Diversity value of Afromontane forest patches within KwaZulu-Natal timber production areas.

by

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Dissertation presented for the degree of Doctor of Philosophy in the Faculty of AgriSciences at Stellenbosch University

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March 2016

Declaration

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December 2015

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General summary

Natural forests are important habitats for many species. In the KwaZulu-Natal Midlands of South Africa these forests naturally exist as small isolated forest patches within a grassland matrix. Recently, much of the extensive grassland matrix has been converted to exotic pine plantations. It remains unclear how this has affected the ecologically important forest arthropods. The overall aim of this study is to determine the state of arthropod diversity in natural forest patches within a timber production landscape, and how best to conserve this diversity. The specific objectives of this study are to: 1) determine the impact of natural forest interpatch distance and forest patch size on epigaeic arthropod diversity; 2) compare arthropod species richness, abundance and composition among natural forests, pine plantations and grasslands; 3) determine how each arthropod functional guild/taxon (detritivores, predators, herbivores, ants and mites) responds to pine plantations, natural forests and grassland, and assess whether exotic pine plantations are able to function as habitat extensions of natural forests compared to the natural reference of grassland.

Natural forest patches and surrounding habitats were sampled for epigaeic arthropods using pitfall traps, Berlese-Tullgren funnels, and active searches. Large and small patches had similar species richness, while assemblages differed significantly. Greater ant richness was recorded in patches with closer interpatch distances, while the opposite was observed for mites. Interaction between patch size and interpatch distance led to large-close patches supporting ant, beetle and spider composition that is different from small-close patches. Additionally, small-distant and small-close patches supported different beetle and ant composition. However, large-close and large-distant patches supported similar overall assemblages. Natural forests surrounded by grassland maintain arthropod diversity better than those surrounded by pines. There were greater differences in assemblages between natural forest-grassland boundaries than between natural forest-pine boundaries, indicating edge effects between pines and natural forests. Furthermore, grassland supported higher ant richness, while the greatest richness of mites and detritivores was in natural forests. Natural forests and their surrounding habitats varied in assemblages among functional guilds, although natural forests and pines were similar in mite, herbivore and predator assemblages. Interestingly, some grassland associated species were often found in adjacent natural forests. Many natural forests associated species were also present in the surrounding pines, yet pine

blocks negatively influenced natural forest associated mite species. All pine associated species were able to occupy adjacent natural forests.

Small patches had higher arthropod diversity than expected, although large and close patches are of greatest conservation priority in this landscape. Nevertheless, effective maintenance of all forest patches must incorporate surrounding natural vegetation. Although pines had a negative impact on species richness, they were also important habitat for some forest species, even though this is associated with loss of grassland species. I show that pines are not true extensions of natural forests, as they do not support all natural forest arthropod species. This study highlights the important role that natural forests play in the conservation of native arthropod biodiversity in a production landscape, and by extension in maintaining ecosystem processes across this landscape.

Algemene opsomming

Natuurlike woude is belangrike habitatte vir baie spesies. In die KwaZulu-Natal Middelande van Suid-Afrika bestaan hierdie woude natuurlik as klein geïsoleerde bos-kolle binne 'n grasveldmatriks. Onlangs is groot dele van die uitgebreide grasveldmatriks omgeskakel na eksotiese denneplantasies. Dit is steeds onduidelik hoe hierdie veranderings die ekologies belangrike geleedpotiges in woude affekteer. Die oorkoepelende doel van hierdie studie was om die toestand van diversiteit van geleedpotiges binne natuurlike bos-kolle in 'n hout-produksielandskap te bepaal en om vas te stel wat die beste manier is om hierdie diversiteit te bewaar. Die spesifieke doelwitte van hierdie studie was om 1) die impak van natuurlike bos inter-kol afstand en bos-kol grootte op grondbewonende geleedpotige-diversiteit te bepaal; 2) geleedpotige-spesiesrykheid, -hoeveelheid en -samestelling tussen natuurlike woude, denneplantasies en graslande te vergelyk; 3) vas te stel hoe elke geleedpotige funksionele-gilde/takson (detritivore, roofdiere, herbivore, miere en myte) op denneplantasies, natuurlike woude en grasslande reageer, en om te bepaal of eksotiese denneplantasies as habitat-uitbreidings van natuurlike woude kan funksioneer met die natuurlike graslande as verwysing.

Grondbewonende geleedpotiges vanaf natuurlike bos-kolle en omliggende habitatte is versamel deur gebruik te maak van putvalle, Berlese-Tullgren tregters, en aktiewe soektogte. Bos-kol grootte het nie spesiesrykheid beïnvloed nie, terwyl spesiessamestelling opmerklik verskil het tussen groot en klein bos-kolle. Hoër mierspesiesrykheid was aangeteken in kolle met naby inter-kol afstande, terwyl die teenoorgestelde waarneming gemaak is vir myte. Interaksie tussen kol grootte en inter-kol afstand het daartoe gelei dat groot en naby kolle mier-, kewer- en spinnekopsamestellings ondersteun het wat verskil van klein en naby kolle.. Klein-ver en klein-naby kolle het ook verskillende kewer- en miersamestellings ondersteun. Maar, indien alle takson in ag geneem word, het groot-naby en groot-ver bos-kolle soortgelyke samestellings ondersteun. Natuurlike woude wat omring word deur grasveld handhaaf geleedpotige-diversiteit beter as dié omring deur dennebome. Daar was groter verskille in samestellings tussen natuurlike bos-grasveld rande as tussen natuurlike bos-dennebome rande, wat 'n aanduiding is van rand-effekte tussen denne en natuurlike woude. Grasveld ondersteun hoër mierspesiesrykheid, terwyl die grootste rykheid van myte en detritivore in natuurlike woude gevind is. Natuurlike woude en hul omliggende habitatte het verskil in hul samestellings van funksionele gildes, alhoewel natuurlike woude en

dennewoude soortgelyke myt-, herbivoor- en roofdiersamestellings gehad het. Interessant genoeg, sommige grasveld-verbonde spesies is dikwels in die omliggende natuurlike woude aangetref. Baie spesies wat in natuurlike woude voorkom was ook teenwoordig in die omliggende dennewoude, maar denneplantasies het 'n negatiewe invloed op natuurlike woud-verbonde mytspesies gehad. Alle denne-verbonde spesies was in staat om die omliggende natuurlike bos te bewoon.

Kleiner bos-kolle het hoër geleedpotige-diversiteit gehad as wat verwag was, alhoewel groot en naby bos-kolle van die hoogste bewaringsprioriteite in hierdie landskap is. Tog moet doeltreffende instandhouding van alle bos-kolle die omliggende natuurlike plantegroei ook inkorporeer. Alhoewel denneplantasies 'n negatiewe impak op spesierykheid gehad het, was hulle ook belangrike habitat vir sommige woudspesies; daar was egter 'n gepaardgaande verlies in grasveldspesies. Ek wys dat dennebome nie ware uitbreidings van natuurlike woude is nie, aangesien hulle nie alle natuurlike bos geleedpotige-spesies ondersteun nie. Hierdie studie beklemtoon die belangrike rol wat natuurlike woude speel in die bewaring van inheemse geleedpotige-biodiversiteit in 'n produksielandskap en dus ook in die handhawing van ekosisteem-prosesse regoor hierdie landskap.

Acknowledgements

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Chapter 1: General introduction

Worldwide, losses of terrestrial biodiversity are increasing at an alarming rate. This is largely due to alteration of natural habitats as a result of anthropogenic disturbances, such as conversion of natural vegetation to agricultural landscapes, habitat fragmentation, changes to fire regimes, climate change and introduction of exotic species (Bradshaw 2012; Brockerhoff *et al*. 2008; Cremene *et al*. 2005; Hundera *et al*. 2013a; Kishimoto-Yamada *et al*. 2013; de Lima *et al*. 2013 Malcolm *et al*. 2006). These disturbances indirectly influence ecosystem structure and functioning, as they are interrelated with biodiversity composition and productivity (Muchoney 2008). The impact that these disturbances have on natural forest biodiversity have been well studied (Basset *et al*. 2008; Floren & Linsenmair 2001; Goehring *et al*. 2002; Kotze & Samways 1999b; Magrini *et al*. 2001; Magura *et al*. 2001; Pryke & Samways 2012; van der Merwe *et al*. 1996), as these disturbances are major threats to natural forests (Eeley *et al*. 2001)

Natural forests

Globally, natural forests are a conservation priority for terrestrial biodiversity, supporting relatively high diversity of both plant and animal species (Eeley *et al*. 1999; 2001; Lawes *et al*. 2000; Lötter & Beck 2004; Kishimoto-Yamada *et al*. 2013; Maleque *et al*. 2009; Schmitt *et al*. 2009; Uys *et al*. 2009; Wilson & Downs 2012). This is due to the structural complexity of natural forests which contain several vegetation strata, with high tree species diversity resulting in closed canopy cover, as well as increased availability of dead wood such as logs and snags (Downs & Symes 2004; Maleque *et al*. 2009; Zhou *et al*. 2009; Zurita 2006). Natural forests can extend their conservation value into other surrounding vegetation types. For example, natural forest patches in the Midlands of KwaZulu-Natal in South Africa shares many arthropod species with grassland (Pryke & Samways 2012). In South Africa, natural forests contain 5.35% of the country's plant species, and some of these species are rare. However, these forests cover only a very small surface area (0.56%) (Hayward *et al*. 2005; Lötter & Beck 2004; Wilson & Downs 2012).

Increase in human population size is a large threat to natural forests. This is due to the fact that more than 1.6 billion people are directly dependent on natural forests for their

survival (Aerts & Honnay 2011). These natural forests are in demand for a number of human activities, including firewood, pasture, and shelter, with many of the remaining forest patches being converted to agricultural landscapes (Islam & Weil 2000; Li *et al*. 2013). Human activities not only affect vegetation cover, but also influence soil structure through increased soil erosion (Li *et al*. 2013).

Natural forests are also threatened by anthropogenic pressures such as habitat fragmentation, which results in numerous forest patches of different sizes (Brockerhoff *et al*. 2008; Daniels *et al*. 2009; Downs & Symes 2004; Echeuerria *et al*. 2007; Eeley *et al*. 1999, 2001; Lawes *et al*. 2000; Uys *et al* 2009). Distances between these forest patches can be progressively increased (Gaspar *et al*. 2008; Mossman *et al*. 2015) because of attrition of remnant patches. Furthermore, plant species diversity is influenced by changes in forest patch size and increased distances between forest patches (Hundera *et al*. 2013b; Lötter & Beck 2004). This is due to limited long-distance seed dispersal abilities of many Afromontane forest tree species (Aerts *et al*. 2006), which negatively influences forest dependant species (Díaz *et al*. 2010; Uys *et al*. 2009). The theory of island biogeography predicts that large patches and patches that are close to other patches support higher animal species richness than small patches and distant patches (MacArthur & Wilson 1967). This is usually associated with close patches being more diverse than distant patches (Fahrig 2003), and this is often attributed to animal limited dispersal abilities, as a result formation of corridors among isolated habitats, has been found to reduce the impacts of habitat fragmentation (Collinge 1996). Furthermore, large patches provide a suitable habitat to a number of different species, as a result of greater variety of soil types and habitat types (Collinge 1996). However, consequences of forest fragmentation lead to small forest patches, which have reduced amount of large canopy trees, resulting in increased wind exposure and increased temperatures (Downs & Symes 2004). For example, reduction of forest patch size, contributes towards the lack of forest interior habitat, while increasing the edge habitat, thus these patches experience environmental conditions that are completely different from those in the original forest patch (Brockerhoff *et al*. 2008; Collinge 1996; Echeuerria *et al*. 2007; Kotze & Lawes 2007; Ries *et al*. 2004). As a result of altered environmental conditions, small patches may experience edge effect, which can contribute towards increased extinction rates of forest specialist species (Collinge 1996; Heliölä *et al*. 2001).

In the KwaZulu-Natal Midlands, South Africa, natural forest patches are naturally surrounded by grassland, and now also by exotic plantations (Wethered & Lawes 2003). Surrounding vegetation is known to play an important role in the conservation of plant and animal diversity of adjacent forest patches (Driscoll *et al*. 2013). For example, there may be presence of edge effects between the contrasting vegetation structure and composition of natural forests and that of the matrix (Harper *et al*. 2005), and intensity of edge effects vary among species, depending on their habitat specialization, with specialized species being more sensitive than generalist species (Peyras *et al*. 2013; Ries *et al*. 2013). These edge effects not only influence faunal movement and species interactions, but they also influence ecosystem structure and functioning, as arthropods play a vital role in many ecosystem processes (Aerts & Honnay 2011; Echeuerria *et al*. 2007; Ries *et al*. 2013; Spector & Ayzama, 2003).

As a result of the matrix impact on natural forest biodiversity, there is now a call for conservation of grassland habitat surrounding Afromontane forest patches, since protection of this habitat will increase native biodiversity (Kotze & Samways 1999a). Furthermore, grassland supports relatively high plant and animal diversity, including many endemic and threatened species (Cremene *et al*. 2005; Lipsey & Hockey 2010). In addition to the conservation value of grassland, natural forest-grassland edges, have edge specialist species, which also increase native biodiversity (Kotze & Samways 2001; Pryke & Samways 2012). However, grassland ecosystems are fire-driven (Bond & Parr 2010), which negatively influences forest patches within this grassland through reduction in forest patch size. In South Africa, grassland ecosystems are largely threatened by being transformed to agricultural lands and exotic plantations (Lipsey & Hockey 2010; Magura 2002; Neke & du Plessis 2004; Pryke & Samways 2003).

Replacement of natural vegetation by exotic plantations is a global threat to native flora and fauna (Murray *et al*. 2009; Zurita *et al*. 2006). This is due to the alteration of microclimatic conditions, vegetation structure and food resources, as plantations provide habitat and resources that are completely different from the original habitat (Le Maitre *et al*. 2002; Murray *et al*. 2009; Zurita *et al*. 2006). Exotic plantations negatively affect forest dependent species, while positively influencing forest generalist, edge and exotic species (Brockerhoff *et al*. 2008; Pryke & Samways 2012; Zurita *et al*. 2006).

Exotic pine plantations, in which many of South African forest patches are embedded, are known to be a major threat to natural forest biodiversity (Dogra *et al*. 2010). Influences of

the surrounding plantation on forest patches are due to changes in biotic and abiotic conditions, which resemble those of the surrounding vegetation at the forest edge (Bieringer & Zulka 2002; Magura 2002; Samways *et al*. 2010). In addition, pine plantations which lack diverse understory vegetation (van der Merwe *et al*. 1996; Sinclair & New 2004), influence epigaeic arthropods that are dependent on ground vegetation and leaf litter deposition (Samways *et al*. 2010; Zou *et al*. 2013). Alteration of natural forests as a result of plantation replacement affect ecosystem processes, through changes in soil acidity, fertility and forest floor turnover rate (Wiezika *et al*. 2007).

Importance of arthropods

Arthropods are an important component of natural biodiversity, they occur in greater abundances and species richness in almost all habitats, from soil to canopy level (Cheli *et al*. 2010; Longcore 2003; Oxbrough *et al*. 2010; Taylor & Doran 2001). Arthropods are important in many ecosystem processes such as influencing soil structure and fertility, pollination, nutrient cycling, decomposition and in food webs acting as herbivores, predators, detritivores and also serve as the main food source for many vertebrates (Cheli *et al*. 2010; Lawes *et al*. 2005; Lencinas *et al*. 2008; Pryke & Samways 2012; Taylor & Doran 2001).

Arthropods are a diverse group that are sensitive to changes in habitat structure and environmental conditions as small habitat changes can have pronounced influence on their ability to survive or reproduce. For example, many epigaeic arthropods rely almost entirely on the resources available within their immediate habitat (Lawes *et al*. 2005; Pryke & Samways 2012). Arthropods are therefore good indicators of ecosystem diversity and heterogeneity (Cheli *et al*. 2010; Lawes *et al*. 2005; Longcore 2003; Pryke & Samways 2012; Uys *et al*. 2010). Furthermore, arthropods are excellent indicators of forest ecosystems, as their response to disturbances also represents responses of other organisms, and therefore indicate the habitat quality of the ecosystem (Langor & Spence 2006; Uys *et al*. 2010). This is due to the fact that arthropods associate strongly with site conditions, because of their limited dispersal abilities, particularly specialist species (Stephens & Wagner 2006; Uys *et al*. 2010). Different arthropod species often have different habitat requirements, and may respond differently to disturbances (Langor & Spence 2006). For example, carabid beetles were found to be indicators of disturbance caused by forest fragmentation, while spiders with high dispersal abilities were uninfluenced by fragmentation, but were rather indicators of forest fires, vegetation development and forest complexity (Maleque *et al*. 2009). However, it

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is important to note that these arthropods may respond differently in another geographical isolated area. As a result Gerlach *et al*. (2013) noted that using multiple arthropod taxonomic groups in conservation studies provide more reliable results than using a narrow range of taxa.

Study area

KwaZulu-Natal province plays a vital role in the conservation of natural forest biodiversity, and it is estimated that approximately one sixth of South Africa's indigenous forests occur in this province (Eeley *et al*. 1999, 2001). However, only 25% of these natural forest patches are in conservation areas of the province, other patches occur in private owned land (Eeley *et al*. 2001). This province is characterized by high annual rainfall, occurring mostly in summer, which is important for the occurrence of natural forests, and temperatures vary between summer and winter seasons (Fairbanks & Benn 2000; Wethered & Lawes 2005). Natural forests in the study area are found in the western half of KwaZulu-Natal, and are associated with the south-east facing slopes of the hills and mountains (Eeley *et al*. 1999, 2001). These natural forest patches are embedded within a matrix of natural grassland, that is deliberately burned annually and this results in a sharp border with the natural forest patches (Wethered & Lawes 2005). Furthermore, natural grassland matrix was previously the dominant vegetation cover surrounding natural forest patches in the province (Wethered & Lawes 2005). However, KwaZulu-Natal province is now largely transformed, resulting in the conversion of natural grassland to agricultural landscapes and/or exotic plantations (Lawes *et al*. 2004). This transformation has led to the reduction of grassland matrix as it is now mostly replaced by exotic plantations (Armstrong 2002; Lawes *et al*. 2004; Wethered & Lawes 2003, 2005). As a result currently, exotic plantations contribute the highest percentage of the total land cover of the region (Pryke & Samways 2012).

Thesis aim, objectives and outline

To conserve arthropods effectively, it is important to first understand how arthropods associate with particular habitats, and how they interact with different vegetation types relative to proximity to similar and different habitat types. This study is not restricted to forest patches, but it incorporates the surrounding vegetation. Results of this work will serve as a guide towards natural forest management in this landscape.

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The overall aim of this study is to determine the state of arthropod diversity in natural forest patches in a timber production landscape in the Midlands of KwaZulu-Natal, South Africa and how best to conserve this diversity. This thesis consists of three data-chapters (Chapters 2-4), which were written as individual manuscripts, as result repetition in these chapters was unavoidable.

As Midlands natural forest patches are embedded within grassland ecosystems, many of these patches are naturally small and distant from each other, due to the effect of natural fires in the grassland matrix. With the theory of island biogeography stating that small and distant forest patches are less species rich than large and close patches (MacArthur & Wilson 1967). In Chapter 2, I aim to test these predictions on epigaeic arthropod species richness and composition in patchy forest remnants within a grassland/forest patch mosaic.

In this landscape, natural forest patches are today surrounded by both grassland and exotic pine plantations, and the effect of the surrounding vegetation on natural forest epigaeic arthropods is unclear. Thus in Chapter 3, I aim to compare arthropod species richness, abundance and composition among natural forest patches, pine plantations and grassland. This chapter also assesses how arthropod assemblages respond to the environmental changes at the boundaries between natural forest patches and the two different types of surrounding vegetation. Based on previous work that open edges have higher edge effects than close edges (Didham & Lawton 1999), I expect greater edge effects between natural forests and grassland, compared to natural forests and pine plantations.

Exotic pine plantations have been previously reported as unsuitable habitat for many epigaeic arthropod species (Baker & Murray 2012; Pryke & Samways 2009; Sinclair & New 2004). Specialist species are known to be highly sensitive to changes in their habitat. However, landscape transformation within the Midlands has led to different vegetation types being in contact with each other, and very little is known about how the different arthropod functional guilds/taxa respond to these vegetation types. Hence, the aim of Chapter 4 is to determine how each arthropod functional guild/taxon (detritivores, predators, herbivores, ants and mites) responds to pine plantations, natural forests and grassland. I also determine how species that commonly occur in the interiors of natural forests, pine plantations and grassland use adjacent habitats. By doing this I will be able to assess whether exotic pine plantations are able to function as habitat extensions of natural forests compared to the natural reference of grassland.

In the final chapter (Chapter 5), I discuss the results obtained throughout the entire study, placing emphasis on the most important results of this study. This chapter also provides some conservation management recommendations in order to improve arthropod conservation within this production landscape, and suggest ways to protect this functionally important component of biodiversity into the future.

Study design

Here I selected forty natural forest patches that had different sizes (27.41-433.80 m) and interpatch distances (42-643.88 m) (Appendix A) in order to address the aims of Chapter 2. In addition, twenty natural forest patches that were adjacent to grassland (ten patches) and pine plantations (ten patches) were also selected, and these patches also varied in size (120.72-451.12 m; Appendix A). To answer questions asked in Chapter 3 and Chapter 4, I used data from the twenty natural forest patches and adjacent habitats. Epigaeic arthropods, which are important in many ecological processes, are often useful indicators for habitat quality assessment, because of their sensitivity to habitat changes, and their response may provide an overview of the how other higher taxa are affected (Gerlach *et al*. 2013). Here these arthropods were sampled in January 2014 and May 2014, using three sampling techniques (active searches, Berlese-Tullgren funnels and pitfall traps), which target different arthropod taxa, and data from the two seasons and techniques were pooled for analyses. There were six arthropod groups sampled: spiders that were identified to genus and species level, beetles identified to family level, ants identified to family and genus where possible, mites, millipedes and cockroaches that were sorted into morphospecies (Appendix B). As a result of taxonomic challenges, analyses were carried out on morphospecies data in of the most sampled arthropods. I opted for this approach as it has been indicated that even though morphospecies approach is not perfect, it can be of great importance towards arthropod conservation (Derraik *et al*. 2002; Gerlach *et al*. 2013; Oliver & Beattie 1996; Samways *et al*. 2010), especially in the absence of taxonomic specialists. Furthermore, after sample sorting into morphospecies, a second person (experienced in that particular taxon) was appointed to validate morphospecies assignment. Prior data analyses for Chapter 4, each species was assigned to a specific functional guild based on their feeding habits (Kwon *et al*. 2013); detritivore (beetles, cockroaches, and millipedes), herbivore (beetles) and predator (spiders and beetles; Appendix B), with the exception of ants and mites which were analysed as generalist taxa due to their complex feeding habits.

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Chapter 2: Conserving a variety of ancient forest patches maintains arthropod diversity

Abstract

Forests are naturally extensive tracts. However, in South Africa natural fires over many millennia have reduced forested areas into small remnants spread throughout a grassland matrix. Small patches, especially distant patches, are generally considered to be adverse for forest specialists, owing to decreased forest interior habitat and increased edge habitat. Here I test this assumption by determining the impact of forest interpatch distance and patch size on epigaeic arthropod diversity in this globally rare vegetation type. Forty patches were selected: ten large (≥100 m diameter) that are distant (>500 m) from other patches, ten large that are close to other patches (<100 m), ten small (≤50 m) that are distant, and ten small-close patches. Each patch had two plots, edge and interior. Arthropods were sampled using pitfall traps, Berlese-Tullgren funnels and active searches. Interiors and edges had similar species richness and composition. Similarly, large and small forest patches supported similar species richness of all taxa, while impact of interpatch distance varied among taxa. Importantly, my results highlighted the importance of both forest patch size and interpatch distance in determining arthropod diversity. Assemblages differed between small-close and large-close patches. Furthermore, large patches supported similar assemblages regardless of interpatch distance. Small-distant and small-close patches housed different beetle and ant composition. I can conclude that large and/or close patches are particularly important for arthropod conservation. Nevertheless, it is also important to conserve a variety of patch sizes at various distances to maximize on overall arthropod composition.

Introduction

According to the theory of island biogeography large patches support greater animal diversity than small patches (Losos & Ricklefs 2010; MacArthur & Wilson 1967). Diversity in large forest patches is mostly dominated by forest specialist species (Soga *et al.* 2013; Yu *et al.* 2014), because these patches are characterized by structurally complex vegetation of mostly shade-tolerant tree and shrub species (Echeverría *et al.* 2007; Jacquemyn *et al.* 2001; Qie *et al.* 2011). However, small patches are characterized by lower structural diversity, and less forest characteristic microclimates e.g. higher temperatures and lower humidity (Bierregaard *et al.* 1992; Gibb & Hochuli 2002; Gove *et al.* 2009; Jokimäki *et al.* 1998). These small patches have proportionately increased edge habitat, which favours more open-habitat species, usually being dominated by shade-intolerant tree and shrub species (Echeverría *et al.* 2007; Heliölä *et al.* 2001). Small patches often lack important factors for forest-associated epigaeic arthropods such as logs and deep leaf litter deposition which serve as refuges and food resources (Gibb *et al.* 2012; Niemelä *et al.* 2007). As a result these small patches have high extinction rates of species requiring habitat features occurring in large patches (Bierregaard *et al.* 1992; Losos & Ricklefs 2010).

Increased interpatch distance is known to significantly influence arthropod movements and diversity, particularly specialist species, because it changes complex vegetation structure to a simpler vegetation structure that have increased edge habitat and altered microclimatic conditions (Bierregaard *et al.* 1992; Losos & Ricklefs 2010). Thus, the theory of island biogeography predicts that distant patches should have lower species richness than close patches (Losos & Ricklefs 2010). However, Fischer *et al.* (2013) have shown that the effect of forest interpatch distance on arthropod diversity differs from one taxon to another depending on their degree of habitat specialisation and traits e.g. hunting strategies and dispersal abilities. As dispersal ability is positively related to animal body size, small animals such as many epigaeic arthropods, are usually negatively affected by increasing forest interpatch distance (Peter *et al.* 2014). In addition, forest specialist arthropod species prefer dense and well connected woody habitats and often have low dispersal abilities, and are sensitive to changes in habitat composition as well as to increased interpatch distance (Fischer *et al.* 2013; Peter *et al.* 2014; Vialatte *et al.* 2010). Increased forest interpatch

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distance decreases arthropod diversity (Brühl *et al*. 2003), as it can lead to changes in gene flow patterns of forest specialist arthropod species and therefore contribute towards specialist extinction (Vandergast & Gillespie 2004). However, distant forest patches may provide a suitable habitat for generalist arthropod species, which have high dispersal abilities (Fischer *et al*. 2013; Vialatte *et al*. 2010).

Arthropods play an important role in many ecosystem processes such as nutrient cycling, decomposition and pollination (Finér *et al*. 2013; Hudewenz *et al*. 2012; Lawes *et al*. 2005). Furthermore, arthropods are also important in food webs as herbivores, omnivores, detritivores and predators, as well as serving as the main food source for many vertebrates (Gerlach *et al*. 2013; Kwon *et al*. 2013; Samways *et al*. 2010). Hence changes in forest patch size and interpatch distance not only influence arthropod assemblages, but also affect interaction between arthropods and other organisms (Gibb & Hochuli 2002; Jokimäki *et al*. 1998). In addition, interaction between arthropod diversity and plant diversity plays a vital role in ecosystem functioning, since plant growth, reproduction and survival often requires arthropods (Peter *et al*. 2014). Arthropods are therefore good indicators of habitat heterogeneity, ecosystem diversity and environmental stressors, as they respond to resources available at point localities (Lawes *et al*. 2005; Pryke & Samways 2012).

Although most of the previous studies on the effect of patch size and interpatch distance on arthropod diversity have supported the theory of island biogeography (Didham *et al*. 1998; Gibb & Hochuli 2002; Kotze & Samways 1999; Soga *et al*. 2013), they also highlighted other important factors that might influence arthropods, such as matrix effects (Prugh *et al*. 2008), and dispersal abilities and feeding habits (Bonte *et al*. 2004; Magura *et al*. 2015). For example arthropods with limited dispersal abilities and specific feeding habits respond negatively to anthropogenic forest fragmentation, while the opposite tends to be true for arthropods with high dispersal abilities and less specific feeding habits (Magura *et al*. 2015). Furthermore, anthropogenic forest fragmentation affects arthropod species as a result of changes in forest patch structure and microclimatic conditions, which are likey to cause edge effects (Murcia 1995). In addition, forest arthropods are negatively affected by reduction of forest patch size, due to low diversity or absence of tree species, variable age classes, large logs and snags, all of which are important for epigaeic arthropod diversity (Maleque *et al*. 2009).

South African ecosystems are largely fire driven (Bond & Parr 2010). Where this occurs in Afromontane grassland, this results in a regular spatial expansion of grassland and concomitant retention and even retraction of natural forests. The result is a globally unusual forest system: a patchy mosaic made up of many small forest patches, which have expanded and contracted over geological time scales (Eeley *et al*. 1999; Kotze & Lawes 2007). These naturally small forest patches are also interesting in that they have had time to undergo ecological relaxation or extinction debt, which is the gradual loss of species from patches due to the metapopulation breakdown, this can be beyond a time scale of recent anthropogenic forest fragmentation and attrition (Hanski 1998; Samways *et al*. 2010). This means that there is the possibility that forest interpatch distance and patch size may result in different arthropod diversity patterns than would be the case with anthropogenic forest fragments.

Here, I aim to determine the impact of natural forest patch size and interpatch distance on epigaeic arthropod diversity in patchy forest remnants within a grassland mosaic. Based on the predictions of the theory of island biogeography (MacArthur & Wilson 1967), I hypothesized that large and close forest patches will have greater species richness than small and distant patches and would also expect species composition to change between patch size and interpatch distance. I will also wish to determine whether large-distant forest patches are as important as large-close forest patches, and also assess the conservation value of small patches. Information from this study will be valuable for managing these remnant forest patches in an environment where transformation of the landscape is taking place mostly by plantation forestry and livestock grazing.

Methods

Study area and sampling design

The study was conducted at Good Hope (29º63S; 29º97E) and Maybole (29º74S; 030º22E) timber production estates, in the Midlands of KwaZulu-Natal, South Africa, and the distance between these two estates is 18 km (Fig. 2.1). Although these are commercial timber plantation areas, >45% of the land surface is left unplanted and is relatively undisturbed natural habitat. This area was chosen as it has a high number of different sized natural forest patches, with varying degrees of interpatch distances, and these forest patches are mostly within a grassland matrix (Fig. 2.2). Afromontane Mistbelt mixed *Podocarpus* forests, which

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occurs in areas with high annual rainfall, dominate this area and are cool, tall forests on well developed and mature soils (Eeley *et al*. 1999; Wethered & Lawes 2005).

Sampling of arthropods was conducted in January 2014 (warm and rainy period) and in May 2014 (cold and dry period), and data for both time periods were combined to increase the number of sampled species. Forty natural forest patches were selected: ten large forest (≥100 m in diameter) patches that are distant (>500 m) from other patches (large-distant patches), ten large patches that are close to other patches (<100 m) (large-close patches), ten small (≤50 m) patches that are distant from other patches (small-distant patches), and ten small patches that are close to other patches (small-close patches) (Fig. 2.1). Within each patch, two plots were established, with one on the patch edge (5 m from edge) and the other in the interior (50 m from edge of large patches or continuous patch size data were used to determine the centre of small patches), giving a total of 80 plots per sampling season. Vegetation surrounding these natural forest patches consists of both grassland and exotic plantations (Fig. 2.1). To get an idea what is found in the natural matrix ten grassland sites were established, these were >50 m from the forest edge. Even though exotic plantations can serve as alternative habitat for some forest species, here they were considered matrix for the natural forest species, as such distant forest patches were patches that were far from natural forest patches only. Furthermore, understanding the effect of different sized forest patches and varying degrees of interpatch distances on epigaeic arthropods is vital as these arthropods have limited dispersal abilities (Uys *et al*. 2009), and are often sensitive to changes in habitat type (Cameron & Leather 2012).

To maximise the range of taxa sampled, three different sampling methods were used: pitfall traps, active searches and Berlese-Tullgren funnels, and for analyses, data from the three techniques were pooled. Pitfall trapping is the most commonly used technique for sampling active epigaeic arthropods (Perner & Schueler 2004; Samways *et al*. 2010). Pitfall traps used here were plastic cups 7.5 cm in diameter and 9.5 cm in depth. At each plot, four pitfall traps that were 2 m apart were quarter filled with 50% ethylene glycol, and sunk so that the rim was flush with the ground surface, and traps were left open in the field for five days. I opted for short, intensive sampling duration (10 days in total per site) because as Duelli *et al*. (1999) suggest, intensive standardized sampling over short periods minimises seasonal effects between sites and results in the same correlative effects as longer, more survey driven sampling. Collected arthropods were preserved in 70% ethyl alcohol.

To collect arthropods that live under stones, among logs and those that avoid pitfall traps, active searches were used (Samways *et al*. 2010), consisting of 20 min of active diurnal searching along a 50 m transect parallel to the forest edge at each plot. Arthropods found on the ground, underneath stones and among logs that serve as refuges for numerous arthropod species (Evans *et al*. 2003) were collected and preserved in 70% ethyl alcohol.

Berlese-Tullgren funnel trapping is commonly used for sampling arthropods that live in leaf litter (Samways *et al*. 2010). This technique is effective as leaf litter arthropods have poor dispersal abilities and are usually restricted to their specific habitats (Uys *et al*. 2009). The method works on the assumption that as the litter is heated and dries out so arthropods will move away from the heat source. This forces arthropods out of the sample and into a collection container. At each plot five litres of leaf litter were collected, and sieved using a bucket covered with a wire mesh (grid size of 4 mm) to remove large debris. Sifted material was transported to the laboratory for arthropod extraction using Berlese-Tullgren funnels. These funnels were 14.5 cm in diameter and 18 cm in height fitted with mesh screens (4 mm grid) on the inside onto which the sifted material containing arthropods were placed. Heat was from a 40 w light bulb above the sample. Glass vials quarter filled with 50% ethylene glycol were attached at the bottom end of each funnel to capture arthropods that moved away from the heat source. Leaf litter samples were left in funnels for two days with continuous heat. Extracted arthropods were washed in water and preserved in 70% ethyl alcohol.

All collected arthropods were sorted into morphospecies and later identified to family, genus and/or species level, where possible. Voucher specimens are housed in the Entomology Museum, Department of Conservation Ecology and Entomology, Stellenbosch University, with the exception of spiders which are housed in the National Collection of Arachnida, National Museum, Pretoria.

Environmental variables (leaf litter deposition, number of logs, and leaf litter moisture content) were measured at each plot during each sampling occasion. Leaf litter deposition was measured using a plastic cup (9.5 cm depth) with centimetre marks, which was inserted into the leaf litter until the soil layer was reached. A plastic cup was used as it can accurately measure leaf litter deposition without including the soil layer, unlike a ruler which can go into the soil layer when inserted into the leaf litter. At each plot, a 50 m transect parallel to the forest edge was established, whereby logs seen within that transect were counted. A log was considered as such if it had a diameter that is equal to or greater than 10 cm (Rabelo et al.

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2004). At each plot leaf litter was collected using a plastic cup (9.5 cm depth), and the wet leaf litter was weighed and later dried at temperatures 40-80°C for a period of 24 hours. Dried leaf litter was weighed and the difference between the wet and the dry leaf litter gave moisture content.

Data analyses

Singletons and doubletons were removed from overall species richness or forest specialist richness analyses, as these may skew the results. Seasonal data were pooled to increase the sample size per sampling unit. Generalized Linear Mixed Models (GLMMs) were calculated using the *MASS* package in R (2015, The R Foundation for Statistical Computing; Venables & Ripley 2002), using the penalized quasilkelihood estimation method and data fitted to a Poisson distribution (Bolker *et al*. 2009). These data were tested for spatial autocorrelation using a semivariogram and found that when including longitude and latitude as a dummy variable as an exponential correlated function improved the semivariogram (Dormann *et al*. 2007). These analyses were done for species richness of each arthropod taxon (ants, spiders, beetles and mites) separately, with the forest interpatch distance, forest patch size, distance from the edge and environmental variables (leaf litter deposition, number of logs and leaf litter moisture content) used to construct a model. To determine interaction between forest patch size, interpatch distance and distance from edge, on species richness forward selection was used. In addition to the overall data, second datasets consisting of only forest associated species were analysed. Species that were found in the interiors of both the natural forests and grassland were considered generalist species here and removed from the overall dataset to create a second dataset termed here 'forest specialist species'. However, these analyses were not carried out on ant data, due to a very small number of forest specialist species (three species), many of the sampled ant species were generalists that occupied the interiors of both grasslands and natural forests.

A Permutational multivariate analysis of variance (PERMANOVA) model, created in PRIMER 6 (2009, PRIMER-E Ltd) was used to determine the response of arthropod assemblage composition. The factors included in the model were forest interpatch distance, forest patch size, distance from the edge and environmental variables (leaf litter deposition, number of logs and leaf litter moisture content) first, and then the interaction between patch

size, interpatch distance and distance from the edge was added to the model. Assemblage composition F- and p- values were calculated using 9999 permutations (Anderson 2006). The weight of common species was reduced using square-root transformation on the data, and analyses were performed using Bray-Curtis similarity measures (Anderson 2001). Differences in assemblage composition across the interaction between forest patch size and interpatch distance were also determined using canonical analysis of principal coordinates (CAP) in PRIMER (Anderson & Willis 2003). These analyses were repeated for each arthropod taxon. A second pairwise PERMANOVA model was created to assess the species composition of natural forest patches (large-close, large-distant, small-close and small-distant) compared to the matrix (grassland) composition. The non-parametric species estimators of Chao2 and Jacknife2 (Hortal *et al*. 2006) were calculated in PRIMER to predict asymptotic species richness. Species accumulation curves were plotted for overall dataset, and for each forest patch category (large-close, large-distant, small-close and small-distant patches).

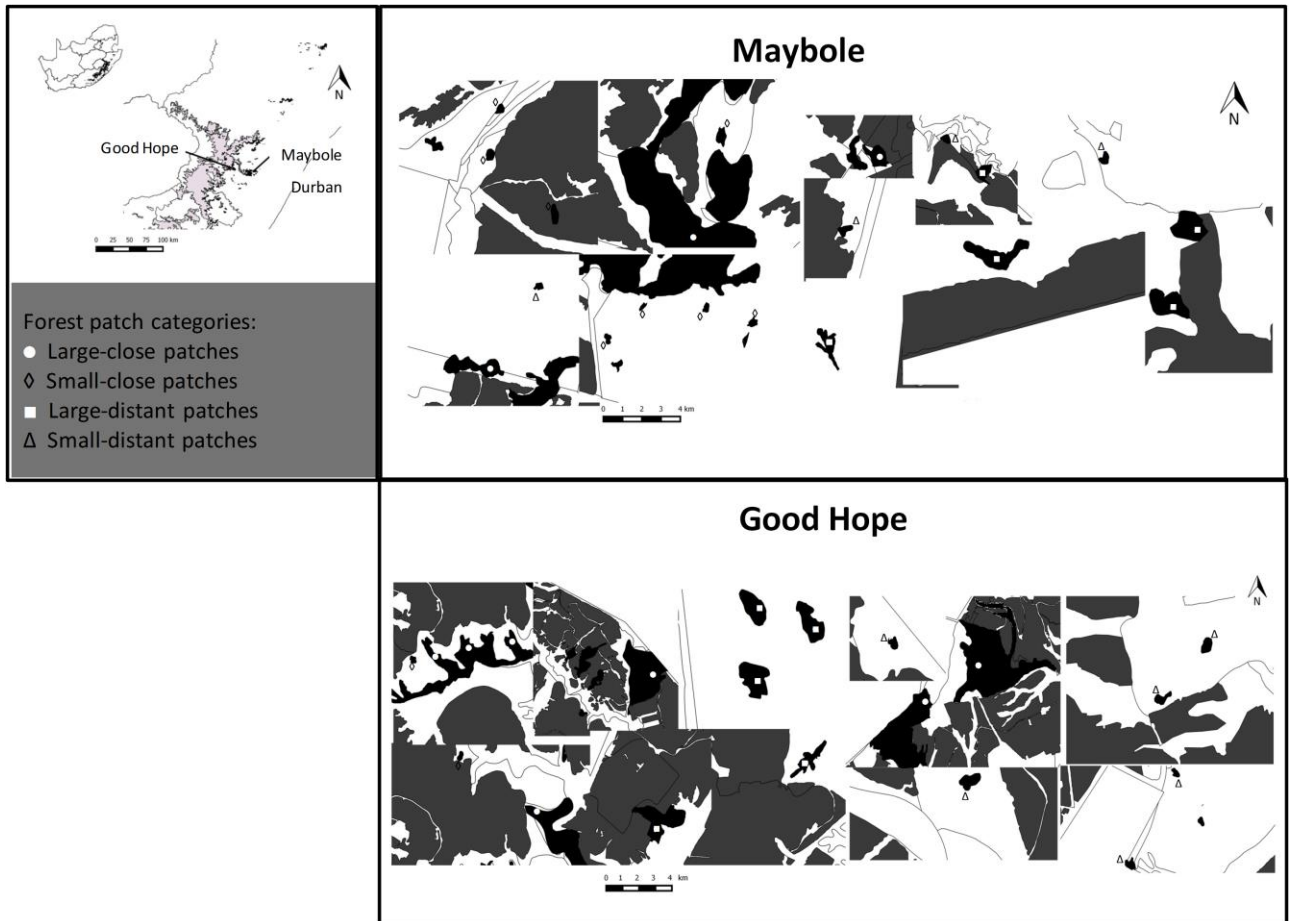**Fig. 2.1** Map of the study sites. The top left map indicates the two plantation estates sampled. The top right map shows natural forest patches sampled in Maybole estate and the bottom map indicates patches sampled in Good Hope estate. Black- natural forests, grey- exotic plantations and white- grassland.

Fig. 2.2 Example of natural forest patches within a grassland matrix sampled here.

Results

A total of 8 002 specimens representing 166 morphospecies of beetles, spiders, ants and mites were collected. Pitfall sampling contributed the highest number (4 569 individuals) of collected individuals, whereas active searches contributed the lowest (558 individuals; Table 2.1). The highest number of individuals captured using pitfall traps was for ants, while the lowest was for mites (Table 2.1). Berlese-Tullgren funnel was the most preferred technique for collecting mites, yet it was unsuitable for sampling spiders, as relatively low number of spider individuals were captured (Table 2.1). However, in the case of active searches, spiders were the most abundant and mites the least abundant (Table 2.1). When data from the three techniques were pooled, ants were the most abundant (2030 individuals) while spiders were the least abundant (712 individuals, Table 2.1). Beetle species richness was the highest recorded (54 morphospecies), while ants were the lowest (25 morphospecies). Overall species estimators indicated similar trends to the observed species richness (Chao2 = 166.35 ± 0.72, Jacknife2 = 159.37; Fig. 2.3). Species accumulation curves of the four natural forest patches were nearly flat, with large-close patches (Choa2 = 144.52 ± 11.27, Jacknifet2 = 163.29), large-distant patches (Choa2 = 145.82 ± 9.82, Jacknife2 =165.87), small-close patches (Choa2 = 199.11 ± 28.68; Jacknife2 = 204.85) and small-distant patches (Choa2 = 164.92 ± 13.70, Jacknife2 = 186.53) (Figs. 2.4).

Overall species and forest specialist species richness of beetles and spiders were uninfluenced by forest patch size, forest interpatch distance, distance from the edge plots, and the interaction between these factors, as well as environmental variables (Tables 2.2-2.3). Overall mite species richness was significantly greater in distant forest patches than close forest patches (Tables 2.2; Fig. 2.5a). However, overall species and forest specialist mite species richness did not differ between large and small patches, and was also uninfluenced by the distance from the edge and environmental variables (Table 2.2). Significantly higher ant richness was recorded in close forest patches than distant forest patches (Table 2.2; Fig. 2.5b). Ant species richness was not influenced by forest patch size, distance from the edge and environmental variables (Table 2.2).

Pairwise comparison showed that none of the natural forest patch types here (different sizes and different interpatch distances) were more or less similar to natural grasslands (Table

2.4). In all arthropod taxa, forest patch size was an important factor structuring arthropod assemblages, with large forest patches supporting species composition that is significantly different from that of small forest patches (Table 2.4). Beetle, spider and ant composition did not differ between distant and close forest patches (Table 2.4). However, forest interpatch distance significantly influenced mite composition, even though p value was closer to 0.05 (Table 2.4). Species composition of all arthropod taxa did not differ significantly between the interior and edge plots (Table 2.4). Interaction between forest patch size and interpatch distance significantly influenced beetle, spider and ant composition (Table 2.4). There were similarities in beetle composition between large forest patches (both distant and close), and between distant forest patches (small and large) (Fig 2.6a). However, beetle composition of large-close patches differed from both small-close and small-distant patches (Fig. 2.6a). Furthermore, small-distant forest patches housed different beetle composition from that of small-close patches (Fig. 2.6a). Beetle composition was significantly influenced by leaf litter moisture content (Table 2.4). Significant differences in spider composition were only detected between large-close and small-close patches (Fig. 2.6b). All measured environmental variables did not influence spider composition (Table 2.4). Similarities in ant species composition were recorded only between large-distant and large-close patches (Fig. 2.6c). Leaf litter deposition and leaf litter moisture content were important variables affecting ant composition (Table 2.4). Interaction between forest patch size and forest interpatch distance did not influence mite composition (Table 2.4; Fig 2.6d). Leaf litter moisture content significantly influenced mite species composition (Table 2.4).

Table 2.1. Number of individuals sampled in each arthropod taxon and sampling technique.

	Pitfall traps	Berlese-Tullgren funnels	Active searches	Overall
Beetles	1302	431	80	1813
Spiders	425	34	253	712
Ants	2484	337	199	3020
Mites	358	2037	26	2457
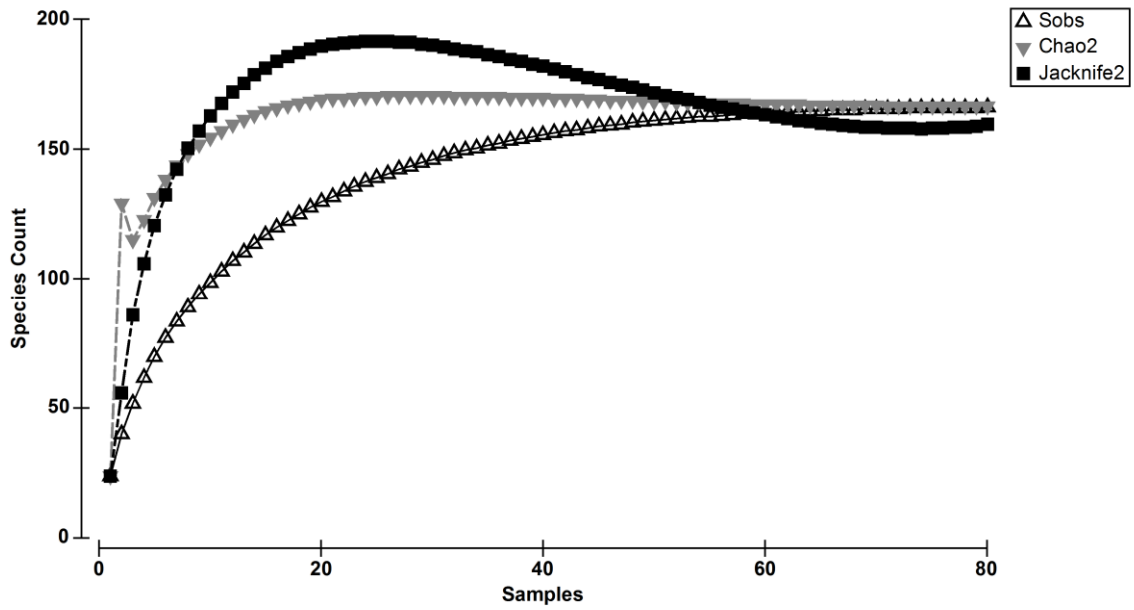
Fig. 2.3 Species accumulation curves for the overall dataset.
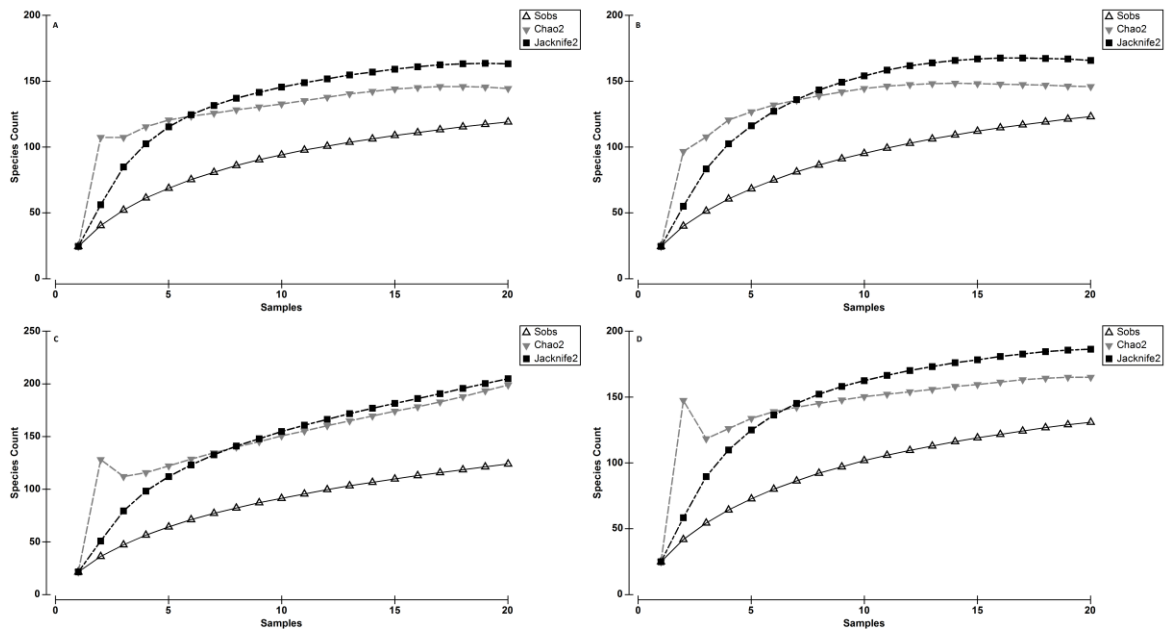
Fig. 2.4 Species accumulation curves for respective forest patch categories (a- large-close, b- large-distant, c- small-close and d- small-distant patches).

Table 2.2. Effect of forest patch size, forest interpatch distance, distance from the edge, the interaction between these factors and environmental variables, on arthropod species richness (overall species). Only significant posthoc tests are shown.

	Beetles				Spiders				Mites				Ants			
	SE	df	t-value	p	SE	df	t-value	p	SE	df	t-value	p	SE	df	t-value	p
Patch size	0.0006	73	0.97	0.33	0.0006	73	0.77	0.44	0.0009	73	0.27	0.78	0.0005	73	0.31	0.76
Forest interpatch distance (FID)	0.0002	73	1.95	0.05	0.0002	73	0.07	0.94	0.0003	73	0.06	0.04 (D > C)	0.0002	73	2.42	0.02 (C > D)
Distance from the edge (DfE)	0.003	73	0.32	0.75	0.003	73	0.23	0.82	0.004	73	1.31	0.19	0.003	73	1.14	0.25
*Patch size*FID*	0.000	73	0.33	0.75	0.000	73	0.57	0.56	0.000	73	1.59	0.11	0.000	73	0.63	0.53
*Patch size*DfE*	0.000	73	1.59	0.11	0.000	73	1.14	0.25	0.002	73	0.66	0.51	0.000	73	0.55	0.58
*FID*DfE*	0.000	73	0.92	0.36	0.000	73	2.01	0.05	0.0006	73	0.09	0.93	0.000	73	1.49	0.14
*Patch size*FID*DfE*	0.000	72	0.39	0.69	0.000	72	0.69	0.48	0.000	72	0.38	0.70	0.000	72	0.60	0.55
Leaf litter deposition	0.03	73	0.73	0.47	0.03	73	1.27	0.21	0.05	73	0.82	0.41	0.03	73	0.75	0.46
Number of logs	0.06	73	0.36	0.72	0.07	73	1.52	0.13	0.09	73	0.49	0.62	0.05	73	1.93	0.06
Leaf litter moisture content	0.04	73	1.45	0.15	0.04	73	0.95	0.34	0.05	73	0.06	0.95	0.04	73	1.92	0.06

Table 2.3. Effect of forest patch size, forest interpatch distance, distance from the edge and the interaction between these factors, on arthropod species richness (forest specialist species).

	Beetles				Spiders				Mites			
	SE	df	t-value	p	SE	df	t-value	p	SE	df	t-value	p
Patch size	0.0006	73	0.42	0.68	0.001	73	0.44	0.65	0.0009	73	0.31	0.75
Forest interpatch distance (FID)	0.0002	73	1.81	0.07	0.0004	73	0.65	0.51	0.0003	73	2.00	0.05
Distance from the edge (DfE)	0.003	73	0.52	0.61	0.005	73	0.49	0.63	0.004	73	1.26	0.21
*Patch size*FID*	0.000	73	0.75	0.45	0.000	73	0.71	0.48	0.000	73	1.10	0.27
*Patch size*DfE*	0.000	73	1.46	0.15	0.000	73	0.06	0.95	0.000	73	1.65	0.10
*FID*DfE*	0.000	73	0.02	0.98	0.0007	73	1.22	0.22	0.000	73	1.06	0.29
*Patch size*FID*DfE*	0.000	72	0.61	0.54	0.000	72	0.24	0.81	0.000	72	0.78	0.44

Table 2.4. Effect of forest patch size, forest interpatch distance, distance from the edge, the interaction between these factors and environmental variables, on assemblage composition (pseudo-F). Only significant posthoc tests are shown, ≠- significantly different.

	Beetles			**Spiders**			**Ants**			**Mites**		
	df	Pseudo-F	p	df	Pseudo-F	p	df	Pseudo-F	p	df	Pseudo-F	p
Patch size	1	3.48	0.0001 (L≠S)	1	1.94	0.03 (L≠S)	1	4.19	0.0008 (L≠S)	1	2.12	0.009 (L≠S)
Forest interpatch distance (FID)	1	1.74	0.05	1	0.68	0.76	1	1.65	0.11	1	1.75	0.04 (C ≠ D)
Distance from the edge (DfE)	1	1.05	0.39	1	0.85	0.59	1	0.69	0.71	1	0.98	0.47
*Patch size*FID*	1	1,76	0.04 (LC ≠ SC, SD & SC ≠ SD, LD)	1	2.36	0.009 (LC ≠ SC)	1	3.09	0.005 (LC ≠ SC, SD; SC ≠ SD, LD & LD ≠ SD)	1	0.81	0.66
*Patch size*DfE*	1	0.63	0.83	1	0.52	0.88	1	0.35	0.95	1	0.69	0.78
*FID*DfE*	1	0.94	0.51	1	0.71	0.72	1	1.09	0.35	1	0.93	0.53
*Patch size*FID*DfE*	1	1.04	0.43	1	1.29	0.23	1	0.62	0.77	1	0.79	0.69
Leaf litter deposition	2	1.39	0.09	2	0.99	0.47	2	2.05	0.009	2	1.20	0.21
Number of logs	1	0.91	0.52	1	0.71	0.69	1	0.87	0.57	1	1.45	0.13
Soil moisture content	2	1.86	0.006	2	1.11	0.33	2	1.70	0.043	2	1.65	0.02

Pairwise comparison of assemblage composition between natural forest patches and grassland

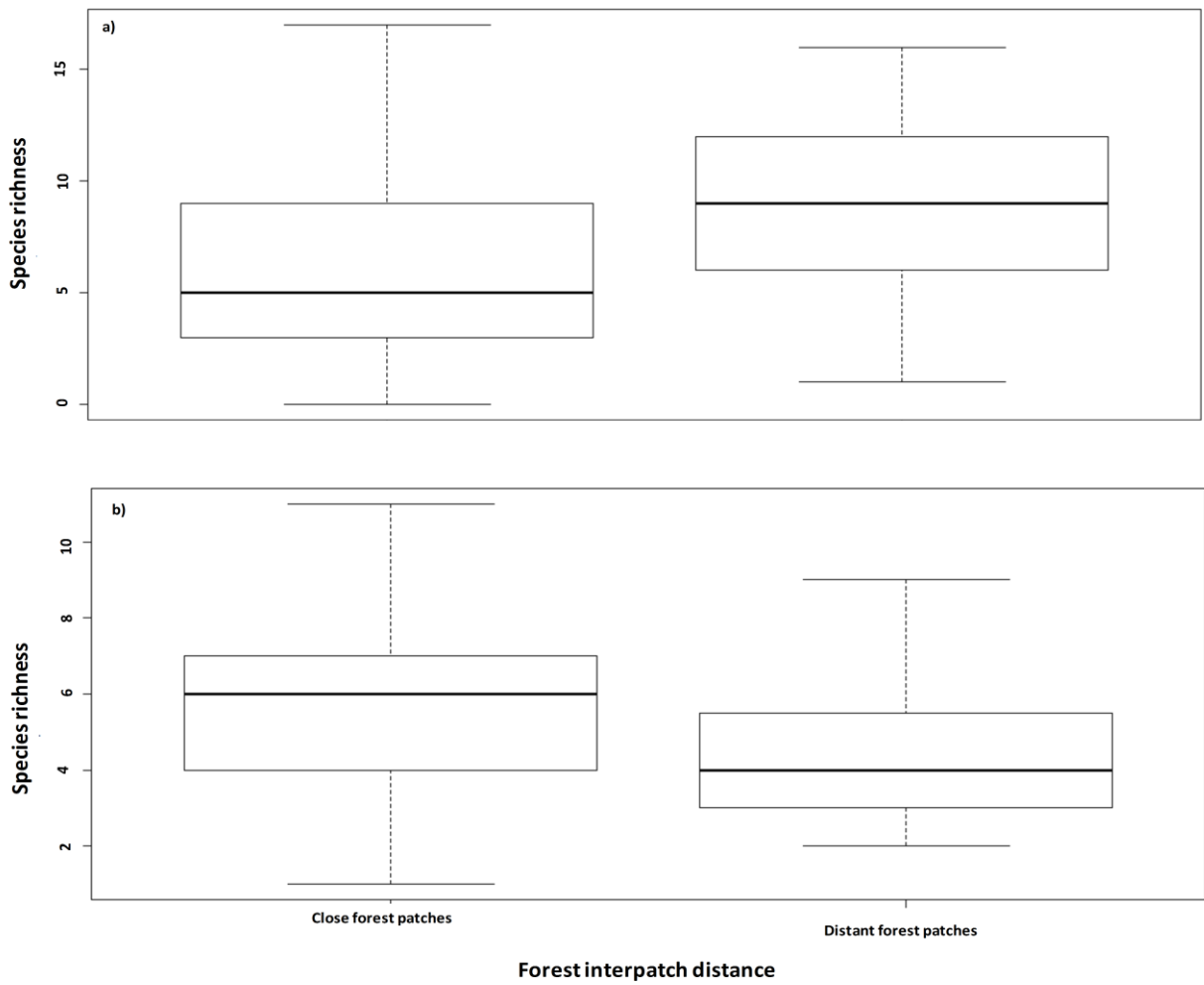|	**Beetles**		**Spiders**		**Ants**		**Mites**	
	t	p	t	p	t	p	t	p
Small-close patches, Grassland	2.52	0.0001	2.09	0.0001	2.38	0.0001	2.06	0.0006
Large-close patches, Grassland	2.98	0.0001	2.29	0.0001	1.84	0.0004	2.31	0.0001
Small-distant patches, Grassland	2.96	0.0001	1.88	0.0003	2.11	0.0001	2.27	0.0003
Large-distant patches, Grassland	2.82	0.0001	2.07	0.0004	1.92	0.005	2.69	0.0003

Fig. 2.5 Effect of forest interpatch distance species richness of (a) mites and (b) ants.
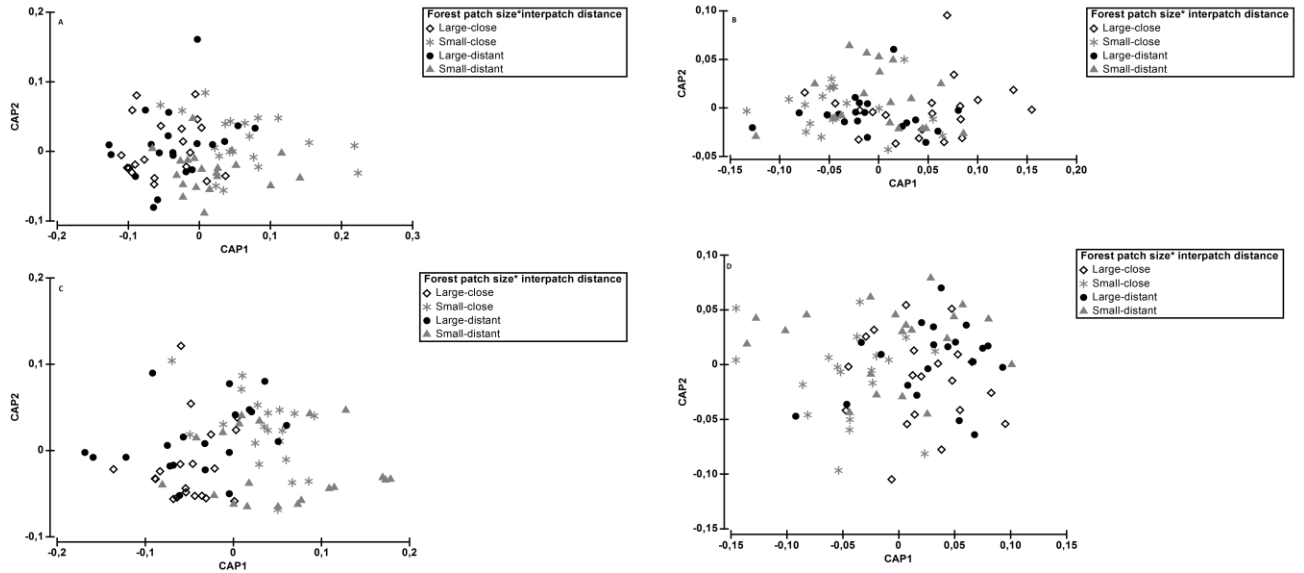
Fig. 2.6 Canonical analysis of principal coordinates of arthropod assemblages (a- beetles, b-spiders, c- ants and d- mites) across the interaction between forest patch size and interpatch distance.

Discussion

This study showed that response of one taxon to forest interpatch distances and forest patch size may not indicate response of other taxa, and this highlights the importance of using a multi-taxon approach. For example, close forest patches provided a suitable habitat for ant species, while they were not suitable for overall mite species, which preferred distant forest patches. Species richness of all taxa did not differ between large and small forest patches, however, when viewing species composition, both forest patch size and interpatch distance were significant factors. My findings further highlighted that large forest patches are vital for arthropod conservation, as large-close patches housed species composition that is similar to that of large-distant patches. I also showed that arthropods sampled here are less sensitive to changes in habitat types, because of the observed similarities in species richness and composition of both overall species and forest specialist species at different distances from the edge (edges and interiors).

Effects of forest patch size and interpatch distance on arthropod species richness

Forest patch size is known to be an important factor in determining species diversity, with the theory of island biogeography stating that large forest patches house greater species richness than small patches (Losos & Ricklefs 2010; MacArthur & Wilson 1967). A number of studies have supported this theory, reporting positive correlation between large forest patches and arthropod diversity (Filgueiras *et al*. 2011; Kotze & Samways 1999; Leal *et al*. 2012; Soga *et al*. 2013), while a negative correlation between large forest patches and ant diversity has also been reported (Gibb & Hochuli 2002; Mitchell *et al*. 2002). However, my findings are contrary to these studies, as I found that species richness of all taxa was uninfluenced by forest patch size, supporting previous studies that large and small patches support similar beetle richness (Araujo *et al*. 2015; Yu *et al*. 2014). Observed similarities in species richness between large and small patches, may be associated with small island effects showing a negative correlation between increase in species richness and increase in forest patch size (Triantis *et al*. 2006). This indicates that decreasing forest patch size do not influence species richness (Burns *et al*. 2009; Triantis *et al*. 2006), species richness is rather maintained in these small patches (Russel *et al*. 2011), as I found unexpectedly higher species richness in these small patches. Furthermore, Sfenthourakis *et al*. (2009) point out that some species are

able to survive in small patches if their habitat requirements are present, as patch size effect vary among taxa.

Possible reasons for the differences between my study and previous ones could be different definitions of large and small forest patches, and different matrix types surrounding these forests. For example, here large forest patches were ≥100 m across and small patches were ≤50 m across, while in another Afromontane grassland/forest mosaic, Kotze & Samways (1999) defined large forest patches as 7-9 ha and small patches as <6 ha. This suggests that when determining the effect of patch size on arthropods, size must be quantified and terms like 'small' and 'large' used only once the sizes have been determined. Natural forest patches here were surrounded by both natural grassland and exotic plantations, which can explain differences between my results and those of Soga *et al*. (2013) on natural forests within a matrix of urbanisation. The effect of reduced patch size on arthropod species richness may therefore be more pronounced when patch reduction/fragmentation is due to harsh land use changes (e.g. urbanisation). For example, in Hungary, high rove beetle species richness was associated with decreasing urbanisation (Magura *et al*. 2013). This may indicate that effects of patch size reduction are less pronounced when changes are comparatively soft (e.g. afforestation with plantation trees), with Oxbrough *et al*. (2012) recording similar arthropod richness in different forest types (both native and plantation).

Predictions of the theory of island biogeography states that close forest patches are species rich than distant forest patches (Laurance 2008). Here this was supported only by ants, which had significantly greater species richness in close forest patches compared to distant forest patches. This shows that even though many of the sampled ant species were generalists, close forest patches are the most preferred habitats. Furthermore, increased forest interpatch distances might cause edge effects, as a result of matrix influences that will negatively influence forest species diversity (Laurance 2008). For instance, greater interpatch distances were reported to reduce diversity of forest associated species as a result of competition for resources between forest species and generalist species from the matrix (Brühl *et al*. 2003; Mäki-Petäys *et al*. 2005). Greater overall mite species richness recorded in distant forest patches than close forest patches, may result from matrix species, since forest specialist species did not differ between distant and close patches. Fujita *et al*. (2008) reported similar results from another taxon (ground beetles), where there was higher ground beetle species richness in forest patches with greater interpatch distances than in the case of

close forest patches. However, for other taxa (beetles and spiders) similarities in species richness were recorded between distant forest patches and close forest patches. These similarities can be associated with high availability of resources in these patches. Additionally, similarities between these forest patches may also be because these patches have been naturally fragmented for a long period, and Losos & Ricklefs (2010) point out, patches that have been distant for a long time, can support similar species richness as close patches. These results support previous work, which found that forest interpatch distance was not an important factor in determining beetle richness (Araujo *et al*. 2015).

Effects of forest patch size and interpatch distance on arthropod assemblage composition

Arthropod assemblage composition of all taxa was significantly influenced by forest patch size, while effect of forest interpatch distance on arthropod assemblages varied among taxa. Dissimilarities in assemblage composition between large and small forest patches, can arise from different vegetation structure and environmental conditions in these patches. For example, two of the measured environmental variables (leaf litter deposition and leaf litter moisture content) here were significant variables influencing beetle, mite and ant composition in these forest patches. Furthermore, small patches usually provide unfavourable habitat for interior associated species, as they most likely lack interior habitat, and they are mainly dominated by edge habitat (Gibb & Hochuli 2002; Soga *et al*. 2013; Vandergast & Gillespie 2004). This can lead to differences in assemblage composition supported by these patches compared to the composition in large forest patches. In addition, my results are similar to previous studies that found differences in arthropod assemblage composition between large and small forest patches (Didham *et al*. 1998; Gibb & Hochuli 2002). However, these results are contrary to those of Yu *et al*. (2014) who recorded similarities in beetle composition between small and large forest patches.

Forest interpatch distance significantly influenced mite assemblage composition, with assemblages in distant patches being different from those in close forest patches, indicating that different species have specific habitat preferences (Díaz-Aguilar *et al*. 2013). These differences might be due to different levels of leaf litter moisture content recorded in each patch. Leaf litter moisture content may influence the forest floor structure, which has been reported to be vital in determining mite communities (Erdmann *et al*. 2012). Furthermore, distant forest patches in Belgium supported lower plant species richness than close forest patches (Jacquemyn *et al*. 2003). Implications of these findings for my study are that

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differences in plant species richness may provide leaf litter layer with different qualities, and this might partly explain dissimilarities recorded here in assemblage composition.

Forest interpatch distance did not independently affect assemblage composition of spiders, beetles and ants. Although these arthropod groups had forest specialist species that often require specific habitat preferences that mainly occur in close forest patches (Fischer *et al*. 2013). Here I show that generalist species response dominates that of specialist species, thus these species are able to occupy different forest patches (Miyashita *et al*. 1998). For example, predatory spiders and carabid beetles, which are mostly generalists are largely influenced by prey availability other than food plants or environmental conditions (Cameron & Leather 2012; Jokimaki *et al*. 1998; Miyashita *et al*. 1998), and some spiders have high dispersal abilities (Cobbold & MacMahon 2012), which can enable them to move from one patch to the other. These similarities may also partly result from the fact that the matrix areas containing plantation trees was not included when defining interpatch distance, with these patches being considered distant only if far from other natural forest patches, with some exotic plantations providing suitable habitat for some forest species (Berndt *et al*. 2008).

Assemblage composition of arthropods (except mites) was affected by an interaction between forest patch size and interpatch distance. Dissimilarities in beetle, ant and spider composition observed between large-close patches and small-close patches can be ascribed to differences in vegetation structure and environmental conditions. Furthermore, small-distant patches supported beetle and ant composition that is different from that of small-close patches. This is reminiscent of the spatial heterogeneity among grassland arthropods in the same region (Pryke & Samways 2015). Furthermore, these forest patches occur in a matrix of mostly grassland, and Blanchet *et al*. (2013) noted that small patches tend to be occupied by generalist or open habitat species from the matrix. However, here both small-distant and small-close forest patches housed assemblage composition that is different from that of the grassland matrix, thus assemblage differences between these patches cannot be linked to matrix effects. In addition, the closeness of small-close patches to other forest patches still results in high species heterogeneity, suggesting differential colonization and establishment in these patches. In terms of conservation, this means that small forest patches (especially close ones) are important in the conservation of arthropods with limited dispersal abilities, as forest arthropods can use these patches as stepping stones, especially from one large patch to another (Godefroid & Koedam 2003). As a consequence I support Blanchet *et al*. (2013) that

to conserve arthropod diversity effectively, forest patches must be large and close to other forest patches.

Even though interaction between forest interpatch distance and forest patch size influenced species composition, no significant differences were detected in arthropod assemblages between large-close patches and large-distant patches, and this emphasises the value of these large patches for arthropod conservation. These similarities can be attributed to the observations of Cook *et al.* (2002) that large-distant forest patches support similar plant species richness with large-close forest patches, and this can result to similarities in arthropod species composition housed by these patches. However, similarities in assemblage composition of spiders, beetles and mites between small-distant patches and large-distant patches may indicate that these forest patches support generalist species from the matrix, which could be detrimental to forest specialists. But I can assume that by now some sort of equilibrium between the two has been established.

Influence of the distance from the edge on arthropod species richness and assemblage composition

Edge and interior plots housed similar species richness and composition of all taxa. Interestingly, these similarities were also observed for forest specialist species, which usually require more stable habitat types, such as interior plots that are structurally complex with high tree species richness and density (Cook *et al*. 2002; Horváth *et al*. 2002; Kacholi 2014). These similarities can be due to edge effects (Laurance 2008), because distance from the edge ranged 5-50 m, leading to species sampled being able to occupy both edge and interior plots (Vandergast & Gillespie 2004).

Conclusions

This study highlights the importance of both forest interpatch distance and forest patch size in the conservation of arthropod diversity. However, effects of these factors vary among arthropod taxa, emphasizing the value of using multi-taxa approach. I found that ant and mite species richness, as well as mite species composition are sensitive to forest interpatch distance, while species richness and composition of other taxa did not differ between close patches and distant patches. Small and large forest patches had similar species richness of all taxa, supporting the existing debate about the conservation of single large or several small (SLOSS) patches (Simberloff & Abele 1982). Interaction between forest interpatch distance

and forest patch size further showed that forest interpatch distance is not important in determining arthropod assemblage composition in large forest patches. However, forest interpatch distance clearly affected beetle and ant composition in small forest patches. Overall, the results emphasize the high conservation value of maintaining a variety of patch sizes at various distances from each other to retain the natural breadth of arthropod diversity.

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Chapter 3: Surrounding vegetation matters for arthropods of small, natural patches of indigenous forests

Abstract

Natural forests are important for terrestrial biodiversity conservation. However, in South Africa, many forest patches are naturally small surrounded by either natural grassland or exotic plantations. Here, I aimed to compare arthropod diversity and composition among natural forest patches, pine plantations and grassland. I also assess how arthropod assemblages respond to the environmental changes at the boundaries between natural forest patches and the two different surrounding vegetation types. Twenty transects were selected, ten natural forests surrounded by pines, and ten natural forests surrounded by natural grassland. Transects ran from natural forest interiors, across the boundary into the interior of the surrounding vegetation. Arthropods were sampled using pitfall traps and active searches. Natural forests surrounded by grassland had higher species richness than those surrounded by pines. Greater arthropod abundance was in grassland edges than edges and interiors of other vegetation types. Pairwise comparisons revealed significant differences in assemblages between all vegetation types. This implies that forest biodiversity in these patches is altered by the main vegetation type in the matrix or in close proximity. Qualitative differences in assemblages between natural forest-grassland boundaries were greater than differences between natural forest-pine boundaries, indicating greater sharing of species between pines and natural forests. My findings emphasize the value of natural forest-grassland edges for conserving arthropod diversity as they add to the local species pool. Overall, I show that when maintaining small isolated natural forest patches, the role of the surrounding vegetation must be considered as it has a major influence on the local patch fauna.

Introduction

Natural forests, which mostly occur in areas of high rainfall, are characterized by structurally complex vegetation (Eeley *et al*. 2001; Fang *et al*. 2014; Joseph *et al*. 2012; Mucina & Rutherford 2006; Robson *et al*. 2009). They also serve as a conservation priority for arthropod biodiversity (Lawes *et al*. 2000). Maleque *et al*. (2009) showed that natural forests are characterized by diverse tree species, have variable age classes, and contain many large logs and snags. As a consequence of this vegetation diversity, natural forests globally may support more than half of the known terrestrial animal, as well as plant, species (Brockerhoff *et al*. 2008).

Forest patches in South Africa are naturally small (usually <1 km^2) (Daniels *et al*. 2009) and are surrounded by grassland or, in recent years, surrounded by commercial plantation vegetation. The influence that the surrounding vegetation has on forest patch biodiversity is either positive or negative depending on the adjacent habitat (Driscoll *et al*. 2013; Kotze & Samways 1999a). Therefore, forest management needs to incorporate the surrounding vegetation within the conservation plan so as to conserve forest biodiversity effectively. The surrounding vegetation can negatively affect forest dependent arthropod species that have limited dispersal abilities, as they require specific forest resources and abiotic factors (Driscoll *et al*. 2013). However, the surrounding vegetation can support some forest species if it is structurally similar to the adjacent forest patch (Driscoll *et al*. 2013; Franklin & Lindenmayer 2009; Ricketts 2001).

In South Africa, natural forests are the smallest land cover type in the country, covering a total area of only about half a percent (Eeley *et al*. 2001), and as elsewhere, contain a relatively high proportion of terrestrial biodiversity (Brockerhoff *et al*. 2008; Eeley *et al*. 2001; Lawes *et al*. 2000). These forests typically make up a patchy landscape of small, dispersed forest patches embedded in a natural fire-driven grassland ecosystem (Bond & Parr 2010; Kotze & Samways 1999a), with anthropogenic attrition of many of the patches (Kotze & Samways 2001), and often surrounded by exotic timber blocks (Wethered & Lawes 2003).

The grassland that surrounds natural forests is important in its own right, especially as it is highly threatened by disturbances such as cattle grazing and frequent fires (Bond & Parr 2010; Kotze & Samways 2001). Activities such as grass cutting and overgrazing can reduce arthropod diversity because of the altered vegetation diversity (Kruess & Tscharntke 2002),

especially as tall grassland supports higher arthropod diversity than short grassland (Morris 2000). In South Africa, grassland mostly occurs in areas with relatively high rainfall and good soils, and often has pockets of natural forests within it (Mucina & Rutherford 2006). Grassland however, is now threatened due to transformation for agriculture and commercial forestry (Neke & du Plessis 2004).

In South Africa and in other parts of the world, blocks of commercial, exotic pine trees (*Pinus* sp.) negatively affect forest biodiversity by replacing native vegetation (Baker & Murray 2012; van Wilgen & Richardson 2012). These blocks are planted in dense stands which change ecosystem structure (Robson *et al*. 2009; Schoeman & Samways 2011). Plantations can also influence soil properties, including soil acidity, fertility and forest floor turnover which then affects the diversity of ground dwelling arthropods (van der Merwe & Africa 1996; Wiezik *et al*. 2007) through sensitivity of arthropods to environmental changes (Pryke & Samways 2012). Many studies have shown that exotic pine blocks support low arthropod diversity compared to natural forests (Brockerhoff *et al*. 2008; Finch 2005; Holmquist *et al*. 2011; Pryke & Samways 2009; Robson *et al*. 2009; Samways *et al*. 1996). Nevertheless, timber plantations can provide valuable habitat for some species (Campbell *et al*. 2011; Brockerhoff *et al*. 2008; Pryke & Samways 2009; Wethered & Lawes 2003), although many of these species are alien, generalists or opportunists (Magoba & Samways 2012; Roets & Pryke 2013; Schoeman & Samways 2011). Furthermore, plantations can negatively affect natural forest specialists such as rare and endemic arthropod species as a result of altered vegetation structure (Taboada *et al*. 2008). This led Oxbrough *et al*. (2005) to encourage establishment of ground vegetation in plantations to enhance arthropod diversity.

Arthropods are an important component of forest biodiversity as they inhabit all local spaces from soil to canopy (Oxbrough *et al*. 2010). They also play an important role in many ecosystem processes, such as nutrient cycling and pollination, while they also serve as a food resources for many vertebrates (Finér *et al*. 2013; Gerlach *et al*. 2013; Hudewenz *et al*. 2012; Lawes *et al*. 2005). Arthropods were used in this study as they are sensitive to environmental changes (Kotze & Samways 2001; Lawes *et al*. 2005; Uys *et al*. 2009), and are easy and cost effective to sample (Gerlach *et al*. 2013; Uehara-Prado *et al*. 2009). Several studies in the KwaZulu-Natal province, South Africa have been conducted on arthropod diversity in these small, sometimes fragmented, forests (Everard *et al*. 1995; Kotze & Lawes 2007; Kotze & Samways 1999a, b, 2001; Lawes *et al*. 2000, 2005; Pryke *et al*. 2013; Uys *et al*. 2009).

However, little is known about the importance of the surrounding vegetation on epigaiec arthropod diversity in these natural forest patches, bearing in mind that adjacent habitats have been recorded to influence arthropod assemblages (Blitzer *et al*. 2012).

Here I aim to compare arthropod (spiders, beetles, mites, ants, millipedes and cockroaches) species richness, abundance and composition among natural forest patches, pine plantations and grassland. I also assess how arthropod assemblages respond to the environmental changes at the boundaries between natural forest patches and the two different surrounding vegetation types making up the matrix. I hypothesized that there will be greater edge effects between grassland and adjacent natural forests than between pine blocks and adjacent forests, because of the observations of Didham & Lawton (1999) that open edges have higher edge effects than closed edges. Understanding the effects of the surrounding vegetation on forest patches will help determine the conservation of these small patches for long term arthropod diversity conservation (Driscoll *et al*. 2013), and how best to design these landscapes for biodiversity conservation in the future.

Methods

Study area

The study was conducted on two estates; Good Hope (29º63S; 29º97E) and Maybole (29º74S; 030º22E), both commercial timber plantations in the Midlands of KwaZulu-Natal, South Africa. In both estates plantation forests cover a high percentage (both pine and eucalypt, even though pines dominate; 52.39% at Good Hope and 59.94% at Maybole) of land cover than natural vegetation (both grassland and natural forests; at 47.61% at Good Hope and 40.06% at Maybole). This area was chosen as it has a high number of natural forest patches that are surrounded either by grassland or pine plantations. Natural forest in the area is dominated by Afromontane Mistbelt mixed *Podocarpus* forest which is characterized as cool, tall forests on well-developed and mature soils (Eeley *et al*. 1999; Wethered & Lawes 2005). These forests are associated with south and south eastern facing slopes on hills and mountains (Eeley *et al*. 1999). Afromontane forests have high annual rainfall which occurs mainly in summer, while temperatures in this region vary moderately between summer and winter (Eeley *et al*. 1999; Mucina & Rutherford 2006; Wethered & Lawes 2005).

Sampling design

Arthropods were sampled in January 2014 and May 2014, these seasons were selected to increase the range of sampled arthropods, and the catches from the two seasons were pooled during data analyses. Twenty sites were selected (Fig. 3.1). Ten were natural forests surrounded by commercial pine blocks, and another ten were natural forests surrounded by grassland, these transects were >400 m away from each other. Sampled natural forest patches were of different sizes, large patches (≥160 m in diameter, 17 patches), and small patches (100-140 m in diameter, three patches; Fig. 3.1). At each site, a transect ran from the natural forest interior, across the forest boundary, and into the interior of the surrounding vegetation. Along each transect four distances from the edge were marked: 50 m from the boundary into the natural forest (forest interior), 5 m into the natural forest (forest edge), 5 m into the surrounding vegetation (matrix edge) and 50 m into the surrounding vegetation (matrix interior). Thus a total of 80 distances from the edge were sampled per sampling season.

Arthropods were sampled using pitfall traps and active searches. These techniques were used as each targets a different group of arthropods. Pitfall trapping is the most commonly used method for sampling active epigaeic arthropods (Perner & Schueler 2004; Samways *et al*. 2010). However, using this technique does not indicate the population density but rather, activity density (Perner & Schueler 2004). Active searches were used for the numerous arthropod species, which live under stones and among logs, and may avoid pitfall traps. Active searching is the preferred technique for collecting arthropods such as millipedes and cockroaches, although favours large bodied arthropods (Samways *et al*. 2010). As each sampling method samples different components of the arthropod diversity, i.e. pitfalls has a bias towards active species and active searches towards large bodied species, these techniques were pooled for data analyses to reduce the biases.

Pitfall traps used here were plastic cups 7.5 cm in diameter and 9.5 cm in depth. At each marked distance from the edge, four pitfall traps, quarter filled with 50% ethylene glycol, were sunk so that the rim was flush with the ground surface, and traps were 2 m apart. Traps were left open in the field for five days. Arthropods from all four pitfall traps were pooled, washed with water and preserved in 70% ethyl alcohol. In addition to pitfalls, at each marked distance from the edge a 50 m transect parallel to the forest edge was established, and 20 min of active diurnal searching was conducted along that transect. Collected arthropods were those seen on

the ground, underneath stones and among logs as they serve as refuges for numerous arthropod species (Evans *et al*., 2003). These arthropods were preserved in 70% ethyl alcohol.

Arthropods were sorted into morphospecies and later identified to family, genus or species where possible. Voucher specimens are housed in the Entomology Museum, Department of Conservation Ecology and Entomology, Stellenbosch University, although spiders are housed in the National Collection of Arachnida, National Museum, Pretoria.

Data analyses

Singletons and doubletons were removed from data analyses, as these may influence the results and arthropods that were used in analyses were spiders, beetles, mites, ants, millipedes and cockroaches. Generalized Linear Mixed Models (GLMMs) were calculated using the *lme4* package in R (2015, The R Foundation for Statistical Computing; Bates 2005). GLMMs were calculated using a Laplace approximation and data fitted to a Poisson distribution (Bolker *et al*. 2009). Models were created for species richness and abundance, and vegetation types (grassland, natural forests adjacent to grassland, pine blocks and natural forests adjacent to pines), distances from the edge and the interaction between these factors were fixed factors, while transects nested within the estate sampled was the random factor. A further set of models that only analysed the forest patches was calculated with forest patch size, surrounding vegetation types (grassland and pine blocks) and the interaction between these factors used as fixed factors and transects nested within the estate sampled was the random factor. χ^2 and p values were provided for the tested parameters. Analyses also showed no over-dispersion of variance for species richness or abundance. Tukey post-hoc tests were performed on significant factors using the *multcomp* package in R (Hothorn *et al*. 2008).

Permutational multivariate analysis of variance (PERMANOVA) in PRIMER 6 (2009, PRIMER-E Ltd) was used to test the effect of vegetation types and distance from the edge (interior and edge) on arthropod assemblage composition, as well as the interaction between these factors. In addition, PERMANOVA was also used to test the effect of forest patch size (large and small), surrounding vegetation types and the interaction between these factors on species composition. F and p values were calculated using 9999 permutations (Anderson 2006). For these analyses, the data were square-root transformed to reduce the weight of common species, and analyses were performed using Bray-Curtis similarity measures (Anderson 2001). Canonical analysis of principal coordinates (CAP) in PRIMER was used to

determine differences in assemblage composition across vegetation types (Anderson & Willis 2003). To investigate patterns of species richness for overall arthropod assemblages sampled, I calculated the non-parametric species estimators of Chao2 and Jacknife2 in PRIMER using 9999 permutations (Hortal *et al*. 2006) for overall data from all vegetation types, as well as for each vegetation type (grassland, natural forests adjacent to grassland, pine blocks and natural forests adjacent to pines).

Different arthropod species require different habitat types (Gallé & Schwéger 2014). It is important to determine which species are indicators of which habitats or shared between habitats, as this can provide valuable information on how natural forest species are affected by the surrounding matrix. As a consequence of this, indicator values (IndVal) that determines which vegetation type a particular species is strongly related to (de Cáceres *et al*. 2010), was calculated using the *indicspecies* package in R (2015, The R Foundation for Statistical Computing; de Cáceres & Legendre 2009). Indicator species were identified based on species abundance and occurrence in a habitat type (Lacasella *et al*. 2015; Samways *et al*. 2010), and significant indicator species had a $p < 0.05$.
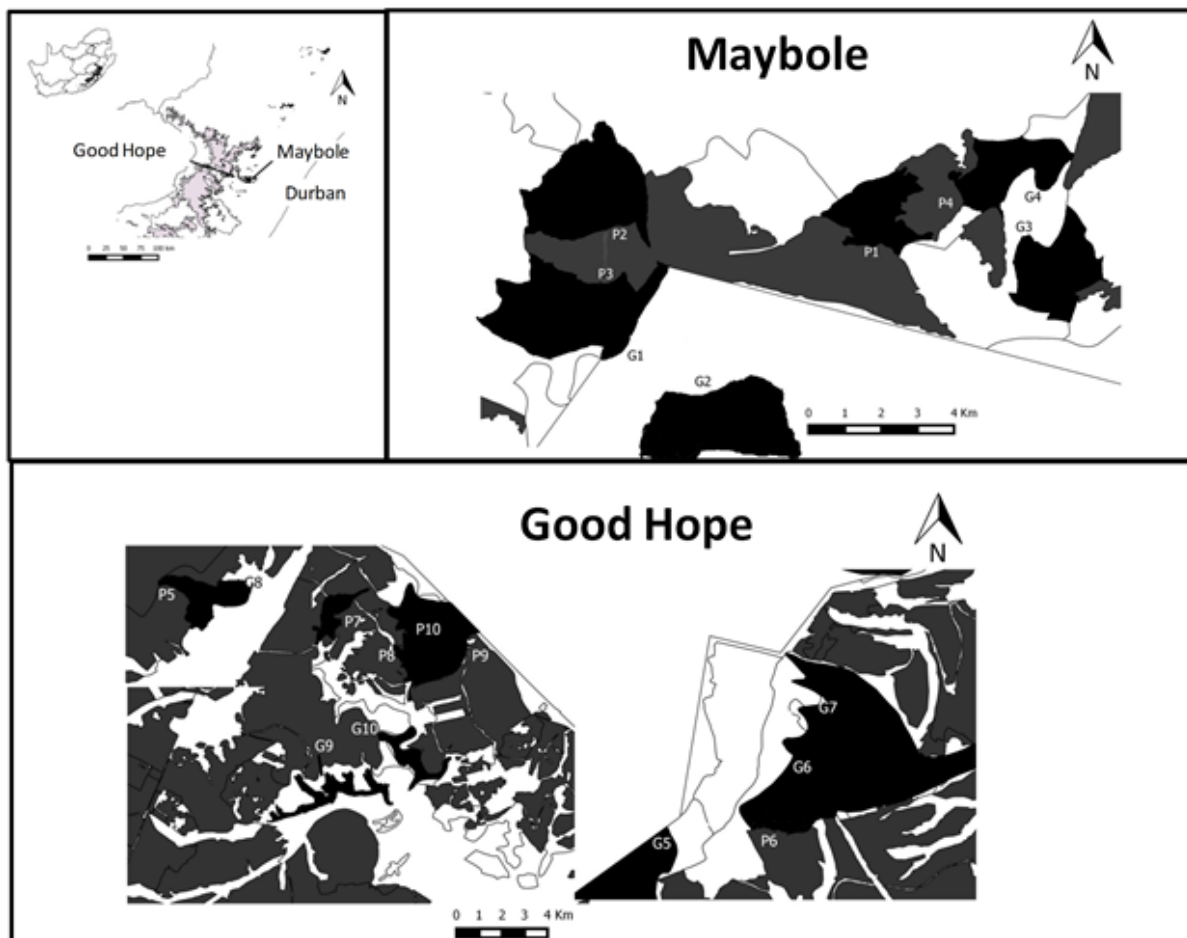
Fig. 3.1 Map indicating the twenty sampled sites. The top left map shows the two plantation estates sampled. The top right map shows the eight sites sampled in Maybole estate, and the bottom map indicates the twelve sites sampled in Good Hope estate, grasslands (*white*), natural forests (*black*) and pine plantations (*grey*).

Results

A total of 4 813 individuals from 122 morphospecies of ants, mites, beetles, spiders, millipedes and cockroaches were collected. The arthropod species accumulation curves reached asymptote, with overall data (Chao2 = 124.91 ± 2.81, Jacknife2 = 127.11), natural forests adjacent to grassland (Chao2 = 104.53 ± 9.00, Jacknife2 = 116.91), grassland (Chao2 = 88.75 ± 8.98, Jacknife2 = 99.91), natural forests adjacent to pines (Chao2 = 94.56 ± 8.48, Jacknife2 = 107.06) and pine blocks (Chao2 = 102.17 ± 14.71, Jacknife2 = 111.87) (Figs. 3.2-3). Grassland had the highest number (32.59%) of sampled arthropod individuals, whereas natural forests adjacent to pines had the lowest (19.78%; Table 3.1). In all vegetation types ants contributed the highest number of collected individuals (Table 3.1). The least abundant taxon in grassland, natural forests adjacent to grassland and those adjacent to pines were cockroaches, while the least abundant taxon in pine blocks were millipedes (Table 3.1). The richest group was beetles, with 43 morphospecies, while millipedes had the lowest species richness (two morphospecies).

Surrounding vegetation significantly affected species richness in natural forests, with natural forests surrounded by grassland being richer than natural forests surrounded by pines (Tables 3.2, Fig. 3.4a). Even though species richness was not independently influenced by distance from the edge, it was significantly influenced by the interaction between vegetation types and distance from the edge, with greater species richness in the edges of natural forests adjacent to grassland than the edges of natural forests adjacent to pines (Fig. 3.4a). Although both forest patch size and the surrounding vegetation types did not influence species richness, interaction between these factors significantly affected species richness, with higher richness in natural forests adjacent grassland (both small and large) than natural forests adjacent to pines (both small and large; Table 3.2). Vegetation types, distance from the edge and the interaction between these factors significantly influenced arthropod abundance (Table 3.2). Overall species abundance was greater in the edges than the interiors (Table 3.2). Arthropod abundance was significantly higher in grassland edges compared to edges and interiors of other vegetation types (Fig. 3.4b). Interiors and edges of natural forests adjacent to pines had the lowest arthropod abundance compared to the interiors and the edges of natural forests adjacent to grassland (Fig. 3.4b). Small natural forest patches had significantly greater arthropod abundance compared to large forest patches (Table 3.2). Higher species abundance was recorded in small natural forest patches adjacent to grassland than large forest patches adjacent to pines (Table 3.2).

Arthropod assemblage composition was significantly influenced by vegetation types (Table 3.2). There were significant differences in arthropod assemblages between all paired vegetation types (the two natural forests were treated as separate vegetation types), even though there were weaker differences between the two natural forests compared to other vegetation types (Table 3.2; Fig. 3.5). Interestingly, there was a large separation between grassland assemblages and assemblages in the adjacent natural forests (Fig. 3.5). Although still significantly different, pine assemblages were grouped closer to those in the adjacent natural forests, indicating a softer edge in the former (Fig. 3.5). Overall assemblage composition between the interiors and the edges did not differ (Table 3.2). Interaction between vegetation types and distance from the edge did not influence species composition (Table 3.2). Assemblage composition was significantly influenced by both forest patch size and the surrounding vegetation types (Table 3.2). However, the interaction between these factors did not influence assemblage composition (Table 3.2).

Indicator value (IndVal) analyses identified three ant species and a weevil as grassland indicators (Table 3.3). Species that frequently occurred in pine blocks were two cockroach species (Table 3.3). Natural forest adjacent to grassland had three mite species and one beetle species, which were indicators of this vegetation type (Table 3.3). However, no sampled species was a unique indicator of natural forests adjacent to pines (Table 3.3). The two natural forests shared two spider and one mite indicator species (Table 3.3). Pine blocks and natural forests adjacent to pines shared a higher number (six) of indicator species, than shared indicators between grassland and natural forests adjacent to grassland (three species; Table 3.3).

Table 3.1 Number of individuals and morphospecies sampled in each arthropod taxon and vegetation type. GF- natural forest adjacent to grassland, G- grassland, PF- natural forest adjacent to pines, P- pine blocks, I- interior, E- edge.

	GF-I	GF-E	G-E	G-I	PF-I	PF-E	P-E	P-I
Ants	249 (13)	309 (14)	679 (23)	611 (23)	195 (13)	282 (12)	311 (15)	289 (14)
Mites	72 (13)	92 (15)	9 (3)	7 (3)	87 (15)	55 (12)	38 (8)	25 (10)
Beetles	202 (19)	129 (27)	77 (19)	67 (19)	111 (20)	100 (19)	109 (20)	128 (17)
Spiders	79 (17)	94 (16)	51 (12)	43 (13)	47 (14)	56 (18)	57 (11)	47 (11)
Cockroaches	1 (1)	2 (2)	2 (1)	0	2 (1)	3 (1)	16 (3)	14 (2)
Millipedes	6 (2)	9 (2)	17 (2)	6 (2)	10 (2)	4 (2)	6 (2)	8 (2)
Overall	609 (65)	635 (76)	835 (60)	734 (60)	452 (65)	500 (64)	537 (59)	511 (56)

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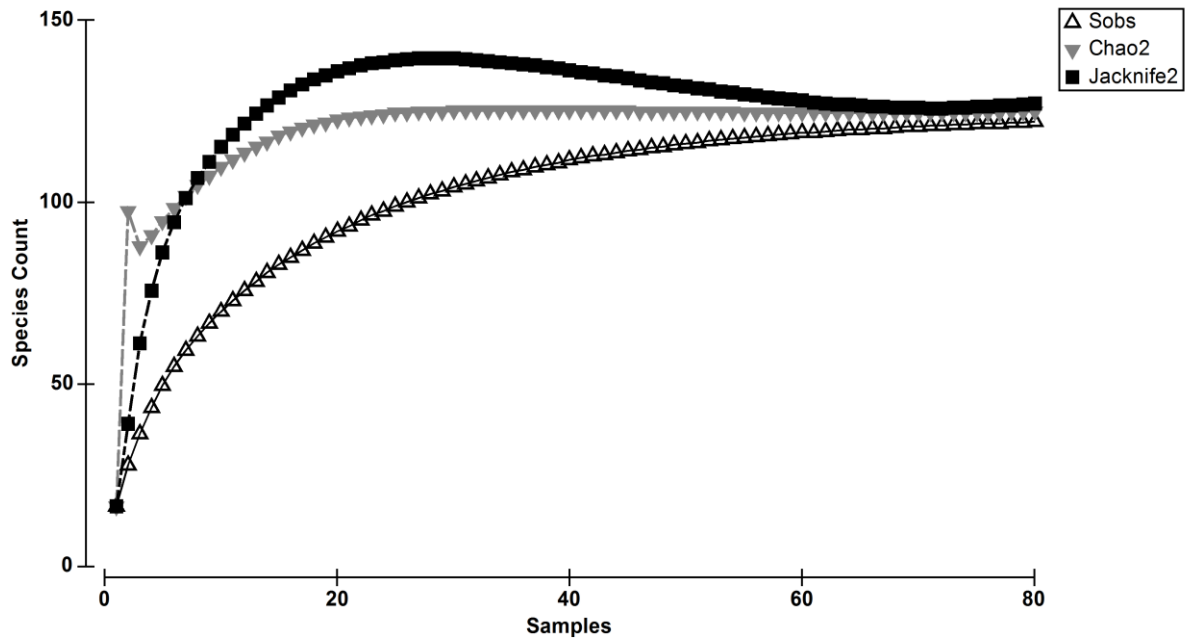
Fig. 3.2 Species accumulation curves for all sampled species.
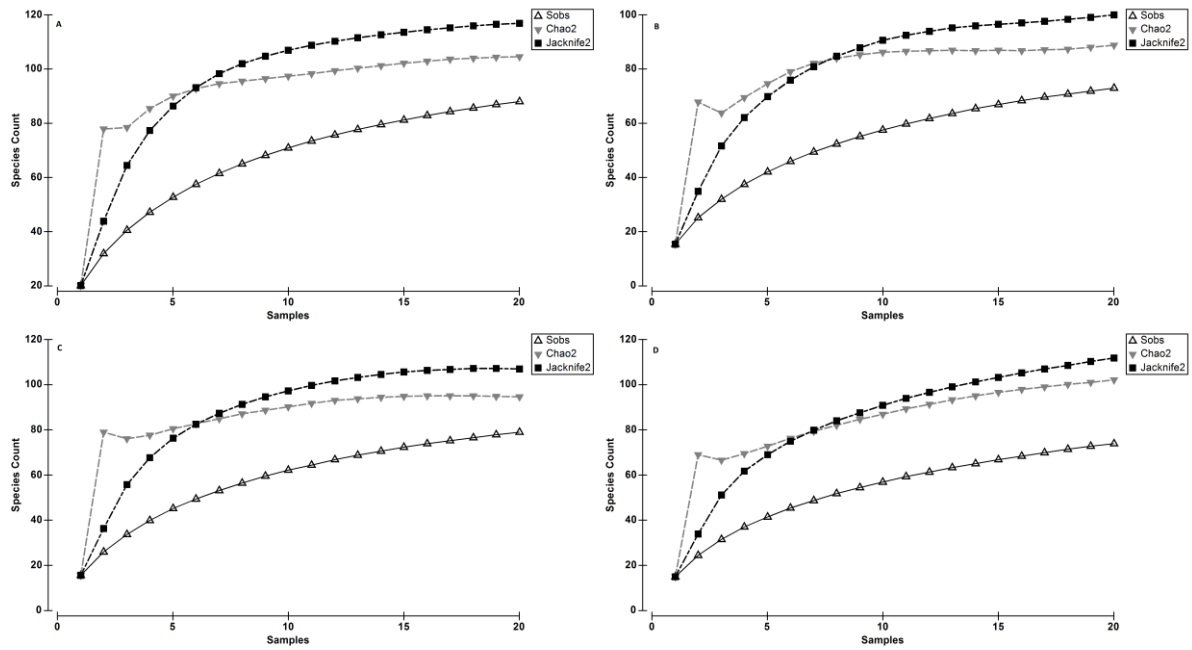
Fig. 3.3 Species accumulation curves for (a) natural forests adjacent to grassland, (b) grassland, (c) natural forests adjacent to pines and (d) pine blocks.

Table 3.2 Effect of vegetation types, distance from the edge (interior/edge) and the interaction between these factors, forest patch size, surrounding vegetation as well as the interaction between factors on species richness, abundance and assemblage composition.

	Species richness			Abundance			Assemblage composition		
	df	χ^2	p	df	χ^2	p	df	Pseudo-F	p
Vegetation types (VT)	3	16.45	0.0009	3	46.58	0.0001	3	5.07	0.0001
Distance from the edge (DE)	1	0.78	0.38	1	8.39	0.004	1	0.93	0.54
VT*DE	7	18.67	0.009	7	56.70	0.0001	3	0.54	0.99
Forest patch size	1	0.25	0.09	1	4.27	0.04	1	1.85	0.02
Surrounding vegetation (SV)	1	7.20	0.07	1	2.46	0.12	1	2.03	0.01
Forest patch size*SV	3	10.85	0.01	3	10.2	0.02	1	1.49	0.07

Pairwise comparison between vegetation types

	SE	z-value	p	SE	z-value	p	t-value		p
Grassland, G-Forest	0.076	3.44	0.003	0.038	6.12	0.0001	2.72		0.0001
G-Forest, P-Forest	0.082	2.89	0.02	0.162	1.77	0.24	1.38		0.01
G-Forest, Pine blocks	0.083	3.41	0.003	0.162	1.18	0.58	2.41		0.0001
Grassland, P-Forest	0.086	0.28	0.99	0.162	3.21	0.004	2.35		0.0001
Grassland, Pine blocks	0.087	0.25	0.99	0.161	2.63	0.03	2.54		0.0001
P-Forest, Pine blocks	0.081	0.57	0.94	0.045	2.15	0.11	1.79		0.0001

Table 3.3 Species with significant indicator values (IndVal) across vegetation types, *** p < 0.001, ** p < 0.01, * p < 0.05. GF- natural forest adjacent to grassland, G- grassland, PF- natural forest adjacent to pines, P- pine blocks, I- interior, E- edge.

	GF-I	GF-E	G-E	G-I	PF-I	PF-E	P-E	P-I
Grassland								
Curculionidae sp. 1 (beetle)			0.53**	0.53**				
Species 3 (ant)			0.59**	0.59**				
Species 4 (ant)			0.83***	0.83***				
Species 5 (ant)				0.46*				
Pine blocks								
Species 1 (cockroach)							0.64***	0.64***
Species 2 (cockroach)							0.47*	0.47*
Natural forest adjacent to grassland								
Species 4 (mite)	0.63**	0.63**						
Species 5 (mite)	0.59**	0.59**						
Species 6 (mite)		0.47*						
Nitidulidae sp. 3 (beetle)	0.67**							
Natural forests adjacent to grassland and those adjacent to pines								
Pachygnatha zappa (spider)	0.49*				0.49*			
Euophrys falciger (spider)	0.71**	071**			0.71**	0.71**		
Species 1 (mite)	0.54*	0.54*			0.54*	0.54*		
Natural forests adjacent to pines and pine blocks								
Carabidae sp. 1 (beetle)					0.73*	0.73*	0.73*	0.73*
Species 2 (mite)					0.67*	0.67*	0.67*	0.67*
Nitidulidae sp. 1 (beetle)					0.86***	0.86***	0.86***	0.86***
Nitidulidae sp. 2 (beetle)					0.67*	0.67		0.67*
Species 3 (mite)					0.58**		0.58**	
Species 1 (ant)						0.73**	0.73**	0.73**
Natural forest adjacent to grassland and grassland								
Allocosa sp. (spider)		0.69**	0.69**	0.69**				
Crematogaster sp. (ant)		0.79***	0.79***					
Species 2 (ant)	0.62*		0.62*	0.62*				
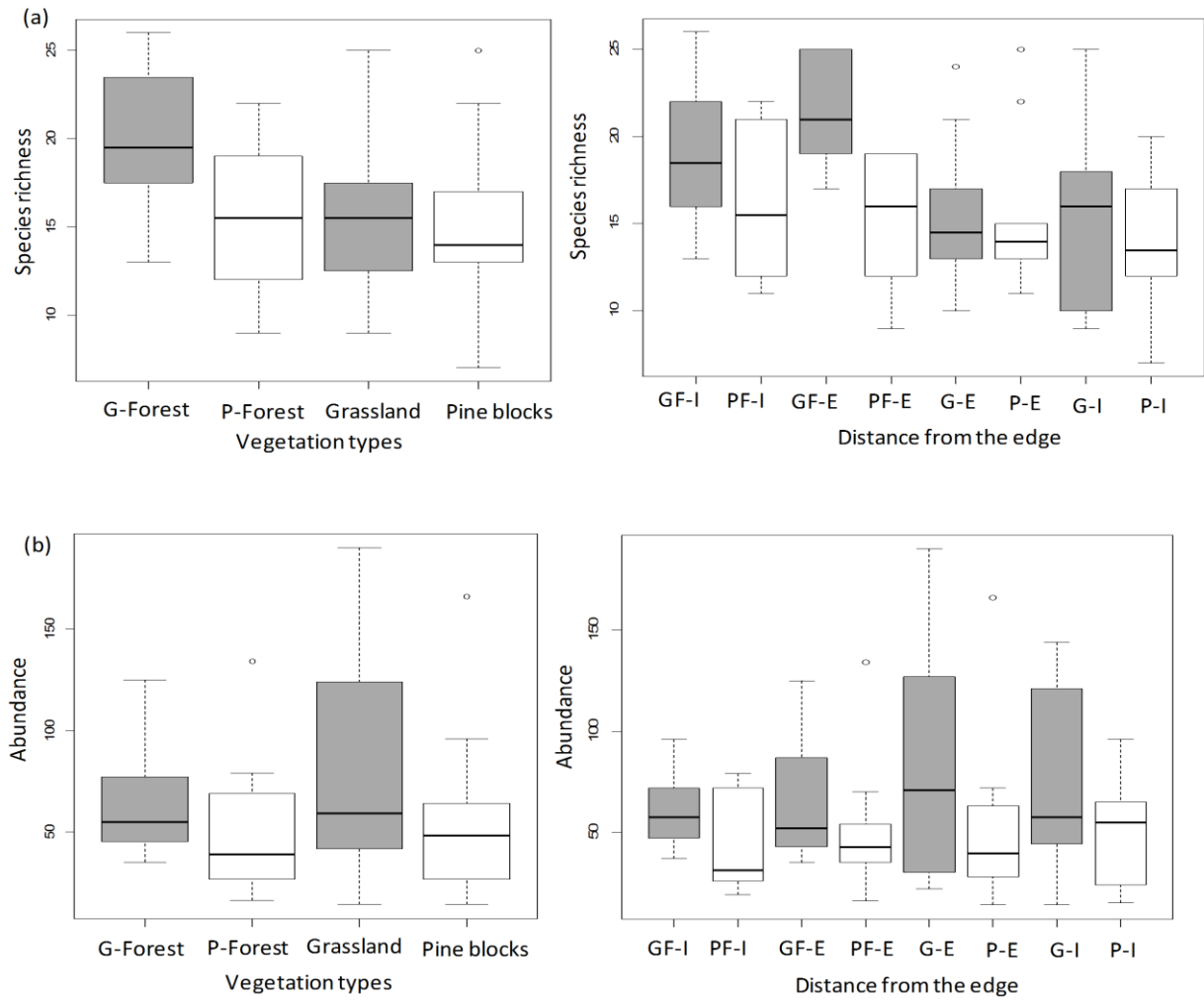
Fig. 3.4 Boxplots showing the effect of forest, matrix and their interaction, as well as the interaction between vegetation types and the distance from the edge on (a) species richness and (b) abundance. G-Forest/GF- natural forest adjacent to grassland, G- grassland, P-Forest/PF- natural forest adjacent to pines, P- pine blocks, I- interior, E- edge.
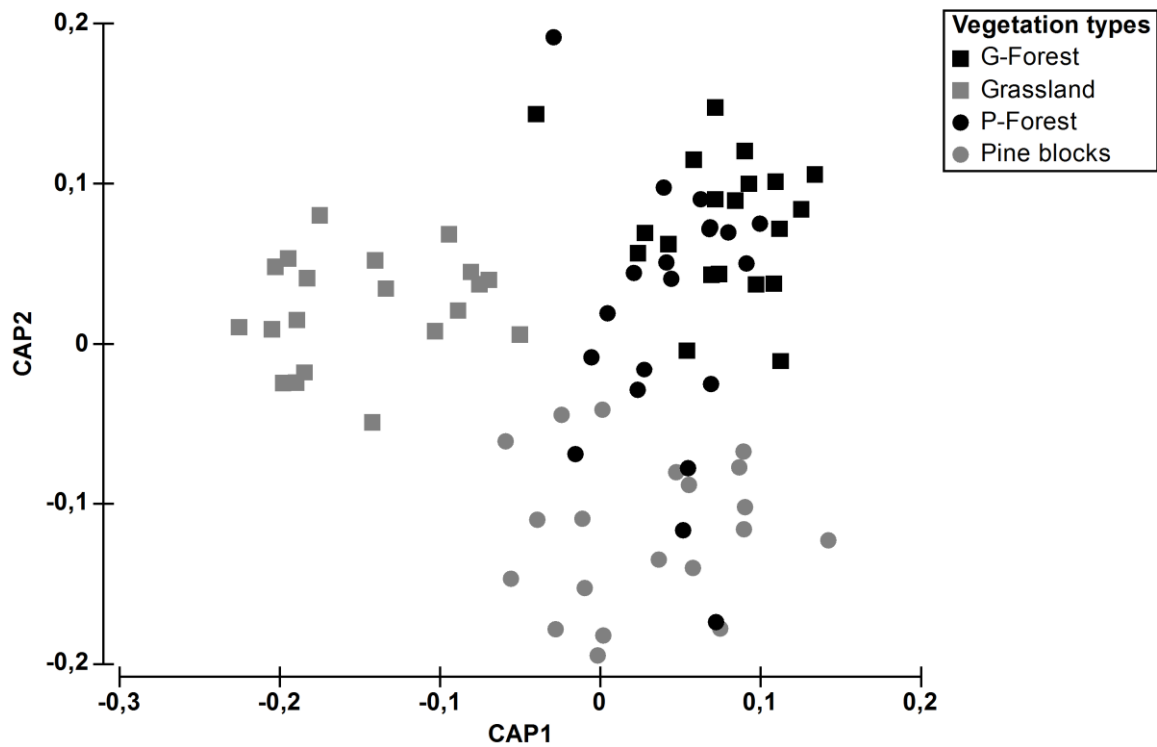
Fig. 3.5 Canonical analysis of principal coordinates (CAP) of arthropod assemblages across different vegetation types. G-Forest- natural forest adjacent to grassland, P-Forest- natural forest adjacent to pines.

Discussion

I found contrasting responses of arthropods to the edges between natural forests and the two different surrounding vegetation types (exotic pines vs. grassland) which made up the matrix. Exotic pine blocks which are structurally similar to natural forests (in terms of canopy vs. that of grassland) distinctly reduced arthropod species richness and abundance in the adjacent natural forests. Furthermore, I found edge effects between pine blocks and adjacent natural forests, with the overlap of assemblage composition between these two vegetation types. This resulted in a significantly different arthropod assemblage composition in natural forests surrounded by pine blocks and natural forests surrounded by grassland. Regardless of assemblage differences between the two natural forests, indicator value (IndVal) showed similarities between these natural forests, as they shared three indicator species (spiders and a mite). This explains the observed overlap of species composition between the two natural forests. However, the surrounding grassland did not influence species diversity of the adjacent natural forests. As a result, natural forests surrounded by grassland supported higher arthropod species richness and abundance than natural forests surrounded by pine blocks. Low diversity in natural forests adjacent to pines was also evident when natural forest patch size was incorporated, with greater diversity in small forest patches adjacent to grassland than large forest patches adjacent to pines.

Higher species richness and abundance recorded here in natural forests adjacent to grassland may be due to the existing positive correlation between forest arthropod diversity and natural forest vegetation (Mgobozi *et al*. 2008). As natural forests are characterized by high habitat quality, unique microclimate, copious leaf litter deposition, and variable plant height, diversity and structure, all of which contribute to rich arthropod assemblages (Christopher & Cameron 2012; Robson *et al*. 2009). Even though these characteristics are also present in natural forests adjacent to pine, their quality might be different from those adjacent to grassland. As Baker & Murray (2012) note that exotic pine blocks may introduce leaf litter that is of low quality into adjacent forests, and exotic plant species provide unfavourable habitat for forest associated arthropods (Mgobozi *et al*. 2008), leading to the diversity decline of those forest species (Gascon *et al*. 1999). I found that response of arthropods to forest-pine boundaries is different from that of forest-grassland boundaries which supported greater arthropod diversity, and this is agreement with previous findings (Ohwaki *et al*. 2015; Pinheiro *et al*. 2010; Tóthmérész *et al*. 2014). Forest edges provide a favourable habitat for natural

forest species, generalist from the matrix and edge species that require variables that occur in both adjacent vegetation types, such as soil moisture, leaf litter deposition, logs and openness (Bogyó *et al*. 2015; Heliölä *et al*. 2001; Magural *et al*. 2002 Pinheiro *et al*. 2010). Here grassland, particularly edges supported higher arthropod abundance than the adjacent natural forests, and this could be because ants are particularly common in these grassland (Kotze & Samways 1999a) and contributed more than half (61%) of the sampled individuals. Additionally, Tóthmérész *et al*. (2014) showed that preference of grassland habitat by arthropods varies among species, and they found higher carabid beetle abundance in grassland than in forests, while the opposite was true for staphylinid beetles.

Here arthropod assemblage composition not only differed between natural forests and the surrounding vegetation (grassland or pine blocks), but even within the natural forests, depending on the vegetation type surrounding the forest patch. This is in contrast to a study by Pryke *et al*. (2013) where there were no significant differences in species richness or assemblage composition of another taxon (dung beetles) between natural forests adjacent to pines and those adjacent to grassland. However, here I included more arthropod taxa and those that appear to be more sensitive in their response to this disturbance, underscoring the importance of multi-taxon studies (Gerlach *et al*. 2013). Sensitivity of arthropods sampled here was also shown, where natural forest patches of different sizes supported different arthopod composition.

Exotic pine plantations support mostly exotic species and generalist species that are able to occupy a variety of habitats, and this may lead to greater edge effects between exotic pine plantations and natural forests (Harper *et al*. 2005). Here this anthropogenic edge clearly affected arthropod assemblages, resulting in the spill-over of arthropod composition between these vegetation types. This may be due to changes in vegetation structure, forest floor, evapotranspiration, nutrient cycling and decomposition (Harper *et al*. 2005; Murcia 1995). Furthermore, this relatively soft edge may also have led to a high number of mite and beetle species that IndVal identified as shared indicators between pine blocks and adjacent natural forests. This indicates that even though exotic pine blocks generally impact negatively on forest arthropods (Pryke & Samways 2009; Robson *et al*. 2009; van der Merwe & Africa 1996), they are able to house some forest species, supporting the findings of Campbell *et al*. (2011) who recorded forest specialist species in pine blocks. However, it is also possible that pine species are using natural forests, and this can be detrimental to natural forest biodiversity,

because some of the pine species might be exotic (Gunther & New 2003) that negatively influence both native plant and arthropod diversity (Hogg & Daane 2015).

Previous studies in South Africa and elsewhere have observed a spill-over of arthropod assemblages between grassland and natural forests (Lacasella *et al*. 2015; Pryke and Samways 2012). However, here I found no edge effect between grassland and adjacent natural forests, with a clear separation of assemblage composition between these vegetation types. This indicates that both natural forest assemblages and grassland assemblages sampled here are sensitive to changes in habitat type. These findings are in agreement with previous work, which found that forests support an arthropod assemblage composition that is significantly different from that in grassland (Bogyó *et al*. 2015; Magura *et al*. 2001; Ohwaki *et al*. 2015; Pinheiro *et al*. 2010; Tóthmérész *et al*. 2014). This emphasises that the quality of forest edges plays an important role in maintenance of arthropod diversity (Molnár *et al*. 2001). Furthermore, forest edges have been found to play a vital role in the conservation of grassland butterfly species (Akeboshi *et al*. 2015), especially in the system I studied here (Pryke & Samways 2001, 2003).

This study supports previous work that to conserve natural forests effectively, the surrounding vegetation needs to be incorporated within the conservation plan (Franklin & Lindenmayer 2009), as I found that the surrounding vegetation significantly influenced natural forest arthropod assemblages, albeit differentially. Natural forests surrounded by grassland conserve arthropod assemblages better than natural forests surrounded by pines, as natural forests surrounded by grassland supported high species diversity. This indicates that the surrounding grassland plays a vital role in maintaining ecological integrity of the adjacent natural forests.

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Chapter 4: Pine plantations as potential range extensions for forest ground-dwelling arthropod functional guilds

Abstract

Natural grassland in South Africa has been extensively replaced by exotic pine plantations, which negatively influence sensitive epigaeic arthropod species. This grassland replacement also influences the patch-matrix dynamics in neighbouring forest patches. In this study, I determine how each arthropod functional guild/taxon (detritivores, predators, herbivores, ants and mites) responds to pine blocks, natural forests and grassland. I also ascertain whether pine blocks act as habitat extensions for natural forest species compared to grassland by assessing how species that commonly occur in the interiors of natural forests, pine blocks and grassland use the adjacent habitat. Arthropods were sampled using pitfall traps and active searches in twenty transects: ten were established from natural forest interiors across the boundary into the interior of the adjacent grassland, while other ten ran from natural forest interior into pine interior. Pine blocks overall had the lowest number of unique species while natural forests had the highest number of unique species. Species richness of all guilds/taxa, with the exception of ants, was higher in natural forest than in grassland. This highlights the complementarity of natural forests and grassland for arthropod conservation. Pine blocks and natural forests supported similar assemblage composition of mites, herbivores and predators. Additionally, arthropod species (except mites) in pine and in natural forest adjacent to pine often spilled over into adjacent habitats. This indicates that even though pine blocks had relatively low species richness of some taxa/guilds, they are being used by certain natural forest species. Thus, these pine blocks are not true extensions of natural forests, although they may be connecting some naturally isolated arthropod populations, which could have important evolutionary consequences. This study illustrates the role of natural forests as important biodiversity refuges, particularly for detritivores and mites within this production landscape. These species often use pine plantations as alternative habitat and may contribute significantly towards ecological processes such as litter decomposition within these altered habitats.

Introduction

Arthropod diversity correlates positively with increased habitat heterogeneity (Borgers *et al*. 2000; Dinnage *et al*. 2012; Jung *et al*. 2014; Lange *et al*. 2014), such as structurally complex natural forests that have small natural features (e.g. logs, snags, coarse woody debris, leaf litter), which have a strong influence on arthropod diversity (Calhoun *et al*. 2014; Hunter 2005; Le Roux *et al*. 2014). For example, heterogeneous leaf litter provides habitat for numerous epigaeic arthropods, as it offers different resources, such as food and nesting sites (Baini *et al*. 2012; de Queiroz *et al*. 2013). In addition, features associated with natural forests play important roles in many ecosystem processes, such as nutrient cycling (Evans *et al*. 2003), and in the maintenance of biodiversity (Calhoun *et al*. 2014; Capps *et al*. 2014).

In South Africa, natural forests often occur within a grassland and/or plantation matrix, and the value of these natural forests in conserving epigaeic arthropods is partly determined by the matrix type surrounding the patch (Chapter 3; Kotze & Samways 1999, 2001). For example, natural forests surrounded by grassland were reported to increase overall arthropod biodiversity, as forest-grassland edges often have arthropod edge specialist species, which add to both grassland specialist and forest specialist assemblages (Chapter 3; Kotze & Samways 2001; Murcia 1995; Pryke & Samways 2012). This is because vegetation at the edges consists of plant species from both adjacent habitats as well as some edge specialists (Kotze & Samways 1999). Furthermore, positive correlation between grassland and arthropod diversity results from high vegetation cover which increases resource availability for arthropods (Ali-Shtayeh *et al*. 2010; Lacasella *et al*. 2015; Morris 2000), while grassland can also serve as an alternative habitat for forest species (Kotze & Samways 1999). However, grassland biodiversity is threatened by disturbances such as grazing by large mammals, fire regimes and establishment of exotic plantations (Ali-Shtayeh *et al*. 2010; Morris 2000). Even though grassland arthropods are mostly opportunistic species, their response to habitat changes such as over grazing by mammals varies between functional guilds (Morris 2000). For example, intensive grazing reduces herbivorous arthropods, while it increases detritivores (e.g. dung beetles), because of the increased food resource (dung) from grazers (Kruess & Tscharntke 2002; Morris 2000). Grassland is also often fire driven, and the effects of fire on arthropods vary among functional guilds (Moranz *et al*. 2013; Morris 2000).

Exotic pine plantations (*Pinus* spp.) globally are a major threat to biodiversity in natural ecosystems (Finch 2005; Murray *et al*. 2009; Robson *et al*. 2009; Pryke & Samways 2009;

Sweaney *et al*. 2015). Pine plantations replace native vegetation, and negatively influence native flora and fauna (Baker & Murray 2012; Moran *et al*. 2000; Pawson *et al*. 2009, 2011; Robson *et al*. 2009) mainly due to loss of native plant and animal species (Finch 2005) and ecosystem homogenisation (Baker & Murray 2012). In addition, the presence of pine leaf litter and needles reduces species richness of native understory vegetation, while increasing richness of exotic plants (Baker & Murray 2012; Sinclair & New 2004). Reduction of understory vegetation is from reduced light penetration from a closed pine canopy, which in turn influences sensitive epigaeic arthropods (Feer 2008; Oxbrough *et al*. 2012; Pryke & Samways 2009; Ratsirarson *et al*. 2002; Robson *et al*. 2009; Yaacobi *et al*. 2007; Uys *et al*. 2009). However, pine plantations in some cases may support high arthropod diversity compared to natural forests, although many of those species are exotic (Berndt *et al*. 2008; Finch 2005; Rastsirarson *et al*. 2002; Yu *et al*. 2014). Presence of pine plantations in natural habitats not only affects native plant and animal species, but also influences ecosystem functioning, which is partly dependent on arthropods that are sensitive to environmental and habitat changes (Baker & Murray 2012; Campos & Hernandez 2013, 2015; Ober & DeGroote 2011; Ratsirarson *et al*. 2002).

Response of epigaeic arthropods to different vegetation types varies among arthropod taxa or functional guilds (Finch 2005; Gerlach *et al*. 2013). This emphasizes the importance of using different arthropod taxa, as generalization based on a single taxon does not indicate the response of the entire arthropod community. Thus, the aim of this study is to determine how each arthropod functional guild/taxon responds to pine blocks, natural forests and grassland. I also determine how species that commonly occur in the interiors of natural forests, pine blocks and grassland use adjacent habitats. By doing this I will be able to assess whether exotic pine blocks are able to function as habitat extensions of natural forests compared to the natural reference of grassland. I hypothesise that exotic pine blocks will negatively affect some arthropods, such as herbivores as they are strongly associated with specific plant species (Debinski *et al*. 2011), and pine blocks will not provide alternative habitat for species normally associated with natural forests, since there is little evolutionary history shared between native arthropods and the exotic plants (Mgobozi *et al*. 2008). Because of taxonomic challenges in the focal area, ants and mites could only sorted into morphospecies, which meant that these two groups had to be analysed as independent taxa and not assigned to any guild, because of their diverse and complex functional roles in ecosystems. For example, ants are vital as predators, herbivores, scavengers and seed

dispersers (Dejean *et al*. 2014; Kwon *et al*. 2014), while mites can act as detritivores, predators or fungivores (Feng *et al*. 2015; Mcmurtry *et al*. 2013).

Methods

Study area and sampling design

In January 2014 and May 2014, sampling was conducted on two timber plantation estates (Good Hope, 29º63S; 29º97E and Maybole, 29º74S; 030º22E) in the Midlands of KwaZulu-Natal, South Africa (Fig. 4.1). In addition to commercial timber plantations dominating this area, historic remnant forest patches (which are classified as Afromontane Mistbelt mixed *Podocarpus* forests (Whetered & Lawes 2005)) and historic grassland are also present in this area. Twenty transects were established: ten were from the interior of the natural forests, across the boundary into the interior of the adjacent grassland, and another ten were from the interior of the natural forests into the interior of the adjacent to pine blocks. Transects were >400 m away from each other to minimize pseudo-replication. Four distances from the edge were marked along each transect: one 50 m from the boundary into the natural forest (forest interior habitat), one 5 m into the natural forest (forest edge habitat), one 5 m into the surrounding habitat (grassland edge or pine block edge habitat) and one 50 m into the surrounding habitat (grassland interior or pine block interior habitat).

Arthropods were sampled using pitfall traps and active searches on two sampling occasions (January 2014 and May 2014). Data from the two sampling occasions and sampling techniques were pooled for analyses. These two sampling techniques were used to increase the range of sampled arthropods, as each targets different arthropod taxa. Pitfall traps are mostly used for sampling active epigaeic arthropods (Perner & Schueler 2004; Samways *et al*. 2010). Active searches mostly target arthropods living under stones and among logs (Perner & Schueler 2004; Samways *et al*. 2010).

Pitfall traps used here were plastic cups 7.5 cm in diameter and 9.5 cm in depth. At each marked distance from the edge, four pitfall traps, quarter filled with 50% ethylene glycol, were sunk so that the rim was flush with the ground surface, and traps were 2 m apart. Traps were left open in the field for a period of five days. Arthropods from all four pitfall traps were pooled, washed with water and preserved in 70% ethyl alcohol. At each marked distance from the edge, 20 min of active diurnal searching was conducted along a 50 m

transect parallel to the forest edge. Collected arthropods were those seen on the ground, underneath stones and among logs. Arthropods were preserved in 70% ethyl alcohol.

Arthropods were sorted into morphospecies and later identified to family, genus or species level where possible. Each morphospecies was also allocated to a broad functional guild: detritivore (beetles and millipedes), herbivore (beetles) and predator (spiders and beetles) (Kwon *et al*. 2013), or analysed as generalist taxa i.e. ants and mites. Voucher specimens are housed in the Entomology Museum, Department of Conservation Ecology and Entomology, Stellenbosch University, with the exception of spiders which are housed in the National Collection of Arachnida, National Museum, Pretoria.

Data analyses

Singletons and doubletons were omitted from the analyses, because these rare species can bias results (Pryke & Samways 2014). To predict asymptotic species richness of the overall data sampled, the non-parametric species estimators of Chao2 and Jacknife2 (Hortal *et al*. 2006) were calculated in PRIMER using 9999 permutations. To determine how each arthropod functional guild/taxon responds to pine blocks, natural forests and grassland, I analysed data only from the interiors of these habitats (>50 m from the edge) to avoid most edge effects. Generalized Linear Mixed Models (GLMMs) were calculated using the *lme4* package in R (2015, The R Foundation for Statistical Computing; Bates 2005), to test the effect of habitat types (pine blocks, natural forests and grassland) on arthropod species richness. Habitat types were used as fixed effects in the model, while commercial plantation estates (Good Hope and Maybole) were used as random effects. Analyses also showed no over-dispersion of variance for species richness of detritivores (Pearson residuals = 1.27), herbivores (Pearson residuals = 0.80), predators (Pearson residuals = 1.21), ants (Pearson residuals = 0.93) and mites (Pearson residuals = 0.76). GLMMs were calculated using a Laplace approximation, and data fitted to a Poisson distribution (Bolker *et al*. 2009), which provided χ^2- and p- values for the tested parameters. The *multcomp* package in R was used to perform Tukey post-hoc tests on significant factors (Hothorn *et al*. 2008). The relative proportion of each functional guild and/or taxon was calculated to assess how they change between vegetation types (pine blocks, grassland and natural forests).

Effect of habitat types on arthropod assemblage composition was tested using Permutational multivariate analysis of variance (PERMANOVA) in PRIMER 6 (2009,

PRIMER-E Ltd). F- and p- values were calculated using 9999 permutations (Anderson 2006). The data were square-root transformed to reduce the weight of common species, and Bray-Curtis similarity measures were used to perform analyses (Anderson 2001). Canonical analysis of principal coordinates (CAP) in PRIMER was also used to detect differences in assemblage composition across habitat types (Anderson & Willis 2003). Analyses were repeated for the different functional guilds (detritivores, herbivores and predators) and taxa (ants and mites). Arthropod community similarities between different habitat types (natural forests, grassland and pine blocks) were determined using the Jaccard index of similarity, [J=C/(A+B-Ć); where C is the number of common species between the two habitats, while A and B represent unique species to each habitat] (Real & Vargas 1996). Similarities between vegetation types were presented using Venn diagrams.

To determine how species that are commonly found in the interiors of natural forests, pine blocks and grassland use the adjacent habitat, I analysed four separate datasets. In each dataset, all the species that were sampled from the interior habitats were selected as representatives for that particular habitat type (excluding singletons and doubletons): 1) Grassland species (GS), which are species commonly associated with interior habitats of grassland; 2) Natural forest adjacent to grassland species (GFS), which are species commonly associated with interiors of these natural forests; 3) Pine species (PS), species commonly associated with interiors of pine blocks; 4) Natural forest adjacent to pine species (FPS), which are species commonly occurring in interiors of these natural forests. GLMMs were used to test the effect of the adjacent habitats on species richness and abundance of species associated with interiors of these various habitats. Commercial plantation estates (Good Hope and Maybole) were used as random effects. GLMMs were calculated using a Laplace approximation, and data fitted to a Poisson distribution (Bolker *et al*. 2009), which provided χ^2- and p- values for the tested parameters. To perform Tukey post-hoc tests on significant factors the *multcomp* package in R was used to (Hothorn *et al*. 2008).
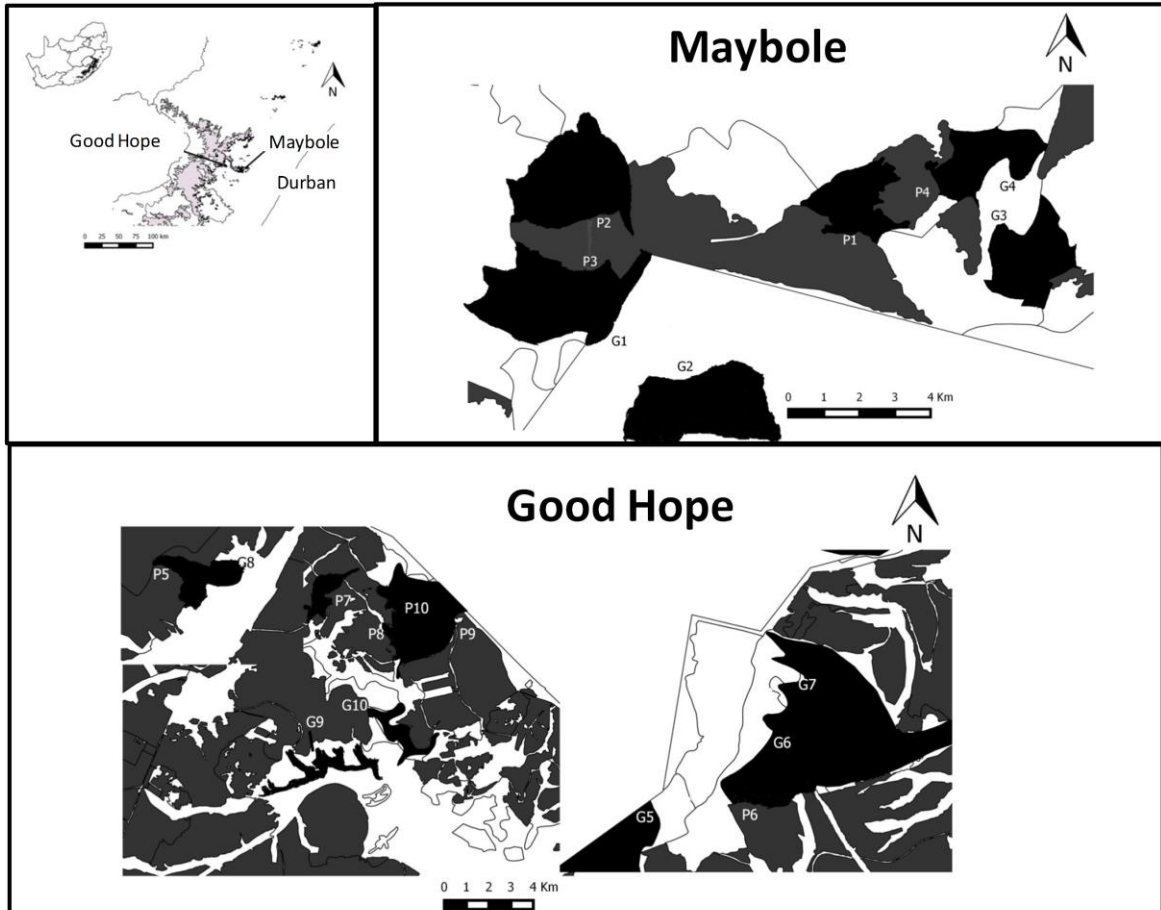
Fig. 4.1 Map indicating the twenty sampled transects. The top left map shows the two plantation estates sampled. The top right map shows the eight transects sampled in Maybole estate, and the bottom map indicates the twelve transects sampled in Good Hope estate, grasslands (*white*), natural forests (*black*) and pine plantations (*grey*).

Results

Overall, 4 605 individuals of 99 morphospecies in the five functional guilds/taxa (predators, ants, detritivores, herbivores and mites) were sampled. Predators were the most species rich functional guild (31 morphospecies), while the least species rich guild were detritivores (10 morphospecies). Species accumulation curves flattened with no major differences between the observed species richness and estimated species richness (Chao2 = 103.17 ± 3.54, Jacknife2 = 107.07).

Response of arthropod functional guilds/taxa to three habitat types (species richness)

Natural forests had the highest number of unique species, while the lowest was recorded in pine blocks (Fig. 4.2). Predators contributed the greatest percentage of unique species in natural forests (Fig. 4.3c). The most species-rich functional guilds/taxa in grassland were herbivores and ants (Figs. 4.3b, d). In pine blocks, unique species belonged to predators (Figs 4.3c). Natural forests and pine blocks shared a high number of mite, predator and detritivore species (Figs. 4.3a, c, e), while the highest number of shared species between natural forests and grassland belonged to detritivores, predators and ants (Figs. 4.3a, c-d). Similarly, numerous predator and ant species were shared between pine blocks and grassland (Figs. 4.3c-d). Ants had the highest number of generalist species (species present in all habitat types), and none of the sampled herbivore species was shared between the three habitat types (Figs. 4.3b, d). Grassland had the highest proportion of ants, while no functional guild/taxon species richness in the natural forests was proportionately larger, compared to other habitat types (Table 4.1). Pine blocks also housed the lowest proportion of herbivore species (Table 4.1).

Detritivore species richness was significantly influenced by habitat type, with higher richness in natural forests and pine blocks, while grassland had the lowest and differed significantly from both pine blocks and natural forests (Tables 4.2-3; Fig. 4.4a). Species richness of herbivores did not differ between grassland and natural forests. However, these natural habitats supported significantly more species than pine blocks (Tables 4.2-3; Fig. 4.4b). Although habitat types significantly influenced predator species richness, posthoc results showed no significant differences between different habitats (Tables 4.2-3; Fig. 4.4c). Grassland had the highest ant richness, while natural forests and pine blocks had similar ant species richness (Tables 4.2-3; Fig. 4.4d). Significantly higher mite species numbers was

recorded in natural forests compared to pine blocks and grassland, which were statistically similar (Tables 4.2-3; Fig. 4.4e).

Response of arthropod functional guilds/taxa to three habitat types (species compositions)

Arthropod assemblage composition of all functional guilds was significantly affected by habitat types (Table 4.2). Detritivore species composition of pine blocks differed significantly from both grassland and natural forests, which supported similar species composition (Tables 4.2-3; Fig. 4.5a). However, the Jaccard index of similarity showed higher similarities of detrivore species between natural forests and pine blocks, than between natural forests and grassland or grassland and pine blocks (Fig. 4.3a). Significant differences in herbivore composition were only detected between grassland and natural forests (Tables 4.2-3; Fig. 4.5b). Grassland predator composition differed significantly from that of both pine blocks and natural forests (Tables 4.2-3; Fig. 4.5c). However, no differences were detected in predator composition between pine blocks and natural forests (Fig. 4.5c). The Jaccard index of similarity showed high sharing of predator species between grassland and pine blocks, between grassland and natural forests, and between natural forests and pine blocks (Fig. 4.3c). Assemblage composition of ants differed significantly between all habitat types. However, there was also sharing of species between all habitat types (Tables 4.2-3; Figs. 4.3d, 4.5d). Assemblage composition of mites did not differ significantly between pine blocks and natural forests (Figs. 4.3e, Fig. 4.5e). However, mite composition of both pine blocks and natural forests were significantly different from grassland composition (Tables 4.2-3; Figs. 4.3e, 4.5e).

Effect of the adjacent habitat on species commonly associated with natural forests, grassland and pine block

Natural forest adjacent to grassland species (GFS) of predators, detritivores and mites were significantly influenced by the adjacent grassland, with the decrease in their richness and abundance from natural forests towards the grassland (Table 4.4; Figs. 4.6-7a, c, e). Although ant GFS richness did not differ between natural forests and the surrounding grassland, species abundance differed, with significantly higher number of individuals in grassland edges (Table 4.4; Figs 4.6-7b). Herbivore GFS richness and abundance was not significantly influenced by the surrounding grassland (Table 4.4; Figs. 4.6-7d). The adjacent natural forest did not influence grassland species (GS) richness of four groups (predators, detritivores, herbivores

and mites) (Table 4.4; Figs. 4.6a, c-e). Interestingly, predator GS abundance was significantly greater in forest edges than grassland interiors (Fig. 4.7a). Grassland had the highest GS abundance of detritiovres and herbivores than the adjacent natural forests (Figs. 4.7 c-d). Ant GS richness and abundance did not differ significantly between the edge and the interior of grassland, and between the edge and the interior of natural forests. However, ant diversity decreased significantly from grassland into the adjacent natural forest (Table 4.4; Figs. 4.6-7b).

There were no significant differences in richness of natural forest adjacent to pine species (PFS) of most functional guilds/taxa from natural forest interiors into pine block interiors (Table 4.4; Figs. 4.6f-i). However, PFS abundance of predators decreased significantly from natural forests into adjacent pine blocks, while ants and detritivores were more abundant in pine blocks than natural forests (Table 4.4; Figs. 4.7f-h). Mite PFS responded negatively into the surrounding pines, with the significant decline in species richness and abundance towards the interiors of the surrounding pines (Table 4.4; Figs. 4.6-7j,). Natural forests adjacent to pines did not influence richness of pine species (PS) (Table 4.4; Figs. 4.6f-j). However, abundance of ant and detritivore PS decreased significantly in adjacent natural forests, while the opposite was observed for mites, which were more abundant in natural forest interiors than in pine interiors (Table 4.4; Figs. 4.7g, h, j).
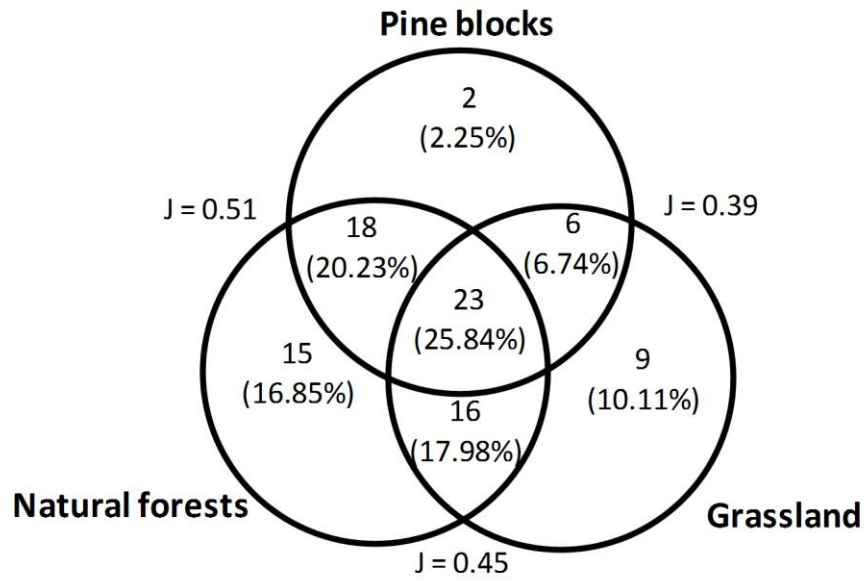
Fig. 4.2 Venn diagram of all sampled arthropod taxa showing the number of species only in pine blocks, natural forests and grassland. J = the Jaccard index of similarity showing similarities between habitat types.
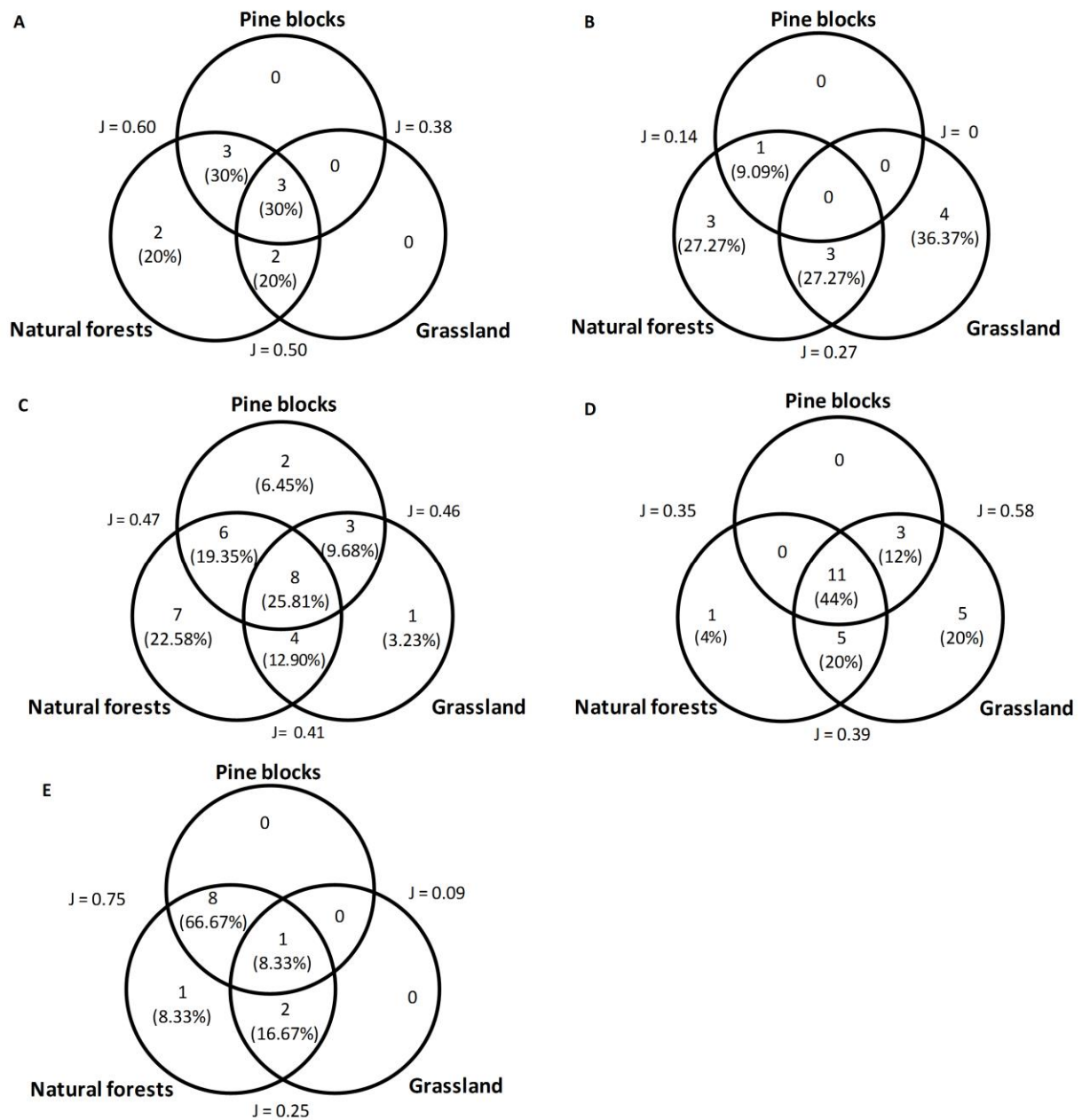
Fig. 4.3 Venn diagrams of shared species of (a) detritivores, (b) herbivores, (c) predators, (d) ants and (e) mites between pine blocks, natural forests and grassland. J = the Jaccard index of similarity showing similarities between habitat types.

Table 4.1 Relative proportion (%) of species richness sampled per habitat type for each functional guild/taxon.

	Natural forest	**Grassland**	**Pine blocks**
Detritivores	10 (13.89%)	5 (9.26%)	6 (12.24%)
Herbivores	8 (11.11%)	6 (11.11%)	1 (2.04%)
Predators	25 (34.72%)	16 (29.63%)	19 (38.78%)
Ants	17 (23.61%)	24 (44.44%)	14 (28.57%)
Mites	12 (16.67%)	3 (5.56%)	9 (18.37%)

Table 4.2 Effect of habitat type on species richness and assemblage composition.

	Species richness			Assemblage composition		
	df	χ^2	p	df	Pseudo-F	p
Detritivores	2	12.00	0.002	2	4.00	0.0001
Herbivores	2	49.28	0.0001	2	1.69	0.02
Predators	2	6.85	0.03	2	2.76	0.0007
Ants	2	21.36	0.0001	2	2.86	0.0005
Mites	2	26.66	0.0001	2	2.22	0.007

Table 4.3 Pairwise comparison of species richness and assemblage composition between the three habitat types.

Species richness	Detritivores			Herbivores			Predators			Ants			Mites		
	SE	z-value	p	SE	z-value	p	SE	z-value	p	SE	z-value	p	SE	z-value	p
Natural forests, grassland	0.41	2.99	0.007	0.39	0.81	0.68	0.19	2.26	0.06	0.15	4.62	0.0001	0.46	0.35	0.0003
Pine blocks, grassland	0.44	2.39	0.04	1.05	2.09	0.08	0.22	0.45	0.89	0.18	2.90	0.01	0.52	1.98	0.11
Pine blocks, natural forest	0.27	0.60	0.81	1.02	2.47	0.03	0.18	1.79	0.17	0.18	1.11	0.51	0.29	2.56	0.03
Species composition															
	t-value	p		t-value	p		t-value	p		t-value	p		t-value	p	
Natural forests, grassland	1.43	0.05		1.51	0.02		2.05	0.0003		1.72	0.006		1.73	0.009	
Pine blocks, grassland	2.65	0.0004		1.36	0.40		1.66	0.009		1.59	0.01		1.56	0.02	
Pine blocks, natural forest	2.22	0.001		1.00	0.54		1.24	0.14		1.73	0.006		1.25	0.15	

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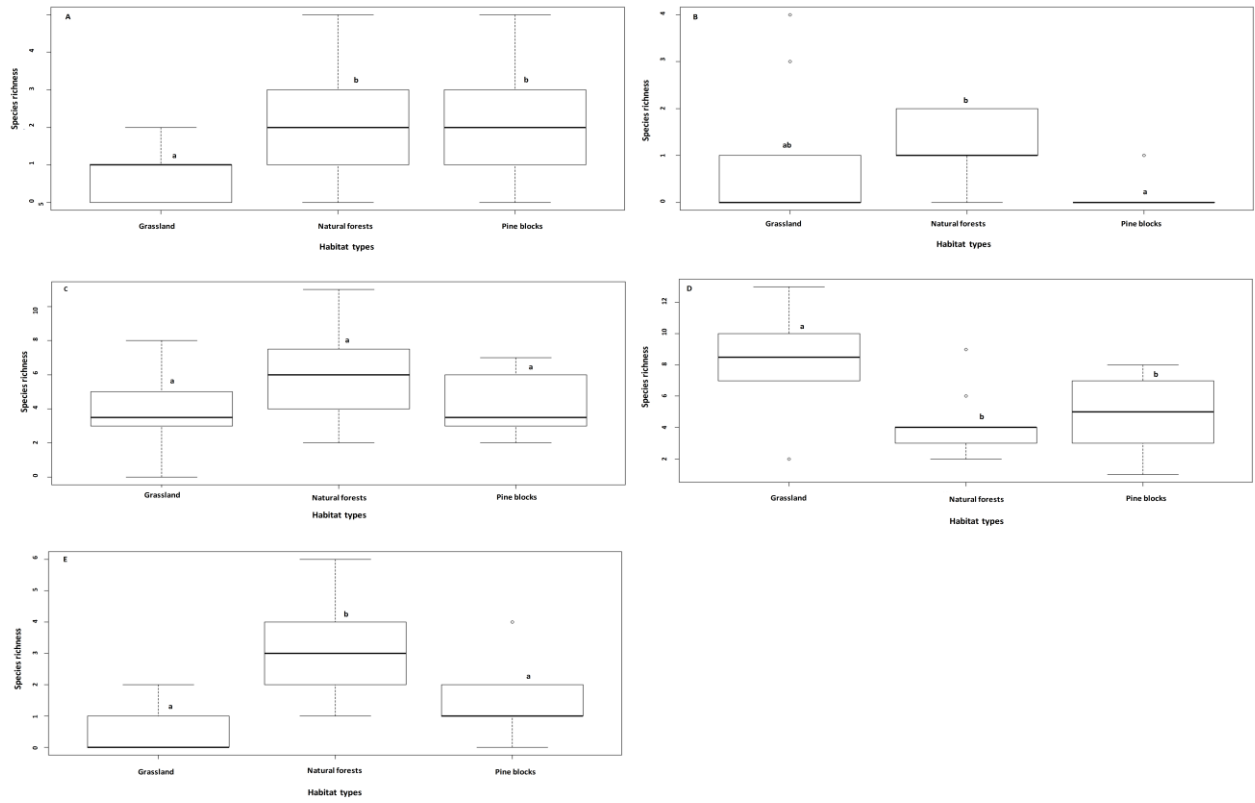
Fig. 4.4 Effect of habitat type on species richness of (a) detritivores, (b) herbivores, (c) predators, (d) ants and (e) mites. Similar letters are not significantly different at p < 0.05.
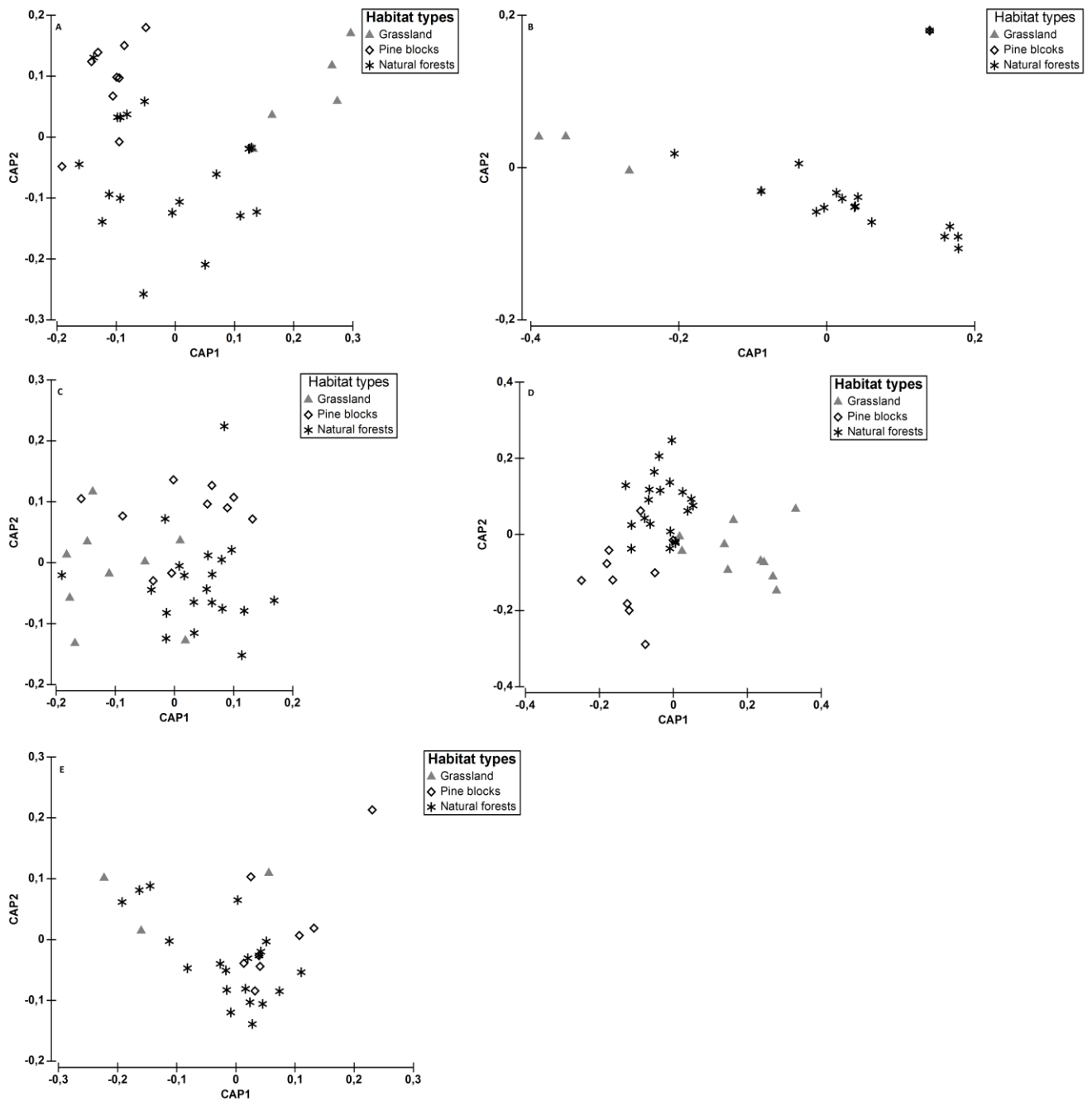
Fig. 4.5 Effect of habitat type on species composition of (a) detritivores, (b) herbivores, (c) predators, (d) ants and (e) mites.

Table 4.4 Effect of the adjacent habitats on richness and abundance of species commonly associated with grassland, natural forests adjacent to grassland, pine blocks and natural forests adjacent to pines.

	Species richness			Abundance			Species richness			Abundance		
	df	χ^2	p	df	χ^2	p	df	χ^2	P	Df	χ^2	p
Natural forests adjacent to grassland							**Grassland**					
Predators	3	29.86	0.0001	3	81.43	0.0001	3	0.77	0.86	3	9.37	0.02
Ants	3	0.28	0.96	3	76.26	0.0001	3	18.78	0.0003	3	280.27	0.0001
Detritivores	3	31.03	0.0001	3	196.84	0.0001	3	1.62	0.65	3	20.01	0.0002
Herbivores	3	1.73	0.63	3	3.08	0.38	3	5.57	0.13	3	23.61	0.0001
Mites	3	48.57	0.0001	3	135.43	0.0001	3	0.29	0.96	3	4.02	0.26
Natural forests adjacent to pines							**Pine blocks**					
Predators	3	2.58	0.46	3	19.97	0.0002	3	0.59	0.89	3	0.97	0.81
Ants	3	0.07	0.99	3	20.33	0.0001	3	2.36	0.50	3	54.57	0.0001
Detritivores	3	0.95	0.81	3	23.17	0.0001	3	0.33	0.95	3	22.84	0.0001
Herbivores	3	8.26	0.04	3	8.26	0.04	0	0	0	0	0	0
Mites	3	12.96	0.005	3	48.27	0.0001	3	1.81	0.61	3	10.76	0.01

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Fig. 4.6 Number of grassland species (*dotted line and the left axis*) and natural forest adjacent to grassland species (*solid line and the right axis*) (a- predators, b- ants, c- detritivores, d- herbivores, e- mites) across different distances from the edge. Number of pine species (*dotted line and the left axis*) and natural forest adjacent to pine species (*solid line and the right axis*) (f- predators, g- ants, h- detritivores, i- herbivores, j- mites) across different distances from the edge. G- grassland, P- pine blocks and F- natural forests.

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Fig. 4.7 Abundance of grassland species (*dotted line and the left axis*) and natural forest adjacent to grassland species (*solid line and the right axis*) (a- predators, b- ants, c- detritiv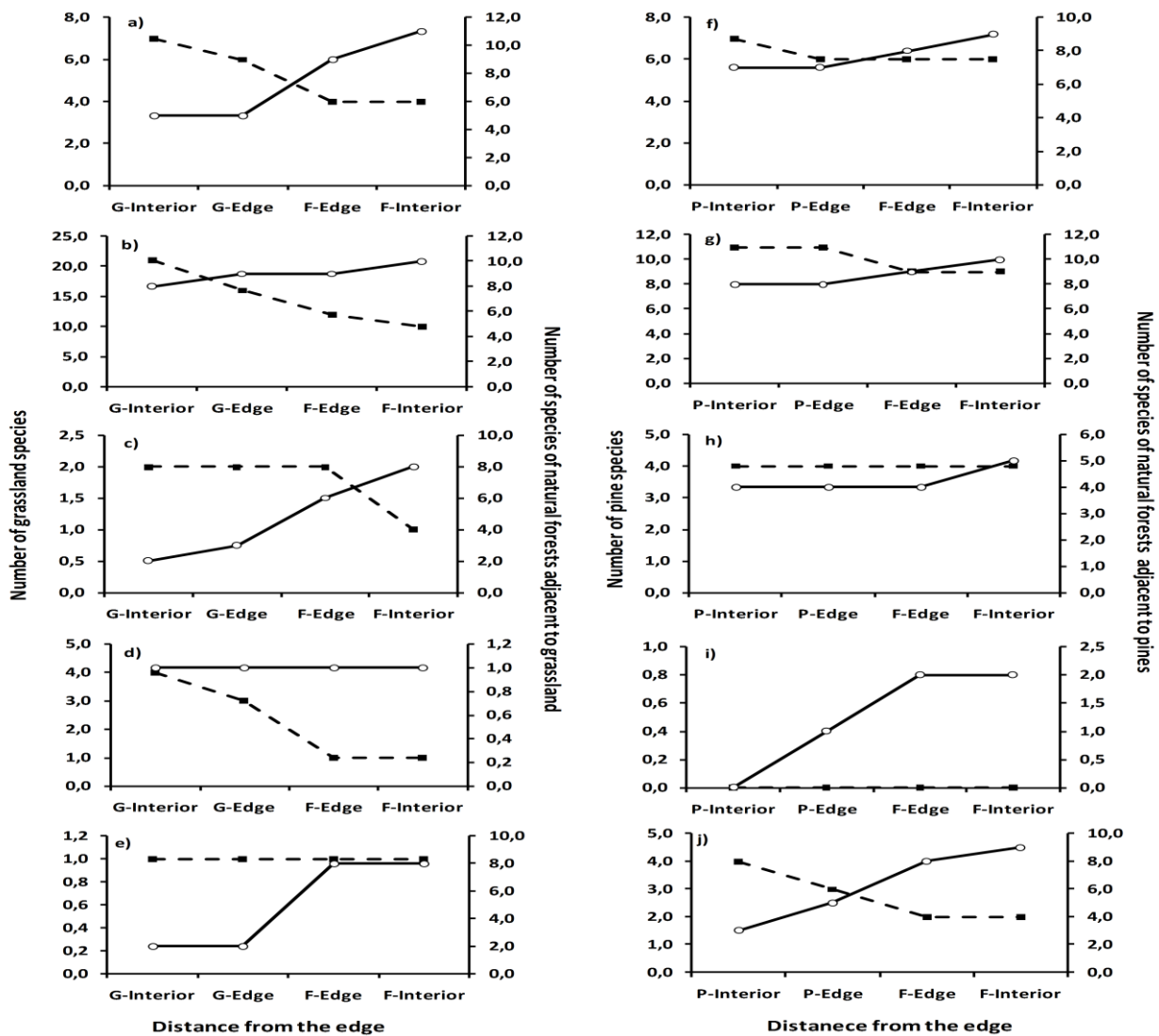ores, d- herbivores, e- mites) across different distances from the edge. Abundance of pine species (*dotted line and the left axis*) and natural forest adjacent to pine species (*solid line and the right axis*) (f- predators, g- ants, h- detritivores, i- herbivores, j- mites) across different distances from the edge. G- grassland, P- pine blocks and F- natural forests.
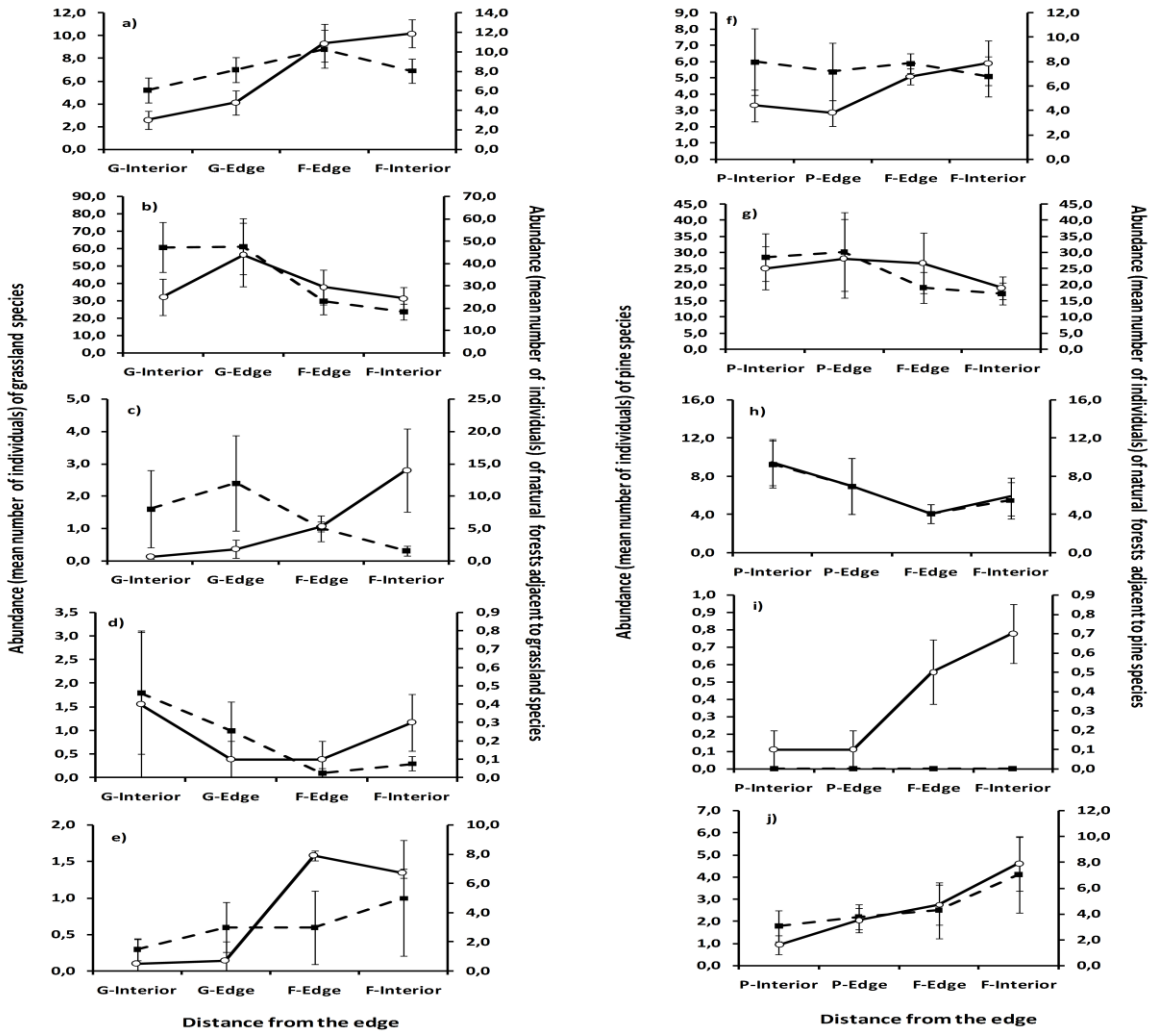
Discussion

Pine blocks had the lowest number of unique species (predators) compared to natural habitat types. This shows that even though pine blocks generally affect arthropod diversity, the intensity of their impact is dependent on the specific guild or taxon being considered. For example, pine blocks supported detritivore species richness that is greater than grassland species richness, while relatively low species richness of herbivores and mites was recorded in pine blocks compared to natural forests. My previous work has shown spill-over of assemblage composition between pine blocks and adjacent natural forests (Chapter 3), and this is also seen here with pine blocks supporting herbivore, predator and mite composition that is similar to that of natural forests, indicating that these blocks can support some forest species. However, there is a possibility that interaction between interior associated species and adjacent habitats may be a result of edge effects (Murcia 1995), since here 50 m distance from the edge was used to classify species of a particular habitat, and it was previously reported that <64 m are effectively all edge for some arthropod species (Pryke & Samways 2012). Furthermore and importantly, pine blocks are a threat to many grassland species, as pine blocks were planted over grassland (Pryke & Samways 2003), and this would result in the reduction of arthropod heterogeneity in these landscapes, particularly ants. Indeed, I found a higher proportion of ants in grassland than in other habitat types. This study shows also that ant grassland species (GS) diversity is sensitive to the adjacent natural forests.

Response of predators to different habitat types

Similarities in predator species richness between different habitat types may be because predators are not directly dependent on leaf litter deposition. Instead, their richness is influenced by prey availability (Liu *et al* 2014; Ratsirarson *et al*. 2002). These similarities in predator richness could also be because spiders are generalist predators that are able to occupy a variety of habitats and respond to different environmental conditions (Bizuet-Flores *et al*. 2015), and here spiders contributed half (51.61%) of the sampled predator species. The generalist nature of predators (Gallé *et al*. 2011) was also evident when grassland species (GS), pine species (PS) and natural forests adjacent to pine species (PFS) were sampled in adjacent habitats. However, my study also highlighted that not all predators are generalist species, as natural forests adjacent to grassland (GFS) had numerous taxa that seemed to be restricted to their specific habitat. This may be associated with different environmental

conditions and vegetation structure, which may affect sensitive predators such as carabids (Tóthmérész *et al*. 2014), with Gallé & Torma (2009) having shown that grassland and natural forests support contrasting predator assemblages. These results are in line with those of other South African studies (Kotze & Samways 1999) where there was a decline of carabid species richness from the natural forest interior into adjacent grassland interior. However, this is in contrast to the previous work which recorded a spill-over of predators from natural forests into the adjacent grassland (Lacasella *et al*. 2015), suggesting perhaps biogeographical differences in response by these predators.

Dissimilarities in grassland predator composition from that of both natural forests and pine blocks may be due to habitat preferences of some predators that prefer sunny and less dense systems (Jansen *et al*. 2013). Furthermore, even though here environmental variables were not measured, variables such as plant species composition and diversity, microclimatic conditions, soil properties and resource availability may differ between habitat types (Feng *et al*. 2014; Franc 2007), and result in different predator composition. However, I also show that numerous species are shared between grassland, pine blocks and natural forests, and this is probably because some of the predators are generalist species (Goncalves-Souza *et al*. 2008; Yaacobi *et al*. 2007). In addition, pine blocks and natural forests are structurally similar in terms of increased shade availability, which correlates strongly with predators such as carabids (Ings & Hartley 1999), and this can lead to similar composition supported by these habitats.

Response of herbivores to different habitat types

Pine blocks significantly influenced herbivore species richness, supporting less species than natural habitat types. This is likely to be a general positive correlation between herbivore richness and plant species richness (Unsicker *et al*. 2006), since pine blocks are more homogenous than natural forests and grassland. Although natural forests and grassland did not differ in species richness, assemblage composition of herbivores differed significantly between these habitats. These differences are probably linked to vegetation compositional and structural differences and abiotic variables such as levels of moisture and insolation (Lacasella *et al*. 2015). However, not all herbivores are sensitive to changes in habitat types, as I found that PFS, PS, GFS and GS are also present adjacent habitats.

Response of ants to different habitat types

Significantly higher ant species richness in grassland than forested habitats could be attributed to the lack of canopy cover in grassland, which results in increased temperatures, increased bare ground and drier soils, all of which can positively influence ant species richness (Radtke *et al*. 2014; Paris & Espadaler 2012). This was also shown when GS diversity decreased significantly from grassland into the adjacent natural forests. In addition, ant species richness decreases with the availability of tree canopy cover as well as with leaf litter deposition (Wiezik *et al*. 2010, 2013, 2015). Ant assemblage composition differed significantly between habitat types. Grassland compositional differences to both natural forests and pine blocks are likely due to differences in vegetation structure and soil temperatures (Fisher & Robertson 2002; Wiezik *et al*. 2010, 2013, 2015). This is similar to previous findings by Pryke & Samways (2012) that grassland has an ant species composition that is different from that of natural forests. Structural differences in plant diversity and complexity between pine blocks and natural forests may explain the detected differences in ant composition. However, the Jaccard index of similarities showed a high number of species shared between grassland and natural forests, grassland and pine blocks, as well as between pine blocks and natural forests. These similarities may have resulted from the positive interaction of GFS, PFS and PS with adjacent habitats, which may be because of the negative correlation between ants and forested habitats in this system.

Response of mites to different habitat types

Although no environmental variables were measured here, elsewhere variables such as shade availability, soil moisture content, logs and leaf litter deposition were found to correlate positively with mite diversity (Badejo *et al*. 2004; Bluhm *et al*. 2015; Murray *et al*. 2009; Ober & DeGroote 2011; Robson *et al*. 2009). These may be linked greater mite species richness observed here in natural forests compared to other habitats, as these variables are mostly found in natural forests (Bokhorst *et al*. 2014; Diaz-Aguilar *et al*. 2013; Napierała *et al*. 2015). Positive association between mites and natural forests was also highlighted when GFS and PFS diversity decreased significantly in adjacent grassland and pine blocks. Grassland ecosystems are driven by fire, which posses a negative effect on soil arthropods that are sensitive to heat (Podgaiski *et al*. 2014), and this may result in the detected decline of mite GFS in the adjacent grassland as well as low species richness recorded in the grassland

here. My results show that that grassland is unfavourable for many mite species, as I recorded relatively low GS, in contrast to the numbers that I recorded in the adjacent natural forests. Furthermore, natural forests and pine blocks have different forest floors, with the natural forest floor being more complex and heterogeneous than that of the pine plantation (Bokhorst *et al*. 2014; Diaz-Aguilar *et al*. 2013; Napierała *et al*. 2015) and which has lower quality leaf litter than natural forest (Baker & Murray 2012). This may explain the observed low species richness in pine blocks, and it is possible that most of mite species sampled here are forest specialist species that require specific environmental conditions (Napierała *et al*. 2015), since I also found that PFS are unable to occupy the surrounding pine blocks. This indicates that natural forests are mite diversity hotspots and refuges in theses landscapes

Although pine blocks supported relatively low mite richness, I found similarities in assemblage composition between pine blocks and natural forests. These similarities can be ascribed to the positive correlation between mite assemblages and closed canopy habitats, as well as a negative correlation between mites and high soil temperatures (Cakir & Makineci 2013). These similarities seem to result from PS that occupies the adjacent natural forests, and this may have negative impact on sensitive forest specialist species. Here I show that presence of pine blocks in these landscape are a major threat to natural forest arthropod diversity, supporting results of Chapter 3 that in which natural forests surrounded by pines support less species than those surrounded by grassland.

Response of detritivores to different habitat types

Detritivores were strongly associated with both natural forests and pine blocks, as these habitat types had the highest species richness although differing from each other compositionally. These results support previous work of Car (2010) who found no significant differences in millipede richness between pine blocks and natural forests. Differences between grassland and the two forested habitats are that grassland lacks leaf litter layer, canopy cover and consequently has a hot and dry soil surface (Campos & Hernandez 2013), while closed canopy forested habitats often have leaf litter deposition that can provide both shelter and protection from desiccation (Car 2010; Medina & Lopes 2014). In addition, here GFS diversity decreased significantly into adjacent grassland.

Grassland and natural forest assemblages were significantly different from those of pine forests. Natural forests are characterized by high levels of leaf litter deposition, bark and rotting logs, whereas pine blocks are mainly dominated by pine species, pine debris, a thick mat of decaying pine needles and a lack of understory vegetation (Murray *et al*. 2009), and this may lead to differences in detritivore composition that each of these habitats support. However, the Jaccard index of similarity showed greater sharing of detritivore assemblages between natural forests and pine blocks, and this may be due to structural similarities (canopy cover). Additionally, both PFS and PS were less sensitive to changes in habitat type, being able to interact with adjacent habitats. Interestingly, natural habitats supported similar assemblage composition, and this may have resulted from GS that were also in the adjacent natural forests. This emphasises the important role that natural forests play in the conservation of detrivores in this production landscape.

Conclusion

This study supports previous work that showed that pine blocks are depauperate in epigaeic arthropods (Pryke & Samways 2009). Natural forests were the most preferred habitat by detritivores, predators and mites, while ants were most species rich in grassland. Although I found that grassland habitats are not habitat extensions for natural forests, I recommend that their conservation in close proximity to these natural forests must be improved, as this will increase native arthropod heterogeneity in these landscapes. This study also highlights the importance of using a multi-guild/taxon approach for land use assessments. As the effect of adjacent habitats on species commonly associated with grassland, pine blocks and natural forests varied between arthropod functional guilds/taxa. Also, I show that many PS and PFS can utilise surrounding habitats, indicating that pine plantations can extend the effective range of some forest arthropod species. This suggests that pine blocks play a role in supporting some forest arthropods, as they shared a high number of species with natural forests, although not all natural forest diversity is supported by pine blocks. This raises an interesting problem, firstly pine forests are not true habitat extensions for natural forests (as not all species are supported), although many species are able to use them. We may therefore be artificially connecting populations of natural forest arthropods that naturally would have remained separate, and doing so might be altering future evolutionarily pathways with largely unknown consequences. I therefore cannot conclude that maintenance of pine blocks is vital for arthropod conservation in these landscapes, as interaction of PFS with the surrounding

pine blocks might have been due to edge effects, and I previously found that pine blocks significantly influence arthropod diversity of the adjacent natural forests (Chapter 3).

Mites and detritivores appear to be highly dependent on the presence of natural forests in these landscapes, highlighting their role as refuges or as an important mesofilter in these production landscapes. When the pine trees are felled, the remaining vegetation is burnt, in about a 10-year cycle in this area, often under an area-wide approach, i.e. all pine blocks in a plantation are felled. Furthermore grassland is burnt annually or at least biannually. This means that natural forests seem to act as a refuge for the detritivores and mites during these periods and then allowing the re-colonisation into the pine blocks or grassland, where they have an important functional role. This shows that these arthropods are of great importance in the functioning of the entire landscape, and therefore maintain healthy ecosystems (Jackson *et al*. 2007; Loreau *et al*. 2001). I further support previous work (Franklin 1993) that to maintain natural forest arthropod diversity, landscape-level approach must be used, as it does not only consider forest patch, instead it incorporates the matrix ecosystem, which have a critical role towards maintenance of forest biodiversity.

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Chapter 5: General discussion

Natural forests of South Africa are under many pressures. Here I show that forest patches in the Midlands of KwaZulu-Natal, South Africa are a conservation hotspot for many arthropod species, supporting a unique assemblage of arthropod species (Chapter 4), yet can be conserved even within a commercial landscape. Furthermore, I show that natural forest patches not only support natural forest arthropod species, but they also house species from other vegetation types that are in contact with these natural forests (Chapters 3 and 4), resulting in increased arthropod heterogeneity. Furthermore, management of vegetation types (grassland and pine blocks) adjacent to these natural forests includes deliberate burning, which affects at least some stage of their life cycles (Bond & Parr 2010; Geldenhuys 1997; van Wilgen *et al*. 2011). During these periods of fire, adjacent natural forests can act as alternative habitats for matrix species, and later allow matrix species to re-colonise pine blocks or grassland where they are involved in important ecological processes (Lawes *et al*. 2005; Ruiz *et al*. 2008). This means that natural forests play an important overall role in ecosystem functioning of the surrounding vegetation, indicating that their conservation will contribute towards arthropod conservation across the entire landscape.

I found that natural forest arthropod diversity is significantly influenced by both forest patch size, and forest interpatch distance (Chapter 2). These results emphasise the importance of using different biodiversity measures (e.g. species richness and species composition), and indicate that conclusions based on the results from a single measure may be unreliable. For example, Chapter 2 shows that forest patch size significantly influenced species composition of all arthropod taxa, with large patches having different assemblage composition from that of small patches. This may result from differences in environmental conditions such as leaf litter deposition and leaf litter moisture content, as these were important factors influencing assemblages of some taxa (Chapter 2). However, large forest patches and small forest patches had similar species richness, and this was unexpected as the theory of island biogeography predicts that large forest patches are richer in species than small forest patches (MacArthur & Wilson 1967). Interestingly, when forest patch assemblages were compared to that of the surrounding grassland, it differed significantly indicating that these similarities cannot be

associated with matrix effects. However, because these patches have been naturally fragmented for longer periods, they might have reached equilibrium.

Influence of forest interpatch distance on species richness and composition varied among taxa, with ants being more species rich in forest patches that are close to other forest patches, and mite species richness and composition being different between distant and close patches (Chapter 2). Although, species composition was significantly influenced by the interaction between forest patch size and interpatch distance, large-distant forest patches and large-close forest patches supported similar assemblages of all taxa sampled here, highlighting the importance of these patches for arthropod conservation (Chapter 2). However, in small forest patches, beetle and ant species composition was significantly influenced by forest interpatch distance, with small-close patches having different assemblages from those of small-distant patches (Chapter 2). From this I can conclude that large forest patches and/or close forest patches are more important for forest arthropod diversity, because arthropods in these patches are less prone to extinction unlike small forest patches (Hanski 1998). I therefore suggest that conservation of large and/or close patches must be the priority in this commercial landscape. However, because natural forests of the KwaZulu-Natal Midlands are naturally small in size, small forest patches, particularly those which are close, must also be considered for conservation, as these can be important stepping stones connecting epigaeic arthropods across the landscape.

In addition to the influence of forest patch size and interpatch distance on natural forest arthropod diversity, the surrounding vegetation was also an important factor (Chapter 3). My results are in accordance with Franklin & Lindenmayer (2009), who show that to successfully conserve natural forest biodiversity, conservation planning must incorporate the surrounding vegetation, as it can have major influences on forest diversity. Furthermore, I found that natural forests adjacent to grassland conserve arthropods better than those adjacent to pines (Chapter 3). This is associated with the positive natural interaction of some arthropods between natural grassland and natural forests (Lacasella *et al*. 2015; Pryke and Samways 2012). Furthermore, positive association of arthropods with grassland was also seen when an indicator value identified a number of ant and herbivore species as grassland indicators, and many of these species were also unique grassland (Chapter 3 and 4). Furthermore, grassland conservation will not only conserve grassland biodiversity, but natural forest biodiversity as well (Chapter 4; Kotze & Samways 1999). For example, in Italy, Lacasella *et al*. (2015)

found that grassland ecosystems provide alternative habitat for forest associated epigaeic arthropod species. Here I have also found that grassland associated species and natural forest adjacent to grassland associated species of most functional guilds/taxa interacted with both grassland and natural forests (Chapter 4). Furthermore, natural edges (forest-grassland) have been found to provide a suitable habitat for a number of arthropods, leading to greater local diversity (Chapter 3; Kotze & Samways 2001; Lacasella *et al*. 2015).

It is important to conserve both natural forests and grasslands together as a unit, because habitat preferences vary between arthropod functional guilds/taxa (Chapter 4). For example, natural forests had the highest number of predator, detritivore and mite species (Chapter 4), and none of these groups were indicators of grassland (Chapter 3). In addition, improved grassland conservation in this commercial landscape is crucial, as grassland ecosystems are now conserved as important remnant ecological networks between natural forests and exotic pine plantations (Samways *et al*. 2010). These ecological networks mitigate the negative impact of pine blocks on natural forest biodiversity. Even though overlap of assemblages between pine blocks and natural forests were observed (Chapters 3 and 4), these pine blocks might be acting as ecological sinks in this landscape (Hess & Fischer 2001), as they threaten native biodiversity (Chapters 3 and 4; Murray *et al*. 2009). This shows that pine blocks are not true extensions of natural forests, as they do not support all forest species (Chapter 4).

As in other studies, here I found that pine blocks provide unfavourable habitat for many arthropod species especially when compared to natural vegetation (Pacheco *et al*. 2009; Pryke & Samways 2009; Ratsirarson *et al*. 2002; Robson *et al*. 2009). This is highlighted in Chapter 3 where I show that pine blocks had the lowest species diversity compared to grassland and natural forests adjacent to grassland. In addition, Chapter 4 revealed a decrease in the diversity of natural forest-associated mite species in adjacent pine blocks, indicating that pine blocks are unable to maintain these species. Possible reasons for the diversity decline can be associated with missing habitat requirements for mites, which likely includes diverse understory vegetation, as Ashford *et al*. (2013) points out that mite diversity of some species is dependent on leaf litter and soil type. Chapter 3 highlighted that pine blocks extend their negative influence into adjacent natural forests. Furthermore, pine blocks introduce leaf litter into adjacent habitats (Robson *et al*. 2009), and that unfavourable leaf litter can contribute towards low species richness and abundance recorded here in natural forests adjacent to pines (Chapter 3).

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Pine effects on natural forests may explain the observed overlap of arthropod assemblages between pine blocks and natural forests (Chapter 3). This overlap was also seen in Chapter 4, through presence of pine associated species in adjacent natural forests. Presence of species from pine blocks in adjacent natural forests can have negative impacts on natural forest biodiversity, because some of these pine associated species might be exotic (Gunther & New 2003) that threaten native plant and arthropod diversity (Hogg & Daane 2015). For example, the presence of Argentine ant in Newlands forest of South Africa (geographically isolated from my study area) was associated with the decline in the diversity of other arthropods (Ratsirarson *et al*. 2002). Similar results were also reported in California, where exotic spider species was shown to reduce native arthropod diversity in natural vegetation through competition for resources with native spiders (Hogg & Daane 2015). These results indicate that planting of exotic pines, not only affects grassland biodiversity (as they are planted in grassland ecosystems) (Pryke & Samways 2003), but also pine plantations disrupt ecosystem functioning and health of natural forests in adjacent habitats, and thus influence the entire landscape.

Despite the negative impact that pine blocks have on native biodiversity of adjacent natural forests, here I found that natural forests surrounded by grassland and those surrounded by pines shared indicator species (Chapter 3). In addition, Chapter 4 showed that these blocks can also serve as alternative habitats for forest generalist species. Pine blocks shared a higher number of arthropod species, particularly detritivores, predators and mites, with natural forests than with grassland or between natural forests and grassland (Chapter 4). Furthermore, I found that some natural forest associated species are able to interact with the surrounding pine blocks (Chapter 4). These findings support previous studies in New Zealand and Australia where exotic pine plantations provided a substitute habitat for forest beetle species (Brockerhoff *et al*. 2005; Gunther & New 2003). Another study in New Zealand found a critically endangered ground beetle species in pine blocks, indicating that plantations can be of importance for conservation of certain species in the absence of natural forests (Berndt *et al*. 2008). However, it is important to mention that interaction of natural forest associated species and pine associated species with adjacent habitats, might be due to edge effect (Harper *et al.* 2005), as interiors of these habitats were established at only 50 m from the edge, and further investigations with increased distance from the edge into the interior would be necessary.

This thesis has shown that the response of arthropod species richness and composition to disturbances vary between different arthropod taxa or functional guilds (Chapters 2, 4), emphasizing that response of a single taxon to habitat changes may not provide a true reflection of how the entire landscape biodiversity is influenced. This is due to the fact that different arthropod taxa have different resource preferences (Maleque *et al*. 2009). I therefore support Gerlach *et al*. (2013) who proposed the use of multi-taxon approach when choosing indicators, as this approach provides the most reliable results.

This study showed that natural forest patches of different sizes and that differ in interpatch distances support different arthropod composition of some taxa. However, it is unclear if differences/similarities in assemblages are caused by species from the surrounding pines, since arthropod sampling here excluded pine blocks surrounding these natural forests, I considered distant forest patches only if far from another natural forest patch. As a result I recommend future studies that determine effect of forest patch size and interpatch distance, should incorporate all matrix vegetation types in the sampling to provide clearer conclusions, especially about the conservation value of distant and small forest patches. Natural forest patches sampled in this study have different shapes, and patch shape might be an important factor influencing natural forest biodiversity. Other areas of interest would be to determine movement patterns of epigaeic arthropods between natural forests and pine blocks. This recommendation is motivated by the observed positive interaction of pine associated species and natural forest adjacent pine associated species with adjacent habitats, being able to occupy interiors of adjacent habitats.

This thesis clearly indicates the need to conserve natural forest patches in the production landscape. I recommend the improved conservation of natural forest patches in this landscape, and for priority to be given to forest patches close to other patches and large forest patches. However, small forest patches should not be ignored as they are suitable habitat for some arthropods. In order to conserve these forest patches successfully, human activities on habitats surrounding these natural forest patches must be minimal, as these activities may have negative consequences on natural forest biodiversity. To increase native arthropod diversity in this production landscape, I recommend that natural forests are conserved with the local grassland as a single conservation unit. This can be done through increased use of grassland as ecological networks (Pryke & Samways 2012) between natural forests and

exotic plantations, and this can reduce the impact that exotic plantations have on natural forests.

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Appendix A

Width and interpatch distances of sampled natural forest patches in Good Hope and Maybole estates.

Chapter 2			Chapters 3 and 4	
Site no.	Forest patch Size (m)	Forest interpatches distance (m)	Site no.	Forest patch size (m)
1	256.07	51.42	1	183.26
2	328.04	85.29	2	264.63
3	433.80	42.00	3	216.07
4	141.53	97.31	4	309.87
5	194.58	87.10	5	194.68
6	109.29	65.66	6	270.34
7	157.53	70.24	7	139.43
8	121.18	42.06	8	451.12
9	104.92	48.72	9	451.12
10	139.65	81.26	10	306.84
11	142.80	514.35	11	289.90
12	107.67	502.44	12	208.93
13	101.82	541.32	13	259.13
14	132.21	513.49	14	209.07
15	103.07	501.43	15	270.17
16	105.16	507.49	16	283.39
17	110.03	512.32	17	380.72
18	102.38	505.73	18	270.34
19	107.04	511.18	19	139.38
20	100.66	511.18	20	120.72
21	41.93	42.42		
22	28.89	91.99		
23	30.55	87.10		
24	40.06	37.99		

25	35.65	97.92
26	37.00	55.29
27	27.41	87.00
28	38.79	50.22
29	31.90	85.05
30	27.99	73.48
31	29.18	501.86
32	28.32	532.93
33	30.18	634.71
34	31.95	509.61
35	31.13	509.61
36	32.60	505.87
37	30.48	505.87
38	37.33	643.88
39	28.36	502.22
40	34.59	582.02

Appendix B

List of arthropod species/ morphospecies recorded in different vegetation types (F- natural forests, G- grassland, P- pie blocks) in the KwaZulu-Natal Midlands, as well as functional guild assignment to species of spiders, beetles, cockroaches and millipedes.

Class/subclass/ order	Superfamily/ family/ subfamily	Scientific name/ morphospecies	Functional guilds	Vegetation types
Araneae	Selenopidae	*Anyphops* sp.	Predator	F
	Cyrtaucheniidae	*Ancylotrypa s*p.	Predator	G
	Araneidae	*Argiope flavipalpis*	Predator	F, G, P
		Araneus nigroquadratus	Predator	P
		Caerostris sexcuspidata	Predator	F
		Gasteracantha sanguinolenta	Predator	F
		Ideocaira triquetra	Predator	F
	Corinnidae	*Afroceto martini*	Predator	F
		Cambalida coriacea	Predator	F, P
		Castianeira sp.	Predator	F
		Copa flavoplumosa	Predator	F
		Trachelas schenkeli	Predator	F
	Linyphiidae	*Metaleptyphantes perexiguus*	Predator	G
		Metaleptyphantes sp.	Predator	F
		Meioneta prosectes	Predator	F, P
		Neriene natalensis	Predator	F, P
		Neriene sp.	Predator	G
		Typhistes gloriosus	Predator	F
		Frontinellina locketi	Predator	F, P
		Agyneta habra	Predator	F
	Lycosidae	*Pardosa* sp.	Predator	F, G
		Proevippa biampliata	Predator	F
		Allocosa sp.	Predator	F, G, P
	Theridiidae	*Theridion* sp.	Predator	F
		Episinus sp.	Predator	G
		Dipoena sp.	Predator	F, G
		Achaearanea sp.	Predator	F

	Steatoda erigoniformis	Predator	F, G
Salticidae	*Heliophanus aberdarensis*	Predator	F
	Euphydrys falciger	Predator	F, G, P
	Thyenula sempiterna	Predator	F
Thomisidae	*Ansiae tuckeri*	Predator	F
	Tmarus foliates	Predator	G
	Xysticus natalensis	Predator	P
	Runcinia aethiops	Predator	G
Tetragnathidae	*Pachygnatha zappa*	Predator	F
	Leucauge levanderi	Predator	F
Uloboridae	Hyptiotes akermani	Predator	F
	Uloborus planipedius	Predator	F
	Uloborus plumipes	Predator	F
Eutichuridae	*Cheiramiona collinita*	Predator	F, P
	Cheiramiona florisbadensis	Predator	G
Clubionidae	*Clubiona abbajensis*	Predator	F
	Clubiona sp.	Predator	F, G
Liocranidae	*Rhaeboctesis denotatus*	Predator	F
	Rhaeboctesis sp.	Predator	F, G, P
Gnaphosidae	*Drassodes* sp.	Predator	F,G,P
	Leptodrassex sp.	Predator	F
Zoropsidae	*Griswoldia melana*	Predator	F, G, P
Zodariidae	*Caesetius bevisi*	Predator	G
Segestriidae	*Ariadna* sp.	Predator	F
Gallieniellidae	*Drassodella melana*	Predator	F, G, P
Hahniidae	*Hahnia lobata*	Predator	F
Nemesiidae	*Lepthercus* sp.	Predator	F, G, P
Nesticidae	*Nesticella* sp. 1	Predator	G
Nephilida	*Nephila fenestrate*	Predator	F
Sparassidae	*Palystella* sp.	Predator	F
Trochanteriidae	*Platyoides* sp.	Predator	F
Scytodidae	Scytodes maritime	Predator	F, P
Miturgidae	*Voraptus affinis*	Predator	G

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	Pholcidae	Quamtana hectori	Predator	F
Coleoptera	Anthicidae	Anthicidae sp. 1	Predator	F, G, P
		Anthicidae sp. 2	Predator	F, P
		Anthicidae sp. 3	Predator	F, G
		Anthicidae sp. 4	Predator	F
	Tenebrionidae	Tenebrionidae sp. 1	Detritivore	F, P
		Tenebrionidae sp. 2	Detritivore	F, G, P
		Tenebrionidae sp. 3	Detritivore	F
		Tenebrionidae sp. 4	Detritivore	F
		Tenebrionidae sp. 5	Detritivore	F
		Tenebrionidae sp. 6	Detritivore	F
	Mordellidae	Mordellidae sp. 1	Herbivore	F
		Mordellidae sp. 2	Herbivore	F
	Aphodiinae	Aphodiinae sp. 1	Detritivore	F
		Aphodiinae sp. 2	Detritivore	F, G
	Scarabaeidae	*Caccobius* sp.	Detritivore	F, G
		Odontoloma sp.	Detritivore	F, G, P
		Onthophagus sp.	Detritivore	F
	Trogidae	*Trox* sp.	Detritivore	G
	Melolothinae	Melolothinae sp. 1	Herbivore	F
		Melolothinae sp. 2	Herbivore	F
		Melolonthinae sp. 3	Herbivore	F
		Melolothinae sp. 4	Herbivore	F, G
		Melolothinae sp. 5	Herbivore	F
	Cetoniinae	Cetoniinae sp. 1	Herbivore	G, F
		Cetoniinae sp. 2	Herbivore	G
	Elateridae	Elateridae sp. 2	Herbivore	F, G,P
		Elateridae sp. 2	Herbivore	G
		Elateridae sp. 3	Herbivore	G
	Cantharidae	Cantharidae sp. 1	Herbivore	F, G, P
	Carabidae	Carabidae sp. 1	Predator	F, P
		Carabidae sp. 2	Predator	F, P
		Carabidae sp. 3	Predator	F, G

	Carabidae sp. 4	Predator	G
	Carabidae sp. 5	Predator	P
	Carabidae sp. 6	Predator	F, P
	Carabidae sp. 7	Predator	F, P
	Carabidae sp. 8	Predator	F, G, P
	Carabidae sp. 9	Predator	F, G, P
	Carabidae sp. 10	Predator	F
	Carabidae sp. 11	Predator	F
Chrysomelidae	Chrysomelidae sp. 1	Herbivore	G
	Chrysomelidae sp. 2	Herbivore	G
	Chrysomelidae sp. 3	Herbivore	F, G
	Chrysomelidae sp. 4	Herbivore	F, G
	Chrysomelidae sp. 5	Herbivore	G
	Chrysomelidae sp. 6	Herbivore	G
Clambidae	Clambidae sp. 1	Detritivore	F
Cleridae	Cleridae sp. 1	Predator	F
Coccinellidae	Coccinellidae sp. 1	Predator	G
	Coccinellidae sp. 2	Predator	F, G, P
	Coccinellidae sp. 3	Predator	G
	Coccinellidae sp. 4	Predator	F, G, P
Cryptophagidae	Cryptophagidae sp. 1	Detritivore	F, G
Curculionidae	Curculionidae sp. 1	Herbivore	F, G, P
	Curculionidae sp. 2	Herbivore	F, P
	Curculionidae sp. 3	Herbivore	F, G, P
	Curculionidae sp. 4	Herbivore	F, G
	Curculionidae sp. 5	Herbivore	F, G, P
	Curculionidae sp. 6	Herbivore	G
	Curculionidae sp. 7	Herbivore	G
	Curculionidae sp. 8	Herbivore	G
Scolytinae	Scolytinae sp. 1	Herbivore	F
Histeridae	Histeridae sp. 1	Predator	F
Nitidulidae	Nitidulidae sp. 1	Detritivore	F, G, P
	Nitidulidae sp. 2	Detritivore	F

		Nitidulidae sp. 3	Detritivore	F, P
		Nitidulidae sp. 4	Detritivore	F, G
		Nitidulidae sp. 5	Detritivore	F
	Staphylinidae	Staphylinidae sp. 1	Predator	F, G, P
		Staphylinidae sp. 2	Predator	F, G, P
		Staphylinidae sp. 3	Predator	P
		Staphylinidae sp. 4	Predator	F,P
		Staphylinidae sp. 5	Predator	F
	Scydmaenidae	Scydmaenidae sp. 1	Predator	F, P
Hymenoptera	Formicidae	Species 1	Ant	F, G, P
		Species 2	Ant	F, G, P
		Camponotus sp.1	Ant	F, G
		Camponotus sp. 2	Ant	F, G
		Crematogaster sp. 1	Ant	F, G, P
		Crematogaster sp. 2	Ant	F, G, P
		Crematogaster sp. 3	Ant	F, G
		Crematogaster sp. 4	Ant	F, G
		Crematogaster sp. 5	Ant	F, G
		Species 3	Ant	F, G, P
		Species 4	Ant	F
		Species 5	Ant	F, G, P
		Species 6	Ant	F, G, P
		Species 7	Ant	F, G, P
		Species 8	Ant	F, G
		Species 9	Ant	F, G
		Species 10	Ant	G, P
		Species 11	Ant	F, G, P
		Species 12	Ant	F
		Species 13	Ant	G
		Species 14	Ant	F, G, P
		Species 15	Ant	F
		Species 16	Ant	G

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	Species 17	Ant	F, G, P
	Species 18	Ant	F, G, P
	Species 19	Ant	G
	Species 20	Ant	G
	Species 21	Ant	G
	Species 22	Ant	G
	Species 23	Ant	F
	Species 24	Ant	G
	Pheidole sp. 1	Ant	F, G, P
	Pheidole sp. 2	Ant	F, G, P
	Tetramorium sp. 1	Ant	F, G, P
	Tetramorium sp. 2	Ant	F, G, P
Acari	Species 1	Mite	F
	Species 2	Mite	F
	Species 3	Mite	G
	Species 4	Mite	F
	Species 5	Mite	F, P
	Species 6	Mite	F, P
	Species 7	Mite	F
	Species 8	Mite	F
	Species 9	Mite	F
	Species 10	Mite	F
	Species 11	Mite	F
	Species 12	Mite	F
	Species 13	Mite	F
	Species 14	Mite	F
	Species 15	Mite	F
	Species 16	Mite	F
	Species 17	Mite	F
	Species 18	Mite	F
	Species 19	Mite	F

Species 20	Mite	F, P
Species 21	Mite	F, G, P
Species 22	Mite	F, G
Species 23	Mite	F, G, P
Species 24	Mite	F
Species 25	Mite	F
Species26	Mite	F
Species 27	Mite	F, P
Species 28	Mite	F, P
Species 29	Mite	F
Species 30	Mite	F
Species 31	Mite	F
Species 32	Mite	F
Species 33	Mite	F
Species 34	Mite	F
Species 35	Mite	F
Species 36	Mite	F, G, P
Species 37	Mite	F, P
Species 38	Mite	F
Species 39	Mite	F
Species 40	Mite	F
Species 41	Mite	F
Species 42	Mite	F, P
Species 43	Mite	F, P
Species 44	Mite	F, P
Species 45	Mite	F
Species 46	Mite	F
Species 47	Mite	F
Species 48	Mite	F
Species 49	Mite	F
Species 50	Mite	F

	Species 51	Mite	F
	Species 52	Mite	F
	Species 53	Mite	F
	Species 54	Mite	F
	Species 55	Mite	F
	Species 56	Mite	F
	Species 57	Mite	G
	Species 58	Mite	P
	Species 59	Mite	F
	Species 60	Mite	F
Diplopoda	Species 1	Detritivore	F, G, P
	Species 2	Detritivore	F, P
	Species 3	Detritivore	F, G, P
Blattodea	Species 1	Detritivore	F, P
	Species 2	Detritivore	G, P
	Species 3	Detritivore	F, P