta-analysis was not conducted due to the heterogeneity in the sampled arthropod groups and the methodology used to collect data in the reviewed studies which may have varying underlying parameters. Vetter (2019) highlighted that although a meta-analysis yields the best estimates and robust results on the subject of interest, data from studies that are highly heterogeneous should not be pooled together. A quantitative or qualitative approach to completing a systematic review article is sufficient if potential disadvantages of a meta-analysis are evident. For the current review, a qualitative and narrative approach was used to synthesise information in studies that met the inclusion criteria, similar to a review by Nielsen *et al.* (2014) investigating species richness in urban environments. The results of the studies were presented in a graphical and tabular format. For each study that met the inclusion criteria, specific information was extracted. This included the geographical region in which the study was conducted to determine its ecozone, the class and the order of the studied arthropod group or groups, the collection methods used, the relevant timber plantation genus, the vegetation types they were compared to, the patterns in species richness and abundance in the compared habitats. Some studies did not identify the Myriapoda subphylum to order level; therefore, only their taxonomic classes (Chilopoda and Diplopoda) were recorded for the purpose of this review. Various studies compared the plantation types of interest for this study with more than one vegetation type; for instance, grasslands and native forests were compared with either of the timber plantation genus in a single study. Such studies were also included in the review and the different vegetation types in each study were specified on the appendix (Table S2 and Table S3).

## 2.3 Results and discussion

The literature search yielded a total of 747 papers eligible for potential inclusion (Figure 2.1). However, 331 records were removed as they were duplicated across the three databases used in the current study. After title and abstract screening, a further 24 records were excluded since they were not published in English. Studies that analysed other non-arthropod invertebrate taxa were further excluded resulting in 283 readings considered for full-text reading. These included those that compared arthropod species richness and abundance in timber plantations of *Pinus* or *Eucalyptus* and other vegetation types. Following the final exclusion of the irrelevant studies, 111 studies from 30 countries in the tropical, subtropical, and temperate zones were used in this review as they met all the inclusion criteria (Figure 2.1).



[a] Indicates articles that reported on non-arthropod invertebrates
[b] Indicates articles that did not have full text reading available

**Figure 2.1.** Flow chart showing the process of the selection of articles reviewed to assess arthropod response to timber plantations (belonging to *Pinus* and *Eucalyptus* genera) globally.

*Dominantly studied arthropod groups in timber plantations*

Hymenopterans are the most studied insect group (studied in 39% of the total number of studies) (Figure 2.2). The order Coleoptera was the second most studied insect group, investigated in at least 32% of the studies. The latter two arthropod groups dominated studies conducted in the Neotropical and Afrotropical regions. The least studied arthropod groups in all the terrestrial ecozones were Acari, Blattodea, Diptera and Hemiptera. Interestingly, none of these orders were studied in Australasia. The number of studies in the Nearctic region were well distributed among all the arthropod groups, except for order Blattodea and Collembola. Lastly, the Indo-Malayan region solely consisted of studies that only considered orders Blatttodea and Acari.

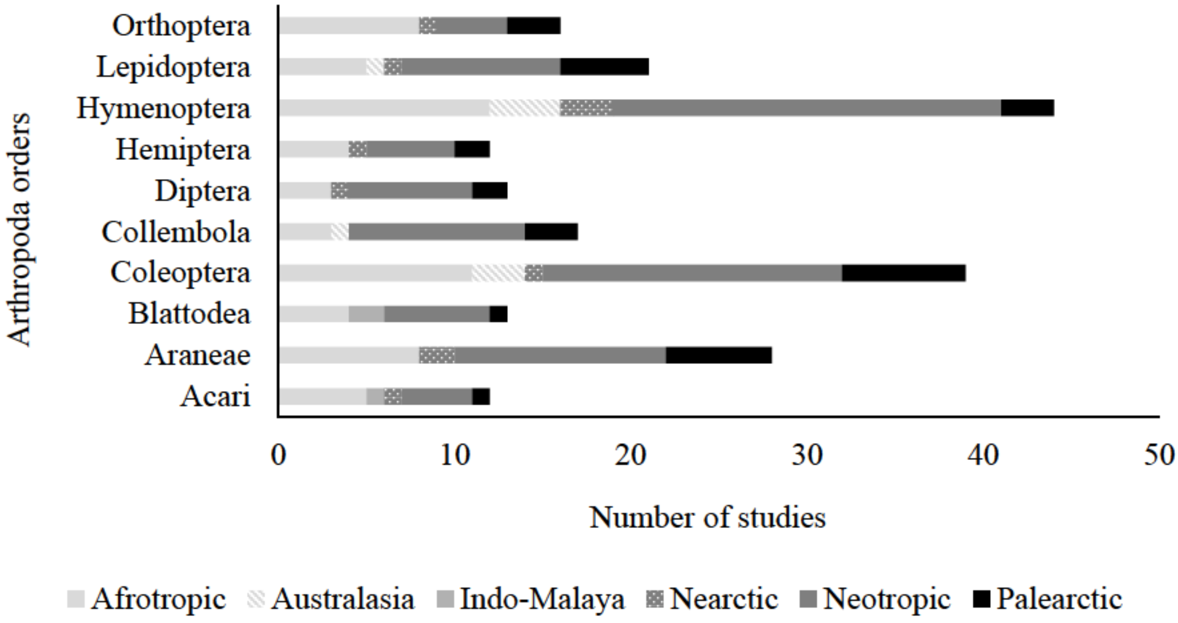


**Figure 2.2.** The predominantly studied arthropod orders across the global terrestrial ecozones in *Pinus* and *Eucalyptus* plantations.

*Global distribution of studies conducted on arthropods in timber plantations and associated trends.*

The response of arthropods to *Pinus* and *Eucalyptus* plantations was first assessed in the 1970s (Figure 2.4a). This was approximately ten years after the plantation industry was internationalised and expanded towards the Southern Hemisphere (Szulecka *et al.*, 2014;

McEwan *et al.*, 2020). The oldest studies were conducted in the Western Australian region (Majer, 1976; Springett, 1976) and reported on similar findings. Majer (1976) surveyed epigaeic ant assemblages in a *Eucalyptus* forest, pine plantations, Hollyoak woodlands, shrublands and a former mining site in the Dwellingup town, Western Australia. This latter study found that ant richness was higher in moderately disturbed native *Eucalyptus* forests than in any other land uses. Springett (1976) compared microarthropod diversity in pine plantations and mixed native forests consisting of *Eucalyptus*, *Banksia,* and *Hakea* trees in the region of Gnangara also in Western Australia and reported that species diversity was higher in the mixed native forest similar to the study by Majer (1976).

A constant increase in published articles on the topic began in the year 2000 (Figure 2.4a). This was due to conservation concerns as some scientists and general public began to view timber plantations as ‘green deserts’ (Hayes *et al.*, 2005; Kanowski *et al.*, 2005), while others recognised their environmental benefits (Binkley, 2005; Friedman, 2005; Brockerhoff *et al.*, 2008; Paquette and Messier, 2010). The number of studies investigating arthropod communities peaked between 2010 and 2019 (Figure 2.4a).

Generally, the selected studies were conducted across all the terrestrial ecozones, with most of the studies based in Brazil (Figure 2.3), the world's largest timber-producing country in the tropical regions (Couto and Dube, 2001). Overall, the neotropical region contained the largest proportion of studies (52% of the total studies (n =58)) (Figure 2.4b). A further 20% (n = 22) and 15% (n = 15) of the selected studies were based in the Palearctic and Afrotropical regions, respectively. Fewer studies were carried out in the Australian (7%, n = 8)) and the Nearctic regions (4%, n = 4), where *Eucalyptus* and *Pinus* plantations naturally occur, respectively (Calviño-Cancela and Van Etten, 2018). The Nearctic and Indo-Malayan (n = 3) regions are understudied (Figure 2.4b).

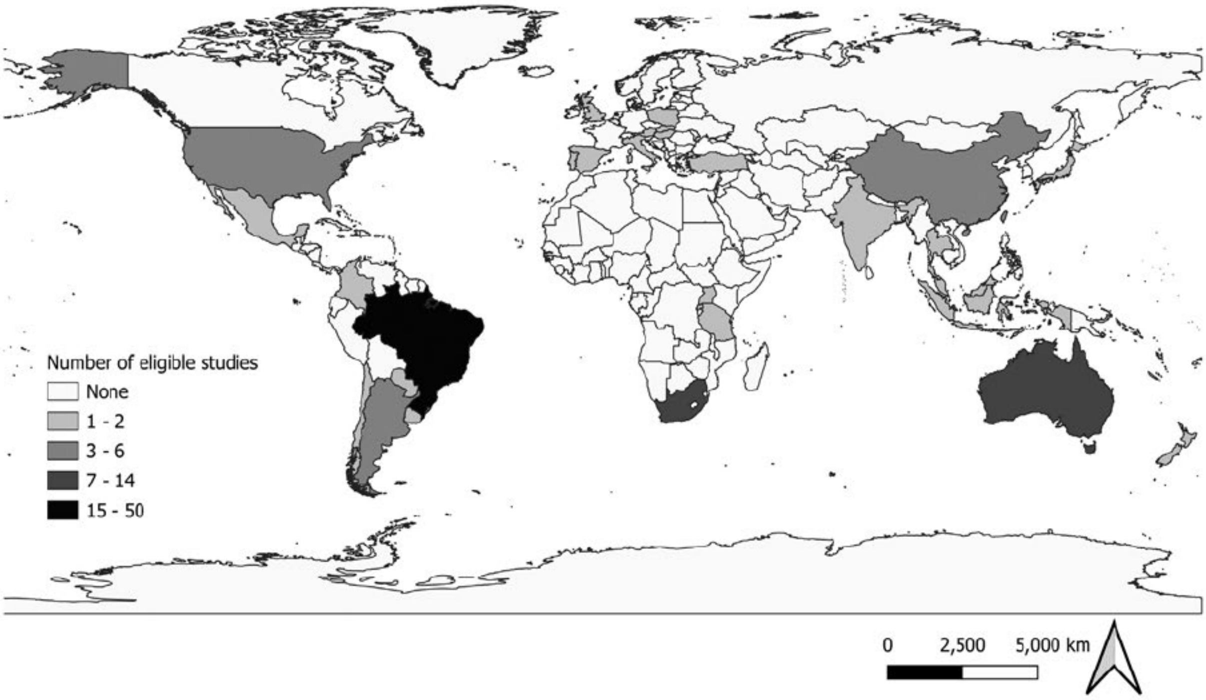


**Figure 2.3.** Map showing the distribution of eligible studies conducted on arthropod response to *Pinus* and *Eucalyptus* plantations per country globally.

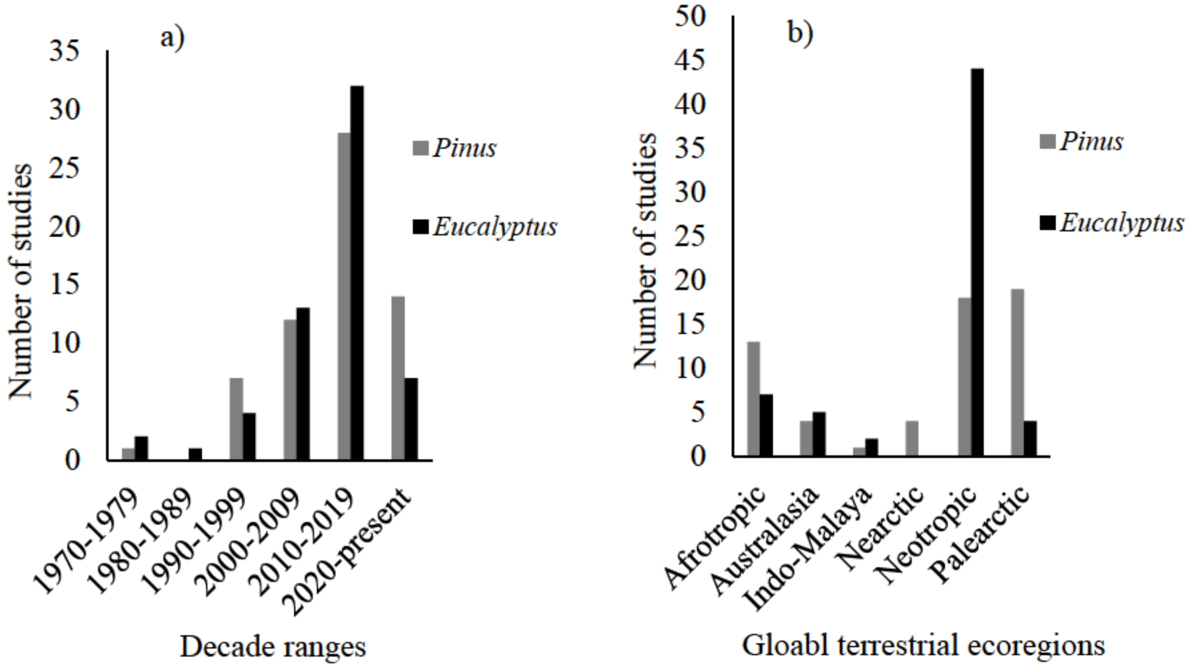


**Figure 2.4.** The number of arthropods studies in (a) *Pinus* and *Eucalyptus* plantations from 1970 to 2022 and (b) the terrestrial ecozones where the studies were conducted.

### Arthropod diversity patterns in timber plantations compared to native vegetation

The response of arthropods to disturbance varies, depending on the ecology and behaviour of the arthropod species or its life history traits. Additionally, plantations may be beneficial or detrimental to arthropods in different regions globally and locally. This may depend on whether the species in the plantation is native or non-native to the region and its invasive potential (Calviño-Cancela and van Etten, 2018). Generally, plantation studies across the globe were based on areas where they were introduced to assess their environmental impact.

About 65% of the studies in the current study reported a decline in arthropod species richness in timber plantations compared to the natural vegetation. In comparison, 21% of the studies concluded that the plantations positively impacted species richness (Supplementary material, Table S2 and Table S3). Nearly half (44%) of the remaining articles found that timber plantations had no effect on arthropod species richness since there was no difference in species richness between the timber plantations and the compared vegetation. Similarly, abundance was negatively affected by the plantations in most studies (51%), with only 27% of the studies reporting a positive impact of timber plantations on arthropod individual abundance (Supplementary material, Table S2 and Table S3). None of the investigated timber tree species showed a clear pattern in arthropod diversity response. However, it appears that Arachnids were less affected by exotic *Eucalyptus* plantations in a few studies (Lo-Man-Hung *et al.*, 2008; Lopes-Rodrigues *et al.*, 2010; Herrmann *et al.*, 2015). These studies were conducted outside the native distribution of *Eucalyptus* trees, including Brazil (Lo-Man-Hung *et al.*, 2008; Lopes-Rodrigues *et al.*, 2010), and Israel (Herrmann *et al.*, 2015). It is also notable that spiders in the above-mentioned studies were collected using different methods which are mist-blowing and pitfall trapping. However, this does not conclude that exotic *Eucalyptus* plantations do not have a negative effect on Arachnids. Therefore, such findings should be considered with caution and more studies should be conducted in the same regions to validate those results.

Previous studies suggest that timber forests may be valuable for arthropod conservation if established within their native ranges (Supplementary material, Table S2 and Table S3) or existing in their natural state. A study by Cunningham *et al.* (2005) focusing on insects in natural *Eucalyptus* forests, *Eucalyptus* plantations and grasslands found that the grasslands and the native *Eucalyptus* forests were more favourable to insect diversity, as they both had high species diversity relative to the plantation. This may be explained by the natural distribution of the *Eucalyptus* tree species within Western Australia, where the study was conducted and the natural state of the *Eucalyptus* forests, with no human-management. Arthropod biodiversity is, therefore, not compromised as the species are adapted to the vegetation. These findings were consistent across *Pinus* forests distributed across the United States of America and Europe, where *Pinus* forests occur naturally (Gillette *et al.*, 2008; Pawson *et al.*, 2008; Smith *et al.*, 2018).

Hurni and Fox (2018) pointed out that *Pinus* and *Eucalyptus* plantations are listed among the frequently planted tree genera in the timber industry at the expense of indigenous forests and grasslands. This may explain why the majority of the studies in our review specifically examined native forests (n = 67) and grasslands (n = 28) as shown in Supplementary material Table S1. Patterns of high arthropod diversity in grasslands and native forests compared to timber plantations were evident in many studies. This includes a study by Cuautle *et al.* (2016) in North America comparing ant species richness between *Eucalyptus* plantations, grasslands, and native Oak forests. The latter study concluded that ant richness and dominance was higher in the native Oak forests and grasslands compared to the plantations. Contrasting observations were reported for springtails and mites comparing the same plantation genus to grasslands in a study by Rieff *et al.* (2016) in South America. Additionally, Rieff *et al.* (2016) specifically focused on subterranean arthropod abundance in *Eucalyptus* plantations and grasslands and found that arthropod abundance was higher in the *Eucalyptus* plantations than in grasslands. Correspondingly, in Portugal, Sousa *et al.* (2004) reported high species richness and abundance of springtails in the *Pinus* plantations compared to the native forests, grasslands, and savannahs. Besides the native distribution of *Pinus* in Portugal (Richardson, 2000), several possible explanations exist for this result. For example, pine plantations are characterised by deep leaf litter in various stages of decomposition (Dames *et al.*, 1998), which is enhanced by common silvicultural plantation treatments such as thinning (Çömez *et al.*, 2021). This provides a suitable habitat for springtails as they are edaphic arthropods that consume algae, fungi, and decaying plant matter (Sousa *et al.*, 2004). Furthermore, the plantations investigated in the study by Sousa *et al.* (2004) were matured and mixed with other woody plant species, which could have made the site more hospitable due to diverse resources.

A large proportion of the selected studies considered timber plantations at their mature stages. Various studies (Costa-Milanez *et al.*, 2014; Van Schalkwyk *et al.*, 2021; Casas-Pinilla *et al.*, 2022) supported that old plantations enhance arthropod species richness and abundance compared to young plantations. A plausible explanation is that as plantations grow taller, light interception reaches the ground easily since tree branches become less dense towards the ground level. As a result, the ground surface becomes more exposed, facilitating the movement of arboreal arthropods such as butterflies (Sant'Anna *et al.*, 2014). Furthermore, it favours the colonisation of understory vegetation which then increases plant species diversity, creating diverse food sources for leaf-feeding insects (Lamb, 1998; Sinclair and New, 2004). Consequently, this will enhance the abundance of predatory arthropods, which feed on other insects. In addition, leaf litter fall will accommodate saprophagous arthropods such as millipedes. Nonetheless, the above factors may be achieved through numerous management regimes to enhance arthropod diversity.

### *The importance of timber plantation management for arthropod communities*

Although most (94%) of the selected articles in the current review did not account for the management regimes implemented on the timber plantations of interest, this is an important aspect that cannot be ignored. Not all timber plantations are structurally similar. Their morphology depends on factors such as their occurrence as a native or an alien plant in the region, the plantation management regime, the plantation design as a mixed or monoculture tree stands, and the intensity of the management regimes applied. Implementing mixed plantations to enhance biodiversity and prevent pest outbreaks has gained a significant reputation in the forestry industry (Abbott, 1993; Hartley, 2002; Ji *et al.*, 2011). This has also been suggested as a suitable method to improve habitat heterogeneity as it allows for the colonisation of understory woody plant species (Carnevale and Montagnini, 2002).

Mixed plantations may consist of the spatial arrangement of different timber tree species composition, various phenotypes and plantations of different ages planted in close proximity (Liu *et al.*, 2018). Wang *et al.* (2019) reported on the success of sustainable forestry practices where arthropod species diversity increased with the transition from monoculture plantations to mixed plantations in a study conducted in Sichuan, China. This is particularly true for *Pinus* plantations which better conserve arthropods when found in mixed stands (Sousa *et al.*, 2004; Alerding and Hunter, 2013; Higgins *et al.*, 2014). Cunningham *et al.* (2005) also found that unmanaged remnant *Eucalyptus* plantations supported more beetle diversity compared to managed monoculture plantations, native forests, and pastures. However, Gillette *et al.* (2008) found that logging in order to enhance old-growth characteristics in a pine plantation improved habitat complexity, increasing spider diversity. This view was supported by Swart *et al.* (2018), who found that felling of pine plantations improved habitat quality for certain arthropods due to increased edge effect. This favoured arthropods associated with open habitats. Therefore, plantation management may have discrete influences on different arthropods.

An important issue emerging from a previous study (Wang *et al.*, 2019) was that the success of arthropod communities in mixed plantations might be scale-dependent, with small mixed plantations supporting a greater diversity of arthropods. Wang *et al.* (2019) further elaborated that planting different tree species in close proximity ameliorates vegetation diversity. This creates habitats that were formerly unavailable at various height profiles while enabling light interception on the forest understory to support herbaceous vegetation. As a result, resource, and food availability increases, subsequently leading to resource partitioning among arthropods within plantation stands. Mixed plantations can mimic natural habitats due to enhanced habitat complexity.

### *The role of adjacent native habitats in shaping arthropod communities in timber plantations*

While plantations act as dispersal corridors for some forest species (Samways *et al.*, 2010), native vegetation may act as biodiversity source areas for plantations. It has been stipulated that plantation forests are favourable when planted adjacent to natural forests due to the canopy cover created, making them a potentially similar habitat to native remnant forests (Lamb, 1998; Norton, 1998; Carnus *et al.*, 2006; Brockerhoff *et al.*, 2008). This creates a hospitable alternative habitat for shade-adapted arthropods. Therefore, plantations reduce the edge effect and improve forest habitat connectivity (Carnus *et al.*, 2006). The views expressed by various authors must be treated cautiously since plantations adjacent to native forests are not always beneficial. The destruction of native forests at the cost of expanding plantations causes the local extinction of specialised plant and animal forest species. In such cases, plantations may not be suitable to function as a secondary forest habitat as they will support more generalist arthropod species (Wang *et al.*, 2019). Moreover, they may enhance further colonisation of exotic species, limiting native forest species from thriving (Finch, 2005; Wang *et al.*, 2019).

### *Knowledge gaps and suggestions for future studies*

Although the current systematic review only included two genera of timber tree species, these were identified as among the most dominant plantation trees for timber production globally (Brown and Ball, 2000; Cubbage *et al.*, 2010). Most of the identified studies were located in Brazil, known for large-scale deforestation of native forests, which are then replaced by timber plantation production (Cubbage *et al.*, 2014).

A limitation of this review was that it did not consider the response of other invertebrate taxonomic groups, such as molluscs and earthworms, which are also excellent indicators of forest health (Uys *et al.*, 2010). Taxon-specific response within arthropod groups is beyond the scope of this review. The main aim was to compare overall arthropod taxonomic diversity patterns between timber plantations and adjacent native vegetation types to obtain a general idea of how this land use affects arthropods and their varying distributional patterns with levels of disturbances. Species richness and abundance are often used as primary measures of biodiversity in ecological studies although they have various limitations. For instance, they do not account for the evenness of the distribution of species within the study site. Additionally, species richness is largely affected by the size and the scale of the sampling area, sampling intensity and taxonomy as some arthropods that are difficult to identify (Fleishman *et al.*, 2006). Similarly, species abundance is depends on the sampling intensity and is takes time to quantify (MacLeod *et al.*, 2011). Their limitations are undisputed; nonetheless, their assessment of homogenous plantations indirectly indicates the susceptibility of such forests to insect pest invasions as the abundance of a single species in a small scale may indicate unhealthy populations which enhances their invasion success.

The studies identified for inclusion in this review only compared plantations and other vegetation types as arthropod habitats. However, there was no consideration of the historical vegetation types prior to the anthropogenic land uses and the climatic variability between countries. Studies that included site comparisons along with the plantations of interest were considered, regardless of the vegetation type being compared to. This may have led to bias as other biotopes, such as grasslands, may not be comparable to plantations since plantations have a distinct morphology with a much denser, higher canopy.

In addition, some comparisons were not made at the landscape level to account for beta diversity in mosaic landscapes, resulting in a positive outcome at a much larger scale than what has been reported. This may overshadow the benefits of plantations at larger scales. Nonetheless, including the management regimes could have assisted in overcoming this limitation to a certain extent. Therefore, plantation forests should be viewed not only as sources of timber but also as an extension of conservation areas. In order to enhance biodiversity conservation, landscape transformation by plantations should mimic untransformed habitats. This will aid in the preservation of the structure of the habitat, species richness, composition, and function to reduce the adverse effects on indigenous species (Aerts and Honnay, 2011).

## 2.4 Conclusion

The impact of timber plantations on arthropods has been considered ambiguous due to the complexity of micro-and macro-environmental factors that contribute to diversity patterns in different bioregions. Generally, arthropod diversity declines with increased habitat simplicity, an attribute of most commercialised timber plantations. However, numerous studies conducted on Arachnids in *Eucalyptus* plantations found that they responded positively to this plantation type. This could imply that *Eucalyptus* plantations may have more complex habitats and prey available favouring spiders relative to pine plantations. Sustainable management practices and the close proximity of adjacent habitats to plantations could make these production landscapes hospitable for arthropods. An important finding emerging in this review is that timber plantations planted within their native ranges have minimal adverse effects on arthropod diversity. Further research should account for the response of above-and below-ground arthropod diversity responses to timber plantations under different management regimes.

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# CHAPTER 3 : What drives multiple arthropod communities in native forests and monoculture timber plantations in the KwaZulu-Natal Midlands?

## Abstract

Timber plantations are increasingly recognised as non-native habitats with conservation potential. This is particularly important for South Africa as these plantations are widespread. Thus, it is necessary to investigate biodiversity response to monoculture timber plantations in this region, particularly arthropod communities, and their ecosystem services. Here, we compared ground-dwelling arthropod diversity (taxonomic and functional), assemblage composition between a natural forest, and monoculture timber plantations (*Pinus* and *Eucalyptus*) in the Natal Midlands and determine their drivers. Arthropods (ants, beetles, spiders, millipedes, and centipedes) were collected at the Umngenipoort Research Facility using pitfall traps over two seasons. Microhabitat environmental data in each forest type were recorded to determine whether arthropods were driven by forest type or environmental factors within those habitats. A total of 4 284 specimens were collected, with most species collected from the native forest. Timber plantations did not result in declines in the overall arthropod diversity. However, different arthropod taxa had unique responses. The native forest had a more heterogeneous habitat structure, with carbon and nitrogen-rich soils, correlating with the species richness of beetles and myriapods. Spiders were mainly driven by season, while ants did not show any microhabitat preferences. Beetle and spider assemblages of the three forest types significantly differed relative to other arthropods. Functional redundancy was evident across all three forests, implying that changes in species richness do not lead to loss in ecosystem functions. This study highlights the need to use complementary facets for biodiversity assessment, as taxonomic diversity may provide limited information on ecosystem functions and how different arthropod groups show unique responses to various environmental factors.

**Keywords:** Arthropod diversity, assemblages, forests, habitat structure

## 3.1 Introduction

Woodlands are essential to the earth's biogeochemical systems as they facilitate the recycling of minerals such as carbon and nitrogen in the biosphere (Damptey *et al.*, 2022). They are well-recognised as reservoirs for terrestrial biodiversity (Damptey *et al.*, 2022, 2023). With native forests becoming more fragmented and timber plantations expanding, the two woody habitats are often compared for biodiversity to assess the conservation potential of timber plantations (Kanowski *et al.*, 2005; Payn *et al.*, 2015). Ribeiro-Troian *et al.* (2009) highlighted how landscape transformation is now mainly driven by human-facilitated disturbances rather than natural causes. Therefore, recent studies have emphasised the need to investigate non-native habitats to sustain viable species populations (Meijer *et al.*, 2011), as they are beginning to dominate human-managed landscapes.

The destruction of natural landscapes into agroforest systems directly alters the diversity and composition of plant species, consequently changing the vegetation type and cover (Feng *et al.*, 2015; Schroeder *et al.*, 2021). This affects the quality and quantity of the resources available to arthropods (Schroeder *et al.*, 2021). Ground-dwelling (epigaeic) arthropods are highly sensitive to such ecosystem modifications. Such modifications have been responsible for arthropod declines reported in recent decades (Feng *et al.*, 2015). Sánchez-Bayo and Wyckhuys (2019) reported that insect species are declining at an annual rate of 2.1% globally due to climate change and intense anthropogenic disturbance causing habitat loss. It is also predicted that 40% of the global insects may become extinct in the next few decades, with the insect orders Hymenoptera and Coleoptera being the most vulnerable taxa (Sánchez-Bayo and Wyckhuys, 2019).

Although the arthropods are prone to extinction owing to land use changes, different taxa may show peculiar responses (Feng *et al.*, 2015). For example, ants and springtails are more associated with soils, relative to other ground-dwelling arthropods, and may escape the disturbance of the above-ground vegetation using soil as their protective agent (Wikars and Schimmel, 2001; Eckert *et al.*, 2022). Similarly, some above-ground arthropods, such as grasshoppers and butterflies, have a high dispersal ability and may escape disturbance events, which increases their survival chances (Samways *et al.*, 1996; Dumbrell and Hill, 2005). However, arthropod groups, such as most myriapods with limited dispersal ability, are often at higher risk in the event of environmental degradation (Car, 2010; Taylor and Victorsson, 2016). Therefore, environmental disturbances may not uniformly affect the community structure of different arthropods.

The practice of planting *Pinus* and *Eucalyptus* timber trees for commercial benefits is widespread across South Africa (Geldenhuys, 1997; Armstrong *et al.*, 1998). It impacts biodiversity and ecosystem functionality (Feng *et al.*, 2015; Maisto *et al.*, 2017). Plantations are often viewed as unsuitable matrices between islands of natural habitats (Ricketts, 2001;

Zahn *et al.*, 2009). This pessimistic perception may be unnecessary for some taxa. Rather, habitat suitability at various scales should also depend on the biotic and abiotic limitations. Spatial heterogeneity and spatial distribution of habitat elements significantly affect species diversity, species traits (Diekötter *et al.*, 2008; Duflot *et al.*, 2014) and their distribution.

Arthropods occupy microhabitats and are thus more responsive to site-specific elements and soil characteristics rather than landscape factors (García-Tejero and Taboada, 2016). They are highly diverse, and many have been suggested to be effective bioindicators of environmental transformation and sustainable forest management (Maleque *et al.*, 2009). These include spiders (da Rosa *et al.*, 2019), ants (King *et al.*, 1998; Sinclair and New, 2004; Majer *et al.*, 2007), and beetles (Davis *et al.*, 2001; García-Suabita *et al.*, 2019). Millipedes and centipedes show idiosyncratic feedback to habitat destruction due to their restricted dispersal ability (Marx *et al.*, 2012; Taylor and Victorsson, 2016).

Understanding how monoculture timber plantations affect arthropod diversity will help determine the ecosystem's resilience, stability, and functionality as well as the local environmental variables that timber producers should prioritise to continue benefiting from the ecosystem functions provided by arthropods. This chapter explores ground-dwelling arthropod diversity patterns, assemblage composition and their drivers in native (Southern Mistbelt forest) and exotic forests of monoculture of *Pinus* and *Eucalyptus* plantations.

The objectives were first to:

1) Compare arthropod diversity patterns and assemblage composition between three forest types (also referred to as habitat types) and in different seasons at the Umngenipoort Research Facility in the Natal Midlands.

2) Identify local environmental drivers of arthropod diversity patterns and assemblage composition between the two main forest types.

3) Identify indicator species for each of the three forest types.

4) Assess the functional composition of arthropods between the different forest types and examine if functional redundancy is masked by taxonomic diversity.

## 3.2 Methods and materials

### *3.2.1 Study area*

The study was conducted at the Umngenipoort Research Facility (29°29′0.1208″ S; 29°54′0.0146″ E) in the Midlands of the KwaZulu-Natal Province, South Africa (Figure 3.1). It is located approximately 50 km northeast of Pietermaritzburg. This area is found at the foothills of the Drakensberg at an altitude of 1500 m above sea level and an average temperature of 24.8°C. It is characterised by clay soils (Supplementary material, Table S4) and a mean annual rainfall of 800 mm, which falls mainly during summer, supporting patches of the native Afromontane forests within and around the study site, also referred to as the Southern Mistbelt forest (Munyai et al., 2021). The forests are dominated by the *Podocarpus henkelii* tree species, coexisting with the evergreen *Afrocarpus Falcatus*, *Calodendrum capense, Celtis Africana*, *Vepris lanceolate* and *Zanthoxylum davyi* woody species (Mucina and Rutherford, 2006). The Mooi River Highland Grassland and commercialised timber plantations form a matrix within these native forest patches (Munyai *et al.*, 2021). The monocultures of timber plantations in this site consist of two species, *Eucalyptus globulus* (bluegum) and *Pinus pinaster* (pine). Within the study site, the native forest had an area of approximately 1.15 km$^2$, while the plantations were distributed across a combined area of 2 km$^2$ (Mthimunye and Munyai, 2022). The vegetation in this site is supported by the perennial Umgeni River, with its tributaries protruding through the various vegetation types.

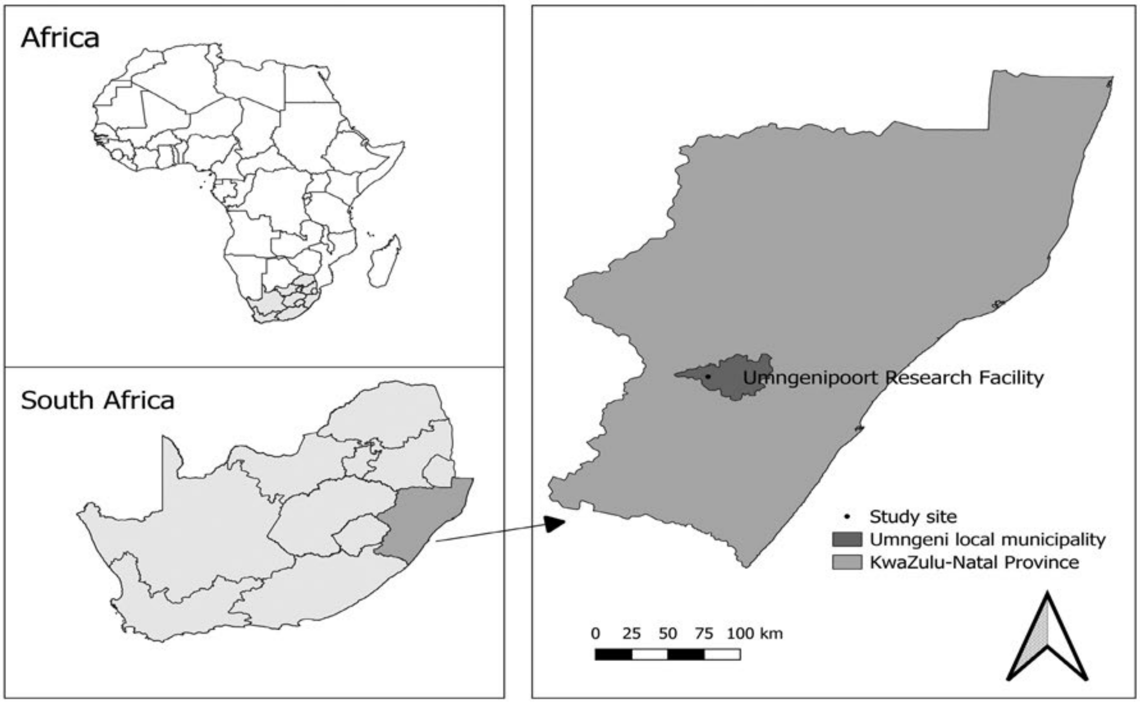

**Figure 3.1.** Map showing the study area, the Umngenipoort Research Facility located in the Midlands of the KwaZulu-Natal province in South Africa.

### *3.2.2 Arthropod sampling*

Epigaeic arthropods were collected using pitfall traps following a procedure outlined by Munyai and Foord (2012). The pitfall traps were transparent plastic cups with a diameter of 62 mm and a depth of 73 mm. Pitfall traps were considered adequate for capturing ground-dwelling arthropods for rapid biodiversity assessment (Hohbein and Conway, 2018). For this study, they were set in a 2 × 5 sampling grid, 10 m apart, resulting in ten pitfall traps per sampling point (replicate) (Figure S1). The pitfall trap was inserted onto the ground such that the mouth of the trap was on the same level as the ground surface. These were half filled with propylene glycol, which has a slow evaporation rate (Hohbein and Conway, 2018) and has no effect on the behaviour of arthropods and, therefore, did not influence their capture rates (Munyai and Foord, 2015). Sampling within each habitat type was replicated seven times, with replicates separated by a distance of over 300 m. The pitfall traps were left open for seven days in November (dry-hot) 2022 and February and March (wet-hot) 2023 to account for seasonal variation. The trapped arthropod samples were collected, washed, sorted, and preserved in 70% ethanol.

*Arthropod identification*

Only arthropods from classes (Insecta (ants and beetles)), Arachnida (spiders), Diplopoda (millipedes) and Chilopoda (centipedes)) were considered in the current study. These were selected as they are taxonomically diverse, are relatively simple to sample and have a quick response to environmental changes due to their rapid regeneration (Maleque *et al.*, 2009). Additionally, ants and beetles consist of various trophic levels and, therefore, can interact with various other taxa. The collected arthropods were identified to the lowest taxonomic level using various identification keys. Beetles were identified to family and some to genus level using Picker *et al.* (2019), then to morphospecies. Confirmation of beetle identification was done at the Ditsong National Museum of Natural History in Pretoria. All ants were identified to genus and, where possible, to species level using available voucher specimens in the School of Life Sciences at the University of KwaZulu-Natal, Pietermaritzburg campus. Ants that could not be identified to species level were assigned to genus and then assigned to morphospecies. Updated and valid ant taxonomic names were further confirmed using Online databases *viz.*, AntWiki (http://www.antwiki.org/, accessed in May 2023) and AntWeb (http://antweb.org/, accessed in May 2023). Centipedes were separated into families using an identification guide by Lawrence (1983). Millipedes and spiders were identified by Prof Tarombera Mwabvu (University of Mpumalanga) and Prof Ansie Dippenaar-Schoeman (Agricultural Research Council), respectively. Individuals that could not be identified to species level were identified to the lowest possible taxonomic ranking (family or genus level) and then morphospecies, following the lower taxonomic group up to which the identification was possible. Despite the lack of species-level identification for some specimens in this study, the family-level or morphospecies can still be useful for assessing the environmental impact and informing conservation (Derraik *et al.*, 2002; Feng *et al.*, 2015). Arthropod voucher specimens are currently kept at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg campus. They will eventually be deposited at the Iziko Museum of Cape Town and Ditsong National Museum of Natural History, Pretoria. Lastly, the collected arthropods were classified into functional guilds based on their broad feeding behaviour, similar to Attwood *et al.* (2008). The functional group classifications included omnivores, detritivores, predators, scavengers, herbivores, coprophages, granivores, nectarivores and honeydew consumers.

### 3.2.3 Drivers and correlates

*Temperature*

Soil temperature was recorded per habitat using two Thermocron iButtons (Semiconductor Corporation, Dallas /Maxin, TX and USA). The iButtions were placed in the soil (1 cm depth) in each habitat at the beginning of the sampling period to record the temperature at one-hour intervals for 12 months (November 2022 to November 2023) to assess seasonal variation. Temperature data obtained from the two iButttons in each habitat were merged, and the monthly minimum, maximum, mean, and standard deviation of the temperature was calculated.

*Soil*

A soil auger was used to randomly collect ten soil subsamples per replicate in each habitat during November 2022. The collected soil was then analysed for physical (% sand, %silt, and %clay) and chemical (soil pH, carbon, and nitrogen content) characteristics by the Soil Analytical Services Lab at Cedara, the Department of Agriculture in Hilton, South Africa.

*Habitat structure*

Habitat structure was measured by considering the horizontal and vertical vegetation distribution following methods proposed by Munyai and Foord (2012). A 1 $m^2$ grid was placed around each pitfall trap to estimate the horizontal vegetation distribution. The percentage of vegetation cover, leaf litter, bare ground, and exposed rock was calculated, recorded, and averaged for each replicate. The vertical vegetation distribution was measured on different height profiles by placing a 1.5 m radius centred over each pitfall trap. The number of times that vegetation was found in contact with a 1.5 m rod for each of the following height intervals: 0–25, 26–50, 51–75, 76–100, 101–125, 126–150, 151+ cm, was counted and averaged for each replicate. This was done in four sampling points around the pitfall trap, positioned at 90° angles from one another (Munyai and Foord, 2012). It was assumed that the canopy cover was present in areas where the height of the vegetation was touching the 151+ cm height interval.

### 3.2.4 Statistical analysis

To compare arthropod species richness across the three habitat types in two different seasons, a two-way ANOVA in IBM SPSS version 29 (Stehlik-Barry and Babinec, 2017) was used. The data was normally distributed and met all parametric test assumptions. Since data for Myriapoda was not normally distributed, generalised linear mixed models were used instead.

A principal component analysis was performed to determine the relationships between the environmental variables and habitat types which were assumed to be responsible for the variation in species richness, using the ‘prcomp’ function. Data was visualised using the ‘ggplot2’ function in R Statistical Software. The first two sets of the PCA explained 68.5% of the variation. The first PCA axes (PC1) explained 54.4% of the variation, while the second PCA axes (PC2) explained only 14.1% of the variation. PC1 was positively correlated with the increased vegetation cover, complexity, as well as soil carbon, nitrogen, and pH, in the native forest, and negatively correlated with an abundance of leaf litter cover, sandy soils, and high soil temperature, which were associated with the plantation sites. The response of arthropod species richness to the computed principal components, season, and habitat type was then modelled using Generalised Linear Mixed Models (GLMM) in R Statistical Software, version 4.3.2 (R Core Development Team, 2023). The GLMM was computed using the Poisson distribution and the loglink function with the loaded package ‘lme4’. The replicates were considered random factors, while the season, habitat type and the principal components were mixed factors. The best model was defined as the one with the smallest Akaike Information Criterion (AIC) value.

An analysis of similarity (ANOSIM) and Similarity Percentage (SIMPER) was conducted in the Primer 6+ software package (Clarke and Gorley, 2006) to compare variations in arthropod species composition across the three habitat types. The Global R statistic produced by an ANOSIM indicates how different (if R is close to one) or similar (if R is close to zero) the compared assemblages are (Hamer and Slotow, 2017). Prior to analysis, the data was square root transformed, and the calculations were computed based on the Bray-Curtis distance, with 999 permutations. Non-metric multidimensional scaling was then used to visualise the variation in assemblages of the different arthropod groups between the three forest types. Points (replicates) closer to one another indicate similarity, while more separated points represent dissimilar replicates. The Jaccard's Similarity Index representing beta diversity was calculated for pairwise habitat comparisons in PAST, version 2.17 (Hammer et at., 2001), with the aid of a SIMPER analysis to confirm the findings.

Species that were indicators of each forest type were determined using the Indicator Value Method (IndVal) (Dufrêne and Legendre, 1997) analysis in R studio statistical software, version 4.3.1, using the ‘ladbsv’ package (R Core Development Team, 2023). Species were combined for both the wet-hot and dry-hot seasons. Only species with indicator values greater than 70% were considered indicator species for that forest type. The various arthropod functional guilds were used to test for variation in functional diversity across the three habitats in R studio statistical software, version 4.3.1 (R Core Development Team, 2023), computed with package 'FD' with the ‘dbFD’ package. Functional divergence and evenness were considered to account for the relative abundance of the different functional groups.

## 3.3 Results

*Collected arthropod fauna*

In total, 4 284 specimens were collected over two seasons, belonging to nine orders in four classes (Insecta (ants and beetles)), Arachnida (spiders), Diplopoda (millipedes) and Chilopoda (centipedes)). The most abundant taxon was beetles, making up 48% of the total number of specimens, followed by ants (28%) and spiders (20%) (Supplementary material, Table S5). Similarly, the highest (88 species) number of species recorded were beetles, while ants and spiders had 35 and 38 species, respectively. Millipedes and centipedes contained only nine and 13 species, respectively.

Arthropods were highly abundant in the natural forests (n = 1832), with the plantations containing slightly fewer individuals (*Pinus*, n = 1396 and *Eucalyptus*, n = 1056) (Supplementary material, Table S5). However, more species and individuals were collected during the dry-hot season than in the wet-hot season (Table 3.1). Ants, beetles, and spiders were fairly distributed across all the habitats, with most millipedes collected from the natural forest (95% of the total individuals of millipedes) and centipedes dominating the pine plantations (61% of the total individuals of centipedes) (Supplementary material, Table S5).

*Arthropod species diversity patterns*

Sample coverage for species richness in each habitat was generally high (>0.80) for most sampled habitats, indicating that the habitats were adequately sampled for most arthropod groups (Figure 3.2). However, the sample coverage for spiders suggested that the sampling was insufficient to capture all the species representative of some habitats, particularly the bluegum plantation (Figure 3.2).

The Shannon–Wiener Diversity Index showed that species diversity was generally high across all the habitats ($H'$ above 3) (Table 3.1). Diversity patterns were more apparent during the dry-hot season, with the pine plantations being less diverse ($H' = 2.71$) and the bluegum plantations having the greatest diversity ($H' = 3.488$). Similarly, the bluegum plantations had more effective species (33 species) and evenness during the dry-hot season (Table 3.1). Nonetheless, the natural forests had the highest number of observed species (Table 3.1, Figure 3.2), with an exception for ants as they did not have a definite habitat preference (F = 1.079, p = 0.35, df = 2) (Figure 3.2, Supplementary material, Table S6).

Species richness of beetles (F = 6.441, p < 0.05, df = 2), spiders (F = 3.629, p < 0.05, df = 2) and myriapods (F = 4.968, p < 0.05, df = 2) significantly differed across the habitats, with more species in the native forest than the two monoculture plantations (Figure 3.2, Supplementary material, Table S6). However, seasonal variation significantly affected beetle (F = 8.704, p < 0.05, df = 1) and spider (F = 3.629, p < 0.05, df = 1) species richness (Supplementary material, Table S6).

**Table 3.1.** Number of arthropod species richness, individuals, and species diversity indices across the three sampled forest types in the wet-hot and dry-hot seasons. The effective number of species values were derived from the Shannon–Wiener Diversity Index (entropy).

| | | **Dry-Hot season** | | | **Wet-Hot season** | |
|---|---|---|---|---|---|---|
| Parameters | **Bluegum** | **Natural forest** | **Pine** | **Bluegum** | **Natural forest** | **Pine** |
| Number of species | 70 | 97 | 64 | 61 | 78 | 59 |
| Number of individuals | 486 | 948 | 839 | 570 | 884 | 557 |
| Shannon–Wiener Diversity Index (entropy) | 3.488 | 3.167 | 2.71 | 3.166 | 3.104 | 3.175 |
| Effective number of species | 33 | 24 | 15 | 24 | 22 | 24 |
| Species evenness | 0.4673 | 0.2446 | 0.2347 | 0.3889 | 0.2856 | 0.4057 |

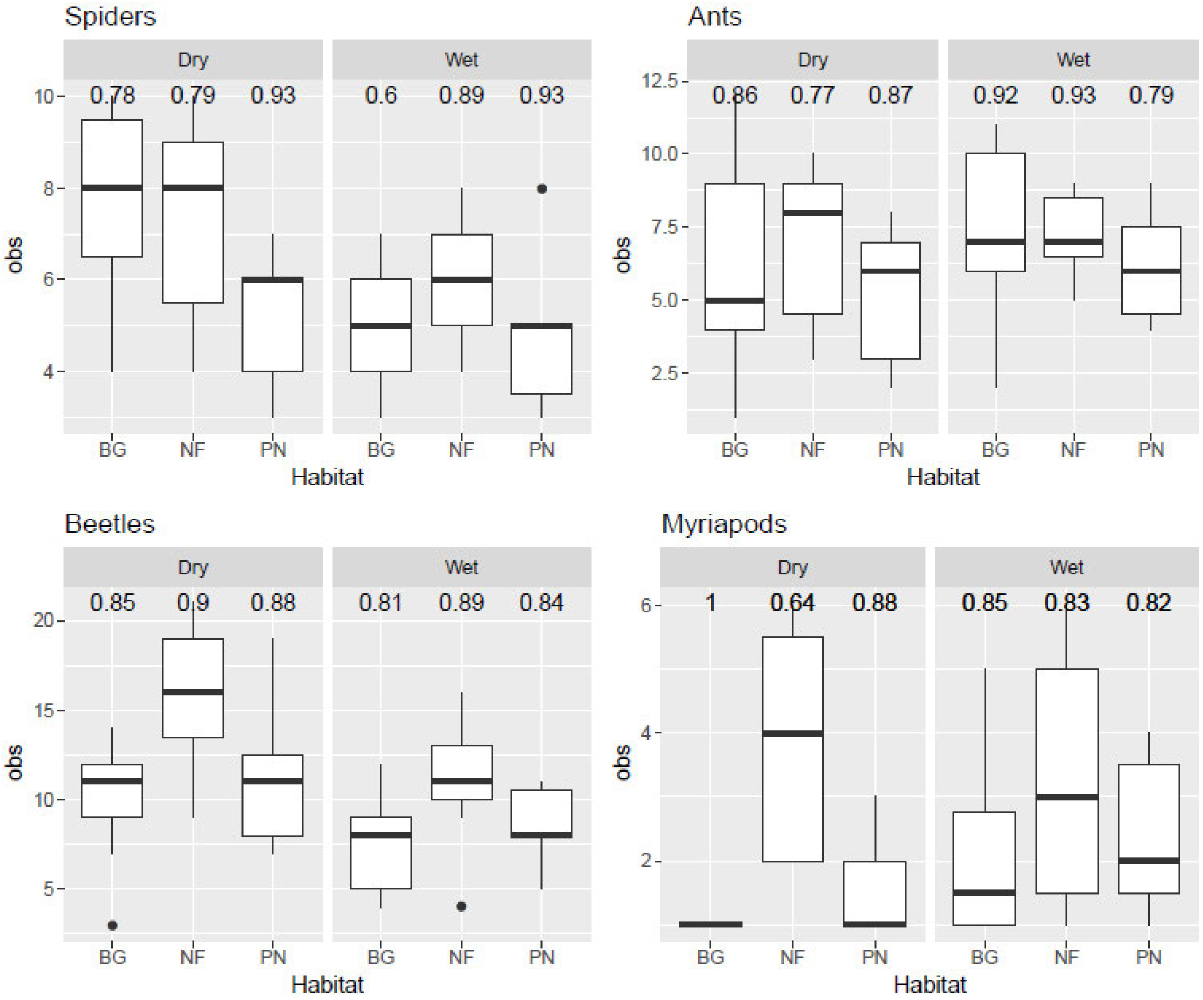

**Figure 3.2.** Boxplots showing the number of observed species (represented by 'obs') of each taxon across the three habitats during the wet-hot and dry-hot seasons and the sample coverage values per taxon in each habitat. The abbreviations of the habitat types are explained as follows: BG = Bluegum, NF = Natural forests and PN = Pine. 'Dry' indicates dry-hot and 'Wet' indicates wet-hot.

### *Drivers of arthropod species richness*

Although the richness of most arthropod species was significantly affected by habitat type, environmental variables (soil temperature, soil type including soil carbon, nitrogen, and pH, as well as vegetation complexity, vegetation cover, leaf litter cover, bare ground, and exposed rock) within those habitats played an important role (Figure 3.3, Table 3.2). PC1 dictates the environmental variables that contribute the most to the variation in habitat differences. A positive increase in PC1 represents the complexity and heterogeneity of the environment, which is characteristic of the native forest. Ant species richness was best explained by habitat type as the ant species richness was positively correlated with the native forest, although the association was not statistically significant (Table 3.2). The species richness of beetles and myriapods was best explained by the PC1, with a positive correlation observed between the beetle species richness and PC1 (estimate = 0.8110 ± 0.2212) as well as myriapod species richness and PC1 (estimate = 0.30699 ± 0.09617) (Table 3.2). Therefore, beetle and myriapod species increased with an increase in soil carbon, soil nitrogen, soil pH and habitat heterogeneity created by the presence of logs, bare ground, rock cover, vegetation cover, as well as vegetation complexity evident in the native forest. The environmental variables that characterised the plantation sites included sandy soils, high temperature and leaf litter cover (Figure 3.3). The best model predicting spider species richness was season (dry-hot versus wet-hot), with the species richness significantly lower during the wet-hot season (estimate = -1.4762 ± 0.4019) (Table 3.2) than in the dry-hot season. Therefore, season, rather than habitat type or the associated environmental variables, greatly affected spider species richness.

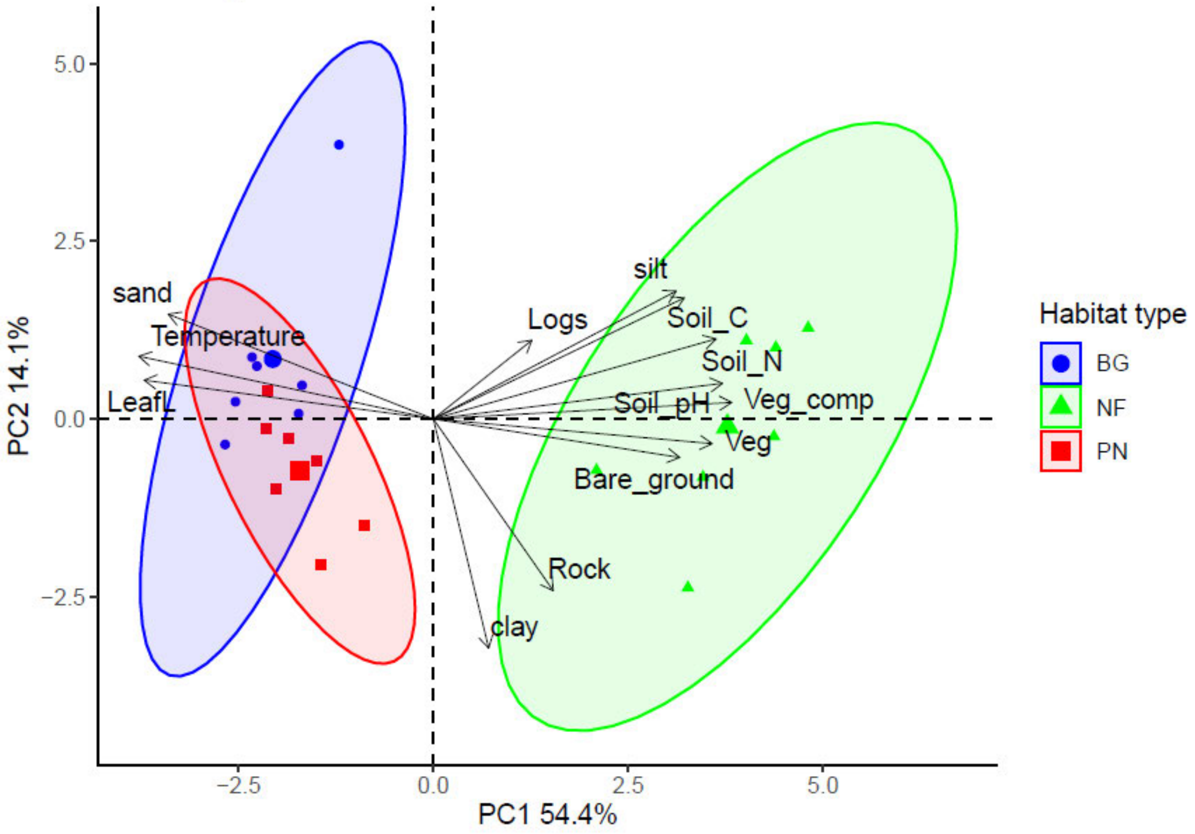

**Figure 3.3.** Principal component analysis (PCA) ordination diagram showing habitat-specific environmental variables that significantly explained variation between the three habitat types, which are indicated by the ellipses at the Umngenipoort Research Facility. PC1 and PC2 explained 68.5% of the variation. The abbreviations of the forest types are explained as follows: BG = Bluegum, NF = Natural forests and PN = Pine

**Table 3.2.** Summary of the GLMM results for the species richness of the various arthropod groups. The results only consist of the best models that explained the species richness of each taxon, following the Akaike information criterion.

| Arthropod group | Factors | Estimate Std. | Error | t-value | Pr(>\|t\|) |
|---|---|---|---|---|---|
| Ants | HabitatNF | 0.18726 | 4.88876 | -0.038 | 0.9699 |
| Beetles | PC1 | 0.8110 | 0.2212 | 3.666 | 0.000687 |
| Myriapods | PC1 | 0.30699 | 0.09617 | 3.192 | 0.00304 |
| Spiders | SeasonWetHot | -1.4762 | 0.4019 | -3.673 | 0.00142 |

### *Arthropod assemblage composition across the forest types*

The assemblage composition of spiders and beetles was clearly distinguishable among the three habitat types (Figure 3.4, Table 3.3). Although all the p-values obtained from an ANOSIM analysis showed significant differences among assemblages of each habitat type, the global R values were more informative in separating the assemblages. The global R values of the beetles and spider assemblages were close to one (Table 3.3), supporting that arthropod assemblages varied among the habitats. In contrast, myriapod and ant communities showed a peculiar response compared to the other groups (Figure 3. 4, Table 3.3), with a global R-value close to zero, indicating similarity in assemblages. In particular, myriapod assemblages in each habitat were not separable, representing similar species composition among the communities of the three habitats. Although ant assemblages were relatively distinguishable, the bluegum and pine plantations had overlapping communities (Figure 3.4).

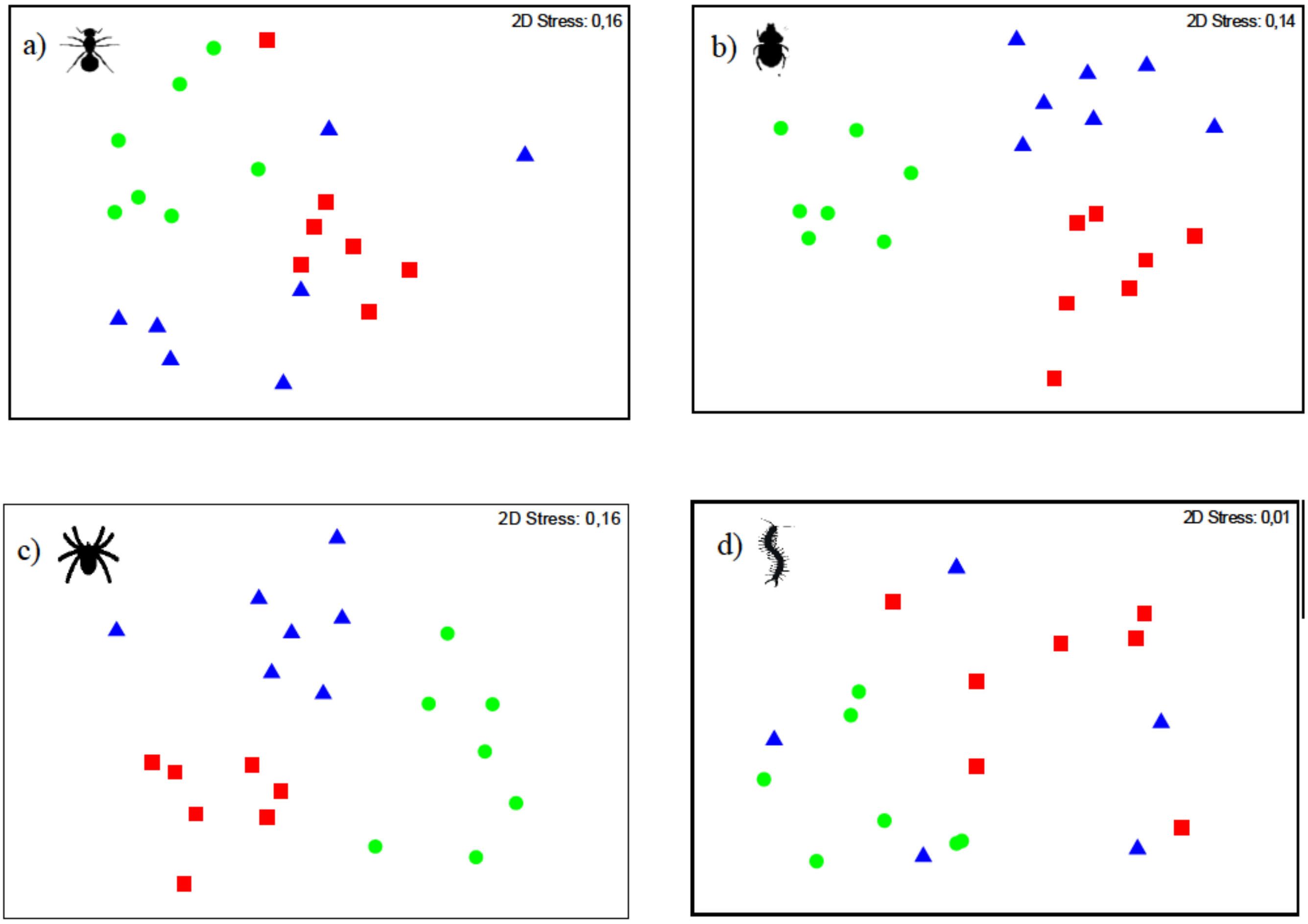

**Figure 3.4.** Non-metric multidimensional scaling (NMDS) plots showing variation among the communities of the various arthropod groups (a = ants, b = beetles, c = spiders, d = myriapods) in the three forest types. The plots are based on the Bray-Curtis similarity used on square root transformed data. The stress levels are shown in each plot. Bluegum plantation = blue triangle, Pine plantation = red square and Natural forest = green circle.

**Table 3.3.** Analysis of similarity (ANOSIM) results depicted by the global R value and the significance level denoting how similar the arthropod assemblages are across the three forest types.

| Taxon | Global R-Value | Significance level |
|---|---|---|
| Ants | 0.44* | $p < 0.05$ |
| Beetles | 0.87 | $p < 0.05$ |
| Spiders | 0.76 | $p < 0.05$ |
| Myriapods | 0.31* | $p < 0.05$ |

*represents similar communities

Many species were shared between the three habitat types (41) (Figure 3.5, Supplementary material, Table S5). However, 58 species were restricted to the natural forest, and the second highest (56) number of species was shared between the natural forest and the bluegum plantations (Figure 3.5). The pine plantation and the natural forest were highly dissimilar in arthropod species composition, and this was supported by the Jaccard's Similarity Index of 0.31, which is close to zero, representing distinct communities and the average dissimilarity percentage of 64%. The bluegum and pine plantations were similar in species composition with Jaccard's Similarity Index of 0.42 and an average dissimilarity of 57%, the lowest among all the habitat comparisons (Figure 3.5).

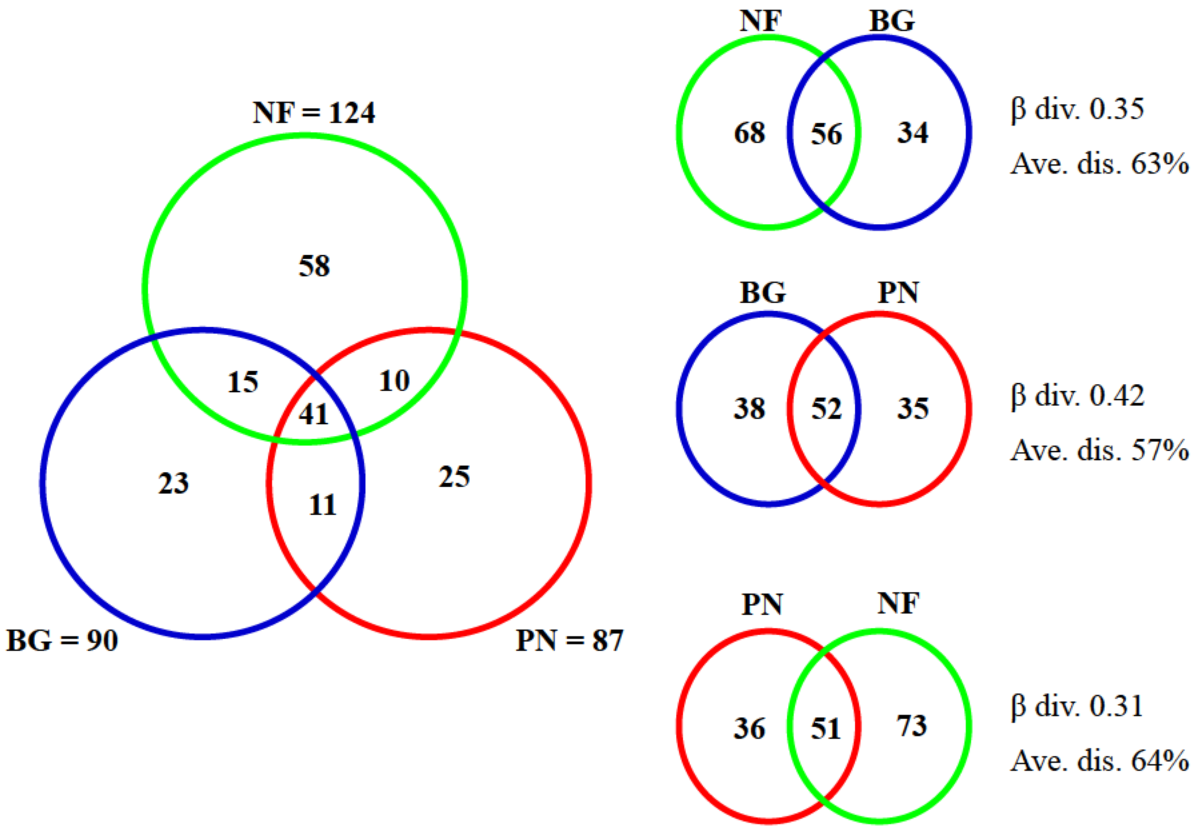

**Figure 3.5.** Total number of species shared and restricted to each habitat type as well as the Jaccard's Similarity Index and average dissimilarity between the paired habitats. The Jaccard's Similarity Index represents beta diversity, while ‘Ave. dis’. represents average dissimilarity obtained from a SIMPER analysis. The abbreviations of the habitat types are explained as follows: BG = Bluegum, NF = Natural forests and PN = Pine.

*Indicator species of the three forest types*

The bluegum plantations only had a single indicator species, the *Copa flavoplumosa* spider, yet the pine plantations were characterised by both beetle and spider indicator taxa, with the Scolytidae_sp1 (a beetle species) being the main indicator species for this habitat (Table 3.4). Although the natural forest had many species associated with it, the common millipede, Polydesmida_sp1 was the primary indicator species, followed by the beetle morphospecies *Erichsonius*_sp1 and Pterostichinae_sp1, which all had an indicator value of over 80% (Table 3.4).

**Table 3.4.** Indicator species for three sampled habitat types in the Umngenipoort Research Facility, Natal Midlands.

| **Habitat type** | **Species** | **Taxa** | **Indicator value (%)** | **P-value** | **Frequency** |
|---|---|---|---|---|---|
| Bluegum Plantation | *Copa flavoplumosa* | Spider | 86 | 0.001 | 6 |
| Natural forest | Polydesmida_sp1 | Millipede | 89 | 0.001 | 10 |
| | *Erichsonius*_sp1 | Beetle | 88 | 0.001 | 18 |
| | Pterostichinae_sp1 | Beetle | 80 | 0.005 | 7 |
| | *Hypoponera* UKZN_03 | Ant | 79 | 0.002 | 7 |
| | *Lepisiota* UKZN_07 | Ant | 77 | 0.001 | 8 |
| | *Anthonomus*_sp1 | Beetle | 76 | 0.003 | 16 |
| | *Vidole helicigyna* | Spider | 73 | 0.001 | 10 |
| | *Melissotarsus beccarii* | Ant | 71 | 0.005 | 5 |
| | Melolonthinae_sp1 | Beetle | 71 | 0.006 | 5 |
| Pine plantation | Scolytidae_sp1 | Beetle | 100 | 0.001 | 7 |
| | *Xenitenus*_sp1 | Beetle | 91 | 0.001 | 9 |
| | *Crozetulus rhodesiensis* | Spider | 90 | 0.001 | 13 |
| | Nitidulidae_sp1 | Beetle | 78 | 0.004 | 20 |
| | *Hahniatabulicola*_sp1 | Spider | 75 | 0.001 | 18 |

### *Arthropod functional groups*

Arthropods in nearly all the considered functional guilds were distributed across the habitat types (Supplementary material, Table S5). Most predators mainly spiders and beetles (mostly rove beetles; family Staphylinidae), were found in the natural forests. Arthropods representing various functional guilds were slightly more evenly distributed in the pine plantation ($F_{eve}$ =

0.07) compared to the other habitat types (natural forests: $F_{eve} = 0.05$, bluegum plantations = $F_{eve} = 0.06$ ) (Table 3.5). Functional divergence was similar across the three habitat types (Table 3.5).

**Table 3.5.** Selected arthropods' functional diversity and evenness across the three habitat types sampled at the Umngenipoort Research Facility in the Natal Midlands.

| **Habitat type** | **Functional divergence** | **Functional evenness** |
|---|---|---|
| Bluegum plantation | 0.75 | 0.06 |
| Natural forest | 0.74 | 0.05 |
| Pine plantation | 0.78 | 0.07 |

## 3.4 Discussion

*Arthropod diversity and assemblages*

The primary objective of this study was to compare arthropod diversity patterns, assemblage composition and determine the drivers of the observed patterns in two monoculture timber plantations (*Pinus* and *Eucalyptus*) and a native forest. This was to elucidate whether plantations were detrimental to soil meso-and-microfauna, which perform essential ecosystem functions. Although biodiversity response to disturbance is complex (Fox, 2013), generally, timber plantations destroy native habitats, contributing to biodiversity declines, and this is also true for some ground-dwelling arthropods (Damptey *et al.*, 2023).

Native forests are highly productive ecosystems known for their importance in preserving biodiversity. The current study found that arthropod species richness was higher in the native forest than in the monoculture timber plantations. This is consistent with the findings of most similar studies worldwide, both on *Pinus* plantations conducted in Spain (Taboada *et al.*, 2010) and Argentina (Munévar *et al.*, 2018) and *Eucalyptus* plantations in studies conducted in Brazil (Martello *et al.*, 2018), China (Wang *et al.*, 2019) and Rwanda (Nsengimana, 2020). Fierro *et al.* (2017) found that the number of beetle species found in the native forest accounted for half the total number of specimens found in all the sampled habitats in the study area (native forests, *Pinus,* and *Eucalyptus* plantations). However, previous studies conducted in the Natal

Midlands (Yekwayo *et al.*, 2017; Eckert *et al.*, 2022) found that timber plantations do not always result in declines in arthropod diversity.

Contrary to the current study, where ant diversity was not significantly different amongst the habitats studied, previous studies (Costa-Milanez *et al.*, 2014; Martello *et al.*, 2018; Aguiar *et al.*, 2022) found that *Eucalyptus* plantations were detrimental to ant taxonomic and functional diversity. Since most ant species were evenly distributed across the study site, the various ecosystem functions provided by ants, such as seed dispersal, soil aeration, nutrient recycling, and decomposition, are possibly preserved (Nsengimana, 2020; Aguiar *et al.*, 2022). Ramón and Donoso (2015) highlighted the ability of ants to survive in nearly any terrestrial ecosystem and how this unique trait contributes to their dominance. Other taxa collected in this study seemed less resilient than ants, as they were negatively affected by habitat differences and microhabitat variations. However, previous studies found that the assemblages of ants (Eckert *et al.*, 2022), spiders (Dippenaar-Schoeman *et al.*, 2013) and beetles (Gunther and New, 2003) were different in plantation sites relative to native vegetation and this was evident in the current study.

### *Drivers of arthropod taxa*

Environmental filters shape taxonomic diversity patterns (Castro *et al.*, 2020). Microhabitat differences among plantation sites may have benefited species favoured by open habitats or different levels of canopy cover. Open habitats attributed to less dense canopy cover in plantations increase light penetration which enhances the establishment of understory vegetation, which are then utilised by arthropods for mating, nesting, and as shelter (Ribeiro-Troian et al., 2009). However, mature timber plantations are generally classified as managed forests, and the arthropod communities from the native forest may have colonised plantations as they mature over the decades (Eckert *et al.*, 2022). Paradoxically, plantations are not as dense in vegetation as the native forests due to less vegetation complexity. Thus, species from the surrounding grasslands would also benefit from the variation in light interception that reaches the ground, resulting in higher temperatures, similar to open habitats such as grasslands (Ohwaki *et al.*, 2017). Such mechanisms may have led to the high number of species shared between the three habitats in this study site, although the assemblages differed. These results are similar to those reported in previous studies in the Natal Midlands (Yekwayo *et al.*, 2017; Eckert *et al.*, 2022) but are from different sites (farms) than the current study. Pine plantations were less suitable for epigaeic arthropods since fewer species were captured in this habitat in high abundances, similarly to previous findings in other geographical regions, e.g., in Germany (Finch, 2005) or Argentina (Munévar *et al.*, 2018). The native forest and the pine plantations had the least number of species shared, suggesting that pine plantations may not meet the habitat requirements of forest arthropod species (Finch, 2005).

Differences in arthropod communities, particularly in ground beetle diversity, have been attributed to soil properties (Finch, 2005). For the current study, we found that the richness of beetle species increases with an increase in soil organic carbon and nitrogen. However, spider species richness and assemblages in forests are supported in highly complex habitats (Scheidler, 1990; da Rosa *et al.*, 2019) enhanced by vegetation structure, understory shrubs, deadwood, litter, and light interception, which also increases prey abundance for spiders to feed on (Finch, 2005; Gallé *et al.*, 2017). These factors are suggested to create more resources (Finch, 2005). Pine plantations had less spider species richness compared to the other habitat types in the current study. This is because pine plantations generally have low arthropod diversity, suggesting that prey abundance is not sufficient to support spiders in this study site. The loss of spiders in this forest type is concerning as the presence of the top predators indicates ecosystem productivity (Cifuentes-Croquevielle *et al.*, 2020). This could imply that pine plantations on this site could be losing their productivity. However, the relatively higher spider species richness in *Eucalyptus* plantations could be attributed to the abundance of other arthropod taxa which spiders feed on, including insect pests that could be present in plantations (Dippenaar-Schoeman *et al.*, 2013).

Mezger and Pfeiffer (2011) conducted a study on ant communities in primary forests of Malaysia and observed that bare ground, vegetation complexity and leaf litter increases the stability of ant diversity (Mezger and Pfeiffer, 2011). This was consistent with the findings of Joseph *et al.* (2019) study on ants and their microhabitats along elevational gradients in the Limpopo province in South Africa. This study found that although elevation decreased the stability of ant species richness, leaf litter and sandy soils regulated ant populations (Joseph *et al.*, 2019). However, for our study, ants were more responsive to habitat than specific small-scale variables. However, Mezger and Pfeiffer (2011) further described how leaf litter quality is associated with soil characteristics. The leaf litter breakdown increases soil nutrients, and good soil quality favours arthropod communities (Ribas and Schoereder, 2007). Thus, complex dynamics within microhabitats explain the ground-dwelling arthropod community structure variation.

### *Arthropod functional diversity*

Morelli *et al.* (2018) suggested that there is a correlation between taxonomic diversity and functional diversity. Having a high number of species in the ecosystem increases the chance of obtaining species of different functional traits, increasing functional diversity (Petchey and Gaston, 2006). However, functional diversity is mainly favoured by the presence of rare species (Rocha-Ortega *et al.*, 2018). Although habitat-specific environmental conditions varied among the forests, arthropod communities were functionally similar, and these findings were identical to those of Castro *et al.* (2020). The loss of functional traits in ground-dwelling fauna has negative cascading effects on the ecosystem, as it would affect other invertebrates as well as plant populations (Arnan *et al.*, 2014). Duffy *et al.* (2007) found that animals in old-growth native forests possess diverse feeding modes within and among various trophic groups. This was not the case for this study, as functional diversity was similar across the three habitat types.

Millipedes and centipedes were combined in this study as they have similar effects on the soil ecosystem because both are bioturbators and enhance aeration in the soil (Kula and Lazorik, 2016), yet their feeding strategies make them unique indicators of forest soil ecosystems. Millipedes, which dominated in the native forest, are known for their major role in decomposition as they feed on organic matter (Cárcamo *et al.*, 2000; Taylor and Victorsson, 2016). Therefore, their presence and dominance in this habitat type could indicate high rates of decomposition favoured by the abundance of organic matter (Nsengimana, 2020). Over time, they improve the soil ecosystem, increasing nutrient availability for other soil organisms (Nsengimana, 2020). Although arthropod size was not measured, the majority of the centipedes found in this study site belong to the order Lithomorpha, which are known for their small body size (Lawrence, 1983). This feature is beneficial for their movement in the dense mat of leaf litter in pine plantations, where they were highly abundant. This could also imply that there was an abundance of prey suitable for such centipede species to feed on since leaf litter is a recommended microhabitat for ground-dwelling arthropods (Nsengimana, 2020).

Predators were the most dominant and diverse functional guild across all the forest types from nearly all the arthropod groups. Cifuentes-Croquevielle *et al.* (2020) mentioned the importance of diverse top predators in ecosystems for the maintenance of complex food chains, which enhances the ecosystem's overall health. However, it is still evident that functionally redundant taxa characterise these forest types as they possess less specialised functions.

## 3.5 Conclusion

Although forest ecosystems are considered biological reservoirs, environmental factors at spatial and temporal scales affect arthropod community structures. In the current study, timber plantations did not result in declines in the overall arthropod diversity. However, different arthropod taxa had unique responses. The native forest was associated with a more heterogeneous habitat structure and soils rich in carbon and nitrogen, correlating with the species richness of beetles and myriapods. Spiders were mainly driven by season rather than habitat type or environmental variables. The assemblages of the three different forests varied only for beetles and spiders. The high number of species shared between the habitats supported the evidence of functional redundancy among the species found in the three forest types. It is recommended that future studies focus on morphological arthropod functional characteristics based on habitat use and quantify how natural forests may have acted as source areas for species in the plantation within the study site to achieve robust results on ecosystem stability.

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# CHAPTER 4 ： Conclusions and recommendations

There has been a growing interest in identifying disturbed areas that still hold sufficient conservation value for species protection, and timber plantations have been suggested to harbour some forest species. South Africa is one of the few countries on the African continent that contains extant patches of the Afromontane forests that have been historically exploited for timber extraction (Moll, 1972; Lawes *et al.*, 2004). These forests are now neighboured by commercialised *Pinus* and *Eucalyptus* plantations, which have mostly replaced native grasslands (Lawes *et al.*, 2004; Malan, 2014). Even so, they are widely distributed along a region considered one of the top three biodiversity hotspots, the Maputaland-Pondoland Albany**.** This has implications on arthropod species' diversity and assemblages as they may have limited ability to disperse compared to vertebrates. Although monoculture timber plantations are generally deemed negative for the environment and biodiversity; distinct taxa may respond differently, and specific mechanisms may drive diversity patterns at spatial scales and temporal scales.

## 4.1 Revisiting the aims and objectives

This study aimed to assess arthropod biodiversity in natural and human-managed ecosystems (monoculture timber plantations) at a global and local scale and the microhabitat-specific factors that drive their diversity patterns. In particular, the objectives of chapter two were to systematically review studies on arthropod diversity patterns and distributions in native vegetation and *Eucalyptus* and/or *Pinus* plantations across different global ecozones and explore the role of adjacent habitats and how management strategies to improve arthropod conservation.

The systematic review yielded 111 studies across 30 countries. Most studies were conducted in the Neotropical region, particularly Brazil, while the highly studied arthropod groups were the insects (particularly ants and beetles). The number of studies conducted on the subject peaked between 2010 and 2019. Arthropod diversity declines were observed in monoculture timber plantations mostly distributed outside their native regions. However, many studies on Arachnids also showed that timber plantations had a minimal effect on their diversity. A possible explanation for this is that *Eucalyptus* plantations may have a relatively more complex habitat than pine plantations, and prey availability may be high in this plantation type. Studies have shown a positive correlation between spider communities, habitat heterogeneity (Scheidler, 1990), and prey availability (Gallé *et al.*, 2017).

Dippenaar-Schoeman *et al.* (2013) reported that spiders tend to feed on pest insects in agroecosystems and this may increase their dominance in such ecosystems. Sustainable plantation management, such as planting mixed plantations, significantly enhances habitat heterogeneity and consequently creates different microhabitats to support diverse arthropods, preventing pest outbreaks (Hartley, 2002; Ji *et al.*, 2011). The modified spatial arrangement of mixed tree species with different phenotypes and variability in age may increase complexity (Carnevale and Montagnini, 2002).

The subsequent chapter compared arthropod diversity and assemblage composition in monoculture timber plantations and natural forests of the Natal Midlands in the KwaZulu-Natal province and the environmental variables responsible for the diversity patterns at a local scale. Functional diversity was also investigated to determine if arthropods in the plantations sufficiently perform the essential ecosystem functions regardless of the patterns in species richness. Pitfall traps were used to collect ground-dwelling arthropods at the Umngenipoort Research Facility. Only specific arthropod groups (ants, spiders, beetles, millipedes, and centipedes) were collected over the wet-hot and dry-hot seasons to assess how different arthropod taxa responded to plantations. Data on various microhabitat environmental variables, such as habitat complexity and soil properties, possibly assumed to influence arthropod communities, were recorded.

In total, 4 284 individuals were collected across the study area. Most species were collected from the native forest, and the beetles were the most dominant taxon collected across all the forest types. Similar studies on this subject have reported similar findings on native forests as these ecosystems are less disturbed and are, therefore, a suitable habitat for native and unique forest species (Wang *et al.*, 2019). This highly heterogenous habitat has more nesting, mating and foraging grounds for ground-dwelling arthropod species (Wang *et al.*, 2019). Conforming to this observation, the native forest in this study correlated with beetle and myriapod (which included centipedes and millipedes) species richness and was characterised by a highly complex habitat with carbon and nitrogen-rich soils. Spider species richness responded more strongly to season than habitat type, with more species collected during the dry-hot season. Although ant species richness was more influenced by habitat type, the differences in ant species richness among the habitats was not statistically significant. Thus, it suggests that arthropod diversity was not necessarily negatively affected by timber plantations. Rather, different arthropod taxa had unique responses and drivers.

Many species were shared among the forest types. However, the assemblage composition of beetles and spiders from each habitat differed, while the assemblage composition of ants and myriapods was not very distinct. A recent study (Eckert *et al.*, 2022) confirmed that timber plantations alter the composition of arthropod species rather than diversity. Additionally, functional redundancy was apparent as there was no evidence of the variation in functional diversity. However, it should be cautioned that functional diversity for this study was measured using functional groups instead of individual species traits. This method groups species based on their broad ecological guild, leading to functionally redundant groups (Petchey et al., 2004).

## 4.2 Contributions of the study

This study confirms that disturbance does not entirely eliminate arthropods. The more resilient groups, with a broader range of environmental tolerance such as ants, survive and take advantage of the remaining available resources (Barrocas *et al.*, 1998; Spencer, 2018). The most sensitive specialists occupying the realised niche within the forests are more threatened by local extinction (Jokimäki *et al.*, 1998) as timber plantations spread. Although these plantations are suggested to put biodiversity at a greater risk of local extinction (Brockerhoff *et al.*, 2008), the ecosystem functions performed by the present arthropods may still be sustained as plantations seem to have less effect on arthropod functional composition. If a single species is lost, another species that performs a similar function may still occupy that niche space.

Arthropods show contrasting responses to different forest types and management. The structural complexity of vegetation is the primary determinant of invertebrate community patterns in forest ecosystems (Maleque *et al.*, 2009). Forests were reported to support more arthropod diversity in studies conducted in the Natal Midlands (Pryke and Samways, 2012; Yekwayo *et al.*, 2016; Theron *et al.*, 2022), yet this was particularly prominent in two scenarios, 1) when they are surrounded by grasslands (natural habitats) and not pine plantations (human-manged habitat) (Pryke and Samways, 2012; Yekwayo *et al.*, 2017), and 2) existing as a small habitat patch area (Yekwayo *et al.*, 2017). None of the previous studies were conducted at the Umngenipoort Research Facility. The current study found that season and habitat complexity play a major role in shaping arthropod diversity patterns. In comparison, the systematic review confirmed that the plantations' status as native or invasive determines how local biodiversity responds. Therefore, various factors are responsible for shaping arthropod diversity patterns at spatial or temporal scales.

## 4.3 Challenges and recommendations for future studies

Ecologists have attempted to explain biodiversity response to environmental changes and ecosystem productivity. However, these should be approached cautiously as generalisations are misleading and result in discrepancies in conservation planning. Arthropods are highly abundant in terrestrial ecosystems, and many of them are used to indicate environmental quality (Maleque *et al.*, 2009). The current study's findings have shown that different arthropod taxa responded to distinct environmental variables. It, therefore, provided a baseline for future studies on the specific taxon to use when investigating variations in certain environmental parameters within habitats to minimise costs spent on investigating multiple taxa.

It is indisputable that the locality in which the study is conducted (key finding of the systematic review), the proximity of plantation sites to native vegetation (Yekwayo *et al.*, 2017) and microhabitat variables (Barton *et al.*, 2009; García-Tejero and Taboada, 2016) may have a major influence on arthropod diversity and assemblages, and different taxa may show contrasting responses. Future studies conducted in the Natal Midlands should determine how other invertebrates, such as molluscs and earthworms, respond, as they are considered good indicators of forest health (Uys *et al.*, 2010). Additionally, timber plantations may possibly be a surrogate habitat for arthropods as they are used by certain forest species. Lastly, it would be beneficial for future studies to consider the historical land uses which dominated the current plantation sites and the regional climatic conditions as they may impact biodiversity on a regional scale.

## 4.4 Final comments and summary of the conclusion

Generalising biodiversity patterns in different land uses is not beneficial for conservation. Some arthropod taxa, such as spiders, were not significantly affected by monoculture timber plantations. It is, therefore, important to assess specific taxa at different scales based on the researcher's objective. In addition, using a single measure of diversity is insufficient for investigating ecosystem productivity as functional diversity among the three habitats suggests that functional arthropod groups are redundant. Yet, species richness significantly differed amongst the habitats for beetles, spiders and myriapods. Environmental filters at various scales drive the diversity and the distribution of arthropods among production landscapes. Local environmental factors and functional diversity should be considered in conservation and habitat rehabilitation projects to maintain and reestablish functional ecosystems.

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## Supplementary material

**Table S1.** Common vegetation types compared with timber plantations in arthropod diversity studies.

| Vegetation type or land-use | Number of studies |
|---|---|
| Grassland | 28 |
| Native forests | 67 |
| Pastures | 19 |
| Savannahs | 10 |
| Secondary forests | 15 |

**Table S2.** Summary of studies that reported arthropod classes that increased or decreased in monoculture *Eucalyptus* plantation type compared to natural vegetation.

| **Author(s)** | **Arthropod class** | ***Eucalyptus* native or introduced in the study region** | **Vegetation/land-use compared to** | **Species richness increased or decreased in plantation?** | **Species abundance increased or decreased in plantation?** |
|---|---|---|---|---|---|
| Audino et al. (2017) | Insecta | Introduced | Native forests | No difference | No difference |
| Barlow et al. (2007) | Insecta | Introduced | Native and secondary forests | Decreased | Increased |
| Beiroz et al. (2014) | Arachnida, insecta and malacostraca | Introduced | Pastures and secondary forests | Increased | Increased |
| Bernardes et al. (2020) | Insecta | Introduced | Savannahs | Decreased | Decreased |
| Braganca et al. (1998) | Insecta | Introduced | secondary forests | Decreased | Increased |
| Bragaqa et al. (1998) | Insecta | Introduced | Native forests | Decreased | Increased |
| Chey et al. (1997) | Insecta | Introduced | Secondary forests | Decreased | Decreased |
| Chey et al. (1998) | Arachnida and insecta | Introduced | Secondary forests | Increased | Decreased |
| Correa et al. (2020) | Insecta | Introduced | Native forests and pastures | Decreased | Decreased |
| Costa-Milanez et al. (2014) | Insecta | Introduced | Savannah | Increased | Increased |
| Cuautle et al. (2015) | Insecta | Introduced | Native forests and grasslands | No difference | Decreased |
| Cunningham et al. (2005) | Insecta | Native | Native forests and pastures | Increased | Increased |
| da Rosa et al. (2019) | Arachnida | Introduced | Native forests and pastures | Decreased | Decreased |
| da Silva et al. (2022) | Entognatha | Introduced | grasslands | Decreased | Decreased |
| De Souza et al. (2012) | Insecta | Introduced | Native forests | Decreased | Decreased |
| de Souza-Campana et al. (2017) | Insecta | Introduced | Native forests | Decreased | - |
| Diniz et al. (2010) | Insecta | Introduced | Pastures and savannahs | Decreased | Decreased |
| Diniz et al. (2012) | Insecta | Introduced | Pastures and savannahs | Decreased | Decreased |
| Dos Santos et al. (2018) | Insecta | Introduced | Native forests and pasture | Decreased | Decreased |
| Fagundes et al. (2011) | Insecta | Introduced | Native forests and grasslands | Decreased | Decreased |
| Fierro et al. (2017) | Insecta | Introduced | Native forests | Decreased | Decreased |
| García-Suabita et al. (2019) | Insecta | Introduced | Pastures and savannahs | Increased | Increased |
| Gardner et al. (2008) | Insecta | Introduced | Native and secondary forests | Decreased | Decreased |

| | | | | | |
|---|---|---|---|---|---|
| Grimbacher et al. (2007) | Insecta | Native | Secondary forests and pastures | Decreased | Increased |
| Gualberto et al. (2021) | Arachnida and insecta | Introduced | Pastures and savannahs | Decreased | - |
| Gunther and New (2003) | Insecta | Introduced | Native Eucalyptus forests | Increased | Increased |
| Hawes et al. (2009) | Insecta | Introduced | Native and secondary forests | No difference | No difference |
| Herrmann et al. (2022) | Arachnida | Introduced | Desert | Increased | Decreased |
| Higuchi et al. (2000) | Insecta | Introduced | Native forests | - | Increased |
| Jayaraman et al. (2017) | Arachnida | Introduced | Native forests | Decreased | - |
| Junqueira et al. (2009) | Insecta | Introduced | Native forests | Decreased | Decreased |
| Lo-Man-Hung et al. (2008) | Arachnida | Introduced | Native and secondary forests | Decreased | Increased |
| Lopes Rodrigues et al. (2010) | Arachnida | Introduced | Grasslands | Increased | Decreased |
| Machado et al. (2019) | Entognatha | Introduced | Native forests | Decreased | Decreased |
| Magrini et al. (2011) | Malacostraca | Introduced | Native forests | - | Increased |
| Majer (1976) | Insecta | Native | Native forests and shrublands | Decreased | Decreased |
| Martello et al. (2018) | Insecta | Introduced | Native forests | Decreased | Decreased |
| Mthimunye and Munyai (2022) | Insecta | Introduced | Native forests | Increased | Increased |
| Munyai et al. (2021) | Insecta | Introduced | Native forests and grasslands | Decreased | Increased |
| Muscardi et al. (2008) | Insecta | Introduced | Native forests | Increased | Increased |
| Neves et al. (2012) | Insecta | Introduced | Savannah and pastures | Decreased | Decreased |
| Nsengimana et al. (2021) | Arachnida, insecta, diplopoda, chilopoda, entognatha, crustacea and Pauropoda | Introduced | Native forests | - | Decreased |
| Nunes et al. (2021) | Arachnida, insecta, entognatha and diplopoda | Introduced | Native forests and pastures | Decreased | Decreased |
| Ojija (2016) | Arachnida, insecta, diplopoda and chilopoda | Introduced | Grasslands | Decreased | Decreased |
| Ortiz et al. (2019) | Entognatha | Introduced | Native forests and pastures | Decreased | Decreased |
| Pellens and Garay (1999) | Arachnida, insecta, entognatha, diplopoda, chilopoda | Introduced | Native forests | Decreased | Decreased |
| Pik et al. (1999) | Insecta | Native | Secondary forests and grasslands | Decreased | Decreased |
| Pompeo et al. (2020) | Insecta | Introduced | Native forests | Decreased | Decreased |
| Pompeo et al. (2017) | Insecta | Introduced | Native forests and pastures | Decreased | Decreased |

| | | | | | |
|---|---|---|---|---|---|
| Pryke and Samways (2012) | Arachnida and insecta | Introduced | Native forests and grasslands | Increased (*Eucalyptus* and *Pinus*) | - |
| Rabello et al. (2021) | Insecta | Introduced | Grasslands, pastures, savannahs | Decreased | - |
| Ribeiro-Troian et al. (2009) | Entognatha | Introduced | Native forests | Increased (*Eucalyptus* and *Pinus*) | Increased (*Eucalyptus* and *Pinus*) |
| Rieff et al. (2016) | Arachnida and entognatha | Introduced | Grasslands | No difference | Increased |
| Santana Gualberto et al. (2021) | Arachnida, insecta, entognatha, chilopoda | Introduced | Savannahs | Decreased | Decreased |
| Schalkwyk et al. (2021) | Arachnida and insecta | Introduced | Native forest and grasslands | Increased | Increased |
| Schnell et al. (2003) | Insecta | Native | Native forests and pastures | Decreased | Decreased |
| Silva-Filho et al. (2020) | Insecta | Introduced | Native forests | - | Increased |
| Suguituru et al. (2011) | Insecta | Introduced | Secondary forests | Increased | Decreased |
| Wang et al. (2019) | Araneae and insecta | Introduced | Native forests | Decreased | Decreased |
| Winck et al. (2017) | Entognatha | Introduced | Native forests and grasslands | Decreased | - |
| Zanuncio et al. (1998) | Insecta | Introduced | Native forests | - | Increased |

**Table S3.** Summary of studies that reported arthropod classes that increased or decreased in monoculture *Pinus* plantation type compared to natural vegetation.

| **Author(s)** | **Class** | ***Pinus* native or introduced to the study region** | **Vegetation compared to** | **Species richness increased or decreased in plantation?** | **Species abundance increased or decreased in plantation?** |
|---|---|---|---|---|---|
| Arif et al. (2021) | Insecta | Introduced | Mixed forests | - | Decreased |
| Baini and Zapparoli (2015) | Chilopoda | Introduced | Native forests | Decreased | - |
| Bieringer and Zulka (2003) | Insecta | Native | Grasslands | Decreased | - |
| Bozdoğan (2020) | Insecta | Native | Native forests | Decreased | Increased |
| Bugs et al. (2014) | Malacostraca | Introduced | Native and secondary forests | Decreased | Decreased |
| Car (2021) | Diplopoda | Introduced | Native forests | - | Increased |
| Casas-Pinilla et al. (2022) | Insecta | Introduced | Native forests | Increased | Increased |
| Catarineu et al. (2018) | Insecta | Introduced | Native forests and grasslands | Decreased | - |
| Chang et al. (2017) | Entognatha | Native | Native forests | Decreased | Decreased |
| Corley et al. 2006 | Insecta | Introduced | Grasslands | Decreased | Decreased |
| Corley et al. (2012) | Insecta | Introduced | Native forests and grasslands | Decreased | Decreased |
| Dalzochio et al. (2018) | Insecta | Introduced | Mixed forests and tamed native tree stands | Decreased | - |
| Donnelly and Giliomee (1985) | Insecta | Introduced | Fynbos | Decreased | Decreased |
| Eckert et al. (2019) | Arachnida, insecta, entognatha, crustacea, diplopoda, chilopoda | Introduced | Grasslands | Decreased | Decreased |
| Fagundes et al. (2011) | Insecta | Introduced | Native forests and grasslands | Decreased | Decreased |
| Feng et al. (2015) | Arachnida and insecta | Native | Grasslands | Decreased | Decreased |
| Fierro et al. (2017) | Insecta | Introduced | Native forests | Decreased | Decreased |
| Gallé et al. (2018) | Arachnida | Native | Native forests | Decreased | Decreased |
| Garcia-Martinez et al. (2017) | Insecta | Introduced | Native forests and pastures | Decreased | Decreased |
| Gillette et al. (2008) | Arachnida | Native | Native forests | Increased | Increased |
| Ienco et al. (2020) | Insecta | Native | Native forests | Decreased | - |
| Kamczyc et al. (2017) | Arachnida | Native | Native forests | Increased | Increased |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| Kovac et al. (2005) | Entognatha | Native | Tamed native tree stands | - | Decreased |
| Liu et al. (2012) | Entognatha | Introduced | Fynbos | Increased | Increased |
| Majer (1976) | Insecta | Native | Native forests and shrublands | Decreased | Decreased |
| Minor (2008) | Entognatha | Introduced | Native forests | Decreased | Increased |
| Moraes et al. (2013) | Insecta | Introduced | Native and secondary forests | Decreased | Decreased |
| Munévar et al. (2018) | Arachnida | Introduced | Native forests | Decreased | Increased |
| Nummelin and Zilihona (2004) | Arachnida and insecta | Introduced | Native forests | - | Decreased |
| Ohwaki et al. (2017) | Insecta | Native | Native forests | Decreased | Decreased |
| Pacheco et al. (2009) | Insecta | Introduced | Secondary forests | Decreased | Decreased |
| Pawson et al. (2008) | Insecta | Introduced | Native forests and pastures | Increased | Decreased |
| Pinto et al. (2018) | Arachnida | Introduced | Native forests and grasslands | Decreased | Decreased |
| Pryke et al. (2013) | Insecta | Introduced | Native forests and grasslands | Decreased | - |
| Renner et al. (2016) | Insecta | Introduced | Native forests | Increased | - |
| Samways and Moore (1991) | Insecta | Introduced | Grasslands | Decreased | Decreased |
| Santoandré et al. (2019) | Insecta | Introduced | Native forests and grasslands | Increased | Increased |
| Santoandré et al. (2019) | Insecta | Introduced | Native forests and grasslands | Increased | Increased |
| Smith et al. (2018) | Arachnida | Native | Native forests | Increased | - |
| Springett (1976) | Arachnida, insecta, entognatha | Native | Native forests | Decreased | - |
| Swart et al. (2018) | Arachnida and insecta | Introduced | Native forests and fynbos | Decreased | - |
| Taboada et al. (2010) | Insecta | Introduced | Native forests | Decreased | - |
| van Der Merwe et al. (1996) | Arachnida | Introduced | Native forests and grasslands | Decreased | - |
| Winkler and Tóth (2012) | Entognatha | Native | Tamed native tree stands and grasslands | Decreased | Decreased |
| Yekwayo et al. (2017) | Arachnida, insecta, entognatha and diplopoda | Introduced | Native forests and grasslands | Decreased | Decreased |
| Yekwayo et al. (2016) | Arachnida, insecta, entognatha and diplopoda | Introduced | Native forests and grasslands | Decreased | Decreased |
| Yu et al. (2014) | Insecta | Native | Native forests | Decreased | No difference |
| Yu et al. (2010) | Insecta | Native | Native forests | Decreased | Increased |

**Table S4.** Coordinates of the sampling points in the three habitats (BG-Bluegum plantation, NF-Natural forest, PN-Pine plantation) and their soil type in the Umngenipoort Research Facility, Natal Midlands.

| Habitat type | Replicate | Coordinates | Soil type |
|---|---|---|---|
| **Bluegum Plantation** | BG1 | 29°29’15.18"S, 29°53’44.16"E | Sandy Loam |
| | BG2 | 29°29’25.44"S, 29°53’48.63"E | Clay |
| | BG3 | 29°29’33.48"S, 29°53’56.22"E | Clay |
| | BG4 | 29°29’38.82"S, 29°53’46.74"E | Clay |
| | BG5 | 29°29’50.94"S, 29°53’45.90"E | Clay |
| | BG6 | 29°29’59.34"S, 29°53’52.98"E | Clay Loam |
| | BG7 | 29°30’5.94"S, 29°53’41.34"E | Clay |
| **Natural Forest** | NF1 | 29°28’41.34"S, 29°53’22.32"E | Silty Clay |
| | NF2 | 29°28’47.88"S, 29°53’31.44"E | Silty Clay Loam |
| | NF3 | 29°28’51.36"S, 29°53’42.72"E | Clay |
| | NF4 | 29°28’46.50"S, 29°53’55.56"E | Clay |
| | NF5 | 29°29’6.90"S, 29°54’13.38"E | Clay |
| | NF6 | 29°29’16.02"S, 29°54’26.40"E | Clay |
| | NF7 | 29°29’12.10"S, 29°54’37.11"E | Clay |
| **Pine Plantation** | PN1 | 29°29’25.44"S, 29°53’46.74"E | Clay Loam |
| | PN2 | 29°30’5.88"S, 29°53’41.52"E | Clay |
| | PN3 | 29°29’43.08"S, 29°53’32.58"E | Clay Loam |
| | PN4 | 29°29’44.28"S, 29°53’0.72"E | Sandy Clay Loam |
| | PN5 | 29°29’37.62"S, 29°53’20.04"E | Clay |
| | PN6 | 29°29’45.42"S, 29°53’23.04"E | Clay |
| | PN7 | 29°29’32.58"S, 29°53’41.88"E | Clay |

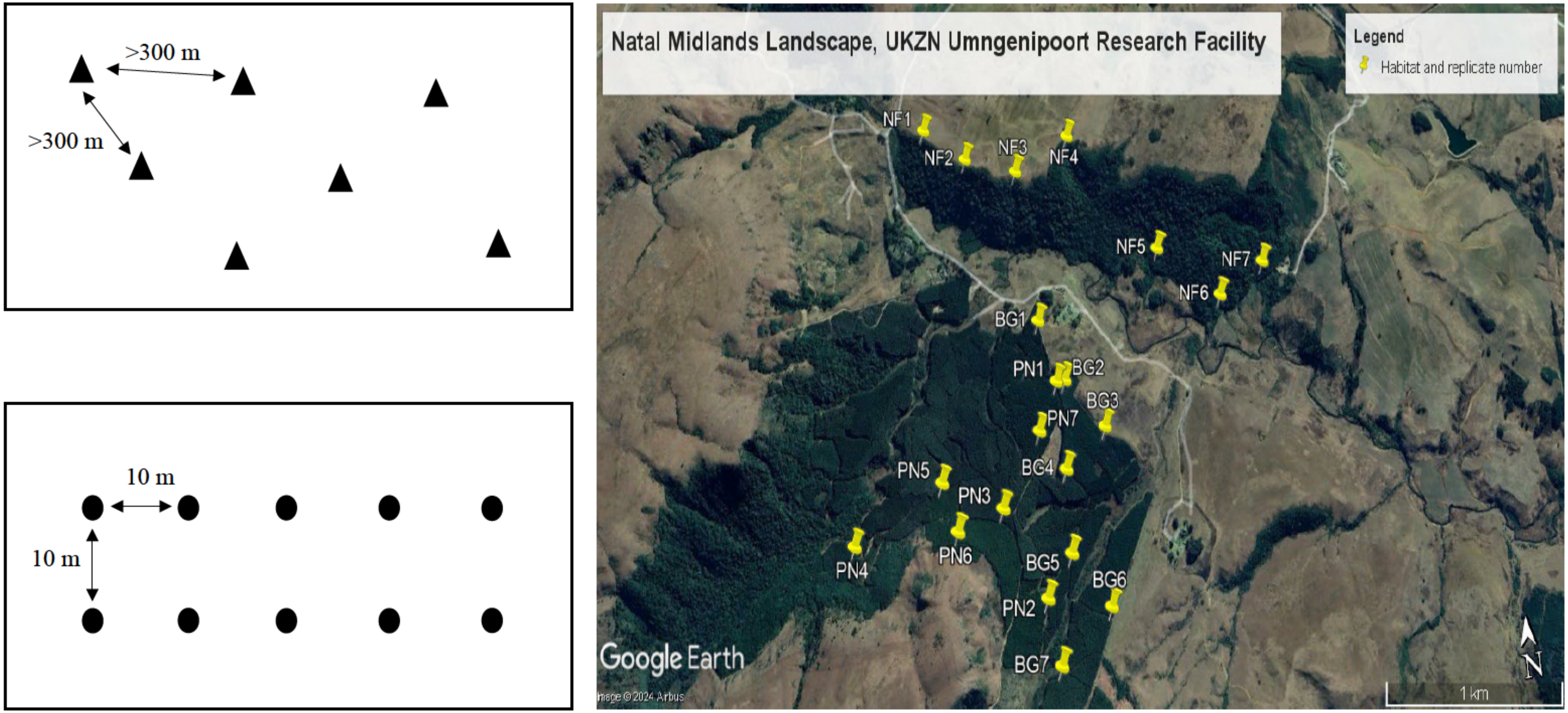

**Figure S1:** Sampling design showing each habitat replicated seven times, with replicates separated by over 300 m and the sampling grip of pitfall traps per replicate. The landscape of the Umgenipoort Research Facility showing the locations of the three habitat types (NF - Natural forests), BG - Blue-gum and PN - Pine plantations, with their replicates, is also shown.

**Table S5.** An inventory of the arthropod species collected across the three habitat types during the dry-hot and wet-hot seasons at the Umngenipoort Research Facility, Natal Midlands.

| | | | **Dry-Hot season** | | | **Wet-Hot season** | | |
|---|---|---|---|---|---|---|---|---|
| **Orders** | **Species** | **Functional guild** | **Bluegum** | **Natural forest** | **Pine** | **Bluegum** | **Natural forest** | **Pine** |
| **Araneae** | *Agyneta natalensis* | Specialist predator | 32 | 50 | 65 | 30 | 73 | 58 |
| | *Allocosa*_sp1 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Argyrodes*_sp1 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Ariadna*_sp1 | Predator | 1 | 6 | 0 | 2 | 7 | 1 |
| | *Austrachelas incertus* | Specialist predator | 35 | 7 | 19 | 6 | 3 | 0 |
| | *Brachytheliscus bicolor* | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Cheiramiona florisbadensis* | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Chresiona*_sp1 | Predator | 3 | 1 | 0 | 0 | 11 | 1 |
| | *Clubiona*_sp1 | Predator | 0 | 0 | 0 | 1 | 1 | 0 |
| | *Copa flavoplumosa* | Predator | 7 | 0 | 0 | 1 | 0 | 0 |
| | *Crozetulus rhodesiensis* | Predator | 8 | 0 | 28 | 2 | 1 | 76 |
| | *Ctenus erythrochelis* | Predator | 2 | 3 | 0 | 0 | 0 | 1 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| *Diphya simoni* | Predator | 2 | 0 | 1 | 0 | 1 | 2 |
| *Dipluridae*_sp1 | Predator | 0 | 0 | 0 | 1 | 0 | 0 |
| *Drassodella montana* | Predator | 0 | 3 | 8 | 0 | 0 | 6 |
| *Euryopis episinoides* | Predator | 0 | 8 | 0 | 0 | 0 | 0 |
| *Evarcha*_sp1 | Predator | 1 | 4 | 0 | 1 | 5 | 0 |
| *Frontinellina locketi* | Predator | 0 | 7 | 0 | 0 | 0 | 0 |
| *Griswoldia urbensis* | Predator | 12 | 0 | 0 | 7 | 7 | 0 |
| *Hahniatabulicola*_sp1 | Predator | 15 | 11 | 75 | 3 | 2 | 17 |
| *Heliophanus*_sp1 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| *Hewittia gracilis* | Predator | 1 | 0 | 0 | 0 | 0 | 0 |
| *Leucauge*_sp1 | Predator | 1 | 3 | 2 | 0 | 0 | 0 |
| *Lycosidae*_sp1 | Predator | 1 | 0 | 0 | 0 | 1 | 2 |
| *Neoscona subfusca* | Predator | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pachygnatha zappa* | Predator | 0 | 11 | 0 | 0 | 1 | 0 |
| *Pardosa*_sp1 | Predator | 1 | 0 | 0 | 0 | 0 | 0 |
| *Salticidae*_sp1 | Predator | 0 | 0 | 0 | 1 | 0 | 0 |
| *Scytodes caffra* | Predator | 0 | 2 | 0 | 7 | 1 | 0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Scytodes*_sp1 | Predator | 1 | 2 | 2 | 0 | 1 | 3 |
| | *Spinotrachelas montanus* | Predator | 6 | 0 | 3 | 6 | 1 | 0 |
| | *Steatoda capensis* | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Thyenula haddadi* | Predator | 1 | 3 | 0 | 0 | 4 | 0 |
| | *Thyenula*_sp1 | Predator | 0 | 0 | 0 | 0 | 0 | 1 |
| | *Trachelas*_sp1 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Vidole helicigyna* | Predator | 0 | 2 | 1 | 2 | 20 | 1 |
| | *Xysticus*_sp1 | Predator | 0 | 0 | 0 | 0 | 0 | 1 |
| | *Zelotes*_sp1 | Predator | 0 | 0 | 1 | 0 | 0 | 0 |
| **Total individuals of Araneae** | | | **131** | **130** | **205** | **70** | **140** | **170** |
| **Total number of species of Araneae** | | | **19** | **23** | **11** | **14** | **17** | **13** |
| **Coleoptera** | Aderidae_sp1 | Herbivore | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Aleochara*_sp1 | Predator | 0 | 1 | 2 | 0 | 0 | 0 |
| | *Aleochara*_sp2 | Predator | 0 | 0 | 0 | 0 | 1 | 0 |
| | Aleocharinae_sp2 | Predator | 0 | 0 | 0 | 0 | 0 | 1 |
| | Aleocharinae_sp3 | Predator | 0 | 0 | 0 | 0 | 0 | 2 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Anobiidae_sp1 | Omnivore | 0 | 1 | 0 | 0 | 0 | 0 |
| | Anthicidae_sp1 | Omnivore | 7 | 4 | 1 | 0 | 4 | 0 |
| | Anthicidae_sp2 | Omnivore | 2 | 1 | 0 | 0 | 0 | 1 |
| | Anthicidae_sp3 | Omnivore | 4 | 0 | 0 | 0 | 0 | 0 |
| | Anthicidae_sp4 | Omnivore | 0 | 0 | 2 | 0 | 0 | 0 |
| | Anthonomus_sp1 | Herbivore | 17 | 97 | 9 | 10 | 16 | 0 |
| | *Aphodius*_sp1 | Detritivore | 0 | 2 | 0 | 0 | 0 | 0 |
| | *Ataenius*_sp1 | Detritivore | 0 | 0 | 1 | 0 | 0 | 0 |
| | *Baeocera*_sp1 | Herbivore | 0 | 1 | 0 | 0 | 1 | 0 |
| | *Caccobius*_sp1 | Detritivore | 0 | 3 | 0 | 0 | 0 | 0 |
| | *Caccobius*_sp2 | Detritivore | 0 | 0 | 0 | 1 | 0 | 0 |
| | *Calosoma auropunctatum* | Predator | 0 | 0 | 0 | 0 | 1 | 0 |
| | *Carabidae*_sp1 | Predator | 0 | 1 | 1 | 0 | 3 | 0 |
| | *Carpophilus*_sp1 | Herbivore | 3 | 0 | 0 | 0 | 0 | 0 |
| | *Cassida*_sp1 | Herbivore | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Catharsius*_sp1 | Detritivore | 0 | 0 | 0 | 0 | 1 | 0 |
| | Cerambycidae_sp1 | Herbivore | 0 | 0 | 3 | 0 | 0 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Cerambycidae_sp2 | Herbivore | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cercyon*_sp1 | Herbivore | 6 | 10 | 2 | 7 | 16 | 1 |
| *Chlaenius aestivus* | Predator | 3 | 13 | 1 | 0 | 2 | 1 |
| *Chlaenius*_sp1 | Predator | 1 | 0 | 0 | 1 | 2 | 0 |
| *Chlaenius*_sp2 | Predator | 0 | 0 | 0 | 0 | 1 | 0 |
| Chrysomelidae_sp1 | Herbivore | 0 | 3 | 0 | 0 | 0 | 0 |
| Clambidae_sp1 | Herbivore | 0 | 1 | 0 | 0 | 0 | 0 |
| *Clivina*_sp1 | Predator | 0 | 0 | 0 | 0 | 0 | 1 |
| Coccinellidae_sp1 | Herbivore | 0 | 1 | 0 | 0 | 0 | 0 |
| Coccinellidae_sp2 | Herbivore | 1 | 0 | 0 | 0 | 0 | 0 |
| Colydiidae_sp1 | Omnivore | 1 | 0 | 0 | 3 | 0 | 2 |
| Colydiidae_sp2 | Omnivore | 0 | 0 | 1 | 0 | 0 | 0 |
| *Conoderus*_sp1 | Omnivore | 1 | 0 | 1 | 0 | 0 | 0 |
| Cucujidae_sp1 | Scavengers | 2 | 1 | 4 | 22 | 1 | 4 |
| Curculionidae_sp1 | Herbivore | 12 | 11 | 28 | 17 | 37 | 25 |
| Curculionidae_sp2 | Herbivore | 0 | 7 | 0 | 1 | 1 | 0 |
| Curculionidae_sp3 | Herbivore | 0 | 3 | 3 | 0 | 3 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Curculionidae_sp4 | Herbivore | 0 | 1 | 0 | 0 | 1 | 0 |
| *Dorcathispa bellicosa* | Herbivore | 0 | 1 | 0 | 0 | 0 | 0 |
| Dytiscidae_sp1 | Predator | 0 | 0 | 1 | 0 | 0 | 0 |
| Elmidae_sp1 | Detritivore | 0 | 5 | 0 | 0 | 0 | 0 |
| Epuraea_sp1 | Detritivore | 0 | 1 | 0 | 0 | 0 | 0 |
| *Erichsonius*_sp1 | Predator | 10 | 269 | 4 | 3 | 125 | 37 |
| *Eusphalerum*_sp1 | Herbivore | 1 | 0 | 0 | 0 | 2 | 0 |
| *Harmonia axyridis* | Nectarivore | 0 | 1 | 0 | 0 | 0 | 0 |
| Harpalinae_sp1 | Predator | 2 | 0 | 1 | 0 | 0 | 1 |
| Histeridae_sp1 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| Histeridae_sp2 | Predator | 28 | 1 | 9 | 16 | 1 | 22 |
| Hydrophilidae_sp1 | Detritivore | 0 | 0 | 1 | 0 | 0 | 2 |
| *Hyphydrus ovatus* | Predator | 1 | 0 | 0 | 0 | 0 | 0 |
| *Lagria vulnerata* | Herbivore | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lagria*_sp1 | Herbivore | 0 | 2 | 0 | 0 | 0 | 0 |
| *Lobiopa*_sp1 | Nectarivore | 0 | 0 | 0 | 0 | 0 | 1 |
| *Margarinotus*_sp1 | Predator | 0 | 0 | 1 | 0 | 0 | 0 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| Melolonthinae_sp1 | Herbivore | 0 | 5 | 0 | 0 | 2 | 0 |
| *Mentophilonthus*_sp1 | Predator | 39 | 45 | 44 | 13 | 37 | 6 |
| Nitidulidae_sp1 | Detritivore | 18 | 55 | 304 | 6 | 15 | 33 |
| Nitidulidae_sp2 | Detritivore | 0 | 0 | 1 | 0 | 0 | 0 |
| Nitidulidae_sp3 | Detritivore | 0 | 1 | 0 | 0 | 1 | 0 |
| *Odontoloma dentinum* | Detritivore | 1 | 5 | 0 | 1 | 13 | 0 |
| *Onthophagini*_sp1 | Detritivore | 0 | 1 | 0 | 0 | 0 | 0 |
| Ophioninae_sp1 | Herbivore | 0 | 0 | 0 | 0 | 1 | 0 |
| *Paracymus aeneus* | Predator | 0 | 0 | 0 | 0 | 1 | 0 |
| Phalacridae_sp1 | Predator | 0 | 0 | 4 | 0 | 0 | 0 |
| Phalacridae_sp2 | Predator | 20 | 0 | 3 | 94 | 0 | 50 |
| *Philonthus*_sp1 | Predator | 0 | 0 | 0 | 0 | 4 | 0 |
| Pselaphinae_sp1 | Predator | 0 | 0 | 0 | 1 | 0 | 0 |
| Pterostichinae_sp1 | Predator | 0 | 8 | 1 | 0 | 7 | 0 |
| Ptiliidae_sp1 | Detritivore | 0 | 1 | 0 | 0 | 0 | 0 |
| Scaphidiidae_sp1 | Herbivore | 0 | 1 | 0 | 0 | 0 | 0 |
| Scaphidiidae_sp2 | Herbivore | 0 | 0 | 0 | 3 | 0 | 0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Scarabaeidae_sp1 | Herbivore | 0 | 1 | 0 | 0 | 0 | 0 |
| | Scarabaeidae_sp2 | Herbivore | 0 | 0 | 0 | 1 | 1 | 0 |
| | Scarabaeidae_sp3 | Herbivore | 0 | 0 | 1 | 0 | 0 | 0 |
| | *Sciobius*_sp1 | Herbivore | 0 | 0 | 0 | 0 | 0 | 1 |
| | Scolytidae_sp1 | Predator | 0 | 0 | 13 | 0 | 0 | 3 |
| | Scydmaeninae_sp1 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Selasia*_sp1 | Herbivore | 0 | 1 | 0 | 0 | 0 | 0 |
| | Staphylinidae_sp2 | Predator | 7 | 4 | 8 | 11 | 14 | 18 |
| | Staphylinidae_sp3 | Predator | 12 | 29 | 7 | 34 | 0 | 9 |
| | Staphylinidae_sp4 | Predator | 0 | 1 | 3 | 0 | 0 | 0 |
| | *Stethorus*_sp1 | Predator | 1 | 0 | 0 | 0 | 0 | 0 |
| | *Tefflus*_sp1 | Predator | 0 | 3 | 0 | 0 | 0 | 0 |
| | *Xeloma*_sp1 | Predator | 0 | 14 | 0 | 0 | 0 | 0 |
| | *Xenitenus*_sp1 | Predator | 1 | 0 | 16 | 0 | 1 | 5 |
| | Zopheridae_sp1 | Omnivore | 1 | 0 | 0 | 0 | 0 | 0 |
| **Total individuals of Coleoptera** | | | **202** | **621** | **482** | **245** | **317** | **226** |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Total number of species of Coleoptera** | | | **27** | **44** | **33** | **19** | **32** | **22** |
| **Hymenoptera** | *Anochetus nr. Pubescens* | Predator | 1 | 0 | 0 | 3 | 0 | 0 |
| | *Brachyponera sennaarensis* | Omnivore | 0 | 0 | 0 | 0 | 1 | 0 |
| | *Camponotus* UKZN_05 (maculatus gp.) | Nectarivore | 1 | 0 | 1 | 0 | 0 | 0 |
| | *Camponotus* UKZN_08 | Nectarivore | 0 | 6 | 0 | 1 | 0 | 0 |
| | *Crematogaster* UKZN_01 (*castanea complex*) | Predator | 2 | 4 | 10 | 3 | 2 | 8 |
| | *Crematogaster* UKZN_02 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Dorylus helvolus* | Predator | 1 | 1 | 0 | 0 | 0 | 0 |
| | *Hypoponera* UKZN_02 | Predator | 0 | 0 | 0 | 0 | 1 | 0 |
| | *Hypoponera* UKZN_03 | Predator | 0 | 3 | 0 | 0 | 8 | 1 |
| | *Hypoponera* UKZN_04 | Predator | 0 | 3 | 0 | 0 | 2 | 0 |
| | *Hypoponera* UKZN_05 | Predator | 0 | 1 | 2 | 1 | 4 | 3 |
| | *Hypoponera* UKZN_06 | Predator | 0 | 0 | 0 | 1 | 0 | 0 |
| | *Lepisiota cf. crinita* | Omnivore | 0 | 0 | 0 | 2 | 0 | 0 |
| | *Lepisiota* UKZN_01 (*capensis* gp.) | Omnivore | 2 | 0 | 2 | 0 | 0 | 0 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| *Lepisiota* UKZN_02 (*capensis* gp.) | Omnivore | 8 | 0 | 23 | 5 | 0 | 7 |
| *Lepisiota* UKZN_07 | Omnivore | 1 | 16 | 0 | 1 | 2 | 0 |
| *Lepisiota* UKZN_08 (*crinita* gp.) | Omnivore | 9 | 0 | 0 | 6 | 0 | 0 |
| *Leptogenys intermedia* | Predator | 0 | 3 | 0 | 0 | 0 | 0 |
| *Melissotarsus beccarii* | Honeydew | 0 | 2 | 0 | 0 | 3 | 0 |
| *Meranoplus peringueyi* | Omnivore | 4 | 0 | 0 | 10 | 0 | 0 |
| *Mesoponera* UKZN_01 | Omnivore | 0 | 0 | 0 | 0 | 0 | 1 |
| *Monomorium* UKZN_01 | Granivore | 3 | 31 | 10 | 11 | 8 | 5 |
| *Monomorium* UKZN_09 | Granivore | 2 | 0 | 0 | 1 | 0 | 0 |
| *Monomorium* UKZN_10 | Granivore | 10 | 3 | 2 | 9 | 18 | 9 |
| *Nylanderia natalensis* | Omnivore | 1 | 1 | 18 | 1 | 0 | 5 |
| *Parasyscia* UKZN_07 | Predator | 0 | 0 | 0 | 0 | 0 | 3 |
| *Pheidole* UKZN_05 | Omnivore | 2 | 0 | 0 | 0 | 0 | 0 |
| *Pheidole* UKZN_07 | Omnivore | 1 | 0 | 3 | 2 | 0 | 4 |
| *Solenopsis* UKZN_03 | Predator | 3 | 4 | 1 | 43 | 37 | 22 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Tetramorium* UKZN_03 (*setigerum* gp.) | Granivore | 31 | 42 | 53 | 29 | 186 | 56 |
| | *Tetramorium* UKZN_09 (*simillimum* gp.) | Nectarivore | 4 | 0 | 0 | 11 | 1 | 1 |
| | *Tetramorium* UKZN_10 (*simillimum* gp.) | Nectarivore | 2 | 0 | 0 | 0 | 1 | 0 |
| | *Tetramorium* UKZN_20 (*squaminode* gp.) | Granivore | 5 | 0 | 1 | 0 | 8 | 2 |
| | *Tetramorium* UKZN_30 (*setigerum* gp.) | Granivore | 2 | 2 | 12 | 11 | 18 | 7 |
| | *Tetramorium* UKZN_32 (*weitzekeri* gp.) | Granivore | 56 | 25 | 0 | 91 | 76 | 1 |
| **Total individuals of Hymenoptera** | | | **151** | **148** | **138** | **242** | **376** | **135** |
| **Total number of species of Hymenoptera** | | | **22** | **17** | **13** | **20** | **17** | **16** |
| **Myriapoda (Chilopoda)** | *Anopsobius*_sp1 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Asanada*_sp1 | Predator | 0 | 0 | 0 | 1 | 0 | 0 |
| | Henicopidae_sp1 | Predator | 0 | 1 | 0 | 0 | 0 | 0 |
| | Lithobiidae_sp3 | Predator | 0 | 0 | 2 | 0 | 2 | 0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Lithobiidae_sp4 | Predator | 0 | 0 | 2 | 5 | 0 | 7 |
| | *Lithobius forficatus* | Predator | 0 | 0 | 1 | 0 | 0 | 0 |
| | *Lithobius microps* | Predator | 0 | 0 | 3 | 1 | 0 | 0 |
| | *Lithobius peregrinus* | Predator | 1 | 2 | 3 | 1 | 2 | 9 |
| | *Lithobius*_sp4 | Predator | 0 | 0 | 0 | 0 | 0 | 3 |
| | *Lithobius*_sp5 | Predator | 0 | 0 | 2 | 0 | 0 | 3 |
| | *Paralamyctes*_sp1 | Predator | 0 | 0 | 0 | 2 | 3 | 1 |
| | *Scolopendridae*_sp1 | Predator | 0 | 0 | 0 | 1 | 0 | 1 |
| | *Scutigerina weberi* | Predator | 0 | 0 | 0 | 0 | 1 | 0 |
| **Total individuals of Chilopoda** | | | **1** | **4** | **13** | **11** | **8** | **24** |
| **Total number of species of Chilopoda** | | | **1** | **3** | **6** | **6** | **4** | **6** |
| **Myriapoda (Diplopoda)** | Odontopygidae_sp1 | Detritivore | 0 | 2 | 0 | 2 | 0 | 2 |
| | Polydesmida_sp1 | Detritivore | 1 | 23 | 1 | 25 | 1 | 2 |
| | Polydesmida_sp2 | Detritivore | 0 | 7 | 0 | 7 | 0 | 1 |
| | Sphaerotheriidae_sp1 | Detritivore | 0 | 2 | 0 | 2 | 0 | 14 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Sphaerotheriidae_sp2 | Detritivore | 0 | 0 | 0 | 0 | 0 | 17 |
| | Sphaerotheriidae_sp3 | Detritivore | 0 | 1 | 0 | 1 | 0 | 2 |
| | Sphaerotheriidae_sp4 | Detritivore | 0 | 2 | 0 | 2 | 0 | 3 |
| | Sphaerothetiidae_sp1 | Detritivore | 0 | 1 | 0 | 1 | 0 | 0 |
| | Spirostreptidae_sp1 | Detritivore | 0 | 7 | 0 | 7 | 1 | 2 |
| **Total individuals of Diplopoda** | | | **1** | **45** | **1** | **47** | **2** | **43** |
| **Total number of species of Diplopoda** | | | **1** | **8** | **1** | **8** | **1** | **9** |

**Table S6.** The statistical tests done to assess the species richness of the different arthropod groups and the results of those statistical tests. The tested factors were the effect of habitat type and season on arthropod species richness at the Umngenipoort Research Facility, Natal Midlands.

| **Taxon** | **Statistical test used** | **Factors** | **P value** | **F value** |
|---|---|---|---|---|
| All arthropods | Two-way ANOVA | Habitat type | <0.05* | 8.289 |
| | | Season | 0.07 | 3.427 |
| | | Interaction (Habitat type and season) | 0.50 | 0.668 |
| Ants | Two-way ANOVA | Habitat type | 0.35 | 1.079 |
| | | Season | 0.32 | 1.002 |
| | | Interaction (Habitat type and season) | 0.94 | 0.065 |
| Beetles | Two-way ANOVA | Habitat type | <0.05* | 6.441 |
| | | Season | <0.05* | 8.704 |
| | | Interaction (Habitat type and season) | 0.61 | 0.499 |
| Spiders | Two-way ANOVA | Habitat type | <0.05* | 3.629 |
| | | Season | <0.05* | 7.032 |
| | | Interaction (Habitat type and season) | 0.25 | 1.434 |
| Myriapods | GLMM | Habitat type | <0.05* | 4.968 |
| | | Season | 0.34 | 0.830 |
| | | Interaction (Habitat type and season) | 0.32 | 1.183 |