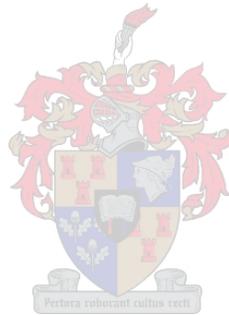# The diversity and distribution of topsoil and leaf litter arthropods in timber plantation landscape mosaics

by

Michelle Eckert

Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in the Faculty of AgriSciences (Department of Conservation Ecology and Entomology), University of Stellenbosch

Supervisor: Dr R. Gaigher
Co-supervisors: Dr J.S. Pryke, Prof M.J. Samways

Department of Conservation Ecology and Entomology
Faculty of AgriSciences
Stellenbosch University

December 2017

DECLARATION

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the owner of the copyright thereof (unless to the extent explicitly otherwise stated), and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: December 2017

i

GENERAL SUMMARY

Landscape planning for conservation is of great importance in high-impact production systems, such as commercial timber plantations. Ecological networks (ENs) have been applied on a large scale in exotic timber plantations in South Africa to mitigate the impacts of forestry by connecting remnant natural areas of high conservation value across the landscape. Natural remnants, such as Afromontane forests and grasslands have received much conservation attention within these ENs, yet the value of conserving grassland on hydromorphic soils remains poorly understood. We also still have limited information on arthropods occurring in the topsoil and leaf litter layer, despite their great functional importance, especially in hydromorphic grasslands. The removal of pine trees from these hydromorphic grasslands is a conservation measure to restore hydrological function within plantation landscapes. However, the effectiveness of restoration for biodiversity has not yet been determined.

The study was conducted in the KwaZulu-Natal Midlands. The diversity and distribution of topsoil and leaf litter arthropods within four dominant biotopes (Afromontane forests, pine plantations, dry grasslands and hydromorphic grasslands) was determined. The biodiversity of hydromorphic grasslands was compared to the other biotopes occurring within an EN-plantation landscape mosaic. In addition, to determining whether restoration leads to successful recovery of the arthropod fauna after the removal of pine trees from hydromorphic grasslands, I compared the diversity of topsoil and leaf litter arthropods between natural untransformed hydromorphic grasslands, restored hydromorphic grasslands and pine plantations.

All the natural untransformed biotopes (i.e. natural forest, dry and hydromorphic grassland) had higher arthropod species diversity compared to the transformed biotope (i.e. pine plantation). Hydromorphic grasslands differed significantly from the other dominant biotopes regarding arthropod assemblage structure, but not in terms of species richness. Thus, hydromorphic grasslands are unique landscape elements that complement the other untransformed biotopes, and contribute to landscape heterogeneity and overall biodiversity within the production landscape. Although hydromorphic and dry grasslands are classified as one vegetation type, I found that here, they were two distinct biotopes, both of which should be conserved separately owing to their unique arthropod assemblages.

After the removal of pine trees from hydromorphic grasslands, the diversity and assemblages of topsoil and leaf litter arthropods have the capacity to recover to levels similar to that of natural hydromorphic grassland. However, contrary to what was expected, the assemblage similarity between the restored and natural hydromorphic grasslands was significantly negatively correlated to time since pine removal. American bramble (*Rubus cuneifolius*), which was more prevalent in older post-restoration sites, had the most significant negative effect on the assemblage similarity between the restored and natural hydromorphic grasslands, causing some restored sites to deviate from the restoration trajectory. Therefore, successful restoration of these hydromorphic grasslands to near natural conditions requires supplementary management inputs through removal and management of *R. cuneifolius* as a key management priority.

ALGEHELE OPSOMMING

Landskapsbeplanning vir bewaring is van groot belang in hoë-impak produksiestelsels, soos houtproduksie. Ekologiese netwerke (ENe) is op groot skaal in eksotiese houtplantasies in Suid-Afrika toegepas om die impak van bosbou te verminder deur die oorblywende natuurgebiede van hoë bewaringswaarde oor die landskap te verbind. Natuurlike oorblyfsels, soos Afromontane woude en grasvelde, het al baie aandag gekry met betrekking tot hul bewaringswaarde binne hierdie ENe, maar ons het steeds min kennis oor die waarde van grasvelde op hidromorfiese grond. Ook, 'n groep organismes waaroor ons nog beperkte inligting op het, maar wat van groot funksionele belang is, die geleedpotiges wat voorkom in die bogrond en blaarvullislaag. Die verwydering van dennebome uit hierdie hidromorfiese grasvelde word geïmplementeer om die hidrologiese funksie binne plantasielandskappe te herstel, maar die effek van restorasie op biodiversiteit is nog nie gemeet nie.

Die studie is in die KwaZulu-Natal, Midlands, uitgevoer. Die diversiteit en verspreiding van bogrondse geleedpotiges binne vier dominante biotope (Afromontane woude, dennewoude, droë grasvelde en hidromorfiese grasvelde) is geëvalueer om die biodiversiteitswaarde van hidromorfiese grasvelde te bepaal, relatief tot die ander biotope wat voorkom in 'n EN-plantasie landskap mosaïek. Daarby, was die sukses van die herstel van geleedpotige biodiversiteit na die verwydering van dennebome van hidromorfiese grasvelde ook bepaal deur die diversiteit van natuurlike, ongetransformeerde hidromorfiese grasvelde, herstelde hidromorfiese grasvelde en denneplantasies te vergelyk.

Al die natuurlike ongetransformeerde biotope (d.w.s. natuurlike woud, droë en hidromorfiese grasvelde) het hoër geleedpotige spesiediversiteit gehad in vergelyking met die getransformeerde biotoop (d.w.s. denneplantasies). Hidromorfiese grasvelde verskil aansienlik van die ander dominante biotope rakende geleedpotige spesiesamestelling, maar nie in spesiesrykheid nie. Dus, hidromorfiese grasvelde is unieke landskapelemente wat die ander ongetransformeerde biotope aanvul, en bydra tot landskap heterogeneiteit en algehele biodiversiteit in die produksie landskap. Alhoewel hidromorfiese en droë grasvelde as een biotoop aanskou word, het ek bevind dat hulle twee afsonderlike biotope was, wat albei as afsonderlike biotope bewaar moet word as gevolg van hul unieke geleedpotige samestellings.

Na die verwydering van dennebome uit hidromorfiese grasvelde, blyk dit dat die diversiteit en samestelling van bogrondse geleedpotiges herstel tot vlakke wat soortgelyk is aan dié van natuurlike hidromorfiese grasvelde. In teenstelling met wat verwag is, was die gelykvormigheid van die samestelling tussen die herstelde en natuurlike hidromorfiese grasvelde aansienlik negatief gekorreleer met die tyd sedert denneboom verwydering. Amerikaanse braambos (*Rubus cuneifolius*), wat meer voorkom in areas wat al vir langer tye gerestoreer is, het die grootste negatiewe uitwerking op die samestelling van die herstelde en natuurlike hidromorfiese grasvelde gehad, wat veroorsaak het dat sommige herstelde areas van die restorasiepad afwyk. Om hierdie hidromorfiese grasvelde suksesvol te herstel tot naby natuurlike toestande, word aanvullende bestuursinsette benodig, met die verwydering en bestuur van *R. cuneifolius* as 'n sleutelbestuursprioriteit.

ACKNOWLEDGEMENTS

I thank the following people and institutions:

DEDICATION

I dedicate this in loving memory of my grandfathers:
Mr. G.B. Eckert (2003) and Mr. A.W. Rossouw (2017)

TABLE OF CONTENT

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

Chapter 1
General introduction

1.1. Biodiversity value in production landscapes

The term "biodiversity" is most commonly used to describe species diversity (Schwarz et al., 1975; Vandermeer and Perfecto, 1995). However, it also includes genetic, ecosystem and habitat diversity (Noss and Cooperrider, 1994), along with their associated ecological and evolutionary processes (Spellerberg and Hardes, 1992; Noss and Cooperrider, 1994). There is a global realization that biodiversity is fundamental within agricultural ecosystems (Thrupp, 2000), as it can provide a variety of important ecological services (Altieri, 1999). Within production systems, biodiversity does not only provide food, fuel and fibre, but also aids in the recycling of nutrients, the regulation of microclimate and hydrological processes, the regulation of unwanted organisms, the detoxification of chemicals (Altieri, 1999) and can aid in the prevention of soil erosion (Perry, 1994).

Darwin (1872) was the first person to notice that ecosystem productivity was dependent on biodiversity. One of his most renowned statements include "The greatest amount of life can be supported by the great diversification of life". Darwin believed that a single plot of land would be more productive with a greater plant diversity, compared to it containing a single plant species. Following Darwin, McNaughton (1977) expanded on this hypothesis (Tilman, 1997). McNaughton (1977) showed that an older and more diverse community of plant species was functionally more stable. Other authors have also noticed that a larger number of species within an ecosystem could lead to more interspecific interactions, which in turn, can affect ecosystem functioning (Odum and Odum, 1953; MacArthur, 1955; Elton, 2000). Since then, numerous studies have found that biodiversity is related to ecosystem stability (Baskin, 1994; Tilman, 1996) and productivity (Tilman et al., 2001b; Tilman et al., 2012). Today these findings are the basis of the "diversity-productivity hypothesis" (Tilman, 1997). A heterogeneous environment is one of the key determinants of greater species richness, which also leads to a taxonomically more diverse community (Pacini et al., 2009).

There is, however, a growing concern about the loss of biodiversity due to the expansion of production landscapes (Eppink et al., 2004). Land use, such as agriculture and forestry, are often considered to be major threats to biodiversity (Mensing et al., 1998, Tilman et al., 2001a; Brockerhoff et al., 2008).

1.2. Plantation forestry and impacts on biodiversity

A current global trend is the transformation of natural environments for the expansion of timber plantations (Ferraz et al., 2013), which is a major conservation concern (Brockerhoff et al., 2008). Numerous studies have been undertaken in plantation forests, which impact biodiversity and productivity (Burger and Zedaker, 1993; Gupta and Malik, 1996; Bird et al., 2000). The simplification of environmental structure (Altieri, 1999), tree harvesting and site preparation practices (Bird et al., 2000), can cause changes in nutrients and organic matter content, changes in trophic systems, and alteration of the soils physical properties (Bird et al., 2004), which could lead to reductions in site productivity (Pritchett and Fisher, 1987). For this reason, there is increasing concern about the impacts that forestry activities can have on hydrology, productivity and biodiversity in intensely managed forestry plantations (Shepard et al., 1993).

Plantation forests generally contribute little to landscape biodiversity (Pryke and Samways, 2012). After Stephens and Wagner (2007) reviewed 35 articles focussing on plantation forests and biodiversity, they found that lower biodiversity in plantation forests was reported in 94% of the reviewed studies. This is because of lower habitat complexity and diversity (Brockerhoff et al., 2008), which leads to plantation forests having lower species diversity compared to natural untransformed biotopes, which are more complex and diverse, such as natural forests and grasslands (Brockerhoff et al., 2008; Pryke and Samways, 2012). In South Africa, the first large scale plantation forest was established in the 1890's (Tewari, 2001), in response to insufficient natural wood resources in the country (Samways et al., 2010). The majority of suitable land for the forestry industry lies within eastern South Africa, especially in Mpumalanga and KwaZulu-Natal. However, these suitable lands occur within the threatened grassland biome (Samways et al., 2010).

One of the greatest global challenges is ensuring efficient agricultural production without compromising biodiversity and ecosystem function (Tscharntke et al., 2012). Therefore, there is need to balance agricultural production and ecosystem stability and functioning is of great importance (Carter, 2001). For this reason, mitigation measures are needed to ensure that plantation forests are ecologically sustainable and that biodiversity within South African landscapes are maintained and conserved. One such measure is through the implementation of ecological networks (ENs).

1.3. Ecological networks in production landscapes

Ecological networks (ENs) are used in South Africa to mitigate the adverse effects plantation forests can have on biodiversity across the landscape (Samways et al., 2010). The aim of ENs is to conserve biodiversity, but also to conserve the structural, compositional and functional complexity of the whole ecosystem across the landscape mosaic (Jongman, 1995; Samways et al., 2010; Pryke and Samways, 2012). On average, about one-third of a given plantation remains unplanted to timber (Samways et al., 2010). These unplanted areas occur at a large spatial scale (Pryke and Samways, 2012), and consist of interconnected patches and corridors of natural or remnant grasslands and natural forests across the landscape, which then form the EN (Jongman, 1995; Samways et al., 2010).

Studies on a wide variety of invertebrate and plant taxa in these ENs have increased our understanding of species diversity and distribution in production landscapes, and also have informed local EN design and management. ENs are important for the conservation of biological diversity and for the provisioning of ecosystem services (Samways et al., 2010). Studies have shown that when the EN corridors is wide enough, they can provide important habitat for a wide range of species (Bazelet and Samways, 2011; Pryke and Samways, 2012; Kietzka et al., 2015; Yekwayo et al., 2016), and can also resemble assemblages which occur within adjacent protected areas, thereby acting as extensions of protected areas (Joubert and Samways, 2014). However, this all depends on the correct management and design of ENs in order to maintain heterogeneity across the production landscape (Bazelet and Samways, 2011; Kietzka et al., 2015). Landscape heterogeneity, or the structural complexity of the landscape matrix, is essential for maintaining landscape biodiversity (Brockerhoff et al., 2008). By having varying sizes and shapes of different or similar types of habitat types, more suitable or alternative habitats for species will increase (Dunning et al., 1992), which leads to greater biodiversity at a landscape and habitat level. Although much research had been done to show the biodiversity value of ENs, only a few areas in the world have implemented the use of ENs (Yu et al., 2006; Jongman et al., 2011), and much more research is needed to improve the design and management of ENs (Samways et al., 2010).

1.4. Delineation and the value of hydromorphic grasslands

Wetland ecosystems are one of the most valuable assets in a landscape, as they contribute to landscape biodiversity and ecosystem functioning (Hansson et al., 2005). Wetlands can provide a variety of ecosystem services, which include water supply and improved water quality (Hannson et al., 2005), and

they also are habitat for a wide range of species (Lu and Wang, 1995; Sabo et al., 2005). Thus, riparian zones and other hydromorphic zones are considered among the most dynamic and biologically diverse ecosystems in the world (Ward, 1989; Tockner et al., 1999; Liu et al., 2003). However, wetlands are often transformed for agricultural production, due to their high organic matter and nutrient content (Reddy and Gale, 1994).

Prior to sustainable land-use planning in the forestry industry, production was maximized by planting trees across the entire landscape, with no consideration for topography (Samways and Pryke, 2016). This led to the landscape being densely covered in planation forests, with trees being planted on hydromorphic (i.e. wetland) soils. This caused alarming effects on natural processes, including hydrological cycles (Neke and du Plessis, 2004), as well as loss of biodiversity (Lawes et al., 1999). After much debate amongst the stakeholders, it was decided that hydrological processes and biodiversity needed to be restored (Samways and Pryke, 2016). The approach focussed on trees which were planted on hydromorphic soils and were causing a disturbance in the functioning of hydrological processes. In response, ENs in South African timber production landscapes in KwaZulu-Natal were designed and established through a process of delineation to help restore grassland and hydromorphic grassland habitats (Joubert and Samways, 2011). Delineation includes the proactive planning to avoid the planting of trees on remaining hydromorphic soils, as well as the removal of planted trees from hydromorphic soils (Dye and Jarmain, 2004). Wetlands typically occur in distinct patches or corridors within a landscape mosaic (Gibbs, 2000), but wetland species' populations occurring in small and isolated patches are more vulnerable to extinction (Moller and Rordam, 1985; Dodd, 1990). Ecological restoration is thus one of the major strategies reversing biodiversity losses to enhance the provisioning of ecosystem services (Bullock et al., 2011). By removing trees from riparian zones and wetlands, water is released from the soil, aiding in the restoration of water courses. This activity addresses the loss of physical, chemical and biological deterioration of the soil (Matthews, 2008).

The process of delineation could be the key to wetland protection and rehabilitation, as it aids in defining the boundaries of hydromorphic soils (Joubert and Samways, 2011). Various authors suggest that restoration success can be measured based on ecosystem processes (Rhoades et al., 1998) and species diversity (van Aarde et al., 1996; Reay and Norton, 1999; Passell, 2000; McCoy and Mushinsky, 2002). Studies that focus on ecosystem processes generally involve study of processes such as nutrient cycling (measured indirectly based on nutrient availability) (Fuhlendorf et al., 2002) and

biological interactions (as it provides information on the resilience of restored ecosystems) (Ruiz-Jaen and Aide, 2005). In contrast, studies that focus on the richness and abundance of organisms generally look at the different trophic levels (Nichols and Nichols, 2003; Weiermans and van Aarde, 2003). It is useful to consider the functional guild species richness, as this also provides information on ecosystem resilience (Peterson et al., 1998). Plants are the most well-studied group (Ruiz-Jaen and Mitchell Aide, 2005; Joubert and Samways, 2011), but some studies have focussed on invertebrate functional groups (Holl, 1995; Majer, 1997; Longcore, 2003), due to their important roles in the ecosystem, such as nutrient cycling (Tian et al., 1997). However, there is still limited information with regards to the influence of delineation and the restoration of hydrological systems on biodiversity within pine plantation landscapes in South Africa (Dye and Jarmain, 2004).

1.5. The importance of soil organisms in production landscapes

Charles Darwin (1881) was one of the first researchers to describe the role of soil organisms in ecosystems for contributing to decomposition of plant matter. Research prior to the 1960's on soil fauna activities, and their role in nutrient recycling, mostly involved earthworms (Huhta, 2007). Today, the role of a variety of soil organisms in providing a variety ecosystem services are being given much more attention (Janzen et al., 2011).

The soil environment is a complex system, containing very complex and diverse biological communities (Ettema and Wardle, 2002). The composition of soil organism communities is strongly dependent on environmental conditions (Bongers and Ferris, 1999), and the small-scale physical and chemical heterogeneity of the soil structure can partly explain the variation of soil biotic communities (Ettema and Wardle, 2002). Soil physical properties which affect soil organisms include the soil texture, pore conditions, moisture content, structure and temperature, whereas the chemical properties which affect soil organisms include the soil pH, nutrient and organic matter content (János, 2012). The diversity of soil organisms is also known to be affected by other factors such as the microclimate of the habitat (Harte et al., 1996), availability of resources (Illieva-Makulec et al., 2006), as well as habitat and landscape complexity and diversity (Vanbergen et al., 2007).

Soil organisms are exceptionally diverse, and although more attention has been given to soil organisms of larger sizes (i.e. macrofauna) compared to smaller soil organisms (i.e. micro- and mesofauna), they all contribute to various ecosystem services (Barrios, 2007). Soil organisms are important as they

contribute to soil formation (Oades, 1993), maintenance of the soil's physical structure (Loranger-Merciris et al., 2007) and the cycling of nutrients (Birkhofer et al., 2011). Soil organisms also influence above ground organisms of higher trophic levels (Bezemer et al., 2005). According to De Ruiter et al. (1995), the stability of soil ecosystem is closely linked to the relative abundance of functional groups within the system, and arthropod functional group diversity can be enhanced through increased habitat heterogeneity (Diekötter et al., 2010). By enhancing habitat heterogeneity, soil arthropod biodiversity also increases, which in turn, promotes ecosystem services associated with these organisms. Therefore, soil organisms play an important role in the quality, fertility and productivity of soils (Woomer and Swift, 1994; Höfer et al., 2001; Giller et al., 2005).

With increasing concerns for the global soil stock (Koch et al., 2013), the term "soil security" has become an important concept (Koch et al., 2012). According to Koch et al. (2012), soil security can be defined as "the maintenance and improvement of soil resources in order to continue to provide ecosystem goods, to maintain biodiversity and to conserve ecosystem services". Soil stocks include soil natural capital (Robinson et al., 2009, Dominati et al., 2010) on which these ecosystems services depend (Robinson et al., 2012). As a reduction in soil fauna can result in the degradation of the soil (Höfer et al., 2001), it is important to improve and maintain the soil's natural capital through sustainable agriculture, as it will contribute to the soil's resilience, fertility, productivity, and ability to provide ecosystem services (Woomer and Swift, 1994; Robinson et al., 2012). In timber plantations, the diversity of soil fauna and their linkage to the whole ecosystem structure and functioning is poorly known (Bernhard-Reversat et al., 2001; Höfer et al., 2001; Warren and Zou, 2002; Barrios, 2007).

1.6. Thesis outline and study aims

The purpose of this study is to gain an in-depth understanding of the diversity and distribution of litter and topsoil arthropods within the ecological networks (ENs) of South African forestry plantation landscapes, with specific focus on biota occurring on hydromorphic soils. Arthropods were selected for this study as they are extremely sensitive to environmental changes (Kotze and Samways, 2001) and are easily and cost effectively sampled (Gerlach et al., 2013). Focussing on leaf litter and topsoil arthropods will be of strategic value, as the impact of forestry management practices on plantation soil quality has been identified as a key concern to the industry (Titshall, 2015). Baseline information of this functionally important and diverse group of organisms is also lacking in South Africa.

The aim of the second chapter in this thesis, is to obtain detailed baseline information on the diversity and assemblage structure of leaf litter and topsoil arthropods in the dominant biotopes within an EN-plantation landscape mosaic. The biotopes selected include indigenous forest, pine plantation, dry grassland, and hydromorphic grassland.

The questions I ask in this chapter are:

1. Does overall and functional guild species richness and assemblage composition differ between the four dominant biotopes?
2. Which environmental variables explain the variation in overall and functional guild species and assemblage composition between the four dominant biotopes?
3. Do hydromorphic grasslands have conservation value compared to other dominant biotopes?

The focus of this chapter is to determine whether hydromorphic grasslands have a unique and characteristic assemblage structure, compared to the other dominant biotopes across the landscape. This will help to determine the unique biodiversity value of hydromorphic soils within a plantation landscape mosaic. Although hydromorphic grasslands within an EN-production landscape has not received much attention as a biotope by itself, I hypothesize that hydromorphic grasslands will have a unique arthropod assemblage compared to dominant biotopes due to the structural and botanical differences between the biotope types. Furthermore, I hypothesize that hydromorphic grasslands to have significant conservation value based on their biological values and ecological roles within ecosystems.

The aim of the third chapter, is to assess the diversity and assemblage structure of leaf litter and topsoil arthropods in naturally occurring hydromorphic grasslands (which have never been planted with pines), delineated hydromorphic grasslands (where pines have been removed) and pine blocks within an EN-plantation landscape mosaic.

The questions I ask in this chapter are:

1. Does species richness and assemblage composition differ between the three biotopes?
2. What effect does 'time since delineation' have on the recovery of hydromorphic, grassland arthropod assemblages?

3. Which environmental variables contribute to, or impede, recovery of restored sites to assemblages that resemble that of natural sites?

The focus of this chapter is to determine whether successful restoration has occurred within delineated hydromorphic sites compared to natural hydromorphic sites. This chapter also determines how long after the delineation processs, the arthropod assemblage structure within delineated hydromorphic grasslands returned to that in the natural hydromorphic grasslands. I hypothesize that the pine blocks would have significantly different assemblages to natural and restored hydromorphic grasslands, due to strong structural and botanical differences. Furthermore, I hypothesize that the restored biotope will have an arthropod assemblage similar to that of the natural biotope, with increasing similarity with increasing time since the pine trees were removed. However, due to altered environmental conditions and inherent effects of disturbance within the restored biotope, I would expect the restoration period would not be rapid.

Finally, I conclude with chapter four. I outline the management options that will best conserve soils and their organisms, which in turn, will promote soil function. Soil health and the conservation of soil biodiversity goes hand-in-hand with creating resilient landscapes and sustainable forestry, and is an area in which conservation and commercial plantation forestry share a common goal.

1.7. References

Altieri M.A. (1999). The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74: 19-31.

Barrios E. (2007). Soil biota, ecosystem services and land productivity. Ecological Economics 64: 269-285.

Baskin Y. (1994). Ecosystem function of biodiversity. BioScience 44: 657-660.

Bazelet C.S. and Samways M.J. (2011). Relative importance of management vs. design for implementation of large-scale ecological networks. Landscape Ecology 26: 341-353.

Bernhard-Reversat F., Laclau J.P., Loubana P.M., Loumeto J.J., Mboukou I.M.C. and Reversat G. (2001). Changes in biological factors of fertility in managed eucalyptus plantations on a savanna soil in Congo. In: Kobayasgi S. (Ed.). Rehabilitation of degraded tropical forest ecosystems: Workshop proceedings. CIFOR, Bogor.

Bezemer T.M., De Deyn G.B., Bossinga T.M., Van Dam N.M., Harvey J.A. and Van der Putten W.H. (2005). Soil community composition drives aboveground plant–herbivore–parasitoid interactions. Ecology Letters 8: 652-661.

Bird S., Coulson R.N. and Crossley D.A. (2000). Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. Forest Ecology and Management 131: 65-80.

Bird S.B., Coulson R.N. and Fisher R.F. (2004). Changes in soil and litter arthropod abundance following tree harvesting and site preparation in a loblolly pine (Pinus taeda L.) plantation. Forest Ecology and Management 202: 195-208.

Birkhofer K., Diekötter T., Boch S., Fischer M., Müller J., Socher S. and Wolters V. (2011). Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. Soil Biology and Biochemistry 43: 2200-2207.

Bongers T. and Ferris H. (1999). Nematode community structure as a bioindicator in environmental monitoring. Trends in Ecology and Evolution 14: 224-228.

Brockerhoff E.G., Jacktel H., Parrotta J.A., Quine C.P. and Sayer J. (2008). Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity Conservation 17: 925-951.

Bullock J.M., Aronson J., Newton A.C., Pywell R.F. and Rey-Benayas J.M. (2011). Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends in Ecology and Evolution 26: 541-549.

Burger J.A. and Zedaker S.M. (1993). Drainage effects on plant diversity and productivity in loblolly pine (Pinus taeda L.) plantations on wet flats. Forest Ecology and Management 61: 109-126.

Carter M.R. (2001). Researching the agroecosystem/environmental interface. Agriculture, Ecosystems and Environment 83: 3-9.

Darwin C. (1872). The origin of species. Thompson and Thomas, Chicago.

Darwin C. (1881). The formation of vegetable mould, through the action of worms. University of Chicago Press, Chicago.

De Ruiter P.C., Neutel A.M. and Moore J.C. (1995). Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269: 1257-1260.

Diekötter T., Wamser S., Wolters V. and Birkhofer K. (2010). Landscape and management effects on structure and function of soil arthropod communities in winter wheat. Agriculture, Ecosystems and Environment 137: 108-112.

Dodd C.K. (1990). Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle Steinotfberis depressuts. Biological Conservation 45: 33-45.

Dominati E., Patterson M. and Mackay A. (2010). A framework for classifying and quantifying the natural capital and ecosystem services of soils. Ecological Economics 69: 1858-1868.

Dunning J.B., Danielson B.J. and Pulliam H.R. (1992). Ecological processes that affect populations in complex landscapes. Oikos: 169-175.

Dye P. and Jermain C. (2004). Water use by black wattle (Acacia mearnsii): implications for the link between removal of invading trees and catchment streamflow. South African Journal of Science 100: 40-44.

Elton C.S. (2000). The ecology of invasions by animals and plants. University of Chicago Press, Chicago.

Eppink F.V., van den Bergh J.C. and Rietveld R. (2004). Modelling biodiversity and land use: Urban growth, agriculture and nature in a wetland area. Ecological Economics 51: 201-216.

Ettema C.H. and Wardle D.A. (2002). Spatial soil ecology. Trends in Ecology and Evolution 17: 177-183.

Ferraz S.F., de Paula Lima W. and Rodrigues C.B. (2013). Managing forest plantation landscapes for water conservation. Forest Ecology and Management 301: 58-66.

Fuhlendorf S.D., Zhang H., Tunnell T.R., Engle D.M. and Cross A.F. (2002). Effects of grazing on restoration of southern mixed prairie soils. Restoration Ecology 10: 401-407.

Gerlach J., Samways M.J. and Pryke J.S. (2013). Terrestrial invertebrates as bioindicators: An overview of available taxonomic groups. Journal of Insect Conservation 17: 831-850.

Gibbs J.P. (2000). Wetland loss and biodiversity conservation. Conservation Biology 14: 325-317.

Giller K.E., Bignell D., Larvelle P., Swift, M.J., Barrios, E., Moreira, F., van Noordwijk, M., Barois, I., Karanja, N. and Huising J. (2005). Soil biodiversity in rapidly changing tropical landscapes: Scaling down and scaling up. Biological Diversity and Functions in Soils: 295-318.

Gupta S.R. and Malik V. (1996). Soil ecology and sustainability. Journal of Tropical Ecology 37: 43-55.

Hansson L.A., Brönmark C., Anders Nilsson P. and Abjörnsson K. (2005). Conflicting demands on wetland ecosystem services: Nutrient retention, biodiversity or both? Freshwater Biology 50: 705-714.

Harte J., Rawa A. and Price V. (1996). Effects of manipulated soil microclimate on mesofaunal biomass and diversity. Soil Biology and Biochemistry 28: 313-322.

Höfer H., Hanagarth W., Garcia M., Martius C., Franklin E., Römbke J. and Beck L. (2001). Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. European Journal of Soil Biology 37: 229-235.

Holl K.D. (1995). Nectar resources and their influence on butterfly communities on reclaimed coal surface mines. Restoration Ecology 3: 76-85.

Huhta V. (2007). The role of soil fauna in ecosystems: A historical review. Pedobiologia 50: 489-495.

Ilieva-Makulec K., Olejniczak I. and Szanser M. (2006). Response of soil micro-and mesofauna to diversity and quality of plant litter. European Journal of Soil Biology 42: S244-S249.

János K. (2012). The importance of soil living organisms in sustainable agricultural land management. Analele Universităţii din Oradea, Fascicula: Protecţia Mediului 19: 86-93.

Janzen H.H., Fixen P.E., Franzluebbers A.J., Hattey J., Izaurralde R.C., Ketterings Q.M., Lobb D.A. and Schlesinger W.H. (2011). Global prospects rooted in soil science. Soil Science Society of America Journal 75: 1-8.

Jongman R.H.G. (1995). Nature conservation planning in Europe: Developing ecological networks. Landscape and Urban Planning 32:169-183.

Jongman R.H.G., Bouwma I.M., Griffioen A., Jones-Walters L. and Doorn A.M. (2011). The Pan European Ecological Network: PEEN. Landscape Ecology 26: 311-326.

Joubert L. and Samways M.J. (2011). Ecological networks: the key to biodiversity conservation. Quest 7: 30-32.

Joubert L. and Samways M.J. (2014). Equivalence of grasslands in an ecological network and a World Heritage Site. Biodiversity and Conservation 23: 2415-2426.

Kietzka G.J., Pryke J.S. and Samways M.J. (2015). Landscape ecological networks are successful in supporting a diverse dragonfly assemblage. Insect Conservation and Diversity 8: 229-237.

Koch A., McBratney A. and Lal R. (2012). Global soil week: Put soil security on the global agenda. Nature 492: 186-186.

Koch A., McBratney A., Adams M., Field D., Hill R., Crawford J., Minasny B., Lal R., Abbott L., O'Donnell A. and Angers D. (2013). Soil security: Solving the global soil crisis. Global Policy 4: 434-441.

Kotze D.J. and Samways M.J. (2001). No general edge effects for invertebrates at Afromontane forest/grassland ecotones. Biodiversity and Conservation 10: 443-466.

Lawes M.J., Everard D. and Eeley H.A.C. (1999). Developing environmental criteria and indicators for sustainable plantation management: The South African perspective. South African Journal of Science 95: 461-469.

Liu H., Lu X. and Zhang S. (2003). Landscape biodiversity of wetlands and their changes in 50 years in watersheds of the Sanjiang Plain. Acta Ecologica Sinica 24: 1472-1479.

Longcore T. (2003). Terrestrial arthropods as indicators of ecological restoration success in coastal sage scrub (California, U.S.A.). Restoration Ecology 11: 397-409.

Loranger-Merciris G., Imbert D., Bernhard-Reversat F., Ponge J.F. and Lavelle P. (2007). Soil fauna abundance and diversity in a secondary semi-evergreen forest in Guadeloupe (Lesser Antilles): Influence of soil type and dominant tree species. Biology and Fertility of Soils 44: 269-276.

Lu X. and Wang R. (1995). Study on wetland biodiversity in China. Chinese Geographical Science 6: 15-23.

MacArthur R. (1955). Fluctuations of animal populations and a measure of community stability. Ecology 36: 533-536.

Majer J.D. (1997). Invertebrates assist the restoration process: An Australian perspective. In: Urbanska K.M., Webb N.R. and Edwards P.J. (Eds.). Restoration ecology and sustainable development. University Press, Cambridge.

Matthews S. (2008). Forestry firm ploughs back into nature. Forestry and Wetlands (Sept/Oct): 29-31.

McCoy E.D. and Mushinsky H.R. (2002). Measuring the success of wildlife community restoration. Ecological Applications 12: 1861-1871.

McNaughton S.J. (1977). Diversity and stability of ecological communities: A comment on the role of empiricism in ecology. The American Naturalist 111: 515-525.

Mensing D.M., Galatowitsch S.M. and Tester J.R. (1998). Anthropogenic effects on biodiversity of riparian wetlands of a northern temperate landscape. Journal of Environmental Management 53: 349-377.

Moller T.R. and Rordam C.P. (1985). Species numbers of vascular plants in relation to area, isolation, and age of ponds in Denmark. Oikos 45: 8-16.

Neke K.S., and du Plessis M.A. (2004). The threat of transformation: Quantifying the vulnerability of grasslands in South Africa. Conservation Biology 18: 466-477.

Nichols O.G. and Nichols F.M. (2003). Long-term trends in faunal recolonization after bauxite mining in the jarrah forest of southwestern Australia. Restoration Ecology 11: 261-272.

Noss R.F. and Cooperrider A.Y. (1994). Saving nature's legacy: Protecting and restoring biodiversity. Island Press, Washington, D.C.

Oades J.M. (1993). The role of biology in the formation, stabilization and degradation of soil structure. Geoderma 56: 377-400.

Odum E.P. and Odum H. (1953). Fundamentals of ecology. Philadelphia, Saunders.

Pacini A., Mazzoleni S., Battisti C. and Ricotta C. (2009). More rich means more diverse: Extending the 'environmental heterogeneity hypothesis' to taxonomic diversity. Ecological Indicators 9: 1271-1274.

Passell H.D. (2000). Recovery of bird species in minimally restored Indonesian thin strips mines. Restoration Ecology 8: 112-118.

Perry D.A. (1994). Forest Ecosystems. Johns Hopkins University Press, Baltimore.

Peterson G., Allen C.R. and Holling C.S. (1998). Ecological resilience, biodiversity, and scale. Ecosystems 1: 6-18.

Pritchett W.L. and Fisher R.F. (1987). Properties and Management of Forest Soils. Wiley, New York.

Pryke J.S. and Samways M.J. (2012). Conservation management of complex natural forests and plantation edge effects. Landscape Ecology 27: 73-85.

Reay S.D. and Norton D.A. (1999). Assessing the success of restoration plantings in a temperate New Zealand forest. Restoration Ecology 7: 298-308.

Reddy K.R. and Gale P.M. (1994). Wetland processes and water quality: A symposium overview. Journal of Environmental quality 23: 875-877.

Rhoades C.C., Eckert G.E. and Coleman D.C. (1998). Effect of pastures trees on soil nitrogen and organic matter: Implications for tropical montane forest restoration. Restoration Ecology 6: 262-270.

Robinson D.A., Hockley N., Dominati E., Lebron I., Scow K.M., Reynolds B., Emmett B.A., Keith A.M., de Jonge L.W., Schjonning P. and Moldrup P. (2012). Natural capital, ecosystem services, and soil change: Why soil science must embrace an ecosystems approach. Vadose Zone Journal 11: 1-20.

Robinson D.A., Lebron I. and Vereecken H. (2009). On the definition of the natural capital of soils: A framework for description, evaluation and monitoring. Soil Science Society of America Journal 73: 1904-1911.

Ruiz-Jaen M.C. and Mitchell Aide T. (2005). Restoration success: How is it being measured? Restoration Ecology 13: 569-577.

Sabo J.L., Sponseller R., Dixon M., Gade K., Harms T., Heffernan J., Jani A., Katz G., Soykan C., Watts J. and Welter J. (2005). Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86: 56-62.

Samways M.J. and Pryke J.S. (2016). Large-scale ecological networks do work in an ecologically complex biodiversity hotspot. Ambio 45: 161-172.

Samways M.J., Bazelet C.S. and Pryke J.S. (2010). Provision of ecosystem services by large scale corridors and ecological networks. Biodiversity and Conservation 19: 2949-2962.

Schwartz C.F., Thor E.C. and Elsner G. (1976). Wildland planning glossary. USDA Forest Service, Pacific Southwest Forest and Range Experimental Station. General Technical Report PSW 13.Shepard J.P., Lucier L.A. and Haines L.W. (1993). Industry and forest wetlands: Cooperative research initiatives. Journal of Forestry 5: 29-33.

Spellerberg I.F. and Hardes S.R. (1992). Biological conservation. Cambridge University Press, Cambridge, England.

Stephens S. and Wagner M.R. (2007). Forest plantations and biodiversity: A fresh perspective. Journal of Forestry 105: 307-313.

Tewari D.D. (2001). Is commercial forestry sustainable in South Africa? The changing institutional and policy needs. Forest Policy and Economics 2: 333-353.

Thrupp L.A. (2000). Linking agricultural biodiversity and food security: The valuable role of agrobiodiversity for sustainable agriculture. International Affairs 76: 283-297.

Tian G., Brussaard L., Kang B.T. and Swift M.J. (1997). Soil fauna mediated decomposition of plant residues under constrained environment and residue quality conditions. In: Cadish G. and Giller K.E. (Eds.). Driven by nature: Plant litter quality and decomposition. CAB International, Wallingford, Oxon.

Tilman D. (1996). Biodiversity: Population versus ecosystem stability. Ecology 77: 350-363.

Tilman D. (1997). Biodiversity and ecosystem functioning. Nature's Services: Societal Dependence on Natural Ecosystems: 93-112.

Tilman D., Fargione J., Wolff B., D'Antonio C., Dobson A., Howarth R., Schindler D., Schlesinger W.H., Simberloff D. and Swackhamer D. (2001a). Forecasting agriculturally driven global environmental change. Science 292: 281-284.

Tilman D., Reich P.B. and Isbell F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance or herbivory. PNAS 109: 10394-10397.

Titshall L. (2015). Managing our soils for sustainable production. SA Forestry Magazine: 1-5.

Tockner K., Pennetzdorfer D., Reiner N., Schiemer F. and Ward J.V. (1999). Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). Freshwater Biology 41: 521-535.

Tscharntke T., Clough Y., Wanger T.C, Jackson L., Motzke I., Perfecto I., Vandermeer J. and Whitbread A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. Biological Conservation 151: 53-59.

van Aarde R.J., Ferreira S.M., Kritzinger J.J., van Dyk P.J., Vogt M. and Wassenaar T.D. (1996). An evaluation of habitat rehabilitation on coastal dune forest in northern KwaZulu-Natal, South Africa. Restoration Ecology 4: 334-345.

Vanbergen A.J., Watt A.D., Mitchell R., Truscott A.M., Palmer S.C.F., Ivits E., Eggleton P., Jones T.H. and Sousa J.P. (2007). Scale-specific correlations between habitat heterogeneity and soil fauna diversity along a landscape structure gradient. Oecologia 153: 713-725.

Vandermeer J. and Perfecto I. (1995). Breakfast of biodiversity: The truth about rainforest destruction. Institute for Food and Development Policy, Oakland.

Ward J.V. (1989). The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society: 2-8.

Warren M.W. and Zou X. (2002). Soil macrofauna and litter nutrients in three tropical tree plantations on a disturbed site in Puerto Rico. Forest Ecology and Management 170: 161-171.

Weiermans J., and van Aarde R.J. (2003). Roads as ecological edges for rehabilitating coastal dune assemblages in northern KwaZulu-Natal, South Africa. Restoration Ecology 11: 43-49.

Woomer P.L. and Swift M.J. (1994). The biological management of tropical soil fertility. Wiley, Chichester, U.K.

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

Yu K., Li D. and Li N. (2006). The evolution of greenways in China. Landscape and Urban Planning 76: 223-239.

Chapter 2
Hydromorphic grasslands for water conservation complement dry grasslands in their litter and topsoil arthropods across landscape mosaics.

ABSTRACT

Natural remnants, such as Afromontane forests and grasslands, have received much attention with regards to their conservation value within ecological networks (ENs), yet the value of grassland on hydromorphic soils remains poorly understood, especially with regards to topsoil and leaf litter macro-arthropods. Here, the aim of this study was to determine the diversity and distribution of topsoil and leaf litter arthropods within four dominant biotopes (indigenous forests, pine plantations, dry grasslands and hydromorphic grasslands) occurring within an EN-plantation landscape mosaic in KwaZulu-Natal, Midlands. Arthropods were collected using three methods, namely pitfall trapping, active searching and the use of Winkler bags to extract leaf litter arthropods. The natural, untransformed biotopes (i.e. natural forest, dry and hydromorphic grassland) had higher species diversity, both ground-living and litter, compared to the transformed biotope (i.e. pine plantation). Hydromorphic grasslands in particular had a relatively high proportion of unique species, and differed significantly from the other dominant biotopes with regard to arthropod assemblage structure, but not in species richness. Dry and hydromorphic grasslands had a high proportion of shared species, although their assemblage structure differed significantly due to differences in soil characteristics, including soil compaction, pH and moisture. Hydromorphic grasslands are a unique and valuable landscape element that contributes to landscape heterogeneity and overall biodiversity within the production landscape. Although hydromorphic and dry grasslands are classified as one biotope, I found that they were two distinct biotopes, both of which should be conserved. While natural biotopes such as indigenous forests and wetlands are well protected under laws and regulations, dry grasslands have been granted very little protection. Owing to their high biological diversity and unique assemblage structure, they contribute to landscape biodiversity and should thus be included in conservation efforts to maintain and conserve overall biodiversity within these landscapes.

2.1. Introduction

Landscape planning for conservation is of great importance in high-impact production systems, such as timber production. Timber plantations are often perceived as a major conservation concern (Brockerhoff et al., 2008) and increased pressure exerted on lands within timber production landscapes, especially on the soil, water and biodiversity, calls for conservation measures to ensure their long-term sustainability (Tetzlaff et al., 2007). The most suitable land for timber production in KwaZulu-Natal (KZN), South Africa, occurs within the threatened grassland biotope, which includes important components such as indigenous forests and wetlands (Eeley et al. 2002; Neke and du Plessis 2004; Samways et al., 2010a). Here, ecological networks (ENs) have been applied on a large scale in exotic timber plantations (Samways et al., 2010a). ENs aim to structurally and functionally connect remnant

14

areas of high natural value across the production landscape (Samways and Pryke, 2016) to mitigate the impact of these production areas (Samways, 2007; Samways et al., 2010a). Pryke and Samways (2012a) found that ENs can function as extensions of protected areas, making them areas of high conservation value. On average, one-third of a plantation landscape remains unplanted to timber to comply with national environmental legislation and industry regulations (Kirkman and Pott, 2002) and these interconnected, unplanted areas form the EN within the plantation landscape (Samways and Pryke, 2016). These ENs consist of natural grasslands, indigenous forests and wetlands, which have different species assemblages and different ecosystem functions in these landscapes (Joubert and Samways, 2011).

Wetland (i.e. hydromorphic soil) ecosystems are valuable assets within a landscape as they contribute to biodiversity and ecosystem functioning (Hannson et al., 2005). Therefore these ecosystems are of great conservation value as they are considered one of the most biologically diverse ecosystems (Ward, 1989; Tockner et al., 1999; Liu et al., 2003), provide a variety of ecosystem services and provide suitable habitat for a wide range of species (Lu and Wang, 1995; Hannson et al., 2005; Sabo et al., 2005). One of the most important ecosystem services provided by wetlands is their significant role in the provision of water (Constanza et al., 1997; Zedler, 2000; Hansson et al., 2005). This particular service depends greatly on water pathways within that landscape at different spatial and temporal scales (Curmi et al., 1998). As a result, wetland ecosystems are susceptible to changes in the quality and quantity of their water supply (Erwin, 2009). Therefore, as grasslands within ENs can improve hydrological functions (Samways et al., 2010a), the planting of trees on hydromorphic soils within these ENs is often avoided (Dye and Jarmain, 2004). This is accomplished through a process termed "delineation" within the South African timber industry (Dye and Jarmain, 2004). Delineation can be defined as either the proactive avoidance of planting of trees on hydromorphic soils, or the removal of planted trees on hydromorphic soils. Natural remnants, such as Afromontane forests and grasslands, have received much attention with regards to their biodiversity value within EN-plantation landscapes (Joubert and Samways, 2014; Samways and Pryke, 2016; Yekwayo et al., 2016). Grasslands as a whole have received much attention, but to date there has been no distinction between dry and wet grasslands, and therefore, the value of grasslands on hydromorphic EN soils still remains poorly understood. As plant assemblages between wet and dry grasslands are visibly different, there is reason to assume the fauna occurring in these biotopes will also be distinct.

Studies on a wide variety of invertebrate (Pryke and Samways, 2012a; Kietzka et al., 2015; Samways and Pryke, 2016, Yekwayo et al., 2016) and plant taxa (Joubert and Samways, 2014; Joubert et al., 2016) in these ENs have increased our understanding of species diversity and their distribution in production landscapes, and have informed local EN design and management. One group of organisms which is of great functional importance to ecosystems is invertebrates occurring in the leaf litter and topsoil layer (Warren and Zou, 2002; Barrios, 2007). The stability of a soil ecosystem is closely linked to the relative abundance and species richness within functional groups (De Ruiter et al., 1995; Barrios, 2007), which include arthropod detritivore, herbivore, omnivore and predator species (Tilman et al., 1997). However, the diversity of soil fauna and their linkage to the whole ecosystem structure and functioning is poorly known (Bernhard-Reversat et al., 2001; Höfer et al., 2001; Warren and Zou, 2002), globally and in South Africa (Janion-Scheeper et al., 2016). Very few studies have been done on these organisms within these landscapes in South Africa (but see Yekwayo et al., 2016), and our knowledge on them remains limited.

This study examines the diversity and assemblage structure of leaf litter and topsoil macro-arthropods within dominant biotopes in an EN-plantation landscape mosaic. I focus on hydromorphic soil grasslands and determine whether this biotope has a unique and characteristic assemblage structure compared to other dominant biotopes within the landscape, as well as which environmental characteristics influence these results. This will help determine the unique biodiversity value of both hydromorphic and dry soils within a plantation landscape. Thus, the objectives of this study are to test 1) whether overall species richness and assemblage structure, along with species richness and assemblage structure of various functional guilds (detritivores, herbivores, omnivores and predators), differed between the four biotopes, 2) which environmental variables best explain the variations in species richness and assemblage structure between the four biotopes. I hypothesize that hydromorphic and dry grasslands will each have a unique arthropod assemblage structure compared to the other dominant biotopes, driven by strong differences in the physical and biotic characteristics of the biotopes. Although hydromorphic soils are structurally similar to dry grasslands, we need to understand how unique these hydromorphic grasslands are to be able to plan and conserve these complex systems within production landscapes.

2.2. Materials and methods

2.2.1. Study area and design

This study was conducted in South Africa on two separate timber plantation estates in KwaZulu-Natal, Midlands. The region is dominated by Midlands Mistbelt Grassland and has sub-tropical climatic conditions with a summer rainfall (Mucina and Rutherford, 2006). The two plantation estates are Good Hope (29°39'09.8"S, 29°57'09.8"E) and Mount Shannon (29°41'11.8"S, 29°58'43.0"E), which were selected here as they both consist of a heterogeneous landscape (Samways and Niba, 2010) (Figure 2.1). These plantations contain commercial pine blocks (*Pinus* spp.), remnant grassland corridors that include dry and hydromorphic grasslands, and Afromontane forest patches. For this study, 10 sites were selected for each of the four dominant biotopes, namely dry grasslands, hydromorphic grasslands, natural forests, as well as pine plantation blocks, making a total of 40 sites. To distinguish between dry and hydromorphic grasslands, I primarily used soil GIS data provided by the Mondi environmental specialist for Midlands (J. Shuttleworth pers. comm.), which was then subsequently verified in the field by assessing general plant composition. Fieldwork was conducted in summer, between February and March 2016.

2.2.2. Arthropod sampling and identification

Some invertebrate families can be under- or overestimated by the type of sampling method used, which emphasises the importance of combining sampling methods to attain the most information and high capture rates for a variety of species (Mommertz et al., 1996; Zanetti et al., 2016). I used pitfall trapping as it is effective at sampling surface-active invertebrates (Standen, 2000; Prasifka et al., 2007), it is simple, efficient (Southwood, 1978), and it is a valuable method for sampling invertebrate assemblages (Hammond, 1990). To complement the pitfall trapping, I also extracted invertebrates which occur at or below the soil surface using Winkler bags (Donegan et al., 1997; Perry et al., 1997) and hand-collected invertebrates (i.e. active searching) to obtain information on species diversity and relative abundance of a wide variety of leaf litter and topsoil invertebrates (Mesibov et al., 1995).

Pitfall trapping was conducted using four 300 ml plastic cups (9.5 cm diameter and 8 cm deep) which were placed in a 2 m^2 grid with the rim of the trap flush with the soil surface. Traps were filled with 50 ml 60% ethylene glycol (with two drops of detergent to break the surface tension). Pitfall traps were left in the field for five days, after which arthropods captured were transferred to 75% ethanol.
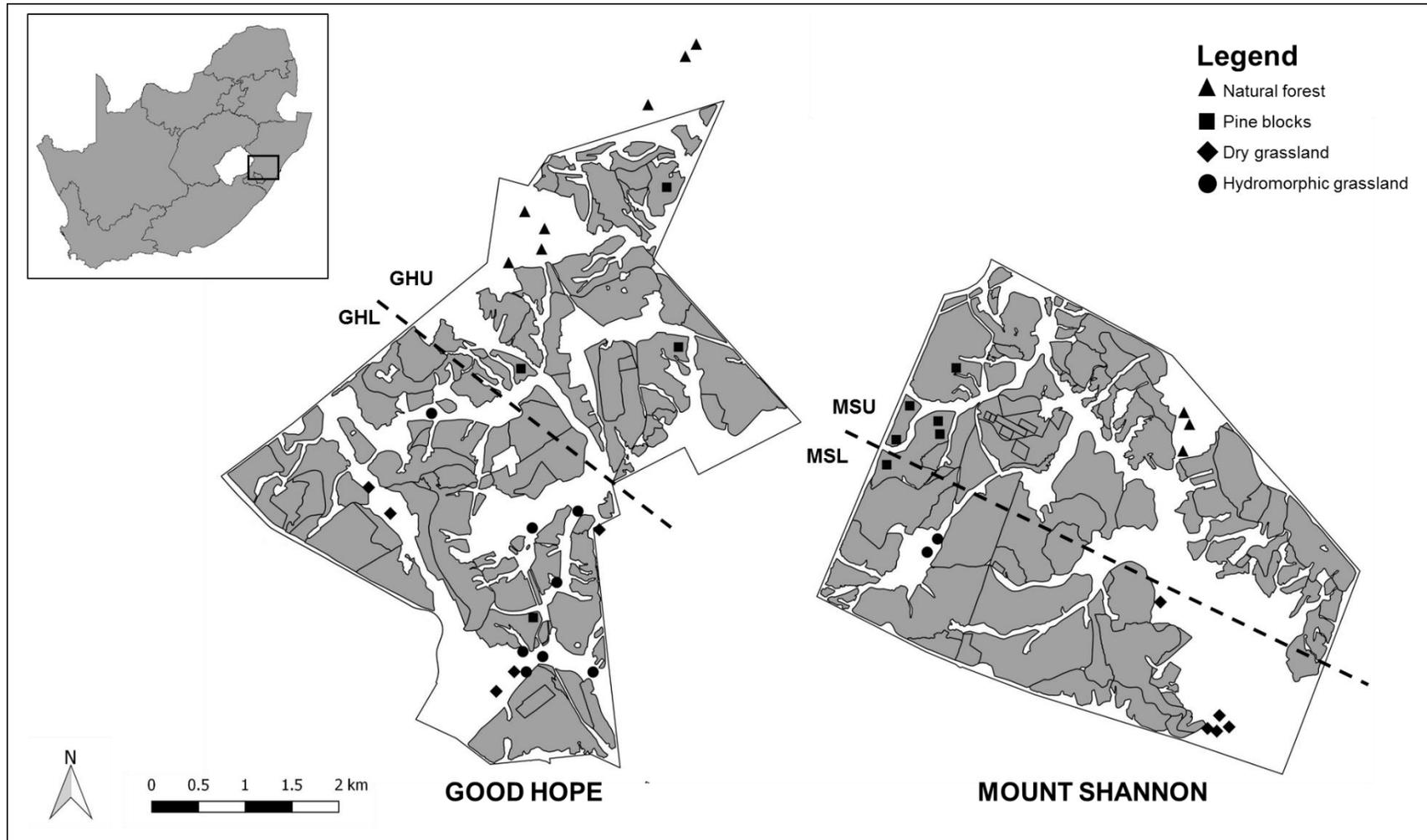
Figure 2.1: The focal estates of Good Hope and Mount Shannon in Midlands, KwaZulu-Natal, South Africa. It illustrates the division of these two plantation estates into four classes (GHU = Good Hope upper, GHL = Good Hope lower, MSU = Mount Shannon upper and MSL = Mount Shannon lower). Plantation blocks (grey) and non-plantation areas (white) are also indicated.

Approximately 2 L of leaf litter was also collected at each site, which was divided into two mesh bags (22 cm by 30 cm, with a mesh size of 0.5 cm), which were placed and enclosed within a Winkler bag for each site. A 130 ml plastic jar was attached to the bottom of the Winkler bag, and contained 50 ml of 70 % ethylene glycol (with two drops of detergent). The leaf litter was allowed to dry out for five days, causing the arthropods to move downwards out of the leaf litter, as litter arthropods instinctively move downwards in search of moist conditions. After five days, the mesh bags were removed from the Winkler bag, and searched for any remaining arthropods within the leaf litter. All arthropods collected from the Winkler bags were preserved for later identification. A 1 m^2 quadrat was also placed at random within each site to actively search for leaf litter and topsoil arthropods. Active searching involved two people searching for arthropods for 10 min within the quadrat. Litter within the quadrat was over turned to detect arthropods under the litter layer.

Arthropods were sorted into morphospecies, counted and identified to family level using relevant literature (Dirsh (1965), Scholtz and Holm (1985), Keep and Ledger (1990), Walker (1991), Dippenaar-Schoeman and Harvey (2000), Picker et al. (2004), Haddad et al. (2006) and Janion-Scheepers et al. (2015)) for Amblypygi, Amphipoda, Blattodea, Coleoptera, Collembola, Dermaptera, Hemiptera, Hymenoptera (Formicidae only), Isopoda, Ixodida, Lithobiomorpha, Opiliones, Oribatida, Orthoptera, Phasmatodea, Polydesmoidea, Pseudoscorpiones, Scorpiones, Sphaerotheriidae, Spirostreptida, Thysanura and Trombidiformes. Specimens of the order Araneae was sent to a spider specialist for identification. The collected spider specimens are now kept in the National Collection of Arachnida at the National Museum, Pretoria. Reference specimens, excluding that of Araneae, are maintained in Stellenbosch University's entomology museum in the Department of Conservation Ecology and Entomology.

2.2.3. Biotic and abiotic environmental variables

Various vegetation and soil characteristics were recorded within each site. At each site, a 1 m^2 quadrat was placed at random. Within the quadrat, a soil moisture and pH meter (Kelway, Inc.) and a soil penetrometer (Lang Penetrometer, Inc.) were used to measure soil moisture, pH and soil compaction. This was recorded three times and the average was used in the analyses. Various vegetation characteristics were also recorded within the quadrat, including percentage vegetation cover, vegetation height, the number of plant species, percentage leaf litter, as well as the percentage cover of herbaceous, shrub and grass species, along with percentage bare ground.

In a 5 m radius surrounding the quadrat, other environmental variables were recorded, including percentage canopy cover, shade, dead wood cover, rock cover and the percentage of trees occurring within 80 m^2. Landscape variables were also calculated in QGIS (version 2.18.0) (QGIS Development Team, 2009). These landscape variables include the slope, elevation, aspect, amount of focal biotope in the surrounding landscape (estimated as the percentage of the sampled biotope type in a 1 km radius around each site), and the percentage of transformed landscape (estimated as the percentage of pine plantation within a 1 km radius of each site).

2.2.4. Data analysis

A species accumulation curve across all biotopes was made in Primer 6 (version 6.1.13) (PRIMER-E, 2008) to determine whether the sampling of arthropods reached an asymptote (Gotelli and Colwell, 2001). Species estimates Chao 2 and Jacknife 2 were included for the species accumulation curve. As observed species richness is strongly dependent on sampling effort (i.e. sample size) (Colwell et al., 2004), non-parametric species richness estimators are used to deal with the problem of sampling effort dependence (Melo, 2004). Chao 2 also produces the least biased estimation of species richness (Colwell and Coddington, 1994; Brose, 2002). Non-parametric species richness estimators, Chao 2 and Jacknife 2, were used, as they are the most capable of estimating the species diversity within a highly diversity community (Colwell and Coddington, 1994). The proportion of shared and unique species between and within biotopes was also calculated.

Generalized linear mixed models (GLMMs) were performed in R (version 3.3.1.) (R Core Team, 2016) using the "lme4" package (Bates et al., 2014), to determine the effect of biotope type on Simpson's Evenness Index, species richness and functional guild species richness. Simpson's Diversity Index (D) was calculated using Primer 6 (version 6.1.13) (PRIMER-E, 2008), of which Simpson's Evenness Index ($E_{1/D}$) was calculated (Samways et al., 2010b). I used the inverse of Simpson's Evenness which shows the larger the value, the less even the assemblage and the greater the diversity of the assemblage. GLMMs were based on either a Poisson error (Consul and Jain, 1973; Bolker et al., 2009) or Gaussian distribution (Goodman, 1963; Bishop, 2006), and log link function was specified for the models. Biotope type (Afromontane forest, dry grassland, hydromorphic grassland and pine blocks) was included as the fixed variable and estate section as a random variable (this factor divides the plantation estates in half to get four regions; see Figure 2.1) to account for the uneven spatial distribution of sites.

Probability (P) and Chi-square (χ^2) values were estimated, after which a Tukey post-hoc test was performed when there were significant effects using the multcomp package in R (Bretz et al., 2002; Bretz et al., 2008) to determine pairwise differences between the four biotopes.

Of 22 recorded environmental variables, some variables were highly correlated, based on Spearman's rank order correlations (Appendix A). To account for this, one variable was selected to include in the initial model between highly correlated variables based on their biological relevance. Eleven environmental variables were selected to include in the final models. The variables selected were elevation, aspect, soil moisture, number of plant species, percentage vegetation cover, leaf litter, shade, rock cover and dead wood. The amount of focal biotope in the landscape and percentage transformed landscape (i.e. pine plantation) within a 1 km radius was also included. For grassland biotopes, environmental variables such as shade and dead wood cover was not included in the models, as it was not applicable to these biotopes.

GLMMs were then conducted in R (version 3.3.1.) (R Core Team, 2016) using the "lme4" package (Bates et al., 2014), to determine which environmental variables best explained the variations in Simpson's Evenness, species richness and functional guild species richness. The initial model included all the selected environmental variables, after which a backward-stepwise selection of variables was done to obtain the model with the best fit. The best models were those that showed no over-dispersion of variance and had the lowest Akaike Information Criterion (AIC) value (Wagenmakers and Farrell, 2004). The grassland sites (dry and hydromorphic) and wooded sites (pine plantations and natural forests) are structurally and compositionally very different and this may obscure finer-scale environmental influences. Thus, two separate models were constructed for grassland and wooded sites.

To visualize the assemblage structure of leaf litter and topsoil arthropods between the dominant biotopes, as well as the assemblage structure of each functional guild, Canonical Analysis of Principal coordinates (CAP) was done in Primer 6 (Samways et al., 2010b). A permutational multivariate analysis of variance (PERMANOVA) was done in Primer 6 to test for significant differences in the arthropod assemblages between the four dominant biotopes, as well as the assemblage structure of each functional guild. "Biotope" was used as a fixed factor and "estate section" was used as a random variable (Figure 2.1). To obtain the Pseudo-F statistic and P-values, the test was permutated 9999 times. The analysis was performed using the Bray-Curtis similarity measure, using square-root

transformed abundance data (Legendre and Gallagher, 2001). Pairwise comparisons were then conducted using PERMANOVA to determine which biotopes were significantly different from each other, with regards to arthropod assemblage and functional guild structure.

Distance-based linear modelling (DistLM) was conducted in Primer 6 to determine which of the recorded environmental variables best described the distributions of leaf litter and topsoil arthropod assemblages and functional guild structure between the wooded sites (natural forest and pine plantation) and grassland sites (dry and hydromorphic grassland). The environmental data used were based on the Euclidean distance measure using a Log (X+1) transformation and normalization (Anderson, 2001). When selecting a model for analysis, the model with the best fit is the model with the lowest AIC value (Budoff et al., 2009; Megraud et al., 2012). Therefore, the DistLM model was run using the forward selection procedure with AICc selection criteria, as the backward selection procedure resulted in models with higher AIC values.

2.3. Results

A total of 9 404 individuals were sampled, consisting of 24 different arthropod orders, 76 arthropod families and 204 species across all biotopes (see Appendix B). The species accumulation curve indicated that the sampled species approached an asymptote (see Appendix C). Species estimators Chao 2 and Jacknife 2, indicated similar trends for species richness (Table 2.1). The dominant arthropod orders were spiders (33 spp.) and beetles (32 spp.) within the wooded biotopes, and beetles (42 spp.) and spiders (34 spp.) within the grassland biotopes. Predators were the most dominant functional guild within the wooded biotopes (57 spp.), followed by omnivores (29 spp.), herbivores (26 spp.) and detritivores (13 spp.). Predators also dominated the grassland biotopes (65 spp.), followed by omnivores (41 spp.), herbivores (35 spp.) and detritivores (16 spp.).

Table 2.1: Species accumulation curve results of overall observed species (Sobs) assemblage structure and functional guild assemblage structure between natural forests, pine blocks, dry grasslands and hydromorphic grasslands. Species estimators Chao 2 and Jacknife 2 included in analysis.

Assemblage	Sobs	Chao 2 ± SE	Jacknife 2 ± SE
Overall	204	214.58 ± 6.73	228.49 ± 9.33
Detritivores	20	20.08 ± 0.71	19.92 ± 0.85
Herbivores	46	52.44 ± 1.74	52.58 ± 2.41
Omnivores	53	60.01 ± 1.87	60.04 ± 2.56
Predators	85	89.30 ± 2.43	93.64 ± 3.55

2.3.1. Response of species richness and evenness to biotope type

Overall species richness was significantly different between biotope types ($\chi^2 = 14.58$, P = 0.002, df = 3) (Figure 2.2A). Overall species richness of pine plantations was significantly lower than natural forests and dry grasslands. Simpson's Evenness was also significantly different between biotope types ($\chi^2 = 68.21$, P < 0.001, df = 3) (Figure 2.2B). Pine plantations and hydromorphic grasslands had significantly lower evenness than natural forests and dry grasslands, indicating lower diversity.

Arthropod detritivore ($\chi^2 = 27.09$, P < 0.001, df = 3) (Figure 2.2C), herbivore ($\chi^2 = 30.72$, P < 0.001, df = 3) (Figure 2.2C), omnivore ($\chi^2 = 33.59$, P < 0.001, df = 3) (Figure 2.2C) and predator ($\chi^2 = 24.34$, P < 0.001, df = 3) (Figure 2.2C) species richness all differed significantly between the four dominant biotopes. Natural forests were significantly higher than all other biotopes for detritivore and predator species richness. Pine blocks were significantly lower in herbivore species richness compared to other biotopes. Omnivore species richness was significantly higher in dry grasslands compared to all other biotopes, while hydromorphic grasslands were significantly richer than natural forests.
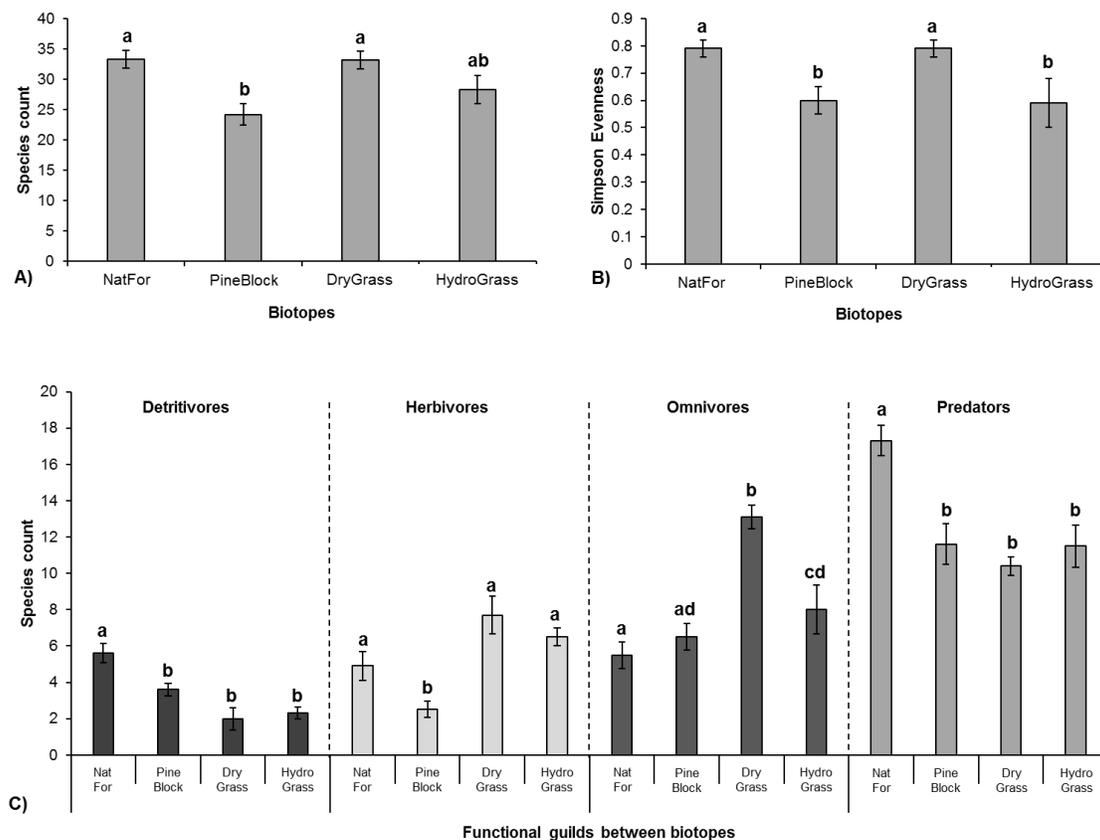
Figure 2.2: Graphical illustration of mean (±SE) overall species richness (A), inversed Simpson Evenness (B) and functional guild species richness (C) between natural forests (NatFor), pine blocks (PineBlock), dry grasslands (DryGrass) and hydromorphic grasslands (HydroGrass). Letters above each bar indicate significantly different means between biotopes based on Tukey's post-hoc tests, with significance of p < 0.05.

23

Table 2.2: Generalized linear mixed model (GLMM) results for overall species richness and functional guild species richness between wooded and grassland biotope types, as well as Simpson's Evenness between all biotope types. Results show the variables selected in the final model, which best explained the variations in species richness and assemblage evenness between the different biotope types. Significant effects from GLMMs for chi-square values indicated with (*). The (+) or (−) value before chi-square values indicate the direction of the relationship based on Spearman's Rank Order correlations.

Response variable	Species richness										Simpson Evenness
Assemblage	Overall		Detritivore		Herbivore		Omnivore		Predator		Overall
Biotope type	Wooded	Grassland	Wooded	Grassland	Wooded	Grassland	Wooded	Grassland	Wooded	Grassland	All biotopes
Landscape and site-scale characteristics											
Site elevation (m)	-	(+) 7.71**	-	(+) 15.51***	-	(+) 3.91*	-	-	-	-	(−) 3.41
Focal biotope (%)	-	-	-	(−) 0.78	(−) 0.01	(+) 0.27	-	-	-	(−) 2.72	(−) 4.24*
Transformed landscape (%)	-	-	-	-	-	-	-	-	(−) 0.17	(+) 4.85*	-
Rock cover (%)	(-) 1.64	-	-	-	-	-	(−) 5.34*	-	-	-	-
Vegetation characteristics											
Number of plant species	(−) 0.47	-	(−) 2.47	(−) 2.74	-	-	(−) 0.27	(+) 1.35	(+) 0.46	-	(−) 0.18
Vegetation cover (%)	(+) 1.95	-	(+) 4.53*	-	(+) 0.37	(−) 0.04	(+) 0.01	-	(−) 1.33	-	(−) 3.08
Leaf litter cover (%)	-	(+) 16.38**	(+) 5.29*	(+) 7.79***	-	-	-	(−) 4.57*	-	(+) 4.70*	(+) 3.68
Soil characteristics											
Soil moisture (%)	-	(−) 2.45	(−) 5.61*	-	-	-	-	(−) 1.26	-	-	(−) 0.48

* P < 0.05; ** P < 0.01; *** P < 0.001

Generalized linear mixed models (GLMMs) showed Simpson's Evenness was influenced by elevation, soil moisture, vegetation cover, number of plant species, leaf litter cover, and percentage of focal biotope (Table 2.2). Overall species richness in wooded biotopes was influenced by vegetation cover, number of plant species and rock cover (Table 2.2). Overall species richness in grassland biotopes can be explained by elevation, leaf litter cover and soil moisture (Table 2.2).

Wooded detritivore species richness was influenced by vegetation cover, leaf litter cover, soil moisture and the number of plant species, whereas grassland detritivore species richness was influenced by site elevation, number of plant species and the percentage of focal biotope (Table 2.2). Wooded herbivore species richness was influenced by vegetation cover and the percentage of transformed landscape (i.e. pine plantation) occurring within 1 km radius, and grassland herbivore species richness was influenced by site elevation, vegetation cover and the percentage of focal biotope (Table 2.2). Wooded omnivore species richness was influenced by vegetation cover, number of plant species and rock cover, whereas grassland omnivore species richness was influenced by the number of plant species, soil moisture and leaf litter cover (Table 2.2). Wooded predator species richness was influenced by the number of plant species, vegetation cover and percentage transformed landscape occurring within 1 km radius, where grassland predator species richness was influenced by leaf litter cover, percentage of focal biotope and transformed landscape occurring within 1 km radius (Table 2.2).

2.3.2. Assemblage and functional guild structure between biotopes

The greatest number of unique species was within dry grasslands (32 spp.) and natural forests (32 spp.), followed by hydromorphic grasslands (26 spp.) and pine blocks (9 spp.) (Table 2.3). The proportion shared species was highest between the two grassland biotopes compared to the two wooded biotopes. Overall arthropod assemblage composition (F = 6.06, P = 0.001, df = 3) (Figure 2.3), along with detritivore (F = 4.77, P = 0.001, df = 3), herbivore (F = 3.15, P = 0.001, df = 3), omnivore (F = 6.09, P = 0.001, df = 3) and predator arthropod assemblage structure (F = 3.82, P = 0.001, df = 3) (Figure 2.4), significantly different among the four biotopes (Table 2.4).

Table 2.3: Proportion unique species (bold) and shared species (italic) between natural forest, pine block, dry grassland and hydromorphic grassland sites.

Biotopes	Natural forest	Pine blocks	Dry grassland	Hydromorphic grassland
Natural forest	**32.00**			
Pine blocks	*37.60*	**12.50**		
Dry grassland	*30.72*	*32.17*	**27.35**	
Hydromorphic grassland	*31.45*	*30.22*	*43.95*	**23.85**
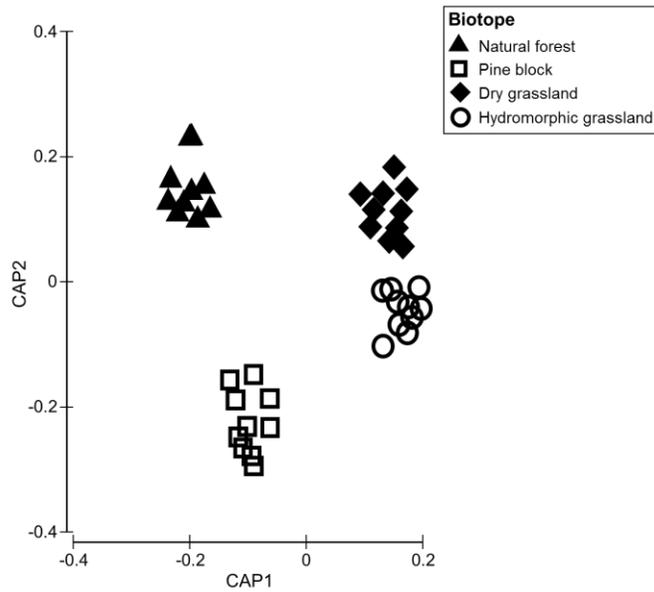
Figure 2.3: Canonical analysis of principal coordinates (CAP) for overall arthropod assemblage structure between natural forest, pine block, dry grassland and hydromorphic grassland sites.
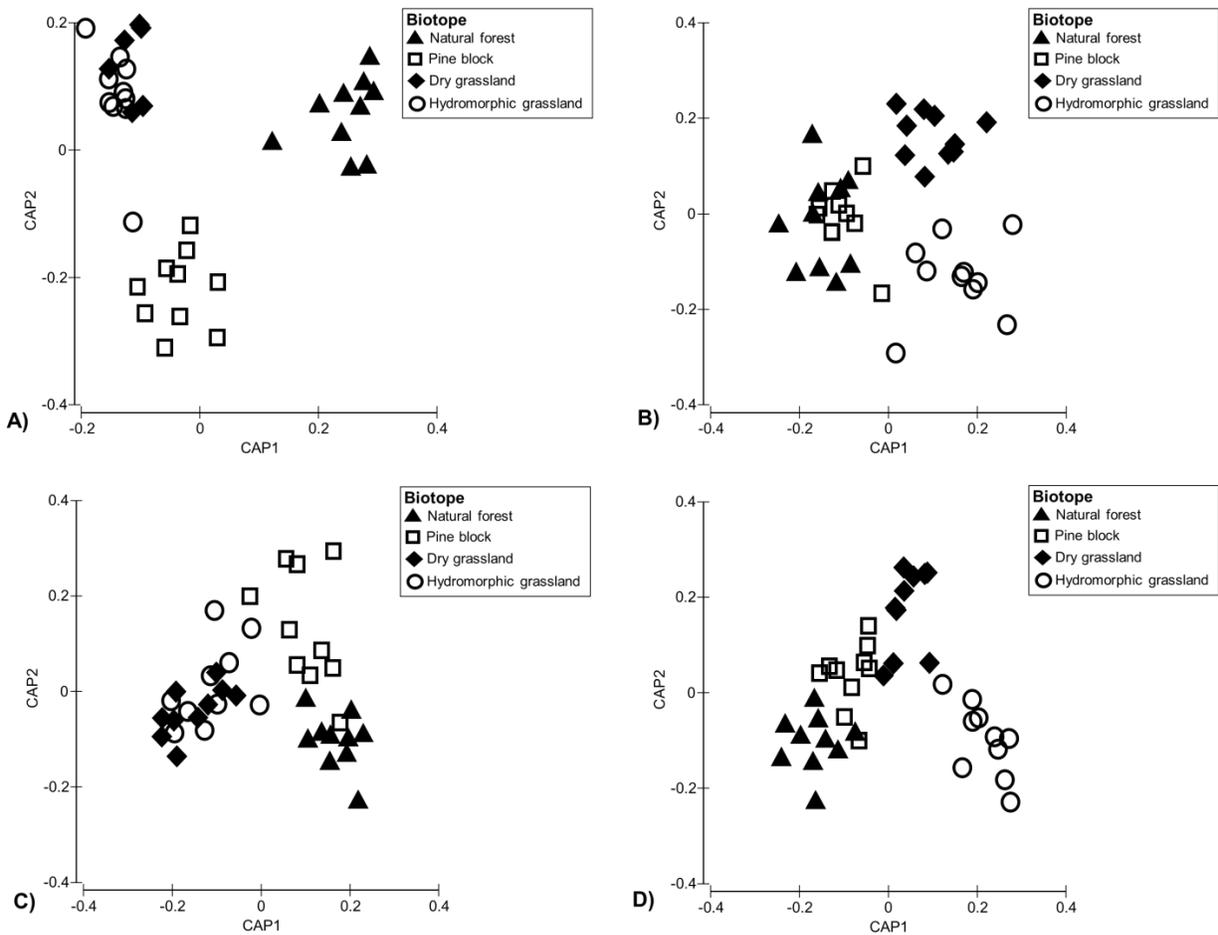
Figure 2.4: Canonical analysis of principal coordinates (CAP) for detritivore (A), herbivore (B), omnivore (C) and predator (D) arthropod assemblage structure between natural forest, pine block, dry grassland and hydromorphic grassland sites.

26

PERMANOVA pairwise tests showed that all biotope types differed significantly from each other with regards to overall assemblage structure (Table 2.4). With regards to functional guild assemblage structure, natural forests had significantly different detritivore assemblages from other biotopes, and the pine blocks differed from hydromorphic grasslands (Table 2.4). Except for natural forests and hydromorphic grasslands, all biotopes differed significantly in herbivore assemblage structure (Table 2.4). Furthermore, all biotopes differed significantly in omnivore assemblage structure, except for natural forests and pine blocks (Table 2.4). Predator assemblage structure differed significantly between all biotopes (Table 2.4).

Table 2.4: PERMANOVA Pseudo-F (bold) and pairwise test (t – value) results for overall arthropod assemblage and functional guilds assemblage structure between natural forest (NatFor), pine block (PineBlock), dry grassland (DryGrass) and hydromorphic grassland (HydroGrass) sites, with significant differences indicated with (*).

Biotopes	Overall	Detritivore	Herbivore	Omnivore	Predator
All sites	**6.06****	**4.77****	**3.15****	**6.09****	**3.82****
NatFor - PineBlock	1.55*	2.39**	1.44*	0.86	1.37*
NatFor - DryGrass	3.12**	2.72***	1.81***	3.52***	2.06**
NatFor - HydroGrass	1.79**	2.24***	1.21	1.88***	1.59**
PineBlock - DryGrass	2.15**	1.50*	1.86**	2.09***	1.46*
PineBlock - HydroGrass	2.35**	1.99**	1.69**	2.09***	2.16**
DryGrass - HydroGrass	1.57**	1.09	2.02**	1.77**	1.30*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Distance based linear modelling (DistLM) analysis showed vegetation cover explained 27.27% of the variation in arthropod assemblage structure for wooded (natural forest and pine plantation) biotopes (Table 2.5). The percentage shade and vegetation cover cumulatively explains 52.81% of the variation in detritivore assemblage structure, whereas the percentage of leaf litter only explains 11.91% of the variation in herbivore assemblage structure (Table 2.5). The number of plant species explains 16.42% of the variation in omnivore assemblage structure, whereas the percentage of vegetation cover explains 24.05% of the variation in predator assemblage structure (Table 2.5).

For grassland (dry and hydromorphic grassland) biotopes, vegetation cover explains 16.35% of the variation in arthropod assemblage structure (Table 2.5). Soil moisture explains 9.98% of the variation in detritivore assemblage structure and 15.87% of the variation in herbivore assemblage structure (Table 2.5). The percentage of vegetation cover explains 20.04% of the variation in omnivore assemblage structure, whereas the percentage of focal biotope explains 14.25% of the variation in predator assemblage structure (Table 2.5).

Table 2.5: Distance based on linear modelling (DistLM) results indicating which environmental variables best describe overall arthropod assemblage and feeding guild assemblage structure between wooded and grassland biotope types. Marginal tests show the contribution of individual variables to the variation in assemblage structures, whereas sequential tests (bold) indicate the subset of variables which best explain the variation in assemblages. Significant effects indicated with (*).

Assemblage	Overall		Detritivore		Herbivore		Omnivore		Predator	
Biotopes	**Wooded**	**Grassland**	**Wooded**	**Grassland**	**Wooded**	**Grassland**	**Wooded**	**Grassland**	**Wooded**	**Grassland**
Landscape and site-scale characteristics										
Site elevation (m)	4.01**	1.61	6.75**	1.39	1.53	1.03	2.57*	0.79	3.63**	1.72*
Site aspect (North)	2.70*	1.67	4.14*	0.83	1.32	2.25*	1.96	1.58	2.52**	2.04**
Site aspect (East)	0.67	1.39	0.33	1.17	0.71	1.04	0.71	1.36	0.71	1.48
Site aspect (South)	2.10*	0.84	2.93	0.36	1.44	1.58	1.86	0.68	1.78	1.36
Focal biotope (%)	1.36	2.48**	0.94	1.08	0.97	3.37**	2.14*	2.37*	1.09	**2.99***
Transformed landscape (%)	1.65	1.70	1.74	1.17	1.75	0.40	1.58	1.44	1.35	2.13**
Shade cover (%)	2.24*	-	**2.74**	-	1.30	-	2.07*	-	2.19*	-
Dead wood cover (%)	2.13*	-	2.83	-	1.63	-	1.23	-	1.94*	-
Rock cover (%)	2.20*	1.33	3.73*	1.50	0.99	1.45	1.59	1.59	1.90*	0.74
Vegetation characteristics										
Number of plant species	3.19**	2.10*	4.85**	1.63	1.12	2.34*	**3.54***	2.48*	2.41*	0.75
Vegetation cover (%)	**6.75***	**3.52***	**14.31***	0.66	2.41**	3.10**	3.49**	**4.51**	**5.70***	1.88*
Leaf litter cover (%)	6.60***	0.78	13.86***	0.69	**2.43**	0.52	3.37**	0.76	5.61***	0.74
Soil characteristics										
Soil moisture (%)	4.58***	3.16**	8.21***	**1.66**	1.46	**3.40**	2.76*	3.79**	4.44***	2.43**

* P < 0.05; ** P < 0.01; *** P < 0.001

28

2.4. Discussion

2.4.1. Effect of biotope type and environmental variables on species richness and assemblage structure

Overall wooded (natural forest and pine plantation) and grassland (dry and hydromorphic grassland) biotopes did not differ significantly from each other with regards to overall arthropod species richness, but they did differ significantly in terms of their arthropod assemblage structure. This corresponds with other studies that show that wooded arthropod assemblages significantly differ from those in grasslands (Pinheiro et al., 2010; Tothmeresz et al., 2014; Bogyó et al., 2015; Ohwaki et al., 2015, Yekwayo et al., 2016). This is to be expected, considering their major structural differences, with other studies showing arthropod species diversity and community structure can be affected by land use and habitat structure (McIntyre et al., 2001; Benton et al., 2003; Weibull et al., 2003). Yet here, even among biotopes within the wooded and grassland categories, there were significant differences in species assemblages. The physical and chemical characteristics of the soil (e.g. soil moisture) and vegetation characteristics (e.g. vegetation cover and leaf litter quantity), were consistent key factors contributing to the variation in overall and functional guild species richness and assemblage structure between the four biotopes. This is in line with previous studies showing that the physical and chemical properties of soil (Ponge, 1999; Hartley et al., 2003), vegetation structure and complexity (Lassau and Hochuli, 2004; Schaffers et al., 2008; Vergnes et al., 2012) and leaf litter quantity and quality (Höfer et al., 1996; Höfer et al., 2001) can contribute to arthropod community structure.

The pine blocks had lower species diversity compared to natural untransformed biotopes. This agrees with Brockerhoff et al. (2008) who found that pine plantations generally have lower species diversity compared to natural habitats. Pine plantations generally are less complex and have less habitat diversity and complexity compared to natural forest (Brockerhoff et al., 2008). Furthermore, more complex habitat structure is often linked to greater arthropod diversity, which is due to greater niche diversity (Samways et al., 1996; Brockerhoff et al., 2008; Pryke and Samways, 2009). My study found that detritivores and predators seemed to be particularly favoured by conditions in the natural forests. Previous studies indicated that the differences in leaf litter quantity (Höfer et al., 1996; Höfer et al. 2001; Yekwayo et al., 2016), rocks and dead wood (Lassau et al., 2005) can have profound effects on invertebrates. With natural forests having a more complex vegetation structure and composition, this could also influence the quality and quantity of leaf litter deposition. Pine plantations have greater quantity of leaf litter deposition, which is of lower quality compared to natural forest. Thus, a more

complex habitat structure can offer a greater variety of resources (Gotellie and Colwell, 2001) and refuges (Bartholomew et al., 2000; Hoddle, 2003) for various species, which could have been the reason for higher predators and detritivores species richness within the natural forest sites. Shade was also a contributing factor to the variation in detritivore species richness between natural forests and pine plantations. Previous studies have shown the temperature of the soil and leaf litter habitat can influence the diversity of topsoil and leaf litter arthropods (Uetz, 1979; Bell et al., 2001). Priha et al. (1999) showed tree density affects soil moisture content by the amount of light which passes through the canopies. Greater shade density is often associated with lower temperatures, which leads to lower evapotranspiration rates, and as a result, keeps the soil moist for longer (Stathers and Bailey, 1986; Kara and Bolat, 2008). Here, natural forest sites had greater shade cover and soil moisture content compared to pine plantations sites. These may also have been contributing factors to the observed high species richness of arthropod detritivores within the natural forests.

Grasslands can have great biological diversity (O'Connor and Kuyler, 2009; Egoh et al., 2011). Here, I found that grasslands and forests supported the most species, with dry grasslands supporting more species than hydromorphic grasslands. This variation between dry and moist grasslands was largely because of soil and vegetation characteristics. Soil compaction was highly correlated to soil moisture content and soil pH. Hydromorphic grasslands had a greater soil moisture content, lower soil pH and significantly lower soil compaction, all of which could contribute to the difference in assemblage structure between these biotopes. Previous studies have shown that soil characteristics and chemistry greatly affect the distribution, activity and movement of arthropods horizontally and vertically within and across the soil substrate (Lafrance, 1968; Fisher et al., 1975; Ponge, 1999; Hartley et al., 2003; Jung et al., 2014). This is supported by the fact that ants, which are known to be highly sensitive to soil abiotic variables (Holway et al., 2002), made up the greatest proportion of species that contributed to the higher species richness in my dry grasslands. Hydromorphic grasslands consisted of a different plant assemblage compared to dry grasslands, which in turn, could influence the quantity and quality of leaf litter deposition. Hydromorphic grasslands had a greater amount of leaf litter cover compared to dry grasslands, which could explain the variation in species diversity (Brockerhoff et al., 2008). Leaf litter deposition is known to increase the structural complexity of the habitat (Robonson et al., 2009). This also increased resources within the habitat, which can positively influence arthropod assemblage compositions.

2.4.2. The conservation value of the two grassland biotopes

I found that hydromorphic grasslands differed significantly from other dominant biotopes with regards to assemblage structure, yet not species richness. This shows that grasslands represent two distinct biotopes. Wet and dry grasslands have different assemblages and conservation values and should be conserved as separate biotopes. Currently the hydromorphic grasslands are well protected by water laws and FSC regulation, due their ecosystem provision of improved water quality. Therefore, the forestry companies have implemented delineation in these areas to protect hydromorphic grasslands and their ecosystem function. Dry grasslands on the other hand have little formal protection, yet in their own right, contributed significantly towards the diversity within these landscapes.

I found dry grasslands to have great conservation value. These grasslands had high arthropod diversity, while having a unique and distinct arthropod assemblage structure compared to other biotope types. However, the areas identified as suitable for timber production in South Africa, lie within the grassland biome (Neke and Du Plessis, 2004) which is critically endangered (Olsen and Dinerstein, 1998; Reyers et al., 2001). Despite numerous studies on the biological and ecological importance of these grassland ecosystems and the pressures exerted on them in South Africa (Samways, 2007; Lipsey and Hockey, 2010; Pryke and Samways, 2012b; Joubert and Samways, 2014; Samways and Pryke, 2016), it has been granted little protection (Neke and Du Plessis, 2004) even though this biome is most in need of conservation (Rebelo, 1997). I urge that conservation efforts should be integrated to include the conservation of this dry grassland biotope, as it has great conservation value in terms of its arthropod species diversity and assemblage composition.

Hydromorphic grasslands had fewer species compared to natural forests and dry grasslands, but still more than the pine plantations. Hydromorphic grasslands had a high proportion of unique species (26 spp.), as did natural forests (32 spp.) and dry grasslands (32 spp.), whereas the pine plantations had fewer unique species (9 spp.). As hydromorphic grasslands have many unique species not found elsewhere in the landscape, their assemblages complement those in the other biotopes (Tilman, 1982; Dunning et al., 1992). A single species can be important due to its unique network position with regards to neighbouring habitats (Lai et al., 2012). They are important in their key roles in ecosystem processes (such as decomposition and productivity) which are often performed by common species (Solan et al., 2004; Hector and Bagchi, 2007; Bellwood et al., 2011), and some even by rare or unique species (Mouillot et al., 2013). The unique species occurring within hydromorphic grasslands included

Araneae (6 spp.), Blattodea (1 spp.), Coleoptera (10 spp.), Hemiptera (3 spp.), Hymenoptera (1 spp.), Orthoptera (3 spp.), Polydesmoidea (1 spp.) and Thysanuara (1 spp.). In view of their distinct functional properties, rare species can perform functions complementary to those performed by other species (Lavergne et al., 2003). This means that they are important in ecosystems as they can increase the functional diversity of local communities, as well as sustain ecosystem functioning (Floder et al., 2010; Mouillot et al., 2011; Richardson et al., 2012). The loss of such species cannot be compensated or replaced easily, nor can their trophic functions be easily replaced by other species (Lai et al., 2012). As rare or unique species are just as important as common species within ecosystems, they should be taken into consideration when setting conservation priorities. Hydromorphic grasslands also shared the most species with dry grasslands (69 spp.), followed by natural forests (50 spp.) and pine blocks (42 spp.).

Although "hydromorphic grassland" is often classified as a sub-group within "grassland", it can also be classified under "wetlands" (Thompson, 1996) which are one of the most valuable assets owing to their significant contribution to landscape biodiversity and ecosystem functioning (Hansson et al., 2005). Wetlands are often associated with agricultural production landscapes due to their high organic matter and nutrient content (Reddy and Gale, 1994), making them of critical conservation concern (Sabo et al., 2005). Futhermore, they can occur in distinct patches or corridors within the landscape (Gibbs, 2000), making species within these small and isolated patches vulnerable to disturbances (Moller and Rordam, 1985; Dodd, 1990). Therefore, hydromorphic grasslands here show great conservation value as they contribute to landscape heterogeneity and connectivity as much as the proclaimed wetland areas, which are biologically diverse (Ward, 1989; Tockner and Ward, 1999; Liu et al., 2003) and of conservational importance (Hansson et al., 2005).

2.5. Conclusion

Landscape and habitat heterogeneity are key factors contributing to the distribution of arthropods and variation in arthropod assemblages. The dominant biotopes within the plantation landscape mosaic harbour distinct species compositions of leaf litter and topsoil arthropods and are influenced by different soil, vegetation and landscape features. As plantation forests are a threat to biodiversity, it is important to conserve as many natural habitats through pro-active planning using delineation of the remaining natural habitats within the landscape to ensure conservation of overall landscape biodiversity. Hydromorphic grasslands within the plantation landscape contribute significantly to

landscape heterogeneity, and subsequently, to landscape biodiversity. Although the primary reason for the conservation of hydromorphic grasslands in these landscapes is to conserve hydrological function, this in effect also conserves diverse arthropod assemblages. This biotope type has a high conservation value with regards to its fauna as it harbours a unique species assemblage, while also sharing many species with other dominant biotopes within the landscape. Interestingly, dry grasslands also make an important and unique contribution to arthropod diversity, emphasising the value of both grassland biotopes. In sum, hydromorphic and dry grasslands contribute to landscape heterogeneity, making them an important and valuable landscape element contributing to overall landscape biodiversity.

2.6. References

Anderson M.J. (2001). A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32-46.

Barrios E. (2007). Soil biota, ecosystem services and land productivity. Ecological Economics 64: 269-285.

Bartholomew A., Diaz R.J. and Cicchetti G. (2000). New dimensionless indices of structural habitat complexity: Predicted and actual effects on a predator's foraging success. Marine Ecology Progress Series 206: 45-58.

Bates D., Maechler M., Bolker B. and Walker S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1: 1-23.

Bell J.R., Wheater C.P. and Cullen W.R. (2001). The implications of grassland and heathland management for the conservation of spider communities: A review. Journal of Zoology 255: 377-387.

Bellwood D.R., Hoey A.S. and Hughes T.P. (2011). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proceedings of the Royal Society of London B: Biological Sciences: 1621-1629.

Benton T.G., Vickery J.A. and Wilson J.D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? Trends in Ecology and Evolution 18: 182-188.

Bernhard-Reversat F., Laclau J.P., Loubana P.M., Loumeto J.J., Mboukou I.M.C. and Reversat G. (2001). Changes in biological factors of fertility in managed eucalyptus plantations on a savanna soil in Congo. In: Rehabilitation of degraded tropical forest ecosystems: Workshop proceedings. CIFOR, Bogor: 179-190.

Bishop C. (2006). Pattern recognition and machine learning. Springer, New York.

Bogyó D., Magura T., Nagy D.D. and Tothmeresz B. (2015). Distribution of millipedes (Myriapods, Diplopoda) along a forest interior-forest edge-grassland habitat complex. ZooKeys 510: 181-195.

Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H. and White J.S.S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology and Evolution 24: 127-35.

Bretz F., Hothorn T. and Westfall P. (2002). On multiple comparisons in R. R News 2(3): 14-17.

Bretz F., Hothorn T. and Westfall P. (2008). Multiple comparison procedures in linear models. COMPSTAT: 423-431.

Brockerhoff E.G., Jacktel H., Parrotta J.A., Quine C.P. and Sayer J. (2008). Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity Conservation 17: 925-951.

Brose U. (2002). Estimating species richness of pitfall catches by non-parametric estimators. Pedobiologia 46: 101-107.

Budoff M.J., Nasir K., McClelland R.L., Detrano R., Wong N., Blumenthal R.S., Kondos G. and Kronmal R.A. (2009). Coronary calcium predicts events better with absolute calcium scores than age-sex-race/ethnicity percentiles: MESA (Multi-Ethnic Study of Atherosclerosis). Journal of the American College of Cardiology 53: 345-352.

Colwell R.K. and Coddington J.A. (1994). Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions: Biological Sciences: 101-118.

Colwell R.K., Mao C.X. and Chang J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85: 2717-2727.

Consul P.C. and Jain G.C. (1973). A generalization of the Poisson distribution. Technometrics 15: 791-799.

Costanza R., d'Arge R., De Groot R., Farber S., Grasso M., Hannon B., Limburg K., Naeem S., O'neill R.V., Paruelo J. and Raskin R.G. (1997). The value of the world's ecosystem services and natural capital. Nature 387: 253-260.

Curmi P., Durand P., Gascuel-Odoux C., Mérot P., Walter C. and Taha A. (1998). Hydromorphic soils, hydrology and water quality: Spatial distribution and functional modelling at different scales. Nutrient Cycling in Agroecosystems 50: 127-142.

De Ruiter P.C., Neutel A.M. and Moore J.C. (1995). Energetics, patterns of interaction strengths and stability in real ecosystems. Science 269: 1257-1260.

Dippenaar-Schoeman A.S. and Harvey M.S. (2000). A check list of the pseudoscorpions of South Africa (Arachnida: Pseudoscorpiones). Koedoe 43: 89-102.

Dirsh V.M. (1965). The African genera of Acridoidea. Cambridge University Press, London.

Dodd C.K. (1990). Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle Steinotfberis depressus. Biological Conservation 45: 33-45.

Donegan K.K., Seidler R.J., Fieland V.J., Schaller D.L., Palm C.J., Ganio L.M., Cardwell D.M. and Steinberger Y. (1997). Decomposition of genetically engineered tobacco under field conditions: Persistence of the proteinase inhibitor I product and effects on soil microbial respiration and protozoa, nematode and microarthropod populations. Journal of Applied Ecology 34: 767-777.

Dunning J.B., Danielson B.J. and Pulliam H.R. (1992). Ecological processes that affect populations in complex landscapes. Oikos: 169-175.

Dye P. and Jarmain C. (2004). Water use by black wattle (Acacia mearnsii): Implications for link between removal of invading trees and catchment streamflow response. South African Journal of Science 100: 40-44.

Eeley H.A.C., Lawes M.J. and Macfarlane D. (2002). Historical change since 1944 in landscape pattern of indigenous forest in the KwaZulu-Natal Midlands. In: Seydack A.H.W., Vorster T., Vermeulen W.H. and van der Merwe J.J. (Eds.). Multiple use management of natural forests and Savanna woodlands: policy refinement and scientific progress. Proceedings of the natural forests and Savanna woodlands symposium III, Kruger Park. Department of Water Affairs and Forestry, Pretoria, South Africa: 68-78.

Egoh B.N., Reyers B., Rouget M. and Richardson D.M. (2011). Identifying priority areas for ecosystem service management in South African grasslands. Journal of Environmental Management 92: 1642-1650.

Erwi K.L. (2009). Wetlands and global climate change: The role of wetland restoration in a changing world. Wetlands Ecology and Management 17: 71-84.

Fisher J., Keaster A. and Fairchild M. (1975). Seasonal vertical movement of wireworm larvae in Missouri: Influence of soil temperature on the genera Melanotus Escholtz and Conoderus Escholtz. Annals of the Entomological Society of America 68: 1071-1073.

Flöder S., Jaschinski S., Wells G. and Burns C.W. (2010). Dominance and compensatory growth in phytoplankton communities under salinity stress. Journal of Experimental Marine Biology and Ecology 395: 223-231.

Gibbs J.P. (2000). Wetland loss and biodiversity conservation. Conservation Biology 14: 325-317.

Goodman N.R. (1963). Statistical analysis based on a certain multivariate complex Gaussian distribution (an introduction). The Annals of Mathematical Statistics 34: 152-177.

Gotelli N.J. and Colwell R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Haddad C.R., Dippenaar-Schoeman A.S. and Wesolowska W. (2006). A checklist of the non-acarine arachnids (Chelicerata: Arachnida) of the Ndumo Game Reserve, Maputaland, South Africa. Koedoe 49: 1-22.

Hammond P.M. (1990). Insect abundance and diversity in the Dumoga-Bone national park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. In: Knight W.J. and Holloway J.D. (Eds.). Insects and rainforests of South East Asia (Wallacea). The Royal Entomological Society of London, London: 197-254.

Hansson L.A., Brönmark C., Anders Nilsson P. and Abjörnsson K. (2005). Conflicting demands on wetland ecosystem services: Nutrient retention, biodiversity or both? Freshwater Biology 50: 705-714.

Hartley S.E., Gardner S.M. and Mitchell R.J. (2003). Indirect effects of grazing and nutrient addition on the hemipteran community of heather moorlands. Journal of Applied Ecology 40: 793-803.

Hector A. and Bagchi R. (2007). Biodiversity and ecosystem multifunctionality. Nature 448: 188-190.

Hoddle M.S. (2003). The effect of prey species and environmental complexity on the functional response of Franklinothrips orizabensis: A test of the fractal foraging model. Ecological Entomology 28: 309-318.

Höfer H., Hanagarth W., Garcia M., Martius C., Franklin E., Römbke J. and Beck L. (2001). Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. European Journal of Soil Biology 37: 229-235.

Höfer H., Martius C. and Beck L. (1996). Decomposition in an Amazonian rain forest after experimental litter addition in small plots. Pedobiologia 40: 570-576.

Holway D.A., Suarez A.V. and Case T.J. (2002). Role of abiotic factors in governing susceptibility to invasion: A test with Argentine ants. Ecology 83: 1610-1619.

Janion-Scheepers C., Deharveng L., Bedos A. and Chown S. (2015). Updated list of Collembola species currently recorded from South Africa. ZooKeys 503: 55-88.

Janion-Scheepers C., Measey J., Braschler B., Chown S.L., Coetzee L., Colville J.F., Dames J., Davies A.B., Davies S.J., Davis A.L. and Dippenaar-Schoeman A.S. (2016). Soil biota in a megadiverse country: Current knowledge and future research directions in South Africa. Pedobiologia 59: 129-174.

Joubert L. and Samways M.J. (2011). Ecological networks: the key to biodiversity conservation. Quest 7: 30-32.

Joubert L. and Samways M.J. (2014). Equivalence of grasslands in an ecological network and a World Heritage Site. Biodiversity Conservation 23: 2415-2426.

Joubert L., Pryke J.S. and Samways M.J. (2016). Past and present disturbances influence biodiversity value of subtropical grassland ecological networks. Biodiversity Conservation 25: 725-737.

Jung J., Racca P., Schmitt J. and Kleinhenz B. (2014). SIMAGRIO-W: Development of a prediction model for wireworms in relation to soil moisture, temperature and type. Journal of Applied Entomology 138: 183-194.

Kara Ö. and Bolat I. (2008). Soil microbial biomass C and N changes in relation to forest conversion in the Northwestern Turkey. Land Degradation and Development 19(4): 421-428.

Keep M.E. and Ledger J.A. (1990). Lice (Phthiraptera), fleas (Siphonaptera) and mites (Trombidiformes, Sarcoptiformes and Mesostigmata) recorded from the larger game species in Natal. Lammergeyer 41: 23-29.

Kietzka G.J., Pryke J.S. and Samways M.J. (2015). Landscape ecological networks are successful in supporting a diverse dragonfly assemblage. Insect Conservation and Diversity 8: 229-237.

Kirkman K.E. and Pott R.M. (2002). Biodiversity conservation in plantation forestry. In: Pierce S.M., Cowling R.M., Sandwith T. and MacKinnon K. (Eds.). Mainstreaming biodiversity in development: case studies from South Africa. The World Bank Environmental Department, Washington, D.C.: 33-42.

Lafrance J. (1968). The seasonal movements of wireworms (Coleoptera: Elateridae) in relation to soil moisture and temperature in the organic soils of southwestern Quebec. The Canadian Entomologist 100: 801-807.

Lai S.M., Liu W.C. and Jordán F. (2012). On the centrality and uniqueness of species from the network perspective. Biology Letters 8: 570-573.

Lassau S.A. and Hochuli D.F. (2004). Effects of habitat complexity on ant assemblages. Ecography 27: 157-164.

Lavergne S., Garnier E. and Debussche M. (2003). Do rock endemic and widespread plant species differ under the leaf–height–seed plant ecology strategy scheme? Ecology Letters 6: 398-404.

Legendre P. and Gallagher E.D. (2001). Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271-280.

Lipsey M.K. and Hockey P.A.R. (2010). Do ecological networks in South African commercial forests benefit grassland birds? A case study of a pine plantation in KwaZulu-Natal. Agriculture, Ecosystems and Environment 137: 133-142.

Liu H., Lu X. and Zhang S. (2003). Landscape biodiversity of wetlands and their changes in 50 years in watersheds of the Sanjiang Plain. Acta Ecologica Sinica 24: 1472-1479.

Lu X. and Wang R. (1995). Study on wetland biodiversity in China. Chinese Geographical Science 6: 15-23.

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

Megraud F., Coenen S., Versporten A., Kist M., Lopez-Brea M., Hirschl A.M., Andersen L.P., Goossens H. and Glupczynski Y. (2012). *Helicobacter pylori* resistance to antibiotics in Europe and its relationship to antibiotic consumption. Gut: 1-9.

Melo A.S. (2004). A critique of the use of jackknife and related non-parametric techniques to estimate species richness. Community Ecology 5: 149-157.

Mesibov R., Taylor R.J. and Brereton R.N. (1995). Relative efficiency of pitfall trapping and hand-collecting from plots for sampling of millipedes. Biodiversity and Conservation 4: 429-439.

Moller T.R. and Rordam C.P. (1985). Species numbers of vascular plants in relation to area, isolation, and age of ponds in Denmark. Oikos 45: 8-16.

Mommertz S., Schauer C., Kösters N., Lang A. and Filser J. (1996). A comparison of D-vac suction, fenced and unfenced pitfall trap sampling of epigeal arthropods in agroecosystems. Annales Zoologici Fennici 33: 117-124.

Mouillot D., Bellwood D.R., Baraloto C., Chave J., Galzin R., Harmelin-Vivien M., Kulbicki M., Lavergne S., Lavorel S., Mouquet N. and Paine C.T. (2013). Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biol 11: e1001569.

Mouillot D., Villéger S., Scherer-Lorenzen M. and Mason N.W. (2011). Functional structure of biological communities predicts ecosystem multifunctionality. PloS One 6: e17476.

Mucina L. and Rutherford M.C. (2006). The vegetation of South Africa, Lesotho and Swaziland. SANBI, Pretoria.

Neke K.S. and du Plessis M.A. (2004). The threat of transformation: quantifying the vulnerability of grasslands in South Africa. Conservation Biology 18: 466-477.

O'Connor T.G. and Kuyler P. (2009). Impact of land use on the biodiversity integrity of the moist sub-biome of the grassland biome, South Africa. Journal of Environmental Management 90: 384-395.

Ohwaki A., Kaneko Y. and Ikeda H. (2015). Seasonal variability in response of ground beetles (Coleoptera: Carabidae) to a forest edge in a heterogeneous agricultural landscape in Japan. European Journal of Entomology 112: 135-144.

Olsen D.M. and Dinerstein E. (1998). The Global 2000: A representation approach to conserving the earth's most biologically valuable ecoregions. Conservation Biology 12: 502-515.

Perry W.B., Christiansen T.A. and Perry S.A. (1997). Response of soil and leaf litter microarthropods to forest application of diflubenzuron. Ecotoxicology 6: 87-99.

Picker M., Griffiths C. and Weaving A. (2004). Field guide to insects of South Africa. Struik Nature, Cape Town.

Pinheiro E.R.S., Duarte L.S., Diehl E. and Harts S.M. (2010). Edge effects on epigaeic ant assemblages in a grassland-forest mosaic in southern Brazil. Acta Oecologica 36: 365-371.

Ponge J.F. (1999). Interaction between soil fauna and their environment. In: Rastin N. and Bauhus J. (Eds.). Going underground: Ecological studies in forest soils. Research Signpost, Trivandrum, Kerala: 45-76.

Prasifka J.R., Lopez M.D., Hellmich R.L., Lewis L.C. and Dively G.P. (2007). Comparison of pitfall traps and litter bags for sampling ground-dwelling arthropods. Journal of Applied Entomology 131: 115-120.

Priha O., Hallantie T. and Smolander A. (1999). Comparing microbial biomass, denitrification enzyme activity, and numbers of nitrifiers in the rhizospheres of Pinus sylvestris, Picea abies and Betula pendula seedlings by microscale methods. Biology and Fertility of Soils 30: 14-19.

PRIMER-E. (2008). PERMANOVA and PRIMER 6. PRIMERE, Lutton, Bedfordshire, UK.

Pryke J.S. and Samways M.J. (2009). Recovery of invertebrate diversity in a rehabilitated cite landscape mosaic in the heart of a biodiversity hotspot. Landscape and Urban Planning 93: 54-62.

Pryke J.S. and Samways M.J. (2012a). Conservation management of complex natural forests and plantation edge effects. Landscape Ecology 27: 73-85.

Pryke J.S. and Samways M.J. (2012b). Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. Journal of Applied Ecology 49: 591-600.

QGIS Development Team. (2009). QGIS Geographic Information System. Open Source Geospatial Foundation. Available at http://qgis.osgeo.org, accessed in March 2016.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org/, accessed in May 2016.

Rebelo A.G. (1997). Conservation. In: Cowling R.M., Richardson D.M. and Pierce S.M. (Eds.). Vegetation of southern Africa. Cambridge University Press, Cambridge, UK: 571-589.

Reddy K.R. and Gale P.M. (1994). Wetland processes and water quality: A symposium overview. Journal of Environmental Quality 23: 875-877.

Reyers B., Fairbanks D.H.K., van Jaarsveld A.S. and Thompson M. (2001). Priority areas for the conservation of South African vegetation: A coarse filter approach. Diversity and Distributions 7: 77-96.

Richardson S.J., Williams P.A., Mason N.W., Buxton R.P., Courtney S.P., Rance B.D., Clarkson B.R., Hoare R.J., St John M.G. and Wiser S.K. (2012). Rare species drive local trait diversity in two geographically disjunct examples of a naturally rare alpine ecosystem in New Zealand. Journal of Vegetation Science 23: 626-639.

Robson T.C., Baker A.C. and Murray B.R. (2009), Differences in leaf-litter invertebrate assemblages between radiata pine plantations and neighbouring native eucalypt woodland. Austral Ecology 34: 368-376.

Sabo J.L., Sponseller R., Dixon M., Gade K., Harms T., Heffernan J., Jani A., Katz G., Soykan C., Watts J. and Welter J. (2005). Riparian zones increase regional species richness by harbouring different, not more, species. Ecology 86: 56-62.

Samways M.J. (2007). Implementing ecological networks for conserving insect and other biodiversity. In: Stewart A.J.A., New T.R. and Lewis O.T. (Eds.). Insect Conservation Biology. CABI, Cambridge: 127-143.

Samways M.J. and Niba A. (2010). Climate and elevational range of a South African dragonfly assemblage. BioRisk 5: 85-107.

Samways M.J. and Pryke J.S. (2016). Large-scale ecological networks do work in an ecologically complex biodiversity hotspot. Ambio 45: 161-172.

Samways M.J., Bazelet C.S. and Pryke J.S. (2010a). Provision of ecosystem services by large scale corridors and ecological networks. Biodiversity and Conservation 19: 2949-2962.

Samways M.J., Caldwell P.M. and Osborn R. (1996). Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. Agriculture, Ecosystems and Environment 59: 19-32.

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

Schaffers A.P., Raemakers I.P., Sýkora K.V. and Ter Braak C.J. (2008). Arthropod assemblages are best predicted by plant species composition. Ecology 89: 782-794.

Scholtz C.H. and Holm E. (1985). Insects of Southern Africa. Butterworths, Cape Town, South Africa.

Solan M., Cardinale B.J., Downing A.L., Engelhardt K.A., Ruesink J.L. and Srivastava D.S. (2004). Extinction and ecosystem function in the marine benthos. Science 306: 1177-1180.

Southwood T.R.E. (1978). Ecological methods. Chapman and Hall, London.

Standen V. (2000). The adequacy of collecting methods for estimating species richness of grassland invertebrates. Journal of Applied Ecology 37: 884-893.

Stathers R.J. and Bailey W.G. (1986). Energy receipt and partitioning in a ginseng shade canopy and mulch environment. Agricultural and forest meteorology 37: 1-14.

Tetzlaff D., Malcolm I.A. and Soulsby C. (2007). Influence of forestry, environmental change and climatic variability on the hydrology, hydrochemistry and residence times of upland catchments. Journal of Hydrology 346: 93-111.

Thompson M. (1996). A standard land-cover classification scheme for remote-sensing applications in South Africa. South African Journal of Science 92: 34-42.

Tilman D. (1982). Resource competition and community structure. Princeton University Press, Princeton, New Jersey.

Tilman D., Knops J., Wedin D., Reich P., Ritchie M. and Sienmann E. (1997). The influence of functional diversity and composition on ecosystem processes. Science 277: 1300-1302.

Tockner K., Pennetzdorfer D., Reiner N., Schiemer F. and Ward J.V. (1999). Hydrological connectivity and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). Freshwater Biology 41: 521-535.

Tothmeresz B., Nagy D.D., Mizser S., Bogyó D. and Magura and T. (2014) Edge effects on ground-dwelling beetles (Carabidae and Staphylinidae) in oak forest-forest edge-grassland habitats in Hungary. European Journal of Entomology 111: 686-691.

Uetz G.W. (1979). The influence of variation in litter habitats on spider communities. Oecologia 40: 29-42.

Vergnes A., Le Viol I. and Clergeau P. (2012). Green corridors in urban landscapes affect the arthropod communities of domestic gardens. Biological Conservation 145: 171-178.

Wagenmakers E.J. and Farrell S. (2004). AIC model selection using Akaike weights. Psychonomic Bulletin and Review 11: 192-196.

Walker J.B. (1991). A review of the ixodid ticks (Acari: Ixodidae) occurring in southern Africa. Onderstepoort Journal of Veterinary Research 58: 81-105.

Ward J.V. (1989). The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society: 2-8.

Warren M.W. and Zou X. (2002). Soil macrofauna and litter nutrients in three tropical tree plantations on a disturbed site in Puerto Rico. Forest Ecology and Management 170: 161-171.

Weibull A.C., Ostman O. and Granqvist A. (2003). Species richness in agroecosystems: The effect of landscape, habitat and farm management. Biodiversity and Conservation 12: 1335-1355.

Yekwayo I., Pryke J.S., Roets F. and Samways M.J. (2016). Surrounding vegetation matters for arthropods of small, natural patches of indigenous forest. Insect Conservation and Diversity: 1-12.

Zanetti N.I., Camina R., Visciarelli E.C. and Centemo N.D. (2016). Active search on carcasses versus pitfall traps: A comparison of sampling methods. Neotropical Entomology 45: 221-226.

Zedler J.B. (2000). Progress in wetland restoration ecology. Trends in Ecology and Evolution 15: 402-407.

Chapter 3
Arthropod diversity and assemblage recovery in hydromorphic grasslands after the removal of pine plantations

ABSTRACT

Wetlands have important roles across many landscapes. Yet many wetland systems are being lost or degraded due to anthropogenic activities, such as plantation forestry. Restoration efforts to restore these wetland systems by removing planted trees from the hydromorphic soils go undocumented, especially in terms of topsoil and leaf litter macro-arthropod biodiversity recovery. Here, I aim to determine whether the diversity of arthropods that occupy hydromorphic grassland topsoil and leaf litter recover after the removal of pine trees. The study took place in the KwaZulu-Natal Midlands, with arthropods collected in three biotopes (natural untransformed hydromorphic grasslands, restored hydromorphic grasslands and commercial pine plantations) using pitfall trapping and active searching. Overall, spider, ant and grasshopper species richness did not differ between the natural and restored grassland, although it was higher in both these than in pine blocks. Overall, spider, beetle, ant and grasshopper assemblages differed significantly between restored grassland and pine blocks, with no significant differences between the restored and natural grasslands. Environmental factors either promoted (corridor width, biotope size, distance to pine block, soil moisture and vegetation cover) or limited (distance to wetland, plant diversity, bramble cover) arthropod assemblage recovery within restored sites. Contrary to expectations, the alien invasive American bramble (*Rubus cuneifolius*) had the greatest effect on the restoration process, rather than time since pine removal. After the restoration of these hydromorphic grasslands, it appears that the diversity and assemblages of topsoil and leaf litter arthropods are recovering to levels similar to that of natural hydromorphic grassland. However, bramble is causing some restored sites to deviate from this trajectory. Therefore, successfully restoration of these hydromorphic grasslands is dependent on the removal and management of bramble.

3.1. Introduction

Wetland ecosystems are important assets across many landscapes through their important roles in provision of water supply (Hannson et al., 2005), nutrient retention (Cui et al., 2009) and for creating habitat for many species (Lu and Wang, 1995; Sabo et al., 2005). They are therefore systems of great biodiversity and economic value (Hannson et al., 2005). However, many of these systems are lost or damaged due to anthropogenic activities (Sieben et al., 2011). They are also being impacted by invasive alien plants (Macdonald, 2004), which negatively affect the structure and functioning of these systems. Therefore, the conservation and rehabilitation of these systems is receiving more attention (Sieben et al., 2011). In South Africa, research on wetland systems has been historically neglected (Malan, 2010). However, there has been a growing interest in understanding wetland systems and the important ecosystem services that they provide (Keddy, 2004). The Working for Wetlands programme

is a national initiative (Ellery et al., 2011) which developed out of the Working for Water programme (Preston, 2003). The wetlands programme is focussed on promoting the protection of remaining wetlands, rehabilitation of degraded wetlands, and on future sustainable use of wetlands. Research on the restoration or rehabilitation of wetland systems is mostly focussed on re-establishment of the historic vegetation composition (MacDonald, 2004), hydrological characteristics (Riddell et al., 2013), and ecosystem services (Grenfell et al., 2007) after the removal of alien invasive plants (Preston, 2003; MacDonald, 2004).

In production systems, such as timber production landscapes, areas are set aside and remain unplanted by timber trees (Louw, 2006). This forms part of conservation programmes to either protect or rehabilitate the biodiversity of wetlands within the landscape, a process locally known as "delineation". Prior to today's sustainable land-use planning in timber production landscapes, production was maximized through the planting of trees across the entire landscape, with no consideration for the topography of the landscape. Natural areas of conservation value, such as wetlands, were lost due to the expansion of production areas. This caused alarming effects on hydrological cycles (Neke and du Plessis, 2004) and caused major losses in biodiversity (Lawes et al., 1999). After much debate among the stakeholders, it was concluded that mitigation measures and restoration efforts were needed to restore the biological and ecological functioning of this important landscape element (Samways and Pryke, 2016). Efforts were then made to restore these wetland systems by removing certain plantation trees which had been planted on wetland soils (Dye and Jarmain, 2004; Joubert and Samways, 2011). Today, this process has been implemented in the ecological networks (ENs) of South African timber production landscapes so as to restore and maintain remnant grassland habitats (Joubert and Samways, 2011), including that of hydromorphic soils. Furthermore, removal of specific trees from wetland areas can aid in the restoration of biodiversity and prevent the physical, chemical and biological deterioration of the soil (Matthews, 2008). However, it is still unclear how the process of delineation and the restoration of hydromorphic grassland systems can affect the biodiversity within plantation landscapes in South Africa (Dye and Jarmain, 2004).

ENs are highly effective at conserving the biodiversity of plants (Joubert and Samways, 2014), dragonflies (Kietzka et al., 2015), grasshoppers (Bazelet and Samways, 2011), small mammals, butterflies and birds (Haddad et al., 2003). However, limited attention has been given to topsoil and leaf litter arthropods (but see Pryke and Samways, 2012; Yekwayo et al., 2016). These organisms are

highly diverse, and contribute to important ecosystem services such as nutrient cycling and decomposition (Birkhofer et al., 2011; Yan et al, 2012), soil formation (Oades, 1993), and the maintenance of the soil physical structure (Loranger-Merciris et al., 2007). Therefore, they are of great functional importance as their presence can influence the quality and health of the soil (Yan et al., 2012), which in turn influences the resilience, productivity of the soil and its ability to provide other important ecosystem services (Woomer and Swift, 1994; Robinson et al., 2012). In general, there is limited knowledge on the diversity of soil fauna and their linkage to the entire ecosystem structure and functioning (Bernhard-Reversat et al., 2001; Höfer et al., 2001; Warren and Zou, 2002; Barrios, 2007) and baseline information on this diverse group of organisms is lacking in South Africa (Louw et al., 2014; Janion-Scheepers et al., 2016).

Restoration success can be measured by improvements in ecosystem processes and in species diversity (van Aarde et al., 1996; Rhoades et al., 1998; Reay and Norton, 1999; Passell, 2000; McCoy and Mushinsky, 2002). Therefore, this study will examine the diversity and assemblage composition of topsoil and leaf litter arthropods in an EN-plantation landscape mosaic, focussing on naturally occurring hydromorphic grasslands (where pine trees have never been planted), restored hydromorphic grasslands (where pine trees have been removed) and commercial pine plantation blocks (grasslands converted to pine plantations). The objectives of this study are: 1) to determine whether species richness and assemblage composition differs between the three biotopes, 2) to assess the effect of time since delineation on the recovery process to see how slowly or rapidly the assemblages recover, and 3) to determine which environmental variables contribute or impede the recovery of restored sites to assemblages that resemble that of natural sites.

Biodiversity and ecosystem services of restored wetlands can recover to levels similar to natural wetlands (Meli et al., 2014), although restoration time can be affected by various biotic and abiotic constraints in grasslands (Bakker and Berendse, 1999). Therefore, I hypothesize that the restored biotope will have an arthropod assemblage similar to that of the natural biotope with an increased similarity with increasing time since the pine trees were removed. However, Mitsch and Wilson (1996) state the restoration of previously afforested wetlands may require more time to recover (close to 20 years) before restoration success can be judged. This is because many of the environmental conditions are significantly altered where pines have been planted (i.e. vegetation and soil characteristics),

resulting in low ecosystem resilience. Therefore, time for recovery where pines had been removed is likely not be rapid.

3.2. Materials and methods

3.2.1. Study area and design

The KwaZulu-Natal (KZN) province of South Africa is an important agricultural and timber production region with its sub-tropical climate (Fairbanks and Benn, 2000). KZN has a remarkably varied topography, geology and climate (King, 1978; Schulze, 1982; Eeley et al., 1999), with warm, wet summers and cool, dry winters (Fairbanks and Benn, 2000). It is covered mostly by indigenous forests, bush thickets and savanna woodlands (Fairbanks and Benn, 2000), with the Midlands Mistbelt grasslands dominating the region (Mucina and Rutherford, 2006). Two plantation estates, Good Hope (29°39'09.8"S, 29°57'09.8"E) and Fabershill (29°40'13.3"S, 29°55'59.5"E), in the KZN Midlands were selected here as they consist of a highly heterogeneous landscape (Samways and Niba, 2010), including natural grasslands, indigenous forests, plantations (*Pinus* spp.), dams, rivers and wetlands (Figure 3.1). Site selection used soil GIS data provided by Mondi (J. Shuttleworth pers. comm.), to determine where natural and restored hydromorphic grasslands occurred within the plantation estates, and later verified in the field. Thirty sites in total were selected, ten for each of the three dominant biotopes: natural hydromorphic grassland, delineated hydromorphic grassland ('restored grassland'), and pine plantation blocks. Sites occurred were within the elevation range 1300-1600 m a.s.l. Sampling was undertaken in summer, January 2017.

3.2.2. Arthropod sampling and identification

Certain invertebrate families can be under- or over-estimated depending on the type of sampling method used (Zanetti et al., 2016). Therefore, two sampling methods were combined to increase capture rates for a greater variety of species (Mommertz et al., 1996). I combined pitfall trapping and direct sampling (i.e. active searching) to collect all arthropods. Pitfall trapping is an effective sampling method for surface-active arthropods, as it is simple and efficient (Southwood, 1978; Standen, 2000; Prasifka et al., 2007). Direct sampling by hand-collecting arthropods complemented the pitfall trapping, as it is a method which can also be used to attain important information on the diversity and abundance of a variety of arthropods which occur in the leaf litter and topsoil layers (Mesibov et al., 1995).
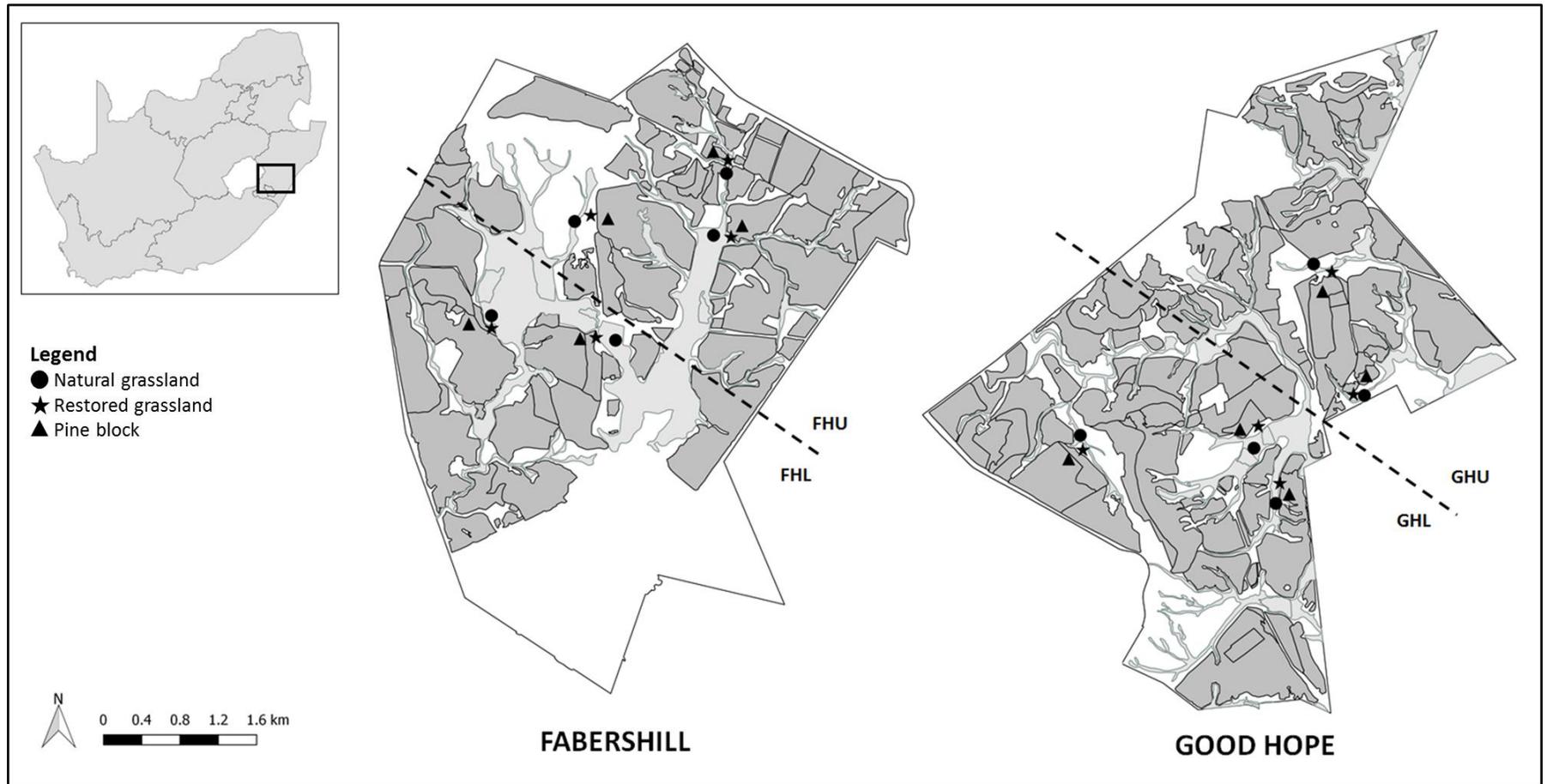
Figure 3.1: The focal estates of Good Hope and Fabershill in Midlands, KwaZulu-Natal, South Africa. Illustrated here is the division of these two plantation estates into 4 sections (GHU = Good Hope upper, GHL = Good Hope lower, FHU = Fabershill upper and FHL = Fabershill lower). Plantation blocks (dark grey), wetlands (light grey) and other non-plantation areas (white) are also indicated.

Pitfall trapping was conducted using four 300 ml plastic cups (9.5 cm diameter and 8 cm deep) which were placed in a 2 m^2 grid, with the rim of the trap flush with the soil surface. Traps were filled with 50 ml 60% ethylene glycol (with two drops of detergent to break the surface tension). Pitfall traps were open for five days, after which arthropods captured were transferred to 75% ethanol. The hand-collection of arthropods was conducted using a 1 m^2 quadrat, which was placed at random within each site. Active searching for leaf litter and topsoil arthropods involved two people searching for 10 min within the quadrat. Litter within the quadrat was turned over to detect arthropods under the litter layer. The top 2 cm of the soil was also disturbed to collect any arthropods in the topsoil layer. Collected arthropods were put into 75% ethanol.

Arthropods were sorted into morphospecies, counted and identified to family level using relevant literature (Dirsh (1965), Scholtz and Holm (1985), Keep and Ledger (1990), Walker (1991), Dippenaar-Schoeman and Harvey (2000), Picker et al. (2004), Haddad et al. (2006) and Janion-Scheepers et al. (2015)) for Amphipoda, Blattodea, Coleoptera, Collembola, Dermaptera, Geophilomorpha, Hemiptera, Hymenoptera (Formicidae only), Isopoda, Ixodida, Lithobiomorpha, Mantodea, Opiliones, Orthoptera, Phasmatodea, Polydesmoidea, Pseudoscorpiones, Sphaero-theriidae, Spirostreptida and Trombidiformes. Specimens in the order Araneae were sent to a spider specialist for identification. Reference specimens, excluding that of Araneae, are maintained in Stellenbosch University's entomology museum in the Department of Conservation Ecology and Entomology. The collected spider specimens are housed in the National Collection of Arachnida at the National Museum, Pretoria.

3.2.3. Biotic and abiotic environmental variables

A 1 m^2 quadrat was placed at random within each site to record various vegetation and soil characteristics. A soil moisture and pH meter (Kelway, Inc.) and a soil penetrometer (Lang Penetrometer, Inc.) was used to measure soil moisture, pH and soil compaction respectively. This was recorded three times and the average was used in the analyses. Vegetation characteristics such as the percentage of vegetation cover, vegetation height, the number of plant species and percentage leaf litter were recorded. Percentage herbaceous, shrub and grass species cover, along with percentage bare ground within the quadrat, were also recorded. Within 80 m^2 of each site (i.e. in a 5 m radius), the environmental variables percentage canopy cover, shade, dead wood cover, bramble cover, rock cover and percentage of trees were recorded. Additional landscape variables were calculated in QGIS (version 2.18.0) (QGIS Development Team, 2009). These included corridor width in which each site occurred, size of focal patch, slope and aspect of each site, amount of focal

biotope in the surrounding landscape (estimated as the percentage of the sampled biotope type in a 1 km radius around each site), and percentage of transformed landscape (estimated as the percentage of pine plantation in a 1km radius around each site), along with the distance to nearest pine block, wetland, river and road.

3.2.4. Data analyses

Using Primer 6 (version 6.1.13) (PRIMER-E, 2008), a species accumulation curve across all biotopes (i.e. natural hydromorphic grassland, restored hydromorphic grassland and pine blocks) was used to determine whether the sampling of arthropods reached an asymptote (Gotelli and Colwell, 2001). Observed species richness is strongly dependent on the sample size (i.e. sampling effort) (Colwell et al., 2004), and therefore, non-parametric species richness estimators were used as they are not dependent on the sample size (Melo, 2004). I chose species estimates Chao 2 and Jacknife 2, as they are non-parametric species richness estimators that are most capable of estimating species diversity in a highly diverse community (Colwell and Coddington, 1994).

In R (version 3.3.1) (R Core Team, 2016), generalized linear mixed models (GLMMs) were performed using the "lme4" package (Bates et al., 2014) to determine the effect of biotope type on overall species richness, as well as species richness of the five most dominant collected arthropod orders (ants, beetles, bugs, grasshoppers and spiders). Models were based on either Poisson error (Consul and Jain, 1973; Bolker et al., 2009) or Gaussian distribution (Goodman, 1963; Bishop, 2006), with a specified log link function. Biotope type (i.e. natural hydromorphic grassland, restored hydromorphic grassland and pine blocks) was included as the fixed variable, whereas estate section was included as a random variable. The estate section divided the location of sites from each of the two plantation estates in half to give four regions (see Figure 3.1). This division was used as a random variable to account for spatial nestedness of sites within the plantations. After the probability (P) and Chi-square (χ^2) values had been estimated, Tukey post-hoc tests were performed where significant effects occurred, using the multcomp package in R (Bretz et al., 2002; Bretz et al., 2008) to determine pairwise differences between biotopes.

Canonical Analysis of Principal Co-ordinates (CAP) was done in Primer 6 to visualize the overall assemblage structure of leaf litter and topsoil arthropods between biotopes (Anderson and Willis, 2003). The same analysis was used for assemblage structure of ants, beetles, bugs, grasshoppers and spiders. To test for significant differences in assemblages between the biotopes, a permutational multivariate analysis of variance (PERMANOVA) was done in Primer for the overall and arthropod

order assemblages. I used biotope type as a fixed factor, and estate class as a random variable (see Figure 3.1). The PERMANOVA was permutated 9999 times to obtain the Pseudo-F statistic and P-values. The analysis was performed using the Bray-Curtis similarity measure, using square-root transformed abundance data (Legendre and Gallagher, 2001). Where significant differences in assemblage composition occurred, I did a pairwise comparison using PERMANOVA to determine which biotopes differed significantly from each other.

I also calculated the proportion of unique species within each biotope type, as well as the proportion of shared species between the biotopes. The Jaccard similarity index, which shows the arthropod community similarity between the different biotopes, was also included. The Jaccard similarity index was calculated using the following formula:

$$J = \frac{C}{A + B - C}$$

where "J" is the Jaccard similarity index, "C" is the number of shared species between two biotope types, "A" is the number of unique species of biotope A, and "B" is the number of species found in biotope B (Real and Vargas, 1996; Yue and Clayton, 2005).

Using the Bray-Curtis similarity measure (Bray and Curtis, 1957) in Primer 6, the assemblage similarity of each restored grassland site to each natural grassland and pine block site was obtained. The average similarity of each restored site to all natural and pine block sites was then calculated and presented using scatterplots. The assemblage similarity between restored and natural grassland, along with the assemblage similarity between the restored grassland and pine blocks, were plotted against time since pine trees had been retrospectively removed (i.e. from earliest time since pine removal, to the latest). Non-parametric Spearman rank order correlations were used to determine the relationship between assemblage similarities and time since pine removal (Lyerly, 1952). As some sites of the restored grassland sites had greater similarity to the natural sites than others, Spearman rank order correlations and scatterplots were used to select environmental variables to determine the relationship between these selected environmental variables and assemblage similarities between restored and natural grassland sites. Where environmental variables were highly correlated ($-0.500 \leq R \geq 0.500$), based on Spearman's rank order correlations (Appendix D), only one ecologically relevant variable from each correlation was included in the analysis. The environmental variables selected for the restored grassland sites were: the corridor width in which

the restored site occurred, size of the restored area, distance to nearest pine block and wetland, soil moisture, vegetation cover, number of plant species, and percentage bramble cover (within a 5 m radius). Mann-Whitney U tests were used to test whether the means of two groups were significantly different (Mann and Whitney, 1947) i.e. to determine whether the two groups (i.e. restored sites with greater and less assemblage similarity to natural sites) differed significantly in terms of the environmental variables.

3.3. Results

A total of 5 016 individuals were sampled, consisting of 21 different arthropod orders, 56 arthropod families and 206 species across all biotopes (see Appendix E). Species accumulation curves indicated observed species reached an asymptote (see Appendix F). Species estimators Chao 2 and Jacknife 2, indicated similar trends for observed species richness (Table 3.1). Overall, the most dominant orders were spiders (60 spp.), beetles (50 spp.), ants (32 spp.), grasshoppers (16 spp.) and bugs (14 spp.). In the natural biotope, the most dominant orders were spiders (47 spp.), beetles (28 spp.), ants (23 spp.). In the restored biotope, the dominant orders were spiders (44 spp.), beetles (29 spp.), ants (29 spp.). Within the pine blocks, the most dominant orders were spiders (20 spp.), beetles (20 spp.) and ants (12 spp.).

Table 3.1: Species accumulation estimators of overall observed species (Sobs) assemblage structure and functional guild assemblage structure between biotope types. Species estimators Chao 2 and Jacknife 2 included in analysis.

Assemblage	Sobs	Chao 2 ± SE	Jacknife 2 ± SE
Overall	206	236.29 ± 11.24	239.00 ± 13.75
Araneae	60	64.99 ± 3.10	60.01 ± 3.09
Coleoptera	50	66.04 ± 3.42	59.92 ± 3.95
Hemiptera	14	18.39 ± 1.88	17.98 ± 1.51
Hymenoptera	32	34.87 ± 1.17	34.82 ± 1.46
Orthoptera	16	18.19 ± 0.85	18.12 ± 0.93

3.3.1. Response of species richness to biotope type

Overall species richness was significantly different between biotope types ($\chi^2 = 20.91$, P < 0.001, df = 2) (Figure 3.2A). Overall species richness was significantly lower within the pine blocks compared to the natural and restored hydromorphic grassland. Spider ($\chi^2 = 25.85$, P < 0.001, df = 2) (Figure 3.2B), ant ($\chi^2 = 30.61$, P < 0.001, df = 2) (Figure 3.2E) and grasshopper ($\chi^2 = 20.12$, P < 0.001, df = 2) (Figure 3.2F) species richness differed significantly between biotopes, with species richness being significantly lower within pine blocks compared to the natural and restored grassland. Beetle ($\chi^2 = 2.70$, P = 0.259, df = 2) (Figure 3.2C) and bug ($\chi^2 = 5.19$, P = 0.075, df = 2) (Figure 3.2D) species richness did not differ significantly between biotopes.

48
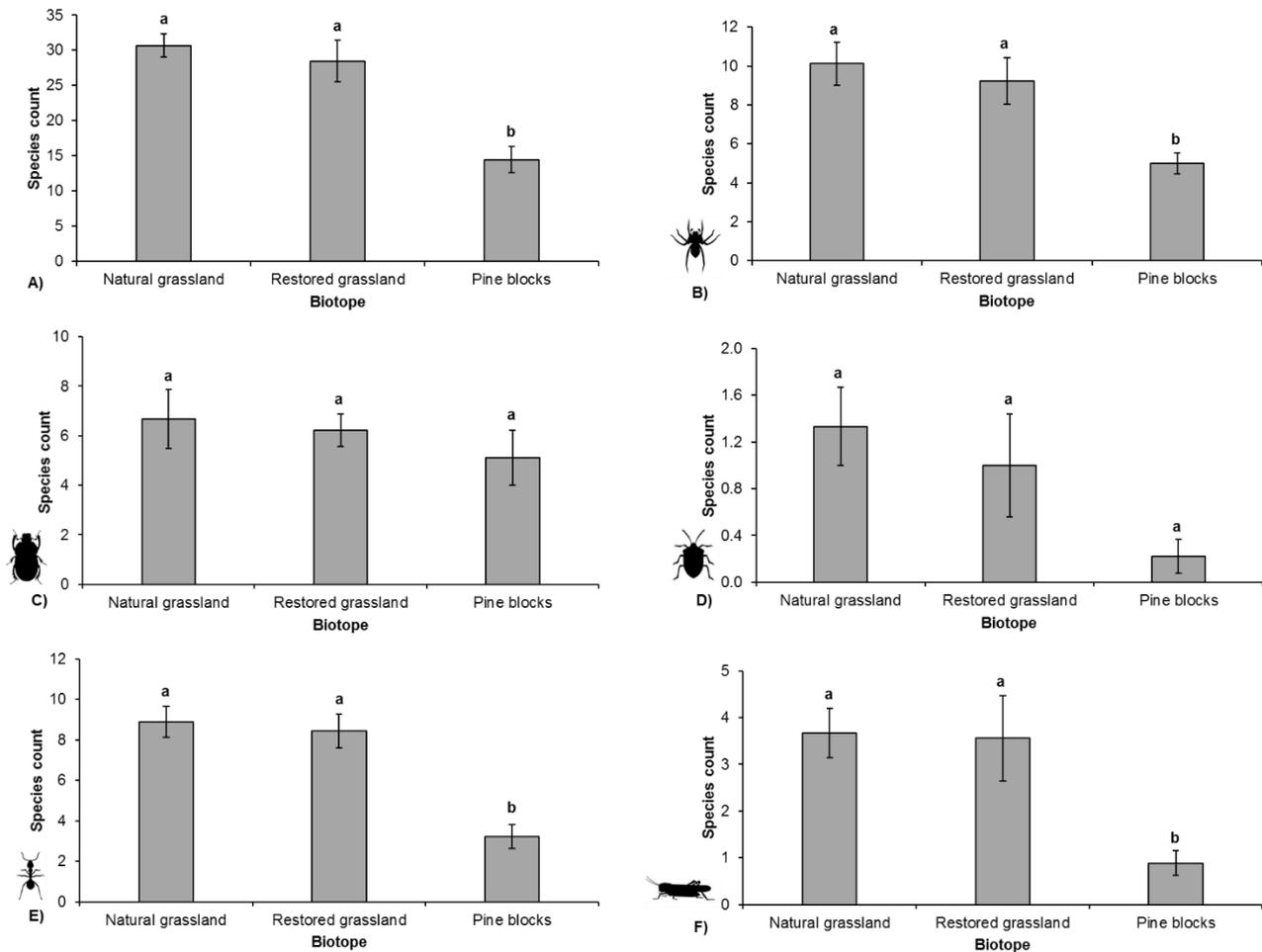
Figure 3.2: Mean (±SE) of A) overall, B) Araneae, C) Coleoptera, D) Hemiptera, E) Hymenoptera and F) Orthoptera species richness between natural grassland, restored grassland and pine blocks. Means with letters in common are not significantly different at p < 0.05, based on Tukey's post-hoc tests.

3.3.2. Assemblage structure of natural, restored and transformed biotopes

Overall arthropod assemblage composition (F = 3.76, P < 0.001, df = 2) (Figure 3.3A) differed significantly between biotopes (Table 3.2). Spider (F = 3.08, P < 0.001, df = 2) (Figure 3.3B), beetle (F = 2.35, P < 0.001, df = 2) (Figure 3.3C), ant (F = 5.73, P < 0.001, df = 2) (Figure 3.3E) and grasshopper (F = 2.26, P = 0.004, df = 2) (Figure 3.3F) assemblages also differed significantly between biotopes (Table 3.2). No significant difference in assemblage composition was found for bugs (F = 1.28, P = 0.103, df = 2) (Figure 3.3D) between biotopes (Table 3.2). For overall arthropod assemblage composition, pine blocks differed significantly from the natural and restored grasslands, but natural and restored grasslands were not significantly different from each other (Table 3.2). Similar results were found for spiders, ants and grasshoppers (Table 3.2). Beetle assemblage composition only differed significantly between pine blocks and restored grassland (Table 3.2).

49
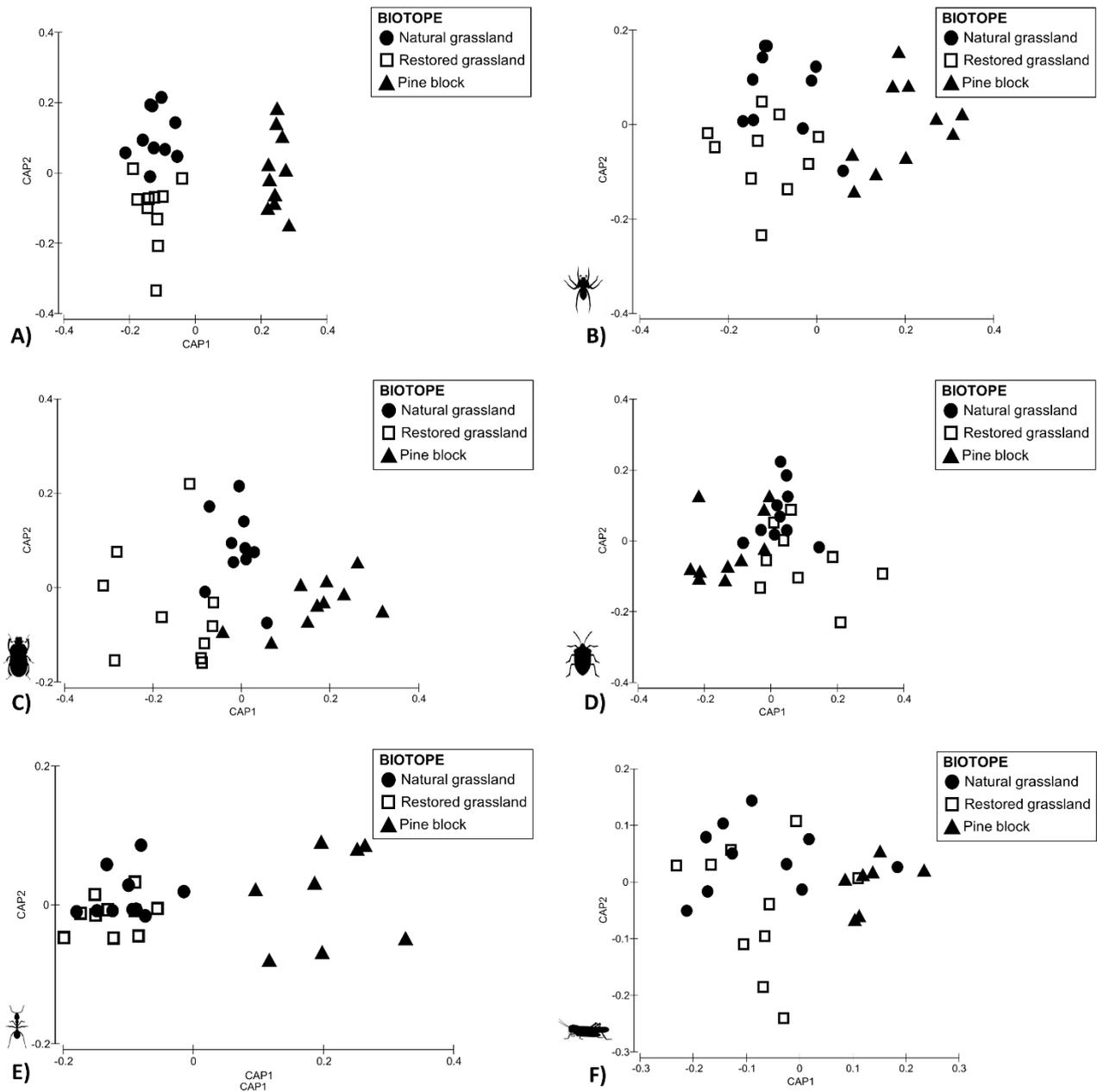
Figure 3.3: Canonical analysis of principal coordinates (CAP) for A) overall B) Araneae, C) Coleoptera, D) Hemiptera, E) Hymenoptera and F) Orthoptera assemblage structures between the natural grassland, restored grassland and pine blocks.

Table 3.2: PERMANOVA Pseudo-F (bold) and pairwise test (t – value) results for overall arthropod assemblage and assemblage structure of the dominant orders between natural grassland (Nat), restored grassland (Rest) and pine blocks (Pine), with significant differences indicated with (*).

Biotopes	Overall	Araneae	Coleoptera	Hemiptera	Hymenoptera	Orthoptera
Nat - Rest	1.03	1.10	1.18	1.18	1.05	1.18
Nat - Pine	2.32**	2.07***	1.37	1.24	2.88***	1.75**
Rest - Pine	2.24**	1.97***	1.95***	0.95	2.81***	1.49*

* P < 0.05; ** P < 0.01; *** P < 0.001

50
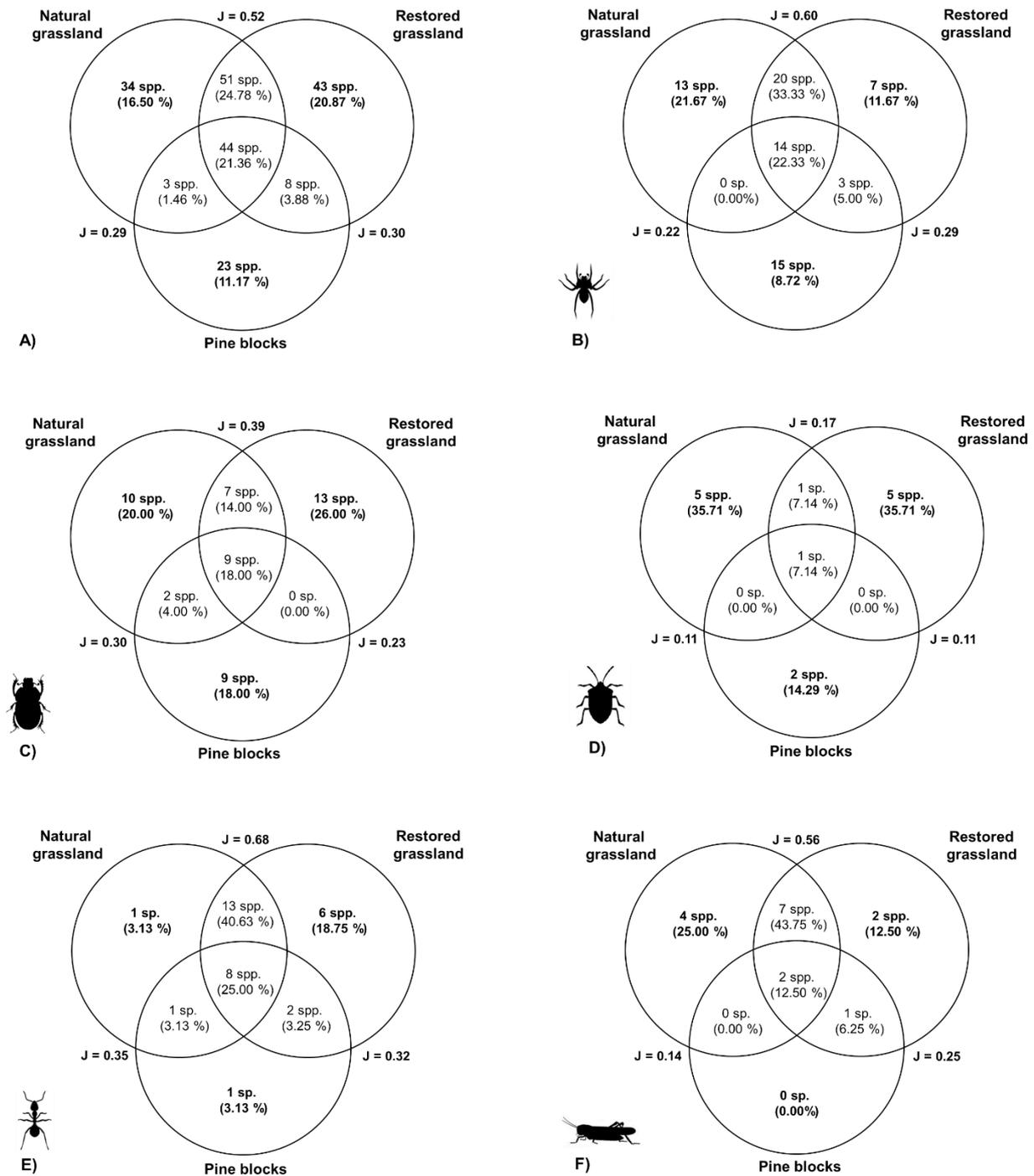
Figure 3.4: Proportion unique species (bold) and shared species for A) overall, B) Araneae, C) Coleoptera, D) Hemiptera, E) Hymenoptera and F) Orthoptera assemblages between natural grassland, restored grassland and pine blocks. Jaccard Similarity Index (J) indicates the percentage of species similarity between biotope types.

Overall, the greatest number of unique species was found within the restored grassland (43 spp.) followed by the natural (34 spp.) grassland and pine blocks (23 spp.) (Figure 3.4A). Greatest number of unique species for spiders was found within the pine blocks (15 spp.), followed by the natural (13 spp.) and restored grasslands (7 spp.) (Figure 3.4B). Greatest number of unique species for beetles was sampled in the restored grassland (13 spp.), followed by the natural grassland (10

51

spp.) and pine blocks (9 spp.) (Figure 3.4C). Greatest number of unique species for bugs was sampled in natural (5 spp.) and restored (5 spp.) grasslands, followed by pine blocks (2 spp.) (Figure 3.4D). Greatest number of unique species for ants was sampled in the restored grassland (6 spp.), followed by natural grassland (1 spp.) and pine blocks (1 spp.) (Figure 3.4E). Greatest number of unique species for grasshoppers was sampled in natural (4 spp.) and restored (2 spp.) grasslands, with no species being unique to pine blocks (Figure 3.4F). Natural and restored grasslands shared the most species with respect to their overall (Figure 3.4A), spider (Figure 3.4B), beetle (Figure 3.4C), bug (Figure 3.4D), ant (Figure 3.4E) and grasshopper (Figure 3.4G) and assemblages. This was verified using the Jaccard Similarity Index, which indicated that natural and restored grasslands were much more similar, compared to natural grassland and pine blocks, as well as restored grassland and pine blocks.

3.3.3. Restorability of hydromorphic grassland assemblages after pine removal

Overall assemblage similarity of restored and natural grasslands was significantly negatively correlated with the time since delineation (Figure 3.5A), whereas the overall assemblage similarity of restored grasslands and pine blocks showed no clear correlation with time since delineation (Figure 3.5B).
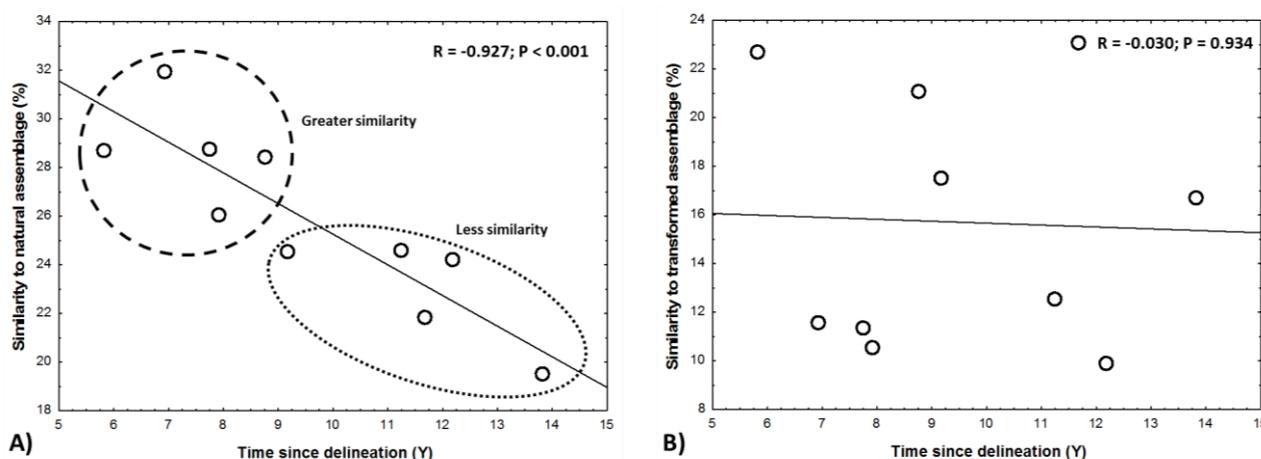
Figure 3.5: Scatterplots of overall arthropod assemblage similarity of restored grasslands to A) natural grassland and B) pine blocks. Trend line is the linear model of time to similarity.

In the case of assemblage similarity between the restored and natural grasslands (Figure 3.5A), some sites had a greater similarity to the natural grasslands than others. Restored sites >9 years old had lower similarity (<25%) to the natural biotopes. Restored sites <9 years old had greater similarity (>25%) to natural biotopes. Arthropod species richness was significantly different between younger and older restored sites ($\chi^2 = 6.61$, P = 0.01, df = 1), being highest in younger (39 ± 4.14) compared to older restored sites (29.8 ± 3.26).
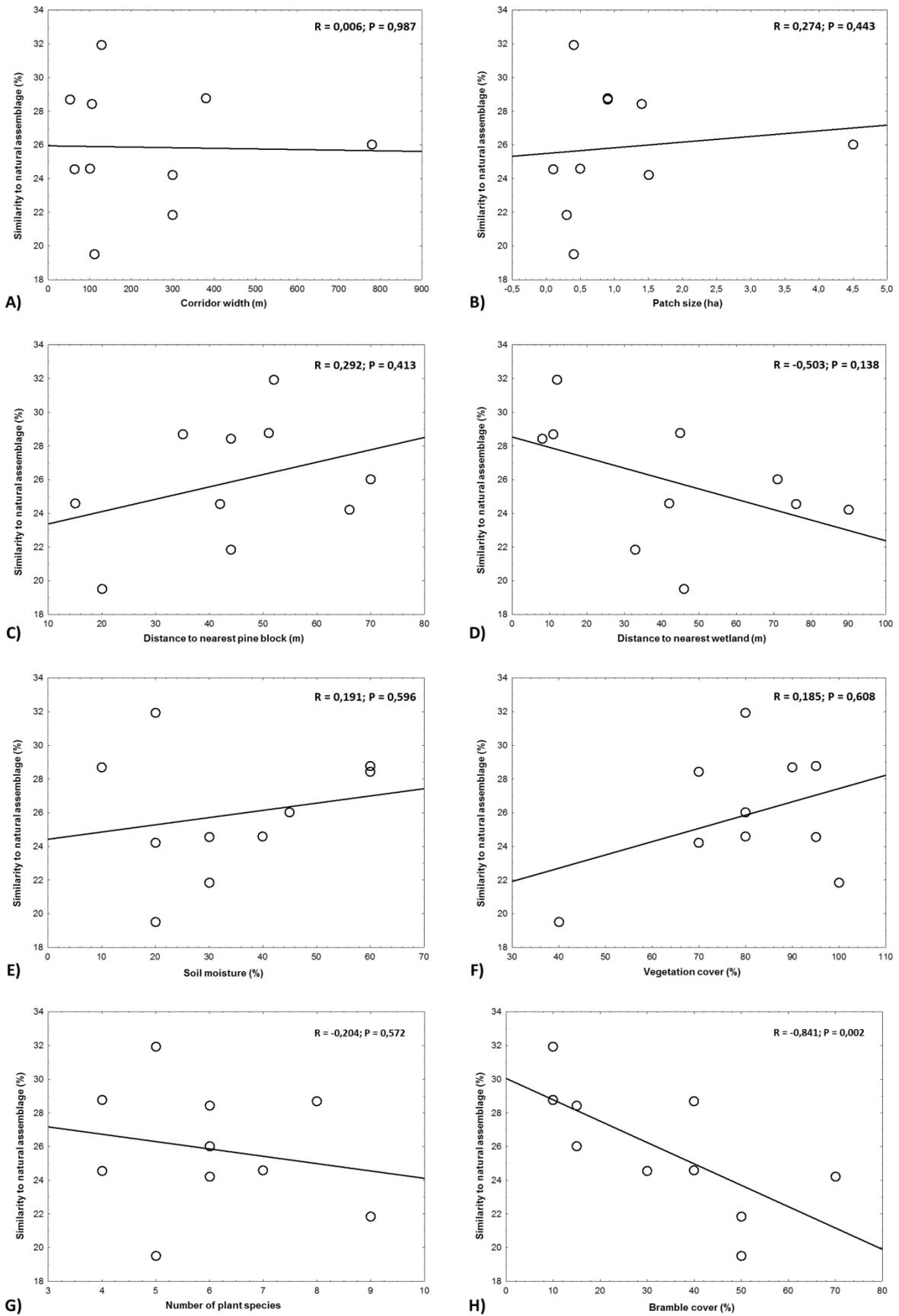
Figure 3.6: Relationships of A) corridor width, B) focal patch size, C) distance to nearest pine block, D) distance to nearest wetland, E) soil moisture, F) vegetation cover, G) plant diversity and H) bramble cover against the assemblage similarity of restored and natural grasslands. Trendline is the linear model of the similarity to the various environmental variables.

53

Different environmental variables correlated with assemblage similarity between restored and natural grasslands (Figure 3.6). Most variables were non-significant and weak, except for bramble cover, which was strongly negatively correlated with similarity to natural grassland (R= -0.84, P=0.002). There was a tendency for increased assemblage similarity between the natural and restored grasslands with an increase in corridor width in which the restored sites occurred (Figure 3.6A), the size of the restored area (Figure 3.6B), distance to the nearest pine block (Figure 3.6C), soil moisture content (Figure 3.6E), and percentage vegetation cover (Figure 3.6F). A decrease in assemblage similarity between the natural and restored grasslands occurred, with an increase in distance to nearest wetland (Figure 3.6D), number of plant species richness (Figure 3.6G), and percentage of bramble cover (Figure 3.6H).

Table 3.3: Non-parametric, Mann-Whitney U test results of environmental variables recorded within restored sites. Shown here are the differences in recorded environmental variables between restored sites with greater and less assemblage similarity to natural sites. Significant differences indicated with (*). SE = standard error.

Environmental variables	Greater similarity		Less similarity		U	Z	P
	Mean	SE	Mean	SE			
Corridor width (m)	289	135.06	175	52	10	0.418	0.676
Patch size (ha)	1.62	0.74	0.56	0.24	5.5	1.358	0.175
Distance to nearest pine block (m)	50.4	5.77	37.4	9.18	6.5	1.149	0.252
Distance to nearest wetland (m)	29.4	12.4	57.4	10.89	5	-1.462	0.144
Soil moisture (%)	39	10.3	28	3.74	9	0.627	0.534
Vegetation cover (%)	83	4.36	77	10.68	12	0.0001	1.000
Plant diversity	6	0.66	6	0.86	11	-0.209	0.835
Bramble cover (%)	18	5.61	48	6.63	1.5	-2.193	0.028*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Values for environmental factors were then compared between restored sites with greater and less assemblage similarity to natural sites (Table 3.3). Amount of bramble cover (within a 5 m radius of each site) was the only variable that was significantly different between the groups (Table 3.3), indicating that bramble was affecting the assemblage similarity of restored grasslands to natural grasslands.

3.4. Discussion

3.4.1. Arthropod diversity and assemblage compositions between natural, restored and transformed biotopes

Natural reference sites are important in restoration studies, as they provide the baseline against which to measure restoration success (Whigham, 1999). Restored sites are often compared to natural sites to determine whether biodiversity and ecosystem function have been restored, which indicates the level of restoration success. I found that restored and natural sites did not differ significantly in both species richness and assemblage composition. This indicates that the removal

of pine trees from hydromorphic grasslands is successful in restoring biodiversity. This is, to some extent, in line with Meli et al. (2014), who showed that biodiversity in restored wetlands can increase to levels similar to those of natural wetlands.

Disturbance is an important component of many ecosystems (Hobbs and Huenneke, 1992). However, when disturbance is too frequent, lower diversity can be expected (Collins and Glenn, 1997; Bongers et al., 2009). This may explain the low species diversity and significantly different arthropod assemblages in the pine blocks, as well as the high species uniqueness in the restored grassland. Harvesting of trees for wood and re-establishment of young seedlings causes the greatest soil disturbance (Tishall, 2015), and can have profound short- or long-term effects on soil chemical and physical properties (Du Toit et al., 2004; Nzila et al., 2004; Smith et al., 2008; Tishall, 2015). Soil biota are known to be sensitive to anthropogenic disturbances (Wolters and Schaefer, 1994; Pankhurst et al., 1997) which in turn is closely linked to soil properties (Six et al., 2004; Wardle et al., 2004; Barrios, 2007; Brussaard et al., 2007). This is likely why the higher species richness and uniqueness were in the restored grassland (with a low level of disturbance), compared to the pine blocks (with a high level of disturbance). Furthermore, I also found beetle and ant species to be more unique in the restored grassland, whereas grasshopper species were more unique in the natural grassland, and spider species most unique species in the pine blocks. This indicates that species and functional groups can respond differently to disturbance (Svensson et al., 2007; Bongers et al., 2009), which results in the community structure and functioning of the ecosystem to vary depending on disturbance regime (Hobbs and Huenneke, 1992; Wardel et al., 1999). Therefore, differences in responses of these arthropod taxa may be because of environmental and anthropogenic disturbance through the restoration process (Riggins et al., 2009).

Restoration was not equal for focal taxa, with some groups showing more pronounced positive responses to restoration than others. Meli et al. (2014) also showed that restoration of wetlands does benefit all organisms equally. Diversity of spiders, ants, and grasshoppers were significantly higher in the restored grassland compared to the pine blocks, and reached levels similar to the natural grassland. Their assemblages were also significantly different from the pine blocks, and more similar to the natural grassland. This indicates that these groups were positively affected by the restoration of these hydromorphic grasslands. Beetle and bug species richness showed no significant difference between the natural, restored and transformed (i.e. pine blocks) biotopes, indicating that their richness is not enhanced by restoration of these hydromorphic grasslands, or that these groups are more tolerant of different land-uses. Furthermore, no significant difference

was found for beetle assemblage composition between the natural grassland, the restored grassland and pine blocks. Even though the species accumulation curve for beetles reached a near asymptote, it appears that they either respond immediately to grassland recovery or are responding to the landscape and not the patch (Wiens et al., 1997; Driscoll and Weir, 2005; Pryke and Samways 2012). Pryke et al. (2013), working in the same system, showed that dung beetles are highly sensitive to land-use. This means that to successfully measure recovery of these systems using beetle assemblages, there needs to be focus on specific taxa within the group rather than the overall assemblage. That bug assemblages did not differ significantly between the natural, restored and transformed biotopes, could be that they are predominantly herbivorous, and likely to be more active on plants than at ground level. Pitfall trapping is more effective for the collection of arthropods which are active at ground level (Zanetti et al., 2016), and not as effective for arthropods which are active on plants. Although active searching for arthropods was included here, more attention was given to topsoil and leaf litter layers than on plants in each sample plot. As estimation of ecological or biological patterns is strongly dependent on sampling effort (Cao et al., 2002) and sample size (Colwell et al., 2004), the bug species richness and assemblages between these biotopes may be due to the low numbers of individuals and species collected here.

3.4.2. Restorability of hydromorphic grassland assemblages and the environmental constraints

Ecological resilience, as defined by Walker et al. (2004), is "the ability of an ecosystem to return to its former, natural condition after a disturbance". Here, the younger restored sites recovered relatively fast, within a few years. Similar results were found by Magoba et al. (2015), showing the removal of alien invasive trees (including *Pinus* species), can lead to the rapid recovery of arthropod assemblages within a few years. This may be an indication of high resilience due to high levels of weakly interacting species (Naeem et al., 1994; Walker, 1995). Also, when more species (with the same ecological functions) occur in an ecosystem, loss of one species (and their functions) is more easily replaced by another species (with the same functions) through ecological equivalence (Loiselle et al. 2007). Here, I found younger restored grassland sites had significantly higher arthropod diversity compared to older restored grassland sites, which agrees with Tilman and Downing (1994) who showed that grassland ecosystems with high biological diversity were more resilient to disturbance and recovered rapidly compared to those with lower biological diversity. However, I found that as time since pine removal increased, similarity between the natural and restored biotope assemblages decreased significantly. This is contrary to expectations, assume that with improved conditions arthropod assemblages would recover to levels similar to natural

conditions. This suggests that some sort of intermediate disturbance effect is at play and/or there were highly dynamic food webs at play where competition and/or predator impacts were still highly volatile.

Landscape- and site-scale factors either promoted or limited similarities between the arthropod assemblages of the natural and restored grasslands. Landscape-scale characteristics of various types can influence recovery of wetlands. These include distance of natural wetlands to restored wetlands (Zobel et al., 1998; Shepherd and Debinski, 2005; Déri et al., 2011), wetland size, and distance to nearest road (Douglas and Johnson, 1994; Daniels and Cumming, 2008; Moreno-Mateos et al., 2012), maintenance of landscape biodiversity (Muller et al., 1998), and management practices (Déri et al., 2011). Riggins et al. (2009) found mechanized disturbance caused by the restoration process could damage soil strata, leading to changes in physical, chemical and biological properties, which influenced restoration rate and success. Furthermore, limitations in recovery of hydrological conditions (Roelofs et al., 1996) and plant assemblages (Verhagen et al., 2001; Seabloom and van der Walk, 2003; Moreno-Mateos et al., 2012) can influence restoration success of degraded wetlands, while successful recovery of wetlands are also influenced by species' dispersal abilities in overcoming environmental barriers (Brady et al. 2002).

Here, the only environmental variable that significantly decreased assemblage similarities between the grasslands (natural and restored) was bramble cover (*Rubus cuneifolius*), notwithstanding that invasive alien plants (IAPs) are a well-known threat to native biodiversity and ecosystem stability (MacDonald et al., 1986; Samways et al., 1996; Richardson and van Wilgen, 2004; Gaertner et al., 2009). Invasive alien plants can have direct and indirect effects on biodiversity (Clusella-Trullas and Garcia, 2017). Presence of IAPs can alter environmental structure and complexity, leading to changes in habitat structure and microclimate (Clusella-Trullas and Garcia, 2017), soil (Magoba and Samways, 2012) and vegetation (Gaertner et al., 2009) characteristics. IAPs can also alter food resources, resulting in cascade affects within the food web (Clusella-Trullas and Garcia, 2017). In addition, IAPs can limit wetland restoration success, as they act as barriers preventing the re-establishment of native plant species (Seabloom and van der Walk, 2003). Here, increased bramble cover clearly interfered with recovery of these ground-living arthropods.

Bramble is a Category 1 alien invasive plant in South Africa (Hansen et al., 2017). Its impact on biodiversity is so great, that under the Conservation of Agricultural Resources Act (CARA) No. 43 of 1983 (CARA, 1983), and under the National Environmental Management: Biodiversity Act

(NEMBA) No. 10 of 2004 (NEMBA, 2004), its occurrence and distribution needs to be limited by either removing or destroying it immediately (Hansen et al., 2017). Brambles are deciduous perennial shrubs (Hansen et al., 2017) with extensive root systems (Erasmus, 1984). Their horizontal roots can grow >10 m at just below the soil surface, and can reach a diameter of <30 mm. The plants also grow vigorously, making dense stands <1.5 m high (Erasmus, 1984). Invasions by woody plants can have a major effect through their canopy increasing shade on the soil surface (Versfeld and van Wilgen, 1986), as well as changing the understory vegetation, which can alter soil characteristics (Samways et al., 1996). Effects are far ranging, with bramble having negative impacts on birds (Reynolds and Symes, 2003), dragonflies (Kietzka et al. 2015) and flower-visiting insects (Hansen et al., 2017). Here, I show that bramble also affects the recovery process of topsoil and leaf litter arthropods after restoration.

Presence of dense bramble stands in the restored biotopes is preventing topsoil and leaf litter arthropod assemblages returning to those that resemble natural sites. As some of these invaded areas occur in small corridors adjacent to pine blocks, fire as a method of management is improbable, and manual removal is the only feasible option (Henderson, 2007). Although the management of this plant is difficult, time consuming and expensive (Boring et al., 1988; Hansen et al., 2017), it must be done as this plant is having a major damaging effect on so many components of the local biodiversity, and likely also on hydrological processes.

3.5. Conclusion

We can never fully restore a degraded system back to its pristine condition, but we can restore a system to where the biodiversity closely resembles that prior to anthropogenic disturbance (Samways and Sharratt, 2010). Wet grassland systems are important elements within a landscape, contributing greatly to landscape heterogeneity and biodiversity. Therefore, the restoration of degraded wetlands has great conservation value. Here, I show that the natural hydromorphic grasslands in a timber plantation landscape has great biodiversity value. Furthermore, restoration of lost or degraded hydromorphic grasslands is highly feasible for recovery of topsoil and leaf litter arthropod assemblages. However, some environmental factors are limiting the successful restoration of certain restored sites. American bramble (*R. cuneifolius*) within these restored sites, is causing sites to deviate from the trajectory where the arthropod assemblages resemble those of natural sites. Therefore, to successfully restore hydromorphic grasslands within these landscapes, removal and management of this alien invasive plant species is a priority, especially to prevent its further spread.

3.6. References

Anderson M.J. and Willis T.J. (2003). Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. Ecology 84: 511-525.

Bakker J.P. and Berendse F. (1999). Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology and Evolution 14: 63-68.

Barrios E. (2007). Soil biota, ecosystem services and land productivity. Ecological Economics 64: 269-285.

Bates D., Maechler M., Bolker B. and Walker S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1: 1-23.

Bazelet C.S. and Samways M.J. (2011). Relative importance of management vs. design for implementation of large-scale ecological networks. Landscape Ecology 26: 341-353.

Bernhard-Reversat F., Laclau J.P., Loubana P.M., Loumeto J.J., Mboukou I.M.C. and Reversat G. (2001). Changes in biological factors of fertility in managed eucalyptus plantations on a savanna soil in Congo. In: Kobayasgi S. (Ed.). Rehabilitation of degraded tropical forest ecosystems: workshop proceedings. CIFOR, Bogor: 179-190.

Birkhofer K., Diekötter T., Boch S., Fischer M., Müller J., Socher S. and Wolters V. (2011). Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. Soil Biology and Biochemistry 43: 2200-2207.

Bishop C. (2006). Pattern recognition and machine learning. Springer, New York.

Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H. and White J.S.S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology and Evolution 24: 127-35.

Bongers F., Poorter L., Hawthorne W.D. and Sheil D. (2009). The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. Ecology Letters 12: 798-805.

Boring L.R., Swank W.T. and Monk C.D. (1988). Dynamics of early successional forest structure in the Coweeta basin. In: Swank W.T. and Crossley D.A. (Eds.). Forest hydrology and ecology at Coweeta. Ecological studies. New York, USA: Springer-Verlag: 161-179.

Brady V.J., Cardinale B.J., Gathman J.P. and Burton T.M. (2002). Does facilitation of faunal recruitment benefit ecosystem restoration? An experimental study of invertebrate assemblages in wetland mesocosms. Restoration Ecology 10: 617-626.

Bray J.R. and Curtis J.T. (1957). An ordination of upland forest communities of southern Wisconsin. Ecological Monographs 27: 325-349.

Bretz F., Hothorn T. and Westfall P. (2002). On multiple comparisons in R. R News 2: 14-17.

Bretz F., Hothorn T. and Westfall P. (2008). Multiple comparison procedures in linear models. COMPSTAT: 423-431.

Brussaard L., De Ruiter P.C. and Brown G.G. (2007). Soil biodiversity for agricultural sustainability. Agriculture, Ecosystems and Environment 121: 233-244.

Cao Y., Larsen D.P., Hughes R.M., Angermeier P.L. and Patton T.M. (2002). Sampling effort affects multivariate comparisons of stream assemblages. Journal of the North American Benthological Society 21: 701-714.

Clusella-Trullas S. and Garcia R.A. (2017). Impacts of invasive plants on animal diversity in South Africa: A synthesis. Bothalia-African Biodiversity and Conservation 47: 1-12.

Collins, S.L. and Glenn, S.M. (1997). Intermediate disturbance and its relationship to within-and between-patch dynamics. New Zealand Journal of Ecology: 103-110.

Colwell R.K. and Coddington J.A. (1994). Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London B: Biological Sciences 345: 101-118.

Colwell R.K., Mao C.X. and Chang J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85: 2717-2727.

Conservation of Agricultural Resources Act (CARA). (1983). No. 43 of 1983. Regulation 15 substituted by regulation 3 of Government Notice R280 of 2001. Available at http://cer.org.za/wp-content/uploads/2014/02/CARA-Regs.pdf, accessed in July 2017.

Consul P.C. and Jain G.C. (1973). A generalization of the Poisson distribution. Technometrics 15: 791-799.

Cui B., Yang Q., Yang Z. and Zhang K. (2009). Evaluating the ecological performance of wetland restoration in the Yellow River Delta, China. Ecological Engineering 35: 1090-1103.

Daniels A.E. and Cumming G.S. (2008). Conversion or conservation? Understanding wetland change in northwest Costa Rica. Ecological Applications 18: 49-63.

Déri E., Magura T., Horváth R., Kisfali M., Ruff G., Lengyel S. and Tóthmérész B. (2011). Measuring the short-term success of grassland restoration: The use of habitat affinity indices in ecological restoration. Restoration Ecology 19: 520-528.

Dippenaar-Schoeman A.S. and Harvey M.S. (2000). A check list of the pseudoscorpions of South Africa (Arachnida: Pseudoscorpiones). Koedoe 43: 89-102.

Dirsh V.M. (1965). The African genera of Acridoidea. Cambridge University Press, London.

Douglas A.J. and Johnson R.L. (1994). Drainage investment and wetlands loss: An analysis of the National Resource Inventory data. Journal of Environmental Management 40: 341-355.

Driscoll D.A. and Weir T.O.M. (2005). Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. Conservation Biology 19: 182-194.

Du Toit B., Dovey S.B., Fuller G.M. and Job R.A. (2004). Effects of harvesting and site management on nutrient pools and stand growth in a South African eucalypt plantation. Site Management and Productivity in Tropical Plantation Forests: 31-43

Dye P. and Jermain C. (2004). Water use by black wattle (Acacia mearnsii): implications for the link between removal of invading trees and catchment streamflow. South African Journal of Science 100: 40-44.

Eeley H.A., Lawes M.J. and Piper S.E. (1999). The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. Journal of Biogeography 26: 595-617.

Ellery W., Grenfell M., Grenfell S., Kotze D., McCarthy T.S., Tooth S., Grundling P.L., Beckedahl H., Maitre D.L. and Ramsay L. (2011). WET-origins: Controls on the distribution and dynamics of wetlands in South Africa. WRC Report (334): 100.

Erasmus D.J. (1984). Bramble farming in South Africa. Department of Agriculture and Water Supply, Pretoria.

Fairbanks D.H. and Benn G.A. (2000). Identifying regional landscapes for conservation planning: A case study from KwaZulu-Natal, South Africa. Landscape and Urban Planning 50: 237-257.

Gaertner M., Den Breeyen A., Hui C. and Richardson D.M. (2009). Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: A meta-analysis. Progress in Physical Geography 33: 319-338.

Goodman N.R. (1963). Statistical analysis based on a certain multivariate complex Gaussian distribution (an introduction). The Annals of Mathematical Statistics 34: 152-177.

Gotelli N.J. and Colwell R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Grenfell M.C., Ellery W.N., Garden S.E., Dini J. and Van der Valk A.G. (2007). The language of intervention: A review of concepts and terminology in wetland ecosystem repair. Water SA 33: 43-50.

Haddad C.R., Dippenaar-Schoeman A.S. and Wesolowska W. (2006). A checklist of the non-acarine arachnids (Chelicerata: Arachnida) of the Ndumo Game Reserve, Maputaland, South Africa. Koedoe 49: 1-22.

Haddad N.M., Bowne D.R., Cunningham A., Danielson B.J., Levey D.J., Sargent S. and Spira T. (2003). Corridor use by diverse taxa. Ecology 84: 609-615.

Hansen S., Roets F., Seymour C.L., Thébault E., van Veen F.J.F. and Pryke J.S. (2017). Alien plants have greater impact than habitat fragmentation on native insect flower visitation networks. Diversity and Distributions DOI: 10.1111/ddi.12656

Hansson L.A., Brönmark C., Anders Nilsson P. and Abjörnsson K. (2005). Conflicting demands on wetland ecosystem services: Nutrient retention, biodiversity or both? Freshwater Biology 50: 705-714.

Henderson L. (2007). Invasive, naturalized and casual alien plants in southern Africa: A summary based on the Southern African Plant Invaders Atlas (SAPIA). Bothalia 372: 215-248.

Hobbs R.J. and Huenneke L.F. (1992). Disturbance, diversity, and invasion: Implications for conservation. Conservation Biology 6: 324-337.

Höfer H., Hanagarth W., Garcia M., Martius C., Franklin E., Römbke J. and Beck L. (2001). Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. European Journal of Soil Biology 37: 229-235.

Janion-Scheepers C., Deharveng L., Bedos A. and Chown S. (2015). Updated list of Collembola species currently recorded from South Africa. ZooKeys 503: 55-88.

Janion-Scheepers C., Measey J., Braschler B., Chown S.L., Coetzee L., Colville J.F., Dames J., Davies A.B., Davies S.J., Davis A.L. and Dippenaar-Schoeman A.S. (2016). Soil biota in a megadiverse country: Current knowledge and future research directions in South Africa. Pedobiologia 59: 129-174.

Joubert L. and Samways M.J. (2011). Ecological networks: the key to biodiversity conservation. Quest 7: 30-32.

Joubert L. and Samways M.J. (2014). Equivalence of grasslands in an ecological network and a World Heritage Site. Biodiversity and Conservation 23: 2415-2426.

Keddy P.A. (2004). Wetland ecology: Principles and conservation. Cambridge University Press, Cambridge.

Keep M.E. and Ledger J.A. (1990). Lice (Phthiraptera), fleas (Siphonaptera) and mites (Trombidiformes, Sarcoptiformes and Mesostigmata) recorded from the larger game species in Natal. Lammergeyer 41: 23-29.

Kietzka G.J., Pryke J.S. and Samways M.J. (2015). Landscape ecological networks are successful in supporting a diverse dragonfly assemblage. Insect Conservation and Diversity 8: 229-237.

King L. (1978). A geomorphology of central and southern Africa: Biogeography and ecology of southern Africa. Monographiae Biologicae 31: 1-17.

Lawes M.J., Everard D. and Eeley H.A.C. (1999). Developing environmental criteria and indicators for sustainable plantation management: The South African perspective. South African Journal of Science 95: 461-469.

Legendre P. and Gallagher E.D. (2001). Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271-280.

Loiselle B.A., Blendinger P.G., Blake J.G. and Ryder T.B. (2007). Ecological redundancy in seed dispersal systems: A comparison between manakins (Aves: Pipridae) in two tropical forests. Seed dispersal: Theory and its application in a changing world. CABI, Wallingford, UK.

Loranger-Merciris G., Imbert D., Bernhard-Reversat F., Ponge J.F. and Lavelle P. (2007). Soil fauna abundance and diversity in a secondary semi-evergreen forest in Guadeloupe (Lesser Antilles): Influence of soil type and dominant tree species. Biology and Fertility of Soils 44: 269-276.

Louw S., Wilson J.R., Veldtman R. and Addison M. (2014). The unknown underworld: Understanding soil health in South Africa. South African Journal of Science 110: 1-4.

Lu X. and Wang R. (1995). Study on wetland biodiversity in China. Chinese Geographical Science 6: 15-23.

Lyerly S.B. (1952). The average Spearman rank correlation coefficient. Psychometrika 17: 421-428.

Macdonald I.A. (2004). Recent research on alien plant invasions and their management in South Africa: A review of the inaugural research symposium of the Working for Water programme: working for water. South African Journal of Science 100: 21-26.

MacDonald I.A.W., Kruger F.J. and Ferrar A.A. (1986). The ecology and control of biological invasions in Southern Africa. Oxford University Press, Cape Town.

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

Magoba R.N., Simaika J.P. and Samways M.J. (2015). Soil compaction and surface-active arthropods in historic, agricultural, alien, and recovering vegetation. Journal of Insect Conservation 19: 501-508.

Malan H. (2010). The status of research on wetland ecology, management and conservation in South Africa. In Ramsar workshop of the STRP National Focal Points of Africa and other wetland experts. Johannesburg, South Africa.

Mann H.B. and Whitney D.R. (1947). On a test of whether one of two random variables is stochastically larger than the other. The Annals of Mathematical Statistics: 50-60.

Matthews S. (2008). Forestry firm ploughs back into nature. Forestry and Wetlands (Sept/Oct): 29-31.

McCoy E.D. and Mushinsky H.R. (2002). Measuring the success of wildlife community restoration. Ecological Applications 12: 1861-1871.

Meli P., Benayas J.M.R., Balvanera P. and Ramos M.M. (2014). Restoration enhances wetland biodiversity and ecosystem service supply, but results are context-dependent: A meta-analysis. PloS one 9: e93507.

Melo A.S. (2004). A critique of the use of jackknife and related non-parametric techniques to estimate species richness. Community Ecology 5: 149-157.

Mesibov R., Taylor R.J. and Brereton R.N. (1995). Relative efficiency of pitfall trapping and hand-collecting from plots for sampling of millipedes. Biodiversity and Conservation 4: 429-439.

Mitsch W.J. and Wilson R.F. (1996). Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications 6: 77-83.

Mommertz S., Schauer C., Kösters N., Lang A. and Filser J. (1996). A comparison of D-vac suction, fenced and unfenced pitfall trap sampling of epigeal arthropods in agroecosystems. Annales Zoologici Fennici 33: 117-124.

Moreno-Mateos D., Power M.E., Comín F.A. and Yockteng R. (2012). Structural and functional loss in restored wetland ecosystems. PLoS Biology 10: e1001247.

Mucina L. and Rutherford M.C. (2006). The Vegetation of South Africa, Lesotho and Swaziland. SANBI, Pretoria, South Africa.

Muller S., Dutoit T., Alard D. and Grevilliot F. (1998). Restoration and rehabilitation of species-rich grassland ecosystems in France: A review. Restoration Ecology 6: 94-101.

Naeem S., Thompson J., Lawler S.P., Lawton J.H. and Woodfin R.M. (1994). Declining biodiversity can alter the performance of ecosystems. Nature 368: 734-737.

National Environmental Management: Biodiversity Act (NEMBA). (2004). No 10 of 2004. Part 2: Invasive species. Accessed from https://www.sanbi.org/sites/default/files/documents/documents/bio-diversityact2004pdf.pdf., accessed in July 2017.

Neke K.S. and du Plessis M.A. (2004). The threat of transformation: Quantifying the vulnerability of grasslands in South Africa. Conservation Biology 18: 466-477.

Nzila J.D.D., Deleporte P., Bouillet J.P., Laclau J.P. and Ranger J. (2004). Effects of slash management on tree growth and nutrient cycling in second-rotation Eucalyptus replanted sites in the Congo. Site Management and Productivity in Tropical Plantation Forests: 15-30.

Oades J.M. (1993). The role of biology in the formation, stabilization and degradation of soil structure. Geoderma 56: 377-400.

Pankhurst C., Doube B.M. and Gupta V.V.S.R. (1997). Biological indicators of soil health. CAB International, Wallingford.

Passell H.D. (2000). Recovery of bird species in minimally restored Indonesian thin strips mines. Restoration Ecology 8: 112-118.

Picker M., Griffiths C. and Weaving A. (2004). Field guide to insects of South Africa. Struik Nature, Cape Town.

Prasifka J.R., Lopez M.D., Hellmich R.L., Lewis L.C. and Dively G.P. (2007). Comparison of pitfall traps and litter bags for sampling ground-dwelling arthropods. Journal of Applied Entomology 131: 115-120.

Preston G. (2003). Invasive alien plants and protected areas in South Africa. In Presentation to World Parks Congress. Durban, South Africa.

PRIMER-E. (2008). PERMANOVA and PRIMER 6. PRIMERE, Lutton, Bedfordshire, UK.

Pryke J.S. and Samways M.J. (2012). Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. Journal of Applied Ecology 49: 591-600.

Pryke J.S., Roets F. and Samways M.J. (2013). Importance of habitat heterogeneity in remnant patches for conserving dung beetles. Biodiversity and Conservation 22: 2857-2873.

QGIS Development Team. (2009). QGIS Geographic Information System. Open Source Geospatial Foundation. Available at http://qgis.osgeo.org, accessed in March 2016.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org/, accessed in May 2016.

Real R. and Vargas J.M. (1996). The probabilistic basis of Jaccard's index of similarity. Systematic biology 45: 380-385.

Reay S.D. and Norton D.A. (1999). Assessing the success of restoration plantings in a temperate New Zealand forest. Restoration Ecology 7: 298-308.

Reynolds C. and Symes C.T. (2013). Grassland bird response to vegetation structural heterogeneity and clearing of invasive bramble. African Zoology 48: 228-239.

Rhoades C.C., Eckert G.E. and Coleman D.C. (1998). Effect of pastures trees on soil nitrogen and organic matter: Implications for tropical montane forest restoration. Restoration Ecology 6: 262-270.

Richardson D.M. and Van Wilgen B.W. (2004). Invasive alien plants in South Africa: How well do we understand the ecological impacts? Working for water. South African Journal of Science 100: 45-52.

Riddell E.S., Everson C., Clulow A. and Mengistu M. (2013). The hydrological characterisation and water budget of a South African rehabilitated headwater wetland system. Water SA 39: 57-66.

Riggins J.J., Davis C.A. and Hoback W.W. (2009). Biodiversity of belowground invertebrates as an indicator of wet meadow restoration success (Platte River, Nebraska). Restoration Ecology 17: 495-505.

Robinson D.A., Hockley N., Dominati E., Lebron I., Scow K.M., Reynolds B., Emmett B.A., Keith A.M., de Jonge L.W., Schjonning P. and Moldrup P. (2012). Natural capital, ecosystem services, and soil change: Why soil science must embrace an ecosystems approach. Vadose Zone Journal 11: 1-20.

Roelofs J.G., Bobbink R., Brouwer E. and de Graaf M.C. (1996) Restoration ecology of aquatic and terrestrial vegetation on non-calcareous sandy soils in the Netherlands. Acta Botanica Neerlandica 45: 517-541.

Sabo J.L., Sponseller R., Dixon M., Gade K., Harms T., Heffernan J., Jani A., Katz G., Soykan C., Watts J. and Welter J. (2005). Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86: 56-62.

Samways M.J. and Niba A. (2010). Climate and elevational range of a South African dragonfly assemblage. BioRisk 5: 85-107.

Samways M.J. and Pryke J.S. (2016). Large-scale ecological networks do work in an ecologically complex biodiversity hotspot. Ambio 45: 161-172.

Samways M.J. and Sharratt N.J. (2010). Recovery of endemic dragonflies after removal of invasive alien trees. Conservation Biology 24: 267-277.

Samways M.J., Caldwell P.M. and Osborn R. (1996). Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. Agriculture, Ecosystems and Environment 59: 19-32.

Scholtz C.H. and Holm E. (1985). Insects of Southern Africa. Butterworths, Cape Town, South Africa.

Schulze R.E. (1982). Agrohydrology and climatology of Natal. Water Research Commission, Pretoria.

Seabloom E.W. and van der Valk A.G. (2003). Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: Implications for restoration. Wetlands 23: 1-12.

Shepherd S. and Debinski D.M. (2005). Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies. Biological Conservation 126(1): 51-61.

Sieben E.J.J., Ellery W.N., Kotze D.C. and Rountree M. (2011). Hierarchical spatial organization and prioritization of wetlands: A conceptual model for wetland rehabilitation in South Africa. Wetlands Ecology and Management 19: 209-222.

Six J., Bossuyt H., Degryze S. and Denef K. (2004). A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics. Soil and Tillage Research 79: 7-31.

Smith T.E., Osborne D.O. and Simpson J.A. (2008). Inter-rotation management impacts on growth and soil properties in hybrid pine plantations on sandy soils in subtropical Australia. Site Management and Productivity in Tropical Plantation Forests: 139-147.

Southwood T.R.E. (1978). Ecological methods. Chapman and Hall, London.

Standen V. (2000). The adequacy of collecting methods for estimating species richness of grassland invertebrates. Journal of Applied Ecology 37: 884-893.

Svensson J.R., Lindegarth M., Siccha M., Lenz M., Molis M., Wahl M. and Pavia H. (2007). Maximum species richness at intermediate frequencies of disturbance: Consistency among levels of productivity. Ecology 88: 830-838.

Tilman D. and Downing J.A. (1994). Biodiversity and stability in grasslands. Nature 367: 363-365.

Titshall L. (2015). Managing our soils for sustainable production. SA Forestry Magazine: 1-5.

van Aarde R.J., Ferreira S.M., Kritzinger J.J., van Dyk P.J., Vogt M. and Wassenaar T.D. (1996). An evaluation of habitat rehabilitation on coastal dune forest in northern KwaZulu-Natal, South Africa. Restoration Ecology 4: 334-345.

Verhagen R., Klooker J., Bakker J.P. and Diggelen R.V. (2001). Restoration success of low-production plant communities on former agricultural soils after top-soil removal. Applied Vegetation Science 4: 75-82.

Versfeld D.B. and Van Wilgen B.W. (1986). Impact of woody aliens on ecosystem properties. In: Macdonald I.A.W., Kruger F.J. and Ferrar A.A. (Eds.). The ecology and control of biological invasions in Southern Africa. Oxford University Press, Cape Town.

Walker B. (1995). Conserving biological diversity through ecosystem resilience. Conservation Biology 9: 747-752.

Walker B., Holling C.S., Carpenter S.R. and Kinzig A. (2004). Resilience, adaptability and transformability in social-ecological systems. Ecology and Society 9: 5.

Walker J.B. (1991). A review of the ixodid ticks (Acari: Ixodidae) occurring in southern Africa. Onderstepoort Journal of Veterinary Research 58: 81-105.

Wardle D.A., Bardgett R.D., Klironomos J.N., Setälä H., Van Der Putten W.H. and Wall D.H. (2004). Ecological linkages between aboveground and belowground biota. Science 304: 1629-1633.

Wardle D.A., Yeates G.W., Nicholson K.S., Bonner K.I. and Watson R.N. (1999). Response of soil microbial biomass dynamics, activity and plant litter decomposition to agricultural intensification over a seven-year period. Soil Biology and Biochemistry 31: 1707-1720.

Warren M.W. and Zou X. (2002). Soil macrofauna and litter nutrients in three tropical tree plantations on a disturbed site in Puerto Rico. Forest Ecology and Management 170: 161-171.

Whigham D.F. (1999). Ecological issues related to wetland preservation, restoration, creation and assessment. Science of the Total Environment 240: 31-40.

Wiens J.A., Schooley R.L. and Weeks Jr. R.D. (1997). Patchy landscapes and animal movements: Do beetles percolate? Oikos: 257-264.

Wolters V. and Schaefer M. (1994). Effects of acid deposition on soil organisms and decomposition processes. In: Benckiser, G. (Ed.). Effects of acid rain on forest processes. Wiley, New York.

Woomer P.L. and Swift M.J. (1994). The biological management of tropical soil fertility. John Wiley and Sons, Chichester.

Yan S., Singh A.N., Fu S., Liao C., Wang S., Li Y., Cui Y. and Hu L. (2012). A soil fauna index for assessing soil quality. Soil Biology and Biochemistry 47: 158-165.

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

Yue J.C. and Clayton M.K. (2005). A similarity measure based on species proportions. Communications in Statistics-Theory and Methods 34: 2123-2131.

Zanetti N.I., Camina R., Visciarelli E.C. and Centemo N.D. (2016). Active search on carcasses versus pitfall traps: A comparison of sampling methods. Neotropical Entomology 45: 221-226.

Zobel M., Van Der Maarel E. and Dupré C. (1998). Species pool: The concept, its determination and its significance for community restoration. Applied Vegetation Science 1: 55-66.

Chapter 4
General discussion

With this thesis, I set out to gain an in-depth understanding of the diversity and distribution of litter and topsoil arthropods within the ecological networks (ENs) of South African forestry plantation landscapes. In Chapter 2, I investigated the response of topsoil and leaf litter arthropod diversity and assemblage structures to various land-uses by looking at four different biotope types within the landscape (including indigenous forest, pine plantation, dry grassland and hydromorphic grassland), as well as how environmental variations affected their diversity and assemblage structures within these biotopes. Attention was given to hydromorphic soil grassland as they are valuable assets within ecosystems (Hansson et al., 2005). However, within the ENs of South Africa, they have not received much attention as a biotope in itself, and therefore their biodiversity value within these systems also remains poorly understood.

In Chapter 2, I demonstrated that natural, untransformed biotopes (i.e. natural forest, dry and hydromorphic grassland) had higher species diversity compared to the transformed biotope (i.e. pine plantations). This corresponds with studies that show pine plantations generally contribute little to landscape biodiversity and have lower species diversity compared to natural biotopes (Armstrong et al., 1998; Pryke and Samways, 2012). Previous studies within these ENs show that the preservation of natural remnant habitats within timber production landscapes is crucial for the conservation and maintenance of a wide range of species (Pryke and Samways, 2012; Joubert and Samways, 2014; Kietzka et al., 2015; Yekwayo et al., 2016). Here in Chapter 2, I also show that set-aside natural areas in these production landscapes are also important for topsoil and leaf litter arthropods. When one considers that the large amount of untransformed land that remains in these landscapes has such a high biodiversity value, this large-scale land sparing approach (i.e. the partitioning of an agricultural landscape for agricultural purposes and the conservation of remnant natural areas) (Phalan et al., 2011) appears to be an appropriate conservation approach for soil and litter arthropods. Even though the practical conservation value of landscape ENs has been questioned (Boitani et al., 2007), these findings contribute to a growing body of work that is providing evidence that ENs can make a significant contribution to biodiversity conservation (Samways and Pryke, 2016).

Furthermore, I showed that natural remnant hydromorphic grasslands are valuable and unique components within ENs that contribute to landscape biodiversity and heterogeneity. Interestingly,

66

the two grassland biotopes (dry and hydromorphic) are two distinct biotopes, and their underlying environmental differences translate into distinctly different arthropod assemblages. Due to the important ecosystem services they provide, hydromorphic grasslands are protected by laws and FSC regulations. However, dry grasslands have not been granted much protection. I therefore suggest conservation efforts must also include the protection of dry grasslands, as both these grassland biotopes play important roles as components within ENs for maintaining arthropod biodiversity in these production landscapes. Furthermore, I strongly recommend the continued preservation of natural remnant hydromorphic grasslands using the land sparing approach, as they contribute to landscape connectivity, which is promoting biodiversity within these highly transformed landscapes. In fact, all of the untransformed biotopes were complementary in their soil and litter arthropod assemblages. By conserving all these different natural remnants, we inherently promote landscape compositional heterogeneity, which is important for the conservation of beta diversity, in the form of species turnover between different landscape elements (Dunning et al., 1992; Fahrig et al., 2011). This is an especially important principle for conservation planning in human-transformed landscapes, where landscape heterogeneity is often lost due to transformation (Benton et al., 2003).

The second part of my thesis investigated the recovery of hydromorphic grassland topsoil and leaf litter arthropod diversity and assemblage composition, as a measure of restoration success following the removal of planted pine trees (Chapter 3). In general, grassland restoration is a high priority for conservation in order to re-establish connections between them in a highly fragmented, transformed landscape (Walker et al., 2004b; Stadler et al., 2007). In Chapter 3, I show that natural and restored hydromorphic grasslands show no significant difference in arthropod species richness or assemblage composition. Therefore, although the aim of restoration of hydromorphic grasslands was initially for hydrological purposes (Joubert and Samways, 2011; Samways and Pryke, 2016), I have shown that it is also beneficial for the re-establishment of functionally important biodiversity. Most restoration studies have focussed on plant diversity and functional composition (Ruiz-Jaen and Aide, 2005; Zalomis and Bond, 2010; Wortley et al., 2013), with fewer studies focussing on arthropod diversity and composition (van Aarde et al., 1996; Nichols and Nichols, 2003; Ruiz-Jaen and Aide, 2005; Wortley et al., 2013). Furthermore, research regarding the restoration of grasslands on former croplands only focussed on plant diversity and assemblages (Walker et al., 2004b; Ruprecht, 2006; Stadler et al., 2007), with apparently no research being done on arthropods. Although Magoba et al. (2015) investigated recovery of arthropod assemblages after the removal of alien invasive trees (including various Pinus species), the study was conducted in the Cape Floristic Region (CFR) of South Africa and focussed on the recovery of fynbos assemblages. Therefore, my

study (Chapter 3) is one of the first to show the restoration success of hydromorphic grasslands regarding arthropod diversity and assemblage composition after the removal of pine trees from hydromorphic soils.

Additionally, I investigated the effect of time since delineation (i.e. time since removal of planted pine trees) on the diversity and assemblage composition of topsoil and leaf litter arthropods, as the restoration success of this process on biodiversity has not previously been measured. In restoration projects, it is important to have natural reference areas to determine the direction of restoration success (Whigham, 1999). Therefore, I compared the diversity and assemblage compositions of topsoil and leaf litter arthropods between naturally occurring hydromorphic grasslands, restored hydromorphic grasslands and pine plantations. In Chapter 3, I show that the restoration of these systems is having a positive effect on arthropod biodiversity and assemblages (i.e. they are reaching levels similar to natural systems), confirming that it is worthwhile investing in restoration efforts. Contrary to what was hypothesized, arthropod assemblages seem to have recovered within the first 5 years of restoration, which is quite rapid. Mitsch and Wilson (1996) suggested the restoration of forested wetlands may require more than 15 years before restoration success could be determined. However, my results, and the results of Magoba et al. (2015), suggest otherwise, and at least for hydromorphic soils, show arthropod assemblages can recover within a few years after the removal of alien invasive trees (such as *Pinus* species). This might be an indication that these assemblages are inherently very responsive to restoration as a result of high resilience (Walker, 1995; Walker et al., 2004a).

However, due to site availability issues, restored sites of 0-5 years after restoration could not be included in this study, although it would have been interesting to see at which exact point in time they have converted back to near-natural assemblages. Also, due to time limitations, I was only able to look at sites which occurred at various times since restoration, as a substitute for the actual monitoring of sites across time. This means that environmental differences and site history may have influenced the results in addition to time since restoration (Driscoll et al. 2010). Therefore, I recommend that a more comprehensive study should follow which monitors the restoration success of hydromorphic grasslands and their assemblages over time, starting with more recently restored areas.

Contrary to what was expected, assemblage similarity between the natural and restored biotope significantly decreased with time since pine removal. Further examination revealed that several

factors were promoting restored assemblages to recover, including an increase in corridor width, biotope size, distance to pine block, soil moisture and vegetation cover. Other factors were limiting the recovery of restored assemblages, including an increase in distance to wetland, number of plant species and American bramble cover (*Rubus cuneifolius*). Therefore, based on these results, it would appear that the areas with the greatest restoration potential are those areas which occur in larger corridors, are larger in size, are closer to natural hydromorphic grasslands, and furthest from pine compartments. Land managers can use these results to improve current restoration efforts by identifying areas that are most likely to respond positively to restoration. This is especially important in this context where time and resources for management can be limited.

Interestingly, *R. cuneifolius* was the most influential factor within the restored sites (Chapter 3). Having high densities of *R. cuneifolius* within some of the restored areas were causing them to deviate from an arthropod assemblage resembling natural areas. Studies within these ENs have shown that bramble can have negative impacts on dragonfly (Kietzka et al., 2015) and flower-visiting insect (Hansen, 2015) assemblages. Here, I also showed that *R. cuneifolius* affects the recovery process of topsoil and leaf litter arthropods after the restoration of hydromorphic grasslands. The removal and management of bramble generally involves cutting (i.e. slashing, mowing or burning), grazing and browsing by livestock, biological control using leaf diseases and insects, or the use of herbicides (Denny, 1999). These need to be repeated constantly for the effective control of this invasive alien plant (IAP). My research (Chapter 3) showed that the restored areas that were most invaded, were the areas that occurred adjacent to pine blocks within very small corridors. Therefore, fire as a method for management in these small corridors would be of high risk to the production blocks. Thus, the only feasible options within the smaller areas closer to the pine blocks would be manual removal (through slashing and mowing) or chemical control. Therefore, in order to comply with the laws and regulations set for this IAP (CARA, 1983; NEMBA, 2004), management needs to make the removal of this plant a priority.

Due to the fact that Chapter 3 was not initially designed to detect the effects of bramble, I was not able to do more rigorous further testing of this effect. Therefore, a more comprehensive study in the future (i.e. a larger sample size and more replicates of different levels of bramble infestation) could provide detailed information of the effect of *R. cuneifolius* on the arthropods inhabiting topsoil and leaf litter. Also, as *R. cuneifolius* was found to be detrimental to restoration success of hydromorphic soil grasslands, it would be interesting to see how topsoil and leaf litter arthropods

recover over time after the removal of bramble. Therefore, I also recommend a long-term study to determine whether these assemblages are recovering after the removal of bramble.

In conclusion, the balance between agricultural production, ecosystem stability and functioning is crucial to ensure sustainable agricultural production (Carter, 2001). Biodiversity within production landscapes is essential, as they play an important ecological role within these systems (Altieri, 1999). Following on from the information provided by my study, future research on the ecological roles of soil biota would provide further justification for their conservation and restoration in these production landscapes. Aside from providing important ecological services (Altieri, 1999), biodiversity is also important for ecosystem resilience (Fischer et al., 2006). Ecosystem resilience is important in production landscapes, as it provides the system with the ability to maintain its ecological integrity to recover from significant external pressures, such as climate change (Adger, 2000) and management practices (Fischer et al., 2006), and it secures the system's ability to provide essential ecosystem services (Elmqvist et al., 2003).

As soil biota are important for sustainable agricultural ecosystems, it is important to encourage management practices that enhance the diversity of these organisms by enhancing their habitat conditions and availability of resources (Altieri, 1999). My thesis provides guidance to land managers on how to conserve these arthropods, by demonstrating that the conservation of remnant natural areas (Chapter 2), as well as the restoration of degraded areas of high conservation value (Chapter 3), is important for the maintenance of topsoil and leaf litter arthropods within these highly transformed landscapes. Therefore, this large-scale EN delineation approach used by the South African forestry is showing huge potential for the conservation of these organisms. Furthermore, the restoration of degraded hydromorphic systems has never been more crucial. Its ecological characteristics (i.e. its natural resilience, the connection between terrestrial and aquatic ecosystems, provides refuges for wide range of species and the provision of habitat connectivity throughout a landscape) contributes to the system's ability to adapt to climate change (Seavy et al., 2009).

In general, the intrinsic value of soil biodiversity is less apparent than for above ground biodiversity (Brussaard et al., 2007). However, these organisms provide important ecosystem services (Oades, 1993; Birkhofer et al., 2011) and play a crucial role maintaining the health and quality of soils, which in turn, affects the productivity of the soil (Woomer and Swift, 1994; Höfer et al., 2001; Giller et al., 2005). However, there is still a great need to understand value and functioning of these organisms in South Africa (Titshall, 2015; Janion-Scheepers et al., 2016). Therefore, by

acknowledging the importance of these organisms in South African soil systems and understanding their conservation value, we can make informed decisions on sustainable agricultural and conservation practices that will help us enhance and maintain soil health into the future.

References

Adger W.N. (2000). Social and ecological resilience: Are they related? Progress in Human Geography 24: 347-364.

Altieri M.A. (1999). The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74: 19-31.

Armstrong A.J., Benn G., Bowland A.E., Goodman P.S., Johnson D.N., Maddock A.H. and Scott-Shaw C.R. (1998). Plantation forestry in South Africa and its impact on biodiversity. Southern African Forestry Journal 182: 59-65.

Benton T.G., Vickery J.A. and Wilson J.D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? Trends in Ecology and Evolution 18: 182-188.

Birkhofer K., Diekötter T., Boch S., Fischer M., Müller J., Socher S. and Wolters V. (2011). Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. Soil Biology and Biochemistry 43: 2200-2207.

Boitani L., Falcucci A., Maiorano L. and Rondinini C. (2007). Ecological networks as conceptual frameworks or operational tools in conservation. Conservation Biology 21: 1414-1422.

Brussaard L., De Ruiter P.C. and Brown G.G. (2007). Soil biodiversity for agricultural sustainability. Agriculture, Ecosystems and Environment 121: 233-244.

Carter M.R. (2001). Researching the agroecosystem/environmental interface. Agriculture, Ecosystems and Environment 83: 3-9.

Conservation of Agricultural Resources Act (CARA). (1983). No. 43 of 1983. Regulation 15 substituted by regulation 3 of Government Notice R280 of 2001. Available at http://cer.org.za/wp-content/uploads/2014/02/CARA-Regs.pdf, accessed in July 2017.

Denny R. (1999). Control of American bramble. Prepared for the Dargle Conservancy, March 2005. Available at http://www.midlandsconservancies.org.za/documents/problemplants/control%-20of%20bramble.pdf, accessed in August 2017.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G. and Gill M. (2010). Fire management for biodiversity conservation: Key research questions and our capacity to answer them. Biological Conservation 143: 1928-1939.

Dunning J.B., Danielson B.J. and Pulliam H.R. (1992). Ecological processes that affect populations in complex landscapes. Oikos 65: 169-175.

Elmqvist T., Folke C., Nyström M., Peterson G., Bengtsson J., Walker B. and Norberg J. (2003). Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment, 1: 488-494.

Fahrig L., Baudry J., Brotons L., Burel F.G., Crist T.O., Fuller R.J., Sirami C., Siriwardena G.M. and Martin J.L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14: 101-112.

Fischer J., Lindenmayer D.B. and Manning A.D. (2006). Biodiversity, ecosystem function, and resilience: Ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4: 80-86.

Giller K.E., Bignell D., Larvelle P., Swift, M.J., Barrios, E., Moreira, F., van Noordwijk, M., Barois, I., Karanja, N. and Huising J. (2005). Soil biodiversity in rapidly changing tropical landscapes: Scaling down and scaling up. Biological Diversity and Functions in Soils: 295-318.

Hansen S., Roets F., Seymour C.L., Thébault E., van Veen F.J.F. and Pryke J.S. (2017). Alien plants have greater impact than habitat fragmentation on native insect flower visitation networks. Diversity and Distributions DOI: 10.1111/ddi.12656.

Hansson L.A., Brönmark C., Anders Nilsson P. and Abjörnsson K. (2005). Conflicting demands on wetland ecosystem services: Nutrient retention, biodiversity or both? Freshwater Biology 50: 705-714.

Höfer H., Hanagarth W., Garcia M., Martius C., Franklin E., Römbke J. and Beck L. (2001). Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. European Journal of Soil Biology 37: 229-235.

Janion-Scheepers C., Measey J., Braschler B., Chown S.L., Coetzee L., Colville J.F., Dames J., Davies A.B., Davies S.J., Davis A.L. and Dippenaar-Schoeman A.S. (2016). Soil biota in a megadiverse country: Current knowledge and future research directions in South Africa. Pedobiologia 59: 129-174.

Joubert L. and Samways M.J. (2011). Ecological networks: The key to biodiversity conservation. Quest 7: 30-32.

Joubert L. and Samways M.J. (2014). Equivalence of grasslands in an ecological network and a World Heritage Site. Biodiversity and Conservation 23: 2415-2426.

Kietzka G.J., Pryke J.S. and Samways M.J. (2015). Landscape ecological networks are successful in supporting a diverse dragonfly assemblage. Insect Conservation and Diversity 8: 229-237.

Magoba R.N., Simaika J.P. and Samways M.J. (2015). Soil compaction and surface-active arthropods in historic, agricultural, alien, and recovering vegetation. Journal of Insect Conservation 19: 501-508.

Mitsch W.J. and Wilson R.F. (1996). Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications 6: 77-83.

National Environmental Management: Biodiversity Act (NEMBA). (2004). No 10 of 2004. Part 2: Invasive species. Accessed from https://www.sanbi.org/sites/default/files/documents/documents/bio-diversityact2004pdf.pdf., accessed in July 2017.

Nichols O.G. and Nichols F.M. (2003). Long-term trends in faunal recolonization after bauxite mining in the jarrah forest of southwestern Australia. Restoration Ecology 11: 261-272.

Oades J.M. (1993). The role of biology in the formation, stabilization and degradation of soil structure. Geoderma 56: 377-400.

Phalan B., Onial M., Balmford A. and Green R.E. (2011). Reconciling food production and biodiversity conservation: Land sharing and land sparing compared. Science 333: 1289-1291.

Pryke J.S. and Samways M.J. (2012). Conservation management of complex natural forests and plantation edge effects. Landscape Ecology 27: 73-85.

Ruiz-Jaen M.C. and Mitchell Aide T. (2005). Restoration success: How is it being measured? Restoration Ecology 13: 569-577.

Ruprecht E. (2006). Successfully recovered grassland: A promising example from Romanian old-fields. Restoration Ecology 14: 473-480.

Samways M.J. and Pryke J.S. (2016). Large-scale ecological networks do work in an ecologically complex biodiversity hotspot. Ambio 45: 161-172.

Seavy N.E., Gardali T., Golet G.H., Griggs F.T., Howell C.A., Kelsey R., Small S.L., Viers J.H. and Weigand J.F. (2009). Why climate change makes riparian restoration more important than ever: Recommendations for practice and research. Ecological Restoration 27: 330-338.

Stadler J., Trefflich A., Brandl R. and Klotz S. (2007). Spontaneous regeneration of dry grasslands on set-aside fields. Biodiversity and Conservation 16: 621-630.

Titshall L. (2015). Managing our soils for sustainable production. SA Forestry Magazine: 1-5.

van Aarde R.J., Ferreira S.M., Kritzinger J.J.,. van Dyk P.J, Vogt M. and Wassenaar T.D. (1996). An evaluation of habitat rehabilitation on coastal dune forest in northern KwaZulu-Natal, South Africa. Restoration Ecology 4: 334-345.

Walker B. (1995). Conserving biological diversity through ecosystem resilience. Conservation Biology 9: 747-752.

Walker B., Holling C.S., Carpenter S.R. and Kinzig A. (2004a). Resilience, adaptability and transformability in social-ecological systems. Ecology and Society 9: 5.

Walker K.J., Stevens P.A., Stevens D.P., Mountford J.O., Manchester S.J. and Pywell R.F. (2004b). The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation 119: 1-18.

Whigham D.F. (1999). Ecological issues related to wetland preservation, restoration, creation and assessment. Science of the Total Environment 240: 31-40.

Woomer P.L. and Swift M.J. (1994). The biological management of tropical soil fertility. Wiley, Chichester, UK.

Wortley L., Hero J.M. and Howes M. (2013). Evaluating ecological restoration success: A review of the literature. Restoration Ecology 21: 537-543.

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

Zaloumis N.P. and Bond W.J. (2011). Grassland restoration after afforestation: No direction home? Austral Ecology 36: 357-366.

Appendix A: Spearman's rank order correlations of all recorded environmental variables across natural forest, pine block, dry grassland and hydromorphic grassland sites. Marked correlations (bold) are significant at $P < 0.05$.

Environmental variables	Site elevation (m)	Soil moisture (%)	Soil compaction (psi)	Soil pH	Vegetation cover (%)	Vegetation height (m)	Number plant species	Leaf litter (%)	Canopy cover (%)	Shade cover (%)	Dead wood (%)
Site elevation (m)	1,000	0,156	**-0,397**	0,033	0,028	-0,069	-0,075	0,194	**0,614**	**0,494**	**0,349**
Soil moisture (%)	0,156	1,000	**-0,739**	**-0,558**	**0,488**	**0,408**	-0,253	-0,045	0,127	0,092	0,016
Soil compaction (psi)	**-0,397**	**-0,739**	1,000	0,308	**-0,324**	-0,112	**0,451**	-0,113	**-0,440**	**-0,399**	-0,306
Soil pH	0,033	**-0,558**	0,308	1,000	**-0,429**	**-0,490**	-0,027	0,189	0,151	0,051	0,176
Vegetation cover (%)	0,028	**0,488**	**-0,324**	**-0,429**	1,000	**0,691**	0,199	**-0,736**	**-0,403**	**-0,435**	**-0,616**
Vegetation height (m)	-0,069	**0,408**	-0,112	**-0,490**	**0,691**	1,000	0,289	**-0,564**	**-0,326**	**-0,373**	**-0,461**
Number plant species	-0,075	-0,253	**0,451**	-0,027	0,199	0,289	1,000	**-0,500**	**-0,354**	-0,273	**-0,479**
Leaf litter (%)	0,194	-0,045	-0,113	0,189	**-0,736**	**-0,564**	**-0,500**	1,000	**0,649**	**0,662**	**0,793**
Canopy cover (%)	**0,614**	0,127	**-0,440**	0,151	**-0,403**	**-0,326**	**-0,354**	**0,649**	1,000	**0,911**	**0,852**
Shade cover (%)	**0,494**	0,092	**-0,399**	0,051	**-0,435**	**-0,373**	-0,273	**0,662**	**0,911**	1,000	**0,822**
Dead wood (%)	**0,349**	0,016	-0,306	0,176	**-0,616**	**-0,461**	**-0,479**	**0,793**	**0,852**	**0,822**	1,000
Rock cover (%)	**0,365**	0,053	-0,074	-0,067	0,291	0,149	**0,327**	-0,211	0,267	0,248	0,085
Tree (%)	**0,334**	0,006	-0,297	0,102	**-0,598**	**-0,436**	**-0,440**	**0,780**	**0,842**	**0,865**	**0,955**
Herbaceous cover (%)	**0,417**	**0,362**	**-0,462**	-0,296	**0,507**	**0,451**	0,229	-0,233	0,244	0,172	-0,074
Shrub cover (%)	0,114	0,108	-0,074	-0,186	0,092	0,092	0,063	-0,119	0,029	0,136	0,127
Grass cover (%)	-0,250	0,022	0,276	-0,132	**0,686**	**0,505**	**0,432**	**-0,777**	**-0,713**	**-0,713**	**-0,835**
Clear ground (%)	-0,246	-0,207	**0,457**	0,054	0,097	0,217	**0,565**	**-0,533**	**-0,579**	**-0,635**	**-0,620**
Site slope (%)	**0,379**	0,140	-0,284	0,092	-0,044	0,009	0,085	0,080	**0,543**	**0,520**	**0,370**
Site aspect	-0,298	-0,294	**0,344**	0,194	0,059	0,065	0,266	-0,160	-0,283	-0,263	-0,282
Focal biotope (%)	-0,059	**-0,369**	0,301	**0,341**	**-0,402**	-0,232	-0,076	0,269	0,246	0,266	0,245
Transformed landscape (%)	0,244	0,037	-0,190	-0,050	0,033	-0,198	-0,096	0,040	-0,079	-0,100	0,016

Appendix A continued

Environmental variables	Rock cover (%)	Tree (%)	Herbaceous cover (%)	Shrub cover (%)	Grass cover (%)	Clear ground (%)	Site slope (%)	Site aspect	Focal biotope (%)	Transformed landscape (%)
Site elevation (m)	**0,365**	**0,334**	**0,417**	0,114	-0,250	-0,246	**0,379**	-0,298	-0,059	0,244
Soil moisture (%)	0,053	0,006	**0,362**	0,108	0,022	-0,207	0,140	-0,294	**-0,369**	0,037
Soil compaction (psi)	-0,074	-0,297	**-0,462**	-0,074	0,276	**0,457**	-0,284	**0,344**	0,301	-0,190
Soil pH	-0,067	0,102	-0,296	-0,186	-0,132	0,054	0,092	0,194	**0,341**	-0,050
Vegetation cover (%)	0,291	**-0,598**	**0,507**	0,092	**0,686**	0,097	-0,044	0,059	**-0,402**	0,033
Vegetation height (m)	0,149	**-0,436**	**0,451**	0,092	**0,505**	0,217	0,009	0,065	-0,232	-0,198
Number plant species	**0,327**	**-0,440**	0,229	0,063	**0,432**	**0,565**	0,085	0,266	-0,076	-0,096
Leaf litter (%)	-0,211	**0,780**	-0,233	-0,119	**-0,777**	**-0,533**	0,080	-0,160	0,269	0,040
Canopy cover (%)	0,267	**0,842**	0,244	0,029	**-0,713**	**-0,579**	**0,543**	-0,283	0,246	-0,079
Shade cover (%)	0,248	**0,865**	0,172	0,136	**-0,713**	**-0,635**	**0,520**	-0,263	0,266	-0,100
Dead wood (%)	0,085	**0,955**	-0,074	0,127	**-0,835**	**-0,620**	0,370	-0,282	0,245	0,016
Rock cover (%)	1,000	0,131	0,295	**0,472**	0,093	-0,111	0,300	-0,032	0,046	-0,019
Tree (%)	0,131	1,000	-0,068	0,211	**-0,827**	**-0,606**	0,382	-0,264	0,228	-0,014
Herbaceous cover (%)	0,295	-0,068	1,000	-0,128	-0,002	-0,139	**0,386**	-0,106	-0,152	-0,048
Shrub cover (%)	**0,472**	0,211	-0,128	1,000	0,039	-0,075	0,143	-0,285	-0,148	**0,340**
Grass cover (%)	0,093	**-0,827**	-0,002	0,039	1,000	**0,433**	-0,281	0,259	**-0,341**	-0,034
Clear ground (%)	-0,111	**-0,606**	-0,139	-0,075	**0,433**	1,000	-0,171	0,173	-0,086	-0,061
Site slope (%)	0,300	**0,382**	**0,386**	0,143	-0,281	-0,171	1,000	0,045	0,092	-0,047
Site aspect	-0,032	-0,264	-0,106	-0,285	0,259	0,173	0,045	1,000	0,137	-0,100
Focal biotope (%)	0,046	0,228	-0,152	-0,148	**-0,341**	-0,086	0,092	0,137	1,000	-0,278
Transformed landscape (%)	-0,019	-0,014	-0,048	**0,340**	-0,034	-0,061	-0,047	-0,100	-0,278	1,000

Appendix B: Arthropods recorded during study period, their functional guild and mean abundance ± standard error (SE) between natural forest (NatFor), pine block (PineBlock), dry grassland (DryGrass) and hydromorphic grassland (HydroGrass) sites.

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Amblypygi	Phrynichidae spp1	Predator	1.00	0.52	0.20	0.14	0.00	0.00	0.10	0.10
Amphipod	Ampithoidae spp1	Detritivore	87.70	14.38	0.30	0.22	0.00	0.00	0.30	0.15
Araneae	Amaurobiidae spp1	Predator	0.90	0.60	1.00	0.56	0.70	0.33	1.00	0.45
	Araneidae spp1	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Clubionidae spp1	Predator	0.70	0.42	0.00	0.00	0.00	0.00	0.30	0.30
	Eutichuriidae spp1	Predator	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
	Gallieniellidae spp1	Predator	1.30	0.60	2.70	1.47	0.30	0.21	0.00	0.00
	Gallieniellidae spp2	Predator	0.10	0.10	0.60	0.27	0.30	0.21	0.30	0.30
	Gnaphosidae spp1	Predator	0.00	0.00	0.80	0.43	0.80	0.29	0.20	0.13
	Linyphiidae spp1	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Linyphiidae spp2	Predator	1.70	0.60	0.50	0.42	0.20	0.20	1.10	0.72
	Linyphiidae spp3	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Linyphiidae spp4	Predator	0.10	0.10	0.20	0.14	0.40	0.22	0.10	0.10
	Linyphiidae spp5	Predator	0.00	0.00	0.70	0.44	0.40	0.31	0.00	0.00
	Linyphiidae spp6	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.13
	Linyphiidae spp7	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Liocranidae spp1	Predator	0.30	0.21	0.00	0.00	0.00	0.00	0.00	0.00
	Lycosidae spp1	Predator	0.80	0.47	0.00	0.00	0.50	0.22	3.40	2.05
	Lycosidae spp2	Predator	0.00	0.00	0.00	0.00	0.00	0.00	1.90	0.66
	Lycosidae spp3	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.80	0.70
	Lycosidae spp4	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.50
	Pholcidae spp1	Predator	0.60	0.31	0.00	0.00	0.00	0.00	0.00	0.00
	Phyxelidae spp1	Predator	1.20	0.49	1.70	1.23	0.50	0.27	0.90	0.41

Appendix B continued

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Araneae	Phyxelidae spp2	Predator	0.30	0.15	0.50	0.23	0.00	0.00	0.00	0.00
	Salticidae spp1	Predator	0.70	0.33	0.00	0.00	0.80	0.47	0.00	0.00
	Salticidae spp2	Predator	1.10	0.35	0.10	0.11	0.90	0.41	0.00	0.00
	Salticidae spp3	Predator	0.50	0.27	0.00	0.00	1.00	0.61	0.10	0.10
	Salticidae spp4	Predator	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
	Scytodidae spp1	Predator	0.50	0.22	0.10	0.11	0.30	0.21	0.00	0.00
	Scytodidae spp2	Predator	0.00	0.00	0.90	0.32	0.40	0.27	0.20	0.20
	Scytodidae spp3	Predator	0.10	0.10	0.30	0.32	0.00	0.00	0.40	0.22
	Segestriidae spp1	Predator	3.20	1.15	0.70	0.63	0.10	0.10	0.40	0.31
	Sparassidae spp1	Predator	1.00	0.52	0.00	0.00	0.40	0.40	1.10	0.53
	Tetragnathidae spp1	Predator	2.10	0.55	7.20	1.85	1.30	0.52	1.90	1.58
	Tetragnathidae spp2	Predator	0.30	0.21	0.00	0.00	0.00	0.00	0.00	0.00
	Tetragnathidae spp3	Predator	0.70	0.30	0.00	0.00	0.00	0.00	0.00	0.00
	Tetragnathidae spp4	Predator	0.00	0.00	0.40	0.23	0.00	0.00	0.00	0.00
	Theridiidae spp1	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.60	0.50
	Theridiidae spp2	Predator	0.40	0.22	0.30	0.22	0.00	0.00	0.40	0.27
	Theridiidae spp3	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Thomisidae spp1	Predator	0.00	0.00	0.00	0.00	0.30	0.21	0.00	0.00
	Thomisidae spp2	Predator	0.00	0.00	0.00	0.00	0.40	0.27	0.00	0.00
	Trachelidae spp1	Predator	0.30	0.15	1.90	0.77	1.50	1.50	0.00	0.00
	Trachelidae spp2	Predator	0.00	0.00	0.00	0.00	0.20	0.20	0.00	0.00
	Zodariidae spp1	Predator	0.00	0.00	0.00	0.00	0.00	0.00	3.20	0.96
	Zodariidae spp2	Predator	0.20	0.20	0.00	0.00	0.00	0.00	0.10	0.10
Blattodea	Blaberidae spp1	Omnivore	0.10	0.10	0.40	0.28	0.10	0.10	0.00	0.00
	Blaberidae spp2	Omnivore	0.10	0.10	0.20	0.21	0.00	0.00	0.00	0.00

Appendix B continued

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Blattodea	Blatellidae spp1	Omnivore	0.00	0.00	0.70	0.44	0.00	0.00	0.00	0.00
	Blatellidae spp2	Omnivore	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
	Blatellidae spp3	Omnivore	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Blattidae spp1	Omnivore	0.00	0.00	0.10	0.11	0.00	0.00	0.00	0.00
Coleoptera	Anthicidae spp1	Omnivore	0.00	0.00	0.10	0.11	0.00	0.00	0.00	0.00
	Anthicidae spp2	Omnivore	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Bostrichidae spp1	Herbivore	0.00	0.00	0.40	0.23	0.10	0.10	0.20	0.13
	Bostrichidae spp2	Herbivore	0.10	0.10	0.00	0.00	0.80	0.70	0.30	0.15
	Bostrichidae spp3	Herbivore	0.00	0.00	0.00	0.00	0.60	0.31	0.20	0.20
	Bostrichidae spp4	Herbivore	1.00	0.45	0.00	0.00	0.30	0.21	0.10	0.10
	Bostrichidae spp5	Herbivore	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.30
	Carabidae spp1	Predator	0.00	0.00	0.10	0.11	0.00	0.00	0.00	0.00
	Carabidae spp2	Predator	0.00	0.00	1.20	0.67	0.80	0.59	0.00	0.00
	Carabidae spp3	Predator	0.10	0.10	0.30	0.22	0.50	0.40	0.10	0.10
	Carabidae spp4	Predator	0.00	0.00	0.00	0.00	0.20	0.20	0.10	0.10
	Carabidae spp5	Predator	0.00	0.00	0.00	0.00	0.10	0.10	0.10	0.10
	Carabidae spp6	Predator	0.00	0.00	0.00	0.00	0.20	0.20	0.50	0.50
	Carabidae spp7	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.21
	Carabidae spp8	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.50	0.22
	Cerambycidae spp1	Herbivore	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Cerambycidae spp2	Herbivore	0.20	0.13	0.00	0.00	0.00	0.00	0.00	0.00
	Chrysomelidae spp1	Herbivore	1.10	0.43	0.30	0.22	7.40	1.92	0.00	0.00
	Chrysomelidae spp2	Herbivore	0.20	0.13	0.00	0.00	0.20	0.20	1.80	0.74
	Chrysomelidae spp3	Herbivore	2.30	1.67	0.10	0.11	0.00	0.00	0.20	0.13
	Chrysomelidae spp4	Herbivore	0.20	0.13	0.00	0.00	0.00	0.00	0.00	0.00

Appendix B continued

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Coleoptera	Chrysomelidae spp5	Herbivore	0.00	0.00	0.10	0.11	0.00	0.00	0.00	0.00
	Chrysomelidae spp6	Herbivore	0.10	0.10	0.10	0.11	0.40	0.27	0.00	0.00
	Chrysomelidae spp7	Herbivore	0.10	0.10	0.00	0.00	1.10	0.48	0.50	0.22
	Chrysomelidae spp8	Herbivore	0.10	0.10	0.40	0.23	0.70	0.50	0.70	0.21
	Cicindelidae spp1	Predator	0.00	0.00	0.00	0.00	0.20	0.13	0.20	0.13
	Coccinelidae spp1	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Coccinelidae spp2	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.13
	Coccinelidae spp3	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Curculionidae spp1	Herbivore	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.20
	Cydnidae spp1	Herbivore	0.00	0.00	0.00	0.00	0.10	0.10	0.30	0.30
	Elateridae spp1	Herbivore	0.00	0.00	0.00	0.00	0.20	0.20	1.10	0.60
	Gyrinidae spp1	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.13
	Hydrophilidae spp1	Omnivore	1.50	0.45	0.40	0.23	0.20	0.13	0.20	0.20
	Hydrophilidae spp2	Omnivore	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Melyridae spp1	Predator	0.60	0.22	0.50	0.23	3.00	0.84	0.30	0.15
	Melyridae spp2	Predator	0.80	0.42	0.00	0.00	0.00	0.00	0.00	0.00
	Melyridae spp3	Predator	0.00	0.00	0.00	0.00	0.60	0.43	0.00	0.00
	Scarabaeidae spp1	Detritivore	1.50	0.79	0.00	0.00	0.30	0.21	0.00	0.00
	Scarabaeidae spp2	Detritivore	2.50	1.85	0.10	0.11	0.30	0.21	0.00	0.00
	Scarabaeidae spp3	Detritivore	0.00	0.00	0.00	0.00	0.50	0.40	0.00	0.00
	Scarabaeidae spp4	Detritivore	0.00	0.00	0.00	0.00	0.20	0.20	0.40	0.40
	Scarabaeidae spp5	Detritivore	0.10	0.10	0.20	0.21	0.50	0.40	0.20	0.13
	Scarabaeidae spp6	Detritivore	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Scarabaeidae spp7	Detritivore	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00
	Scarabaeidae spp8	Detritivore	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.13
	Staphylinidae spp1	Predator	1.70	0.70	1.90	0.89	0.50	0.22	1.20	0.39

Appendix B continued

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Coleoptera	Staphylinidae spp2	Predator	31.60	5.97	5.10	1.22	4.60	1.93	2.90	0.99
	Staphylinidae spp3	Predator	0.60	0.43	1.20	1.04	0.10	0.10	0.00	0.00
	Staphylinidae spp3	Predator	2.60	0.78	0.50	0.53	0.00	0.00	1.60	1.60
	Tenebrionidae spp1	Omnivore	0.00	0.00	0.10	0.11	0.10	0.10	0.20	0.20
	Tenebrionidae spp2	Omnivore	0.00	0.00	0.00	0.00	0.40	0.27	0.10	0.10
	Tenebrionidae spp3	Omnivore	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Tenebrionidae spp4	Omnivore	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
	Tenebrionidae spp5	Omnivore	0.40	0.22	9.80	5.05	0.90	0.55	0.60	0.27
Collembola	Isotomidae spp1	Detritivore	0.30	0.21	0.00	0.00	0.20	0.20	0.20	0.13
Dermaptera	Forficulidae spp1	Predator	0.20	0.13	0.00	0.00	0.60	0.31	0.00	0.00
Hemiptera	Aphididae spp1	Herbivore	0.40	0.22	0.10	0.11	0.00	0.00	0.00	0.00
	Cicadellidae spp1	Herbivore	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Cicadellidae spp2	Herbivore	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Cicadellidae spp3	Herbivore	0.00	0.00	0.00	0.00	0.80	0.36	0.80	0.29
	Cicadellidae spp4	Herbivore	0.00	0.00	0.00	0.00	0.20	0.13	0.00	0.00
	Cicadellidae spp5	Herbivore	0.00	0.00	0.00	0.00	1.30	0.45	0.50	0.31
	Cicadellidae spp6	Herbivore	0.00	0.00	0.10	0.11	0.10	0.10	0.00	0.00
	Coreidae spp1	Herbivore	0.00	0.00	0.00	0.00	0.20	0.20	0.00	0.00
	Pentatomidae spp1	Herbivore	0.00	0.00	0.10	0.11	0.00	0.00	0.00	0.00
	Pyrrhocoridae spp1	Herbivore	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
	Pyrrhocoridae spp2	Herbivore	0.40	0.31	0.00	0.00	0.00	0.00	0.00	0.00
	Pyrrhocoridae spp3	Herbivore	1.70	0.60	0.00	0.00	0.20	0.20	0.20	0.13
	Reduviidae spp1	Predator	0.00	0.00	0.00	0.00	0.10	0.10	0.60	0.34
	Reduviidae spp2	Predator	0.60	0.43	1.20	1.04	0.10	0.10	0.00	0.00

Appendix B continued

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Hemiptera	Reduviidae spp3	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Reduviidae spp4	Predator	4.80	1.90	0.30	0.32	0.20	0.20	0.20	0.20
	Reduviidae spp5	Predator	1.20	0.66	0.40	0.28	0.40	0.40	0.00	0.00
	Reduviidae spp6	Predator	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
	Reduviidae spp7	Predator	0.20	0.13	0.00	0.00	0.90	0.60	0.60	0.34
	Reduviidae spp8	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Reduviidae spp9	Predator	0.00	0.00	0.00	0.00	0.20	0.20	0.00	0.00
	Reduviidae spp10	Predator	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Reduviidae spp11	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Tessaratomidae spp1	Herbivore	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Tessaratomidae spp2	Herbivore	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Tessaratomidae spp3	Herbivore	0.20	0.13	0.00	0.00	0.00	0.00	0.00	0.00
	Tingidae spp1	Herbivore	0.00	0.00	0.00	0.00	0.20	0.13	0.00	0.00
Hymenoptera	Formicidae spp1	Omnivore	18.40	4.22	3.30	1.64	4.80	1.49	1.30	0.84
	Formicidae spp2	Omnivore	19.80	4.66	10.60	4.14	13.60	4.30	13.40	3.22
	Formicidae spp3	Omnivore	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Formicidae spp4	Omnivore	0.80	0.53	0.00	0.00	0.00	0.00	0.00	0.00
	Formicidae spp5	Omnivore	3.20	1.84	1.70	0.94	0.20	0.20	0.00	0.00
	Formicidae spp6	Omnivore	0.20	0.20	0.10	0.11	2.20	0.73	1.30	0.78
	Formicidae spp7	Omnivore	0.00	0.00	1.90	1.08	2.60	2.60	0.50	0.50
	Formicidae spp8	Omnivore	0.00	0.00	0.40	0.42	8.00	4.39	0.00	0.00
	Formicidae spp9	Omnivore	0.10	0.10	0.30	0.22	39.10	14.18	77.30	55.07
	Formicidae spp10	Omnivore	0.00	0.00	0.60	0.22	7.80	3.41	2.10	0.86
	Formicidae spp11	Omnivore	0.00	0.00	0.30	0.22	45.50	22.35	20.70	12.15

Appendix B continued

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Hymenoptera	Formicidae spp12	Omnivore	0.00	0.00	3.40	1.60	6.00	3.81	0.30	0.21
	Formicidae spp13	Omnivore	0.00	0.00	0.40	0.32	32.20	20.80	8.00	4.29
	Formicidae spp14	Omnivore	0.00	0.00	0.00	0.00	0.90	0.46	0.00	0.00
	Formicidae spp15	Omnivore	0.00	0.00	0.00	0.00	1.80	0.55	0.80	0.59
	Formicidae spp16	Omnivore	0.30	0.30	0.00	0.00	60.30	20.85	10.10	4.68
	Formicidae spp17	Omnivore	0.00	0.00	0.00	0.00	3.30	1.56	0.00	0.00
	Formicidae spp18	Omnivore	0.00	0.00	0.00	0.00	0.40	0.40	0.00	0.00
	Formicidae spp19	Omnivore	0.00	0.00	0.00	0.00	13.80	8.06	11.50	11.50
	Formicidae spp20	Omnivore	0.00	0.00	0.00	0.00	5.80	2.49	3.60	3.60
	Formicidae spp21	Omnivore	0.10	0.10	0.00	0.00	0.60	0.34	3.50	1.77
	Formicidae spp22	Omnivore	0.00	0.00	0.00	0.00	0.30	0.30	0.50	0.50
	Formicidae spp23	Omnivore	0.00	0.00	0.00	0.00	3.00	3.00	0.00	0.00
	Formicidae spp24	Omnivore	0.00	0.00	0.00	0.00	3.80	3.80	0.00	0.00
	Formicidae spp25	Omnivore	0.00	0.00	0.00	0.00	19.50	10.86	7.80	5.27
	Formicidae spp26	Omnivore	0.00	0.00	0.00	0.00	0.50	0.31	0.00	0.00
	Formicidae spp27	Omnivore	0.00	0.00	0.00	0.00	0.70	0.70	0.00	0.00
	Formicidae spp28	Omnivore	0.00	0.00	0.00	0.00	0.00	0.00	1.30	0.54
	Formicidae spp29	Omnivore	0.00	0.00	0.00	0.00	1.00	1.00	0.10	0.10
	Formicidae spp30	Omnivore	0.20	0.20	0.00	0.00	0.00	0.00	0.00	0.00
	Formicidae spp31	Omnivore	0.00	0.00	0.00	0.00	0.10	0.10	0.10	0.10
	Formicidae spp32	Omnivore	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
Isopoda	Porcellionidae spp1	Detritivore	14.40	2.43	3.50	1.33	0.30	0.21	0.40	0.27
Ixodida	Ixodidae spp1	Predator	2.20	0.96	0.00	0.00	0.00	0.00	0.00	0.00
	Ixodidae spp2	Predator	0.00	0.00	0.40	0.23	0.00	0.00	0.40	0.40

Appendix B continued

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Ixodida	Nuttalliellidae spp1	Predator	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
Lithobiomorpha	Lithobiidae spp1	Predator	5.10	0.91	3.90	1.14	3.30	2.97	0.30	0.21
Opiliones	Sclerosomatidae spp1	Predator	0.40	0.22	0.20	0.21	0.00	0.00	0.00	0.00
	Sclerosomatidae spp2	Predator	0.00	0.00	0.40	0.32	0.00	0.00	0.00	0.00
	Sclerosomatidae spp3	Predator	0.00	0.00	0.00	0.00	0.40	0.40	0.00	0.00
Oribatida	Phthiracaridae spp1	Detritivore	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
Orthoptera	Acrididae spp1	Herbivore	0.00	0.00	0.00	0.00	2.00	0.63	1.30	0.40
	Acrididae spp2	Herbivore	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
	Acrididae spp3	Herbivore	0.00	0.00	0.00	0.00	0.20	0.20	0.00	0.00
	Acrididae spp4	Herbivore	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.26
	Acrididae spp5	Herbivore	0.00	0.00	0.00	0.00	0.40	0.27	0.00	0.00
	Gryllidae spp1	Omnivore	0.00	0.00	0.00	0.00	0.20	0.13	0.50	0.31
	Gryllidae spp2	Omnivore	0.00	0.00	0.20	0.21	0.00	0.00	0.20	0.20
	Tetrigidae spp1	Herbivore	0.20	0.13	2.20	1.80	2.10	1.07	1.00	0.58
	Tettigidae spp2	Herbivore	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.20
	Tettigidae spp3	Herbivore	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
	Tettigonidae spp1	Omnivore	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
	Tridactylidae spp1	Detritivore	1.50	0.54	17.80	6.33	2.50	2.28	0.90	0.41
Phasmatodea	Heteronemiidae spp1	Herbivore	0.40	0.27	0.00	0.00	0.00	0.00	0.20	0.20
Polydesmoidea	Dalodesmidae spp1	Detritivore	0.80	0.42	0.30	0.16	0.40	0.40	0.00	0.00

Appendix B continued

Order	Family and species number	Functional guild	NatFor		PineBlock		DryGrass		HydroGrass	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Polydesmoidea	Dalodesmidae spp2	Detritivore	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
Pseudoscorpiones	Cheridiidae spp1	Predator	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
	Chtoniidae spp1	Predator	0.20	0.13	0.00	0.00	0.00	0.00	0.00	0.00
Scorpiones	Ischnuridae spp1	Predator	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00
Solifugae	Solifugae spp1	Predator	0.00	0.00	0.00	0.00	0.90	0.41	0.00	0.00
Sphaerotheriida	Sphaerotheriidae spp1	Detritivore	2.40	1.28	0.00	0.00	0.00	0.00	0.00	0.00
	Sphaerotheriidae spp2	Detritivore	2.30	1.43	2.00	1.03	0.00	0.00	0.00	0.00
Spirostreptida	Odontopygidae spp1	Detritivore	0.60	0.34	0.00	0.00	0.00	0.00	0.00	0.00
	Spirostreptidae spp1	Detritivore	0.00	0.00	0.20	0.14	0.00	0.00	0.00	0.00
Thysanura	Lepismatidae spp1	Detritivore	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
Trombidiformes	Trombidiidae spp1	Predator	0.20	0.13	0.00	0.00	0.00	0.00	0.00	0.00
	Trombidiidae spp2	Predator	1.00	0.47	0.00	0.00	0.40	0.22	0.10	0.10
	Trombidiidae spp3	Predator	0.50	0.27	0.00	0.00	0.10	0.10	0.20	0.20
	Trombidiidae spp4	Predator	0.00	0.00	0.00	0.00	2.10	0.62	0.30	0.21

Appendix C: Species accumulation curves for A) overall, B) detritivore, C) herbivore, D) omnivore and E) predator arthropod species sampled across natural forest, pine block, dry grassland and hydromorphic grassland sites. Species estimates "Choa 2" and "Jacknife 2" included.
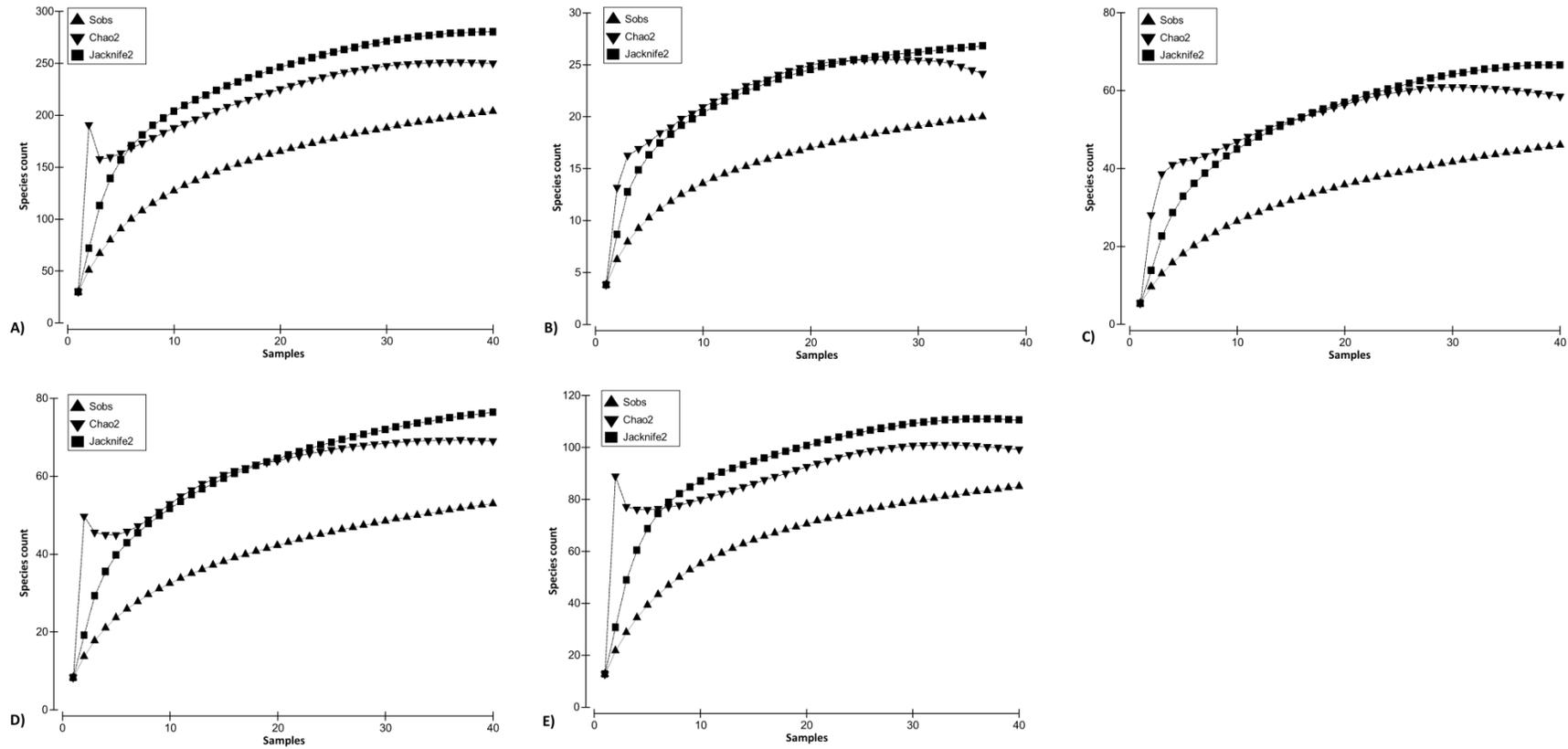
Appendix D: Spearman's rank order correlations of all recorded environmental variables across natural hydromorphic grassland, restored hydromorphic grassland and pine block sites. Marked correlations (bold) are significant at P < 0.05.

	Elevation (m)	Corridor width (m)	Size of biotope (Ha)	Site slope gradient (%)	Site aspect	Time since delineation (Years)	Distance to river (m)	Distance to road (m)	Distance to pine block (m)	Distance to wetland (m)
Elevation (m)	1.000	0.088	0.273	**-0.401**	**-0.598**	-0.118	0.164	-0.128	0.000	0.197
Corridor width (m)	0.088	1.000	-0.319	**-0.375**	-0.016	0.325	**-0.494**	0.212	**0.902**	**-0.656**
Size of biotope (Ha)	0.273	-0.319	1.000	-0.191	-0.193	**-0.716**	0.318	0.294	-0.201	0.243
Site slope gradient (%)	**-0.401**	**-0.375**	-0.191	1.000	**0.562**	0.125	0.272	-0.133	**-0.461**	0.331
Site aspect	**-0.598**	-0.016	-0.193	**0.562**	1.000	0.112	0.126	0.204	-0.040	-0.040
Time since delineation (Years)	-0.118	0.325	**-0.716**	0.125	0.112	1.000	0.050	**-0.435**	0.089	0.084
Distance to river (m)	0.164	**-0.494**	0.318	0.272	0.126	0.050	1.000	-0.294	**-0.647**	**0.868**
Distance to road (m)	-0.128	0.212	0.294	-0.133	0.204	**-0.435**	-0.294	1.000	0.318	**-0.384**
Distance to pine block (m)	0.000	**0.902**	-0.201	**-0.461**	-0.040	0.089	**-0.647**	0.318	1.000	**-0.803**
Distance to wetland (m)	0.197	**-0.656**	0.243	0.331	-0.040	0.084	**0.868**	**-0.384**	**-0.803**	1.000
Focal biotope (%)	0.277	**-0.532**	**0.783**	-0.042	-0.287	**-0.659**	0.499	0.097	**-0.487**	**0.517**
Pine plantation (%)	0.308	-0.055	0.143	-0.316	**-0.793**	-0.077	-0.106	**-0.386**	0.023	-0.001
Soil moisture (%)	0.102	**0.570**	-0.143	**-0.421**	-0.085	0.008	**-0.451**	0.202	**0.648**	**-0.570**
Soil compaction (psi)	-0.041	**-0.477**	0.055	**0.422**	0.183	-0.034	**0.533**	-0.075	**-0.611**	**0.550**
Soil pH	0.066	**-0.454**	-0.093	**0.440**	0.096	0.085	0.146	-0.240	-0.351	0.220
Vegetation cover (%)	0.037	**0.726**	**-0.509**	-0.314	-0.076	0.336	**-0.678**	0.083	**0.724**	**-0.652**
Vegetation height (m)	-0.334	**0.642**	**-0.439**	-0.221	0.115	**0.372**	**-0.525**	0.203	**0.642**	**-0.663**
Plant diversity	-0.203	**0.646**	**-0.367**	-0.212	0.079	0.277	**-0.622**	0.240	**0.732**	**-0.738**
Leaf litter cover (%)	-0.024	**-0.780**	**0.431**	**0.367**	0.169	-0.274	**0.732**	-0.097	**-0.790**	**0.767**
Canopy cover (%)	0.230	**-0.812**	**0.594**	0.258	-0.080	**-0.475**	**0.714**	-0.131	**-0.813**	**0.794**
Shade cover (%)	0.243	**-0.811**	**0.585**	0.264	-0.056	**-0.474**	**0.719**	-0.137	**-0.812**	**0.790**
Dead wood cover (%)	0.023	**-0.851**	**0.400**	**0.372**	0.050	-0.181	**0.671**	-0.245	**-0.876**	**0.825**
Rock cover (%)	0.233	0.124	-0.035	-0.092	-0.218	0.035	-0.124	0.012	0.255	-0.193
Tree density (%)	0.204	**-0.814**	**0.587**	0.254	-0.047	**-0.476**	**0.711**	-0.121	**-0.814**	**0.768**
Bramble cover (%)	-0.161	**0.454**	**-0.469**	0.077	-0.045	**0.642**	-0.246	-0.120	**0.375**	-0.215
Herbaceous cover (%)	-0.046	**0.767**	-0.355	-0.343	-0.127	0.276	**-0.555**	0.232	**0.744**	**-0.702**
Grass cover (%)	-0.101	**0.650**	**-0.629**	-0.193	0.048	**0.478**	**-0.639**	0.028	**0.648**	**-0.585**
Bare ground (%)	-0.302	**0.528**	**-0.380**	-0.199	-0.029	**0.403**	**-0.427**	0.059	**0.576**	**-0.536**

Appendix D continued

	Focal biotope (%)	Pine plantation (%)	Soil moisture (%)	Soil compaction (psi)	Soil pH	Vegetation cover (%)	Vegetation height (m)	Plant diversity	Leaf litter cover (%)	Canopy cover (%)
Elevation (m)	0.277	0.308	0.102	-0.041	0.066	0.037	-0.334	-0.203	-0.024	0.230
Corridor width (m)	**-0.532**	-0.055	**0.570**	**-0.477**	**-0.454**	**0.726**	**0.642**	**0.646**	**-0.780**	**-0.812**
Size of biotope (Ha)	**0.783**	0.143	-0.143	0.055	-0.093	**-0.509**	**-0.439**	**-0.367**	**0.431**	**0.594**
Site slope gradient (%)	-0.042	-0.316	**-0.421**	**0.422**	**0.440**	-0.314	-0.221	-0.212	**0.367**	0.258
Site aspect	-0.287	**-0.793**	-0.085	0.183	0.096	-0.076	0.115	0.079	0.169	-0.080
Time since delineation (Years)	**-0.659**	-0.077	0.008	-0.034	0.085	0.336	**0.372**	0.277	-0.274	**-0.475**
Distance to river (m)	**0.499**	-0.106	**-0.451**	**0.533**	0.146	**-0.678**	**-0.525**	**-0.622**	**0.732**	**0.714**
Distance to road (m)	0.097	**-0.386**	0.202	-0.075	-0.240	0.083	0.203	0.240	-0.097	-0.131
Distance to pine block (m)	**-0.487**	0.023	**0.648**	**-0.611**	-0.351	**0.724**	**0.642**	**0.732**	**-0.790**	**-0.813**
Distance to wetland (m)	**0.517**	-0.001	**-0.570**	**0.550**	0.220	**-0.652**	**-0.663**	**-0.738**	**0.767**	**0.794**
Focal biotope (%)	1.000	0.235	**-0.396**	0.271	-0.030	**-0.705**	**-0.661**	**-0.671**	**0.640**	**0.809**
Pine plantation (%)	0.235	1.000	0.008	-0.236	0.185	-0.015	-0.081	-0.099	-0.144	0.018
Soil moisture (%)	**-0.396**	0.008	1.000	**-0.466**	**-0.369**	**0.546**	**0.416**	**0.525**	**-0.498**	**-0.516**
Soil compaction (psi)	0.271	-0.236	**-0.466**	1.000	0.166	**-0.507**	-0.298	**-0.444**	**0.529**	**0.516**
Soil pH	-0.030	0.185	**-0.369**	0.166	1.000	-0.185	-0.300	-0.140	0.179	0.191
Vegetation cover (%)	**-0.705**	-0.015	**0.546**	**-0.507**	-0.185	1.000	**0.653**	**0.785**	**-0.853**	**-0.813**
Vegetation height (m)	**-0.661**	-0.081	**0.416**	-0.298	-0.300	**0.653**	1.000	**0.865**	**-0.746**	**-0.795**
Plant diversity	**-0.671**	-0.099	**0.525**	**-0.444**	-0.140	**0.785**	**0.865**	1.000	**-0.790**	**-0.809**
Leaf litter cover (%)	**0.640**	-0.144	**-0.498**	**0.529**	0.179	**-0.853**	**-0.746**	**-0.790**	1.000	**0.861**
Canopy cover (%)	**0.809**	0.018	**-0.516**	**0.516**	0.191	**-0.813**	**-0.795**	**-0.809**	**0.861**	1.000
Shade cover (%)	**0.803**	0.003	**-0.504**	**0.511**	0.206	**-0.821**	**-0.805**	**-0.818**	**0.870**	**0.995**
Dead wood cover (%)	**0.617**	-0.049	**-0.667**	**0.514**	0.249	**-0.776**	**-0.702**	**-0.768**	**0.904**	**0.867**
Rock cover (%)	-0.043	0.292	0.069	-0.227	**0.419**	0.078	-0.089	0.157	-0.182	-0.184
Tree density (%)	**0.819**	0.044	**-0.538**	**0.516**	0.253	**-0.821**	**-0.801**	**-0.818**	**0.870**	**0.979**
Bramble cover (%)	**-0.553**	0.118	0.119	-0.114	0.061	**0.478**	**0.650**	**0.578**	**-0.509**	**-0.580**
Herbaceous cover (%)	**-0.557**	0.109	**0.516**	**-0.444**	**-0.411**	**0.667**	**0.809**	**0.718**	**-0.760**	**-0.807**
Grass cover (%)	**-0.788**	-0.101	**0.416**	**-0.431**	-0.021	**0.902**	**0.600**	**0.733**	**-0.796**	**-0.811**
Bare ground (%)	**-0.512**	0.177	0.254	**-0.384**	-0.152	0.257	**0.644**	**0.501**	**-0.542**	**-0.713**

Appendix D continued

	Shade cover (%)	Dead wood cover (%)	Rock cover (%)	Tree density (%)	Bramble cover (%)	Herbaceous cover (%)	Grass cover (%)	Bare ground (%)
Elevation (m)	0.243	0.023	0.233	0.204	-0.161	-0.046	-0.101	-0.302
Corridor width (m)	**-0.811**	**-0.851**	0.124	**-0.814**	**0.454**	**0.767**	**0.650**	**0.528**
Size of biotope (Ha)	**0.585**	**0.400**	-0.035	**0.587**	**-0.469**	-0.355	**-0.629**	**-0.380**
Site slope gradient (%)	0.264	**0.372**	-0.092	0.254	0.077	-0.343	-0.193	-0.199
Site aspect	-0.056	0.050	-0.218	-0.047	-0.045	-0.127	0.048	-0.029
Time since delineation (Years)	**-0.474**	-0.181	0.035	**-0.476**	**0.642**	0.276	**0.478**	**0.403**
Distance to river (m)	**0.719**	**0.671**	-0.124	**0.711**	-0.246	**-0.555**	**-0.639**	**-0.427**
Distance to road (m)	-0.137	-0.245	0.012	-0.121	-0.120	0.232	0.028	0.059
Distance to pine block (m)	**-0.812**	**-0.876**	0.255	**-0.814**	**0.375**	**0.744**	**0.648**	**0.576**
Distance to wetland (m)	**0.790**	**0.825**	-0.193	**0.768**	-0.215	**-0.702**	**-0.585**	**-0.536**
Focal biotope (%)	**0.803**	**0.617**	-0.043	**0.819**	**-0.553**	**-0.557**	**-0.788**	**-0.512**
Pine plantation (%)	0.003	-0.049	0.292	0.044	0.118	0.109	-0.101	0.177
Soil moisture (%)	**-0.504**	**-0.667**	0.069	**-0.538**	0.119	**0.516**	**0.416**	0.254
Soil compaction (psi)	**0.511**	**0.514**	-0.227	**0.516**	-0.114	**-0.444**	**-0.431**	**-0.384**
Soil pH	0.206	0.249	**0.419**	0.253	0.061	**-0.411**	-0.021	-0.152
Vegetation cover (%)	**-0.821**	**-0.776**	0.078	**-0.821**	**0.478**	**0.667**	**0.902**	0.257
Vegetation height (m)	**-0.805**	**-0.702**	-0.089	**-0.801**	**0.650**	**0.809**	**0.600**	**0.644**
Plant diversity	**-0.818**	**-0.768**	0.157	**-0.818**	**0.578**	**0.718**	**0.733**	**0.501**
Leaf litter cover (%)	**0.870**	**0.904**	-0.182	**0.870**	**-0.509**	**-0.760**	**-0.796**	**-0.542**
Canopy cover (%)	**0.995**	**0.867**	-0.184	**0.979**	**-0.580**	**-0.807**	**-0.811**	**-0.713**
Shade cover (%)	1.000	**0.870**	-0.184	**0.980**	**-0.587**	**-0.812**	**-0.821**	**-0.712**
Dead wood cover (%)	**0.870**	1.000	-0.248	**0.860**	**-0.380**	**-0.776**	**-0.727**	**-0.580**
Rock cover (%)	-0.184	-0.248	1.000	-0.185	0.019	0.172	0.104	0.260
Tree density (%)	**0.980**	**0.860**	-0.185	1.000	**-0.570**	**-0.815**	**-0.822**	**-0.714**
Bramble cover (%)	**-0.587**	**-0.380**	0.019	**-0.570**	1.000	**0.509**	**0.494**	**0.536**
Herbaceous cover (%)	**-0.812**	**-0.776**	0.172	**-0.815**	**0.509**	1.000	**0.482**	**0.675**
Grass cover (%)	**-0.821**	**-0.727**	0.104	**-0.822**	**0.494**	**0.482**	1.000	0.353
Bare ground (%)	**-0.712**	**-0.580**	0.260	**-0.714**	**0.536**	**0.675**	0.353	1.000

Appendix E: Arthropods recorded during study period, their functional guild and mean abundance ± standard error (SE) between natural hydromorphic grassland (Natural), restored hydromorphic grassland (Restored) and pine block (Pine) sites.

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Amphipod	Ampithoidae spp1	Detritivore	0.20	0.13	0.60	0.40	0.10	0.10
Araneae	Amaurobiidae spp1	Predator	0.10	0.10	0.80	0.42	0.40	0.31
	Araneidae spp1	Predator	0.20	0.13	0.20	0.13	0.30	0.30
	Araneidae spp2	Predator	0.10	0.10	0.20	0.20	0.00	0.00
	Araneidae spp3	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Clubionidae spp1	Predator	0.50	0.22	0.20	0.13	1.40	0.72
	Corinnidae spp1	Predator	0.00	0.00	0.80	0.80	0.00	0.00
	Corinnidae spp2	Predator	0.10	0.10	0.10	0.10	0.00	0.00
	Gallieniellidae spp1	Predator	0.40	0.22	1.00	0.54	0.40	0.40
	Gnaphosidae spp1	Predator	0.40	0.22	0.40	0.27	0.70	0.37
	Gnaphosidae spp2	Predator	0.70	0.30	0.60	0.50	1.40	0.65
	Gnaphosidae spp3	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Linyphiidae spp1	Predator	0.30	0.30	0.60	0.34	0.20	0.20
	Linyphiidae spp2	Predator	1.00	0.39	0.70	0.33	1.50	0.48
	Linyphiidae spp3	Predator	0.00	0.00	0.10	0.10	9.00	7.25
	Linyphiidae spp4	Predator	0.00	0.00	0.00	0.00	0.20	0.20
	Lycosidae spp1	Predator	0.20	0.20	1.20	1.09	0.10	0.10
	Lycosidae spp2	Predator	2.40	1.97	1.30	0.75	0.00	0.00
	Lycosidae spp3	Predator	1.30	0.88	1.70	0.99	0.00	0.00
	Lycosidae spp4	Predator	7.80	3.30	4.20	1.53	0.00	0.00
	Lycosidae spp5	Predator	0.80	0.39	1.60	1.28	0.20	0.13
	Lycosidae spp6	Predator	0.70	0.47	1.00	0.47	0.00	0.00
	Lycosidae spp7	Predator	0.30	0.21	0.30	0.21	0.10	0.10
	Lycosidae spp8	Predator	1.10	0.48	3.30	1.78	0.00	0.00

Appendix E continued

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Araneae	Lycosidae spp9	Predator	2.70	1.41	0.60	0.50	0.20	0.13
	Lycosidae spp10	Predator	0.30	0.21	0.30	0.21	0.00	0.00
	Lycosidae spp11	Predator	0.00	0.00	0.20	0.13	0.00	0.00
	Lycosidae spp12	Predator	0.40	0.31	0.30	0.21	0.00	0.00
	Lycosidae spp13	Predator	0.90	0.31	0.00	0.00	0.00	0.00
	Lycosidae spp14	Predator	1.50	0.92	0.00	0.00	0.00	0.00
	Lycosidae spp15	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Lycosidae spp16	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Lycosidae spp17	Predator	0.30	0.21	0.10	0.10	0.00	0.00
	Lycosidae spp18	Predator	0.00	0.00	0.00	0.00	0.10	0.10
	Nemisiidae spp1	Predator	0.10	0.10	0.80	0.42	0.60	0.40
	Nemisiidae spp2	Predator	0.50	0.31	0.00	0.00	0.00	0.00
	Oxyopidae spp1	Predator	0.10	0.10	0.10	0.10	0.00	0.00
	Philodromidae spp1	Predator	0.30	0.15	0.00	0.00	0.00	0.00
	Philodromidae spp2	Predator	0.10	0.10	0.10	0.10	0.00	0.00
	Pholcidae spp1	Predator	0.00	0.00	0.10	0.10	0.10	0.10
	Salticidae spp1	Predator	0.10	0.10	1.50	0.86	0.00	0.00
	Salticidae spp2	Predator	0.50	0.40	0.60	0.27	0.00	0.00
	Salticidae spp3	Predator	0.50	0.31	1.20	0.42	0.00	0.00
	Salticidae spp4	Predator	1.40	0.95	0.20	0.13	0.00	0.00
	Salticidae spp5	Predator	0.50	0.31	0.30	0.30	0.00	0.00
	Salticidae spp6	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Salticidae spp7	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Salticidae spp8	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Salticidae spp9	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Salticidae spp10	Predator	0.00	0.00	0.10	0.10	0.00	0.00

Appendix E continued

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Araneae	Scytodidae spp1	Predator	0.00	0.00	0.10	0.10	0.10	0.10
	Theridiidae spp1	Predator	0.20	0.20	0.30	0.21	0.00	0.00
	Theridiidae spp2	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Theridiidae spp3	Predator	0.20	0.13	0.20	0.20	0.00	0.00
	Theridiidae spp4	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Thomisidae spp1	Predator	0.10	0.10	0.10	0.10	0.00	0.00
	Thomisidae spp2	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Thomisidae spp3	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Thomisidae spp4	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Trachelidae spp1	Predator	0.10	0.10	0.10	0.10	2.00	1.39
	Uloboridae spp1	Predator	0.00	0.00	0.00	0.00	0.10	0.10
Blattodea	Blaberidae spp1	Omnivore	0.10	0.10	0.60	0.40	0.40	0.22
	Blaberidae spp2	Omnivore	0.00	0.00	0.00	0.00	0.10	0.10
	Blatellidae spp1	Omnivore	0.00	0.00	0.10	0.10	0.00	0.00
Coleoptera	Bostrichidae spp1	Herbivore	0.00	0.00	0.00	0.00	0.20	0.13
	Bostrichidae spp2	Herbivore	0.50	0.31	1.10	0.43	0.00	0.00
	Bostrichidae spp3	Herbivore	0.40	0.27	1.60	0.83	0.10	0.10
	Carabidae spp1	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Carabidae spp2	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Carabidae spp3	Predator	1.10	1.10	0.00	0.00	0.00	0.00
	Carabidae spp4	Predator	0.00	0.00	0.00	0.00	0.30	0.15
	Carabidae spp5	Predator	0.00	0.00	0.00	0.00	0.20	0.13
	Carabidae spp6	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Carabidae spp7	Predator	0.00	0.00	0.00	0.00	0.40	0.22

Appendix E continued

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Coleoptera	Carabidae spp8	Predator	3.10	1.31	1.70	1.00	0.00	0.00
	Carabidae spp9	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Carabidae spp10	Predator	0.00	0.00	0.00	0.00	0.10	0.10
	Carabidae spp11	Predator	0.20	0.13	0.60	0.50	0.40	0.16
	Carabidae spp12	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Carabidae spp13	Predator	0.20	0.20	0.00	0.00	0.00	0.00
	Carabidae spp14	Predator	0.10	0.10	0.00	0.00	0.10	0.10
	Chrysomelidae spp1	Herbivore	0.00	0.00	0.20	0.13	0.00	0.00
	Chrysomelidae spp2	Herbivore	0.60	0.31	0.20	0.20	0.00	0.00
	Chrysomelidae spp3	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Chrysomelidae spp4	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Chrysomelidae spp5	Herbivore	0.20	0.13	0.00	0.00	0.00	0.00
	Chrysomelidae spp6	Herbivore	0.10	0.10	0.00	0.00	0.00	0.00
	Chrysomelidae spp7	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Chrysomelidae spp8	Herbivore	0.10	0.10	1.10	0.53	0.00	0.00
	Chrysomelidae spp9	Herbivore	0.00	0.00	0.00	0.00	0.20	0.20
	Coccinelidae spp1	Predator	0.30	0.21	0.20	0.13	0.00	0.00
	Coccinelidae spp2	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Curculionidae	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Gyrinidae spp1	Predator	9.50	6.58	2.50	2.50	10.20	5.55
	Gyrinidae spp2	Predator	1.60	1.22	0.80	0.33	0.40	0.31
	Meloidae spp1	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Meloidae spp2	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Meloidae spp3	Herbivore	0.10	0.10	0.00	0.00	0.00	0.00
	Meloidae spp4	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Meloidae spp5	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00

Appendix E continued

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Coleoptera	Melyridae spp1	Herbivore	0.00	0.00	0.20	0.13	0.00	0.00
	Scarabaeidae spp1	Herbivore	0.00	0.00	0.00	0.00	0.50	0.31
	Scarabaeidae spp2	Detritivore	0.40	0.22	1.00	0.33	0.20	0.13
	Scarabaeidae spp3	Detritivore	0.30	0.30	0.10	0.10	0.10	0.10
	Scarabaeidae spp4	Detritivore	0.00	0.00	0.10	0.10	0.00	0.00
	Scarabaeidae spp5	Detritivore	0.00	0.00	0.00	0.00	0.10	0.10
	Scarabaeidae spp6	Detritivore	0.10	0.10	0.30	0.21	0.00	0.00
	Scarabaeidae spp7	Detritivore	0.00	0.00	0.10	0.10	0.00	0.00
	Scarabaeidae spp8	Detritivore	0.00	0.00	0.00	0.00	0.20	0.20
	Staphylinidae spp1	Predator	4.00	1.28	3.10	1.54	7.80	3.23
	Staphylinidae spp2	Predator	1.10	0.41	0.30	0.15	1.60	1.10
	Staphylinidae spp3	Predator	0.10	0.10	0.00	0.00	1.40	0.90
	Tenebrionidae spp1	Omnivore	0.50	0.31	0.80	0.59	2.80	2.28
	Tenebrionidae spp2	Omnivore	0.40	0.22	0.70	0.50	0.00	0.00
	Tenebrionidae spp3	Omnivore	1.10	0.82	0.00	0.00	0.00	0.00
	Tenebrionidae spp4	Omnivore	0.00	0.00	0.00	0.00	0.10	0.10
Collembola	Isotomidae spp1	Detritivore	4.40	2.60	4.40	2.22	30.50	12.43
Dermaptera	Forficulidae spp1	Predator	0.00	0.00	0.40	0.22	0.00	0.00
Geophilomorpha	Geophilidae spp1	Omnivore	0.00	0.00	0.00	0.00	0.80	0.33
Hemiptera	Pentatomidae spp1	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Pentatomidae spp1	Herbivore	0.10	0.10	0.00	0.00	0.00	0.00
	Pyrrhocoridae spp1	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00

Appendix E continued

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Hemiptera	Reduviidae spp1	Predator	1.00	0.33	0.40	0.22	0.20	0.13
	Reduviidae spp2	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Reduviidae spp3	Predator	0.20	0.20	0.50	0.50	0.00	0.00
	Reduviidae spp4	Predator	0.00	0.00	8.40	8.29	0.00	0.00
	Reduviidae spp5	Predator	0.20	0.13	0.00	0.00	0.00	0.00
	Reduviidae spp6	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Reduviidae spp7	Predator	0.50	0.34	0.00	0.00	0.00	0.00
	Reduviidae spp8	Predator	0.10	0.10	0.00	0.00	0.00	0.00
	Reduviidae spp9	Predator	0.00	0.00	0.00	0.00	0.20	0.20
Hymenoptera	Formicidae spp1	Omnivore	27.00	18.58	34.00	20.69	0.30	0.21
	Formicidae spp2	Omnivore	9.40	3.19	18.80	7.26	0.40	0.27
	Formicidae spp3	Omnivore	18.40	11.21	19.00	14.27	3.10	1.56
	Formicidae spp4	Omnivore	2.00	1.32	2.40	1.38	0.00	0.00
	Formicidae spp5	Omnivore	0.00	0.00	0.80	0.42	0.40	0.40
	Formicidae spp6	Omnivore	0.80	0.47	0.20	0.13	0.00	0.00
	Formicidae spp7	Omnivore	0.00	0.00	1.60	1.30	0.00	0.00
	Formicidae spp8	Omnivore	3.20	0.61	3.20	0.96	0.00	0.00
	Formicidae spp9	Omnivore	0.50	0.17	0.20	0.20	0.00	0.00
	Formicidae spp10	Omnivore	22.40	10.54	2.30	1.08	2.10	1.15
	Formicidae spp11	Omnivore	4.20	1.57	0.90	0.48	0.00	0.00
	Formicidae spp12	Omnivore	0.00	0.00	0.10	0.10	0.00	0.00
	Formicidae spp13	Omnivore	1.80	1.21	1.00	0.80	0.00	0.00
	Formicidae spp14	Omnivore	0.60	0.43	0.70	0.33	0.00	0.00
	Formicidae spp15	Omnivore	3.50	2.84	7.60	6.30	0.10	0.10
	Formicidae spp16	Omnivore	0.00	0.00	4.00	2.70	0.90	0.71

Appendix E continued

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Hymenoptera	Formicidae spp17	Omnivore	0.20	0.13	0.40	0.31	0.00	0.00
	Formicidae spp18	Omnivore	0.00	0.00	0.70	0.70	0.00	0.00
	Formicidae spp19	Omnivore	0.80	0.51	0.10	0.10	0.00	0.00
	Formicidae spp20	Omnivore	0.60	0.50	0.60	0.27	0.00	0.00
	Formicidae spp21	Omnivore	0.10	0.10	0.00	0.00	0.10	0.10
	Formicidae spp22	Omnivore	0.10	0.10	0.00	0.00	0.00	0.00
	Formicidae spp23	Omnivore	0.00	0.00	0.10	0.10	0.00	0.00
	Formicidae spp24	Omnivore	0.00	0.00	0.10	0.10	0.00	0.00
	Formicidae spp25	Omnivore	0.20	0.20	0.20	0.13	0.00	0.00
	Formicidae spp26	Omnivore	7.90	5.54	6.20	3.12	0.10	0.10
	Formicidae spp27	Omnivore	0.00	0.00	0.10	0.10	0.00	0.00
	Formicidae spp28	Omnivore	0.20	0.20	0.10	0.10	0.00	0.00
	Formicidae spp29	Omnivore	2.30	1.20	1.50	0.86	1.20	0.55
	Formicidae spp30	Omnivore	2.30	2.09	0.30	0.30	0.50	0.50
	Formicidae spp31	Omnivore	0.20	0.13	0.90	0.60	0.00	0.00
	Formicidae spp32	Omnivore	0.00	0.00	0.00	0.00	0.10	0.10
Isopoda	Porcellionidae spp1	Detritivore	0.00	0.00	0.00	0.00	4.50	1.72
	Porcellionidae spp2	Detritivore	0.00	0.00	0.10	0.10	0.00	0.00
Ixodida	Ixodidae spp1	Predator	0.00	0.00	0.00	0.00	0.20	0.20
Lithobiomorpha	Lithobiidae spp1	Predator	0.70	0.33	0.50	0.22	1.40	0.56
	Lithobiidae spp2	Predator	0.00	0.00	0.00	0.00	0.20	0.20
Mantodea	Mantidae spp1	Predator	0.20	0.13	0.10	0.10	0.00	0.00

Appendix E continued

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Opiliones	Sclerosomatidae spp1	Omnivore	0.20	0.20	0.50	0.31	0.00	0.00
	Sclerosomatidae spp2	Omnivore	0.70	0.50	0.10	0.10	0.60	0.27
Orthoptera	Acrididae spp1	Herbivore	0.80	0.25	0.50	0.22	0.00	0.00
	Acrididae spp2	Herbivore	0.70	0.33	0.10	0.10	0.00	0.00
	Acrididae spp3	Herbivore	0.10	0.10	0.40	0.40	0.00	0.00
	Acrididae spp4	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Acrididae spp5	Herbivore	0.10	0.10	0.40	0.22	0.00	0.00
	Acrididae spp6	Herbivore	0.20	0.20	0.00	0.00	0.00	0.00
	Acrididae spp7	Herbivore	0.20	0.13	0.00	0.00	0.00	0.00
	Gryllidae spp1	Omnivore	0.50	0.22	0.50	0.34	0.40	0.40
	Gryllidae spp2	Omnivore	0.00	0.00	0.60	0.50	0.20	0.13
	Gryllidae spp3	Omnivore	0.30	0.15	0.80	0.33	0.00	0.00
	Gryllidae spp4	Omnivore	1.40	1.40	0.00	0.00	0.00	0.00
	Gryllidae spp5	Omnivore	0.10	0.10	0.00	0.00	0.00	0.00
	Tettigidae spp1	Herbivore	0.90	0.41	1.40	0.72	0.00	0.00
	Tettigidae spp2	Herbivore	0.10	0.10	0.60	0.27	0.00	0.00
	Tettigidae spp3	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
	Tridactylidae spp1	Detritivore	3.20	1.02	4.80	2.67	33.90	25.09
Phasmatodea	Heteronemiidae spp1	Herbivore	0.00	0.00	0.10	0.10	0.00	0.00
Polydesmoidea	Dalodesmidae spp1	Detritivore	0.20	0.20	0.20	0.13	0.00	0.00
	Dalodesmidae spp2	Detritivore	0.00	0.00	0.20	0.13	0.00	0.00
	Dalodesmidae spp3	Detritivore	0.10	0.10	0.20	0.13	1.40	0.79
	Dalodesmidae spp4	Detritivore	0.10	0.10	0.40	0.40	0.10	0.10

Appendix E continued

Order	Family and species number	Functional guild	Natural		Restored		Pine	
			Mean	SE	Mean	SE	Mean	SE
Polydesmoidea	Dalodesmidae spp5	Detritivore	0.00	0.00	0.20	0.13	2.00	1.20
	Dalodesmidae spp6	Detritivore	0.00	0.00	0.00	0.00	0.10	0.10
Pseudoscorpiones	Cheridiidae spp1	Predator	0.00	0.00	0.10	0.10	0.00	0.00
Sphaerotheriida	Sphaerotheriidae spp1	Detritivore	0.00	0.00	0.30	0.30	0.00	0.00
	Sphaerotheriidae spp2	Detritivore	0.00	0.00	0.00	0.00	0.20	0.20
Spirostreptida	Odontopygidae spp1	Detritivore	0.00	0.00	0.50	0.40	0.10	0.10
	Spirostreptidae spp1	Detritivore	0.20	0.20	0.30	0.15	0.20	0.13
	Spirostreptidae spp2	Detritivore	0.20	0.20	0.00	0.00	0.00	0.00
	Spirostreptidae spp3	Detritivore	0.10	0.10	0.10	0.10	0.10	0.10
	Spirostreptidae spp4	Detritivore	0.00	0.00	0.00	0.00	0.10	0.10
Trombidiformes	Anystidae spp1	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Anystidae spp2	Predator	0.10	0.10	0.10	0.10	0.10	0.10
	Anystidae spp3	Predator	0.00	0.00	0.10	0.10	0.00	0.00
	Trombidiidae spp3	Predator	0.00	0.00	0.10	0.10	0.00	0.00

Appendix F: Species accumulation curves for A) overall, B) ant, C) beetle, D) bug, E) grasshopper and F) spider arthropod species sampled across natural hydromorphic grasslands, restored hydromorphic grasslands and pine block sites. Species estimates "Chao 2" and "Jacknife 2" included.