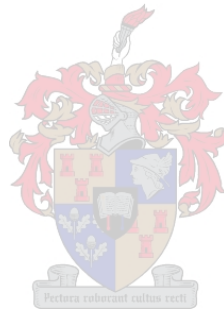


Biodiversity conservation in a fragmented landscape: arthropod assemblages in smaller corridors within a production landscape

by

Julia van Schalkwyk

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



Supervisors: Dr. James S. Pryke and Prof. Michael J. Samways

Department of Conservation Ecology and Entomology

Faculty of AgriSciences

Stellenbosch University

March 2015

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 sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights, and that I have not previously in its entirety, or in part, submitted it for obtaining any qualification.

October 2014

All rights reserved

Overall summary

Habitat loss and fragmentation are major threats to global biodiversity. A cornerstone of traditional conservation involves setting aside land as formally protected areas (PAs). However, for effective biological conservation in the long term there needs to be connectivity between these PAs. When possible, improved connectivity can be achieved using natural corridors at a landscape scale. Even better is to establish a network of corridors and nodes in the form of ecological networks (ENs). ENs are currently being employed by commercial forestry companies in South Africa. While larger corridors and nodes are considered optimum, factors other than design, such as management and environmental heterogeneity, have also been found to be important for species maintenance. This study aims to explore the role of corridor width in driving the composition of invertebrate assemblages across a transformed landscape in KwaZulu-Natal, South Africa, and to investigate other possible environmental variables significant for species distributions.

In Chapter 2, I investigated the contribution of smaller grassland corridors within a timber production matrix to overall biodiversity conservation using two important bioindicator taxa. Ants and dung beetles were sampled in grassland corridors of three size classes, plantation blocks and a nearby PA, iMpendle Nature Reserve. The two taxa showed differential responses to landscape level fragmentation. Dung beetles showed a decrease in species richness and corresponding increase in species turnover with increased fragmentation, while ants were unaffected, although counter intuitively smaller corridors even contained more unique ant species compared to larger corridors. Dung beetle assemblages also showed strong differences between the PA and grassland corridors. While the conservation effectiveness of large corridors undoubtedly exceeds that of smaller corridors, for ants it seems that smaller corridors contribute to their overall conservation within this production landscape.

In Chapter 3, I explore the importance of spatial and environmental factors for species distribution across this landscape. Dung beetles were split into functional guilds according to size and nesting behaviour for analyses. Within grassland corridors, tunnelling dung beetle species richness was sensitive to landscape level fragmentation, especially for larger species, while elevation and vegetation type influenced ant species richness. Since rolling dung beetles showed a close association with the PA, the marked difference in dung beetle assemblages between these two land-uses may be due to the presence of pellet producing grazers in the protected area and their replacement by pat producing cattle in the grassland corridors. Other environmental variables that

were found to be important for dung beetle species composition were elevation, vegetation type, and soil hardness. For ant species composition, only elevation was found to be important.

In conclusion, as large corridors were comparable to the PA in dung beetle and ant species richness, ENs act as extensions of formally PAs, given that they are large enough. Nevertheless, smaller corridors had surprisingly high species richness. Including additional information other than species data improved our knowledge of the underlying factors that drive dung beetle species composition. Even though dung beetle and ant species responded differentially to habitat fragmentation, environmental heterogeneity seemed important for both taxa. Incorporating habitat heterogeneity into the current management scheme may improve the conservation effectiveness within this transformed landscape.

Algehele samevatting

Die vermindering en fragmentasie van natuurlike habitat is 'n groot bedreiging vir globale biodiversiteit. 'n Belangrike tradisionele benadering tot natuurbewaring behels die afbakening van land vir formele beskermde areas (BAs). Ten einde effektiewe biologiese bewaring oor die langtermyn te verseker moet daar verbinding wees tussen hierdie BAs. Indien moontlik kan verbeterde verbinding verkry word deur die gebruik van natuurlike gange op 'n landskaps-vlak. Nog beter is om 'n netwerk van gange en nodes in die vorm van ekologies netwerke (ENe) saam te stel. ENe word tans deur kommersiële bosboumaatskappye in Suid Afrika aangewend. Terwyl groter gange en nodes as optimaal beskou word, is ander faktore behalwe ontwerp, soos bestuur en omgewingsheterogeniteit, ook al gevind as belangrik vir die onderhouding van spesies. Hierdie studie is gemik daarop om die rol van gangwydte as dryfkrag vir die samestelling van invertebraatversamelings oor 'n getransformeerde landskap in KwaZulu-Natal, Suid-Afrika, te ondersoek, asook ander moontlike omgewingsveranderlikes wat belangrik vir spesiesverpreidings kan wees.

In Hoofstuk 2 het ek die bydrae van kleiner gange tot totale biodiversiteit-bewaring ondersoek deur twee belangrike bio-indikator taxa te bestudeer. Miere en miskruiers is versamel in grasland-gange van drie grootte-klasse, plantasie blokke en 'n naby geleë BA, iMpendle Natuurreservaat. Die twee taxa het verskillende reaksies tot landskaps-vlak fragmentasie getoon. Miskruiers het 'n verlaging in spesiesrykheid en 'n gesamentlike verhoging in spesiesomset met verhoogde fragmentasie gewys, terwyl miere nie geaffekteer is nie, alhoewel kleiner gange het trouens meer unieke mierspesies bevat as groter gange. Die miskruiersversamelings in die BA het ook opmerklik verskil van dié in die grasland-gange. Alhoewel die bewaringsdoeltreffendheid van groot gange beslis dié van kleiner gange oorskry, kom dit voor dat kleiner gange wel bydra tot die totale bewaring van miere binne hierdie produksielandskap.

In Hoofstuk 3 het ek die belangrikheid van ruimtelike en omgewingsfaktore vir spesiesverspreiding oor hierdie landskap ondersoek. Miskruiers is ook in funksionele groepe verdeel volgens grootte en nes-gedrag vir aparte analise. Binne grasland-gange was tonnellende miskruierspesies sensitief vir landskaps-vlak fragmentasie, veral groter spesies, terwyl hoogte bo seevlak en vegetasie tipe mier spesiesrykheid beïnvloed het. Aangesien rollende miskruierspesies 'n nabye assosiasie met die BA gewys het, mag die opmerklike verskil in miskruier versamelings tussen hierdie twee grondgebruike 'n gevolg wees van die aanwesigheid van korrel-mis produserend beweiders in die BA en hulle vervanging deur nat-mis produserende beeste in die grasland-gange. Omgewingsveranderlikes

uitsluitende ganggrootte wat belangrik gevind is vir miskruier spesiessamestelling was hoogte bo seevlak, vegetasie tipe en grond-hardheid. Vir mier spesiessamestelling was slegs hoogte bo seevlak belangrik.

Om af te sluit, aangesien groot gange vergelykbaar was met die BA in miskruier en mier spesiesrykheid, tree ENe op as uitbreidings van BAs, mits hulle groot genoeg is. Desnieteenstaande het kleiner gange 'n verbasende hoë spesiesrykheid gehad, veral onder miere. Die insluiting van addisionele inligting buiten spesiesdata het ons kennis van die onderliggende faktore wat miskruier spesiessamestelling dryf verbeter. Alhoewel miskruier- en mierspesies verskillend gereageer het op habitat fragmentasie, het dit voorgekom asof omgewingsheterogeniteit belangrik was vir die spesiesverspreiding van beide taxa. Die insluiting van habitatheterogeniteit binne die huidige bestuursplan mag die doeltreffendheid van bewaring binne hierdie getransformeerde landskap verbeter.

Acknowledgements

Deep gratitude goes to:

- The Green Landscapes Programme (DST/NRF grant) for funding this project
- Mondi International for funding for lodging, field site access and logistics
- My supervisors, Dr. James Pryke and Professor Michael Samways for guidance, development and understanding
- The Department of Conservation Ecology and Entomology at Stellenbosch University for infrastructure, administrative and technical support.
- Ezemvelo KZN Wildlife for permission and access to field sites on iMpendle Nature Reserve (Permit nr: OP 2175/2013 & OP 2177/2013)
- Dr. René Gaigher and Prof. Michael Samways for help with ant identification
- Dr. Francois Roets for help with beetle identification
- My brother Ockert van Schalkwyk (Heghlu'meH QaQ jajvam!) and Ian van Vuuren for assistance with fieldwork
- My Ma en Pa

Table of Contents

Declaration	II
Overall summary	III
Algehele samevatting	V
Acknowledgements	VII
Table of contents	VIII

Chapter 1: General introduction 1

Global biodiversity crisis	1
Risk remediation	1
Formally protected areas	1
Conservation outside of formally protected areas	2
Understanding transformed landscapes	2
Conservation in transformed landscapes – ecological networks	3
The study area	4
The grasslands of KwaZulu-Natal, South Africa	4
Plantation forestry in South Africa	5
Ecological networks in KwaZulu-Natal	5
Advances in understanding conservation in transformed landscapes	6
Limitations to understanding of fragmented communities	7
The study organisms	8
Objectives and thesis outline	9
References	10

Chapter 2: All corridors are equal, but some are more equal than others - dung beetle and ant assemblage responses to grassland corridor size within a timber production landscape

.....	26
Abstract	26
Introduction	26
Methods	31
Results	35
Discussion	44
Arthropod species richness	44

Arthropod species composition	46
Species turnover within biotope	48
The value of smaller corridors	49
References	51

Chapter 3: Beyond corridor size - a continuum model approach to dung beetle and ant assemblage structures in a fragmented grassland

66

Abstract	66
Introduction	66
Methods	69
Results	73
Discussion	79
The influence of corridor width	79
Important environmental gradients	80
The role of fire and grazing management	81
Improving the fragmentation model	83
References	84

Chapter 4: Conclusion

95

References	98
------------------	----

Appendix A	100
Appendix B	101
Appendix C	104
Appendix D	105
Appendix E	106

Chapter 1

General introduction

Global biodiversity crisis

At the present moment, the earth is experiencing an accelerated loss of biodiversity (Sodhi & Ehrlich 2010), altered species interactions (Tylianakis *et al.* 2008), and a decrease in the associated ecosystem functioning and services (MEA 2005). The socio-economic advantages that accompany intact biodiversity, such as sustainable food and water provisioning for human consumption, are also threatened (Chapin *et al.* 2000; Thrupp 2000).

Habitat loss and fragmentation are widely accepted drivers of biodiversity loss (Lawton & May 1995; Pimm *et al.* 1995; Wilcove *et al.* 1998; Walker & Steffen 1999; Pimm & Raven 2000; Laurance & Cochrane 2001; Tscharntke *et al.* 2002). Across all continents, landscapes are undergoing intense human-driven modifications including clearing, inappropriate fire regimes, exotic invasions and climate change. These stressors not only act separately, but considerable interaction is also possible among them (Steffen *et al.* 2009; Lindenmayer *et al.* 2010; Sutherst *et al.* 2011). Ultimately the original and natural ecosystems are reduced to minor isolated patches wherein the habitat of many species have been greatly reduced, degraded and fragmented and species recruitment and distribution become limited or restricted, until their survival and the ecological functioning of these systems are put at severe risk (Pimm *et al.* 1995; Sala *et al.* 2000).

Risk remediation

Formally protected areas

A significant structural approach to the conservation of local, regional and global biodiversity involves setting apart land officially dedicated to the protection and maintenance of nature (Gaston *et al.* 2006; Gaston *et al.* 2008). To make conservation through protected areas (PAs) as effective as possible, biotic inventories are prioritized in an attempt to identify biodiversity hotspots, i.e. areas of conservation importance (Myers *et al.* 2000). These hotspots are currently made up of 35 biogeographic regions (Sloan *et al.* 2014) and include an estimated 77% of all mammal, bird, reptile and amphibian species and 50% of all plant species (Mittermeier *et al.* 2004).

Of the earth's terrestrial surface, about 12.7 % is currently part of a formally PA (Bertzky *et al.* 2012). A major portion of the global conservation budget goes to the care and establishment of these areas (James *et al.* 2001). Politically, this is a practical extent of land, but it is undoubtedly far from the

50% needed to sustain viable populations of suites of native species, represent ecosystems across their range of variation, and encourage ecosystem resilience (Soulé & Sanjayan 1998; Noss & Cooperrider 2003; Pressey *et al.* 2003; Terborgh 2006; Noss *et al.* 2012). Insufficient funds and the increasing and conflicting demands for land by an ever increasing human population makes attaining sufficient land for formal reserve networks to act effectively unlikely (Perrings *et al.* 2006). Establishing links between current conserved areas is also often problematic, or where possible, these areas consist of privately or communally owned land (Chown *et al.* 2003; Perrings *et al.* 2006). Transfrontier Conservation Areas is the exception because these areas require a unique level of international co-operation.

Using biotic inventories to identify areas of conservation importance also poses some problems, as species data are not always available. Furthermore, reserve layouts tend to be suboptimal, involving little planning to optimize their conservation value, particularly regarding climate change, and are often not large enough to sustain long-term viable populations (Margules & Pressey 2000; Reyers *et al.* 2002; Chown *et al.* 2003; Goodman 2003; Opdam & Wascher 2004). Friction between PAs and various surrounding land-uses leads to other complications, such as poaching and alien vegetation encroachment (Pimentel & Stachow 1992; Reyers *et al.* 2002). The static nature of established reserves also makes them less adaptable to political and environmental changes.

It is clear that PAs alone will not slow global biodiversity loss (Rodrigues *et al.* 2004). In order to avoid the additional loss of biodiversity and maintain ecosystem functioning, innovative management approaches are necessary (MEA 2005). Consequently, more importance is being placed on conserving biodiversity outside of formally PAs (Goodman 2003; Solomon *et al.* 2003; Dudley *et al.* 2005).

Conservation outside of formally protected areas

Understanding transformed landscapes

The conservation management of transformed landscapes entails a sound understanding of how organisms are distributed through space (Fischer & Lindenmayer 2006; Pryke & Samways 2014). In this regard, conceptual landscape models could be helpful tools (McIntyre & Hobbs 1999; Lindenmayer & Fischer 2003; Manning *et al.* 2004). The landscape model most frequently used in fauna research and conservation in human-transformed landscapes is the “fragmentation model”, which stems from the theory of island biogeography, or island biogeography theory (IBT) (MacArthur & Wilson 1967). The fragmentation model describes a range of natural patches spread throughout a

dominating and less hospitable transformed “matrix” (Saunders *et al.* 1991; Harrison & Bruna 1999; Debinski & Holt 2000; Haila 2002; Fahrig 2003).

Three key assumptions of the fragmentation model include: 1) a clear contrast exists between human defined patches and the rest of the landscape, 2) numerous organisms view these human-defined patches as agreeable “habitat patches”, and 3) the relationship between landscape patterns (e.g. patch size, patch isolation, patch shape) and species distribution patterns is of interest and is a sensible surrogate for the ecological processes causally connected to species distribution patterns (Fischer & Lindenmayer 2006). Recommendations for conservation arising from this model are: 1) large patches are typically more important than smaller patches, 2) patches are more important than the matrix, 3) corridors increase connectivity, and 4) patches situated close together are better than patches situated farther apart (Diamond 1975).

Conservation in transformed landscapes – ecological networks

Movement between distinct habitats is an important part of the ecology of many species. Connectivity is not only important for certain species, but is central to many ecosystem processes (Benett & Mulongoy 2006). Probably the most obvious example is aquatic ecosystems, which functionally depend on physical connections between their upper and lower reaches (e.g. flooding) (Benett & Mulongoy 2006). The maintenance and restoration of some sort of “connectivity” between ecosystem elements is therefore considered the most obvious solution to counteract the negative impacts of fragmentation (Crooks & Sanjayan 2006).

With consideration of these problems, a range of concepts has been developed within the theoretical framework of landscape ecology, including wildlife corridors, landscape links, and ecoducts (Turner *et al.* 2001; Turner 2005). A more recent addition to this list of concepts is the ecological network (EN), broadly defined as large scale interconnected natural corridors and patches that connect habitats for organism movement on both evolutionary and ecological timescales (Beier & Noss 1998; Jongman 1995).

Corridors can be defined as movement corridors for focal species (Hilty *et al.* 2006). Such corridors are currently being utilized in landscape design in both urban and agricultural settings for biodiversity conservation (Smith & Hellmund 1993; Burel & Baudry 1995; Rosenberg *et al.* 1997; Jongman & Pungetti 2004; Nasi *et al.* 2008). Corridors can only be of conservation value if animals in the landscape use them to bring about connectivity (Beier & Noss 1998). Although some authors argue that such evidence is lacking (e.g. Simberloff *et al.* 1992), others have found corridors to increase organism movement (Haas 1995; Sutcliffe & Thomas 1996; Gonzalez *et al.* 1998; Haddad

1999; Mech & Hallett, 2001) and gene flow between patches (Aars & Ims 1999; Hale *et al.* 2001; Mech & Hallett 2001). On the other hand, increasing connectivity across the landscape may also promote the spread of diseases, catastrophic disturbances (e.g. wild fires), or facilitate the spread of exotic species (Simberloff & Cox 1987; Simberloff *et al.* 1992; Hess 1994). There is also the possibility of corridors luring animals to lower quality habitats where they may experience higher mortality (see Hobbs 1992). Despite these concerns, corridors have been found to increase population sizes (Fahrig & Merriam 1985; Dunning *et al.* 1995; Haddad & Baum 1999) and maintain biodiversity (Gonzalez *et al.* 1998). Apart from increased local and general diversity, other benefits that can arise from effective conservation of human influenced areas include advanced ecological resilience, reduced soil erosion, improved hydrological processes and enhanced beneficial organisms for biological control of pest species (Duelli & Obrist 2003).

By protecting areas of assumed or known high species richness (core areas) and connecting them through corridors that should increase species movement across unsuitable areas, ENs are intended to ensure biodiversity conservation (Boitani *et al.* 2007). Fragmentation model based conservation management is centred on a mosaic of patches and corridors with importance placed on the total amount of predefined “habitat”, patch shape and size, and the spatial organization of patches (Andrén 1994; Fahrig 2003). Good quality, large habitat corridors and important nodes are therefore considered optimal in EN design, while less confidence is given to smaller, disturbed corridors (Samways *et al.* 2010).

The study area

The grasslands of KwaZulu-Natal, South Africa

From a biodiversity conservation viewpoint, KwaZulu-Natal (KZN) Province, South Africa, is internationally significant (Goodman 2003). It is situated within the biologically rich transition zone between the northern tropical biota and southern subtropical biota on the eastern coast of Africa and forms part of the Maputaland-Pondoland-Albany biodiversity hotspot.

The inland area of KZN constitutes part of the distribution of South Africa’s grassland biome. The South African grassland biome covers an area of about 339 240 km² (373 990 km² including Lesotho and Swaziland) and contains 73 vegetation types (Mucina & Rutherford 2006). These grasslands contain high diversity and endemism of plant and animal species and are also considered South Africa’s most productive in terms of agriculture (Mentis & Huntley 1982). Cultivation, urbanisation,

overgrazing and mining, together account for 35% of transformation of the grassland biome (Reyers *et al.* 2005), and it is considered the most threatened biome in South Africa.

Plantation forestry in South Africa

With only 0.02% of the country's land surface being covered by the forest biome (Mucina & Rutherford 2006), natural wood sources are scarce in South Africa. In reaction to this, the first large scale, exotic timber plantations were established in the 1890's (King 1938; Tewari 2001). Over the last decade, the surface dedicated to commercial forestry in South Africa has increased from 1.2% to 1.6% (Schoeman *et al.* 2013).

Plantation forestry is known to have negative impacts on biodiversity (Armstrong *et al.* 1998; Richardson 1998; Lindenmayer *et al.* 2003; Bremer & Farley 2010). Plantation forestry not only results in land-use change, but alien trees form the prime component of commercial forestry in many parts of the world, with these trees often diffusing into surrounding unplanted areas (Simberloff *et al.* 2010). In South Africa, approximately 1.3 million ha are planted exclusively with trees exotic to the country (Kirkman & Pott 2002). Invasive alien trees of great commercial importance in South Africa include *Pinus*, *Acacia* and *Eucalyptus* species, which together poses major threats to both the country's water supplies and biodiversity (Wittenberg & Cock 2001; Le Maitre *et al.* 2004). Furthermore, to grassland specialists the timber matrix is inhospitable (Armstrong & van Hensbergen 1996) and acts as a barrier or filter that impedes movement between remnants of natural grassland (Samways & Kreuzinger 2001; Bieringer & Zulka 2003).

Ecological networks in KwaZulu-Natal

A major component of the land suitable for plantation forestry in South Africa is within Mpumalanga and KwaZulu-Natal (KZN) provinces, within the highly threatened grassland, wetland and forest biomes (Eeley *et al.* 2002; Neke & du Plessis 2004; DWAF 2006). Plantation forestry is considered a key driver of the critically endangered status of vegetation types within the grassland biome (Neke & du Plessis 2004; Mucina & Rutherford 2006).

Fortunately, as a commercial operation, plantation forestry is required to be environmentally sensitive. In the mid-1990's large forestry companies began seeking certification regarding products produced in a biodiversity and socio-economically friendly way, and by 1995 both Mondi and Sappi

(currently the largest private growers in South Africa) had implemented the Forest Stewardship Council (FSC) international standards (Kirkman & Pott 2002).

A stakeholder-owned, non-profit organization, the FSC accredits private companies worldwide to conduct the FSC certification process on sustainable forestry and annual examinations (FSC 1996). Currently, forestry is the single most regulated land use in South Africa (DWAF 2006). To date, the timber industry has demonstrated proactive involvement in attempting to reduce its environmental impact through research related to protecting remnant natural and semi-natural areas within the plantation forestry matrix (see Hartley 2002). On average, one-third of any given plantation remains unplanted to timber, and it is these unplanted areas which form complex ENs of interconnected nodes, corridors and special landscape features (Jongman 1995; Kirkman & Pott 2002; Samways 2007a,b).

Advances in understanding conservation in transformed landscapes

Numerous studies have addressed how fragmentation influences biodiversity (reviewed by Fahrig 2003). Landscape features considered important for population and community ecology include: patch area (Kruess & Tscharntke 2000), patch quality (Hanski & Singer 2006), the ratio of habitat edge to interior (Radeloff *et al.* 2000), isolation of habitat fragments (Collinge 2000), patch diversity (Varchola & Dunn 2001), as well as microclimate (Braman *et al.* 2000). Recent additions to our understanding of the spatial ecology of insects include differential reactions of predators and prey (With *et al.* 2002), genetic change in insect populations (Ronce & Kirkpatrick 2001), as well as temporal changes in landscape structure (Onstad *et al.* 2001).

Previous studies on ENs in South Africa's grassland biome have produced valuable guidelines for conservation management in these areas. EN functioning as supporting systems in providing ecosystem services are considered to be negatively influenced by two main obstacles, namely disturbance (Kinzig & Samways 2000; Pryke & Samways 2003) and size (Pryke & Samways 2001; Field 2002; Pryke & Samways 2003). The recommended minimum width for grassland linkages is 250 m (Pryke & Samways 2001). Habitat quality and connectivity to natural patches outside of the forestry matrix is of great importance in conserving invertebrate species within these corridors (Pryke & Samways 2003; Bullock & Samways 2005). An edge zone (the influence one habitat type can have on an adjacent habitat type) of approximately 30 m stretching from the pine plantation edge into the grassland corridors has been established for several taxa (Pryke & Samways 2012). Management practices have been found to be of greater importance than design for certain taxa

(Bazelet & Samways 2011). Physical landscape features such as rockiness and elevation may serve as potential surrogates for biodiversity and a better understanding of the combined role of fire and grazing has been developed (Crous *et al.* 2013; Joubert *et al.* 2014).

Limitations to understanding of fragmented communities

Although they are implemented in only a few areas in the world, a large amount of conceptual effort has gone into the biodiversity value of ENs (Yu *et al.* 2006; Jongman *et al.* 2011). The justification for ENs is based on Island Biogeography Theory (IBT) (MacArthur & Wilson 1967), metapopulation theory with its idea of source-sink dynamics (Hanski 1999) and the more general outlook of landscape ecology (Turner *et al.* 2001; Turner 2005). It is also supported by the fact that habitat fragmentation is unquestionably among the principal threats to species survival (Wilcove *et al.* 1998, but see also Fahrig (2003)).

Even though habitat destruction and fragmentation are strong drivers of biodiversity decline (Saunders *et al.* 1991; Fahrig 1997; McGarigal & Cushman 2002; Fahrig 2003) and known to affect communities at the landscape or local scale (Chacoff & Aizen 2006), numerous factors other than the spatial distribution of habitat remnants may contribute to animal distribution patterns (Fischer & Lindenmayer 2006). Examples include land-use intensity (Thomas *et al.* 2001), resource distributions (Halley & Dempster 1996) as well as competition and predation (Tscharntke *et al.* 1998). Not only will the relative strength and synergistic effects of these environmental factors define the community composition, but also, given species specific ecological characteristics, their functional structure (Burel *et al.* 1998).

Furthermore, the relevance of IBT in understanding fragmented ecosystems is considered to be limited (Laurance 2008): 1) It provides insufficient predictions regarding expected changes in community compositions in fragments over time and the species expected to be most vulnerable. 2) Edge effects can play key roles in determining species extinctions and ecosystem change, but are not considered by IBT. 3) The matrix of modified vegetation can have major influences on fragment connectivity, is also ignored by IBT. Depending on the nature of the matrix, it may facilitate or impede dispersal between habitat patches (Cronin 2007). The matrix may also influence colonisation and extinction dynamics within fragments via organism spillover (e.g. Pereirae & Daile 2006; Holt 2010), which may occur if the matrix is not entirely hostile to species (when it contains usable resources). 4) Other common anthropogenic disturbances associated with fragmentation are not considered. 5) The many other diverse impacts of fragmentation on ecosystem properties, such as trophic structures of communities, are also not taken into account by IBT. Despite the increased

awareness of those landscape features that drive insect population and community variation, the links between landscape change and insect dynamics are still riddled with clear knowledge gaps (see Hunter 2002).

The study organisms

Arthropod biomass and abundance dominate biodiversity in most parts of the world, making them a vital part of ecosystems (Major *et al.* 2003). Arthropods rely almost completely on those resources available locally and contribute significantly to conservation as they play important functional roles, such as improving soil structure, nutrient cycling, pollination, seed dispersal and maintaining plant community composition as well as other animal populations (Majer & Nichols 1998; Stork & Eggleton 1992; Rohr *et al.* 2007). In general, arthropods have also been found to be sensitive to a range of disturbance types (Madden & Fox 1997; Witt & Samways 2004).

Beetles represent a significant part of the grassland fauna in terms of overall abundance, species richness and the range of functional groups they represent (Thiele 1977; Bohac 1999; Woodcock *et al.* 2005). Dung beetles (Scarabaeidae) have been considered an excellent indicator taxon for landscape diversity studies, being ecologically sensitive, and showing compositional responses to small changes in the local environment (Nichols *et al.* 2008). Dung beetles show sensitivity to habitat change (Nielsen 2007; Gardner *et al.* 2007) and subtle land use changes (Almeida *et al.* 2011), as well as fragmentation and isolation (Klein 1989; Andresen 2003; Nichols *et al.* 2007; Escobar *et al.* 2008). This sensitivity is not restricted to one habitat type or region, and has been shown for different areas of the world and habitats as diverse as the Kalahari Desert (Davis *et al.* 2008), to the rainforests of Borneo (Davis *et al.* 2001) to the scrublands of the Mediterranean (Numa *et al.* 2009).

Since light intensity could determine habitat selection by dung beetles (Doubé 1983; Menezes & Gutierrez 1996), they may be highly sensitive to the impacts of forestry practices. Dung beetles also react quickly to changes in resource availability and the nature of the dung producing ruminants (Lumaret *et al.* 1992). With large herbivores being an important part of grassland systems as well as the livelihoods of the local people in KwaZulu-Natal, dung beetles can provide an important link between different trophic levels.

In many areas of the world ants (Formicidae) have been extensively studied and are often used in studies investigating changes that occur within terrestrial environments (Andersen 1990, 1995, 1997a, b), including impacts of management practices, habitat disturbances and rehabilitation success (Andersen 1990; Majer & Kock 1992; Bestelmeyer & Wiens 1996; French & Major 2001;

Perfecto & Vandermeer 2002; Hoffmann & Andersen 2003; Underwood & Fisher 2006). Numerous studies have employed ants as bioindicators of ecological processes (Culver & Beattie 1983; Majer 1983; Andersen & Sparling 1997). Since they are capable of altering habitats and regulating resource distribution to other organisms, many ant species can be seen as the terrestrial ecosystem engineers among insects (Jones *et al.* 1994). The variety of ecological roles performed by ants further makes them a suitable group for exploring the effects of edges along fragmented landscapes (Ivanov & Kieper 2010), which is why they were chosen along with dung beetles as study organisms in the present study.

Objectives and thesis outline

Since plantation forestry using alien trees poses a major risk to local biodiversity (Samways & Kreuzinger 2001), ecological networks are vital in adjusting this land-use into a more sustainable practice in South Africa.

A number of studies have found an increase in beta diversity associated with an increase in environmental heterogeneity as a result of fragmentation (see Didham *et al.* 1998; Limolino & Perault 2000; Pardini 2004; Pardini *et al.* 2005). Despite the fact that smaller habitat islands contain 1) impoverished communities, 2) involve a lower frequency and strength of biotic interactions (Holt 2010), 3) demonstrates greater extinction probability (Kuussaari *et al.* 2009), and 4) are often devoid of rare, fragment-area-sensitive species, these negative local effects at the patch scale may be numerically overcompensated in terms of total species richness by the higher beta diversity among patches (Tscharnkte *et al.* 2002). The present study is aimed at exploring the role played by corridor width in determining local arthropod assemblage structures. Specifically, the contribution of smaller corridors to conservation within the ENs in KwaZulu-Natal was determined using dung beetles and ants as target taxa (Chapter 2). As they provide firebreaks necessary for fire management within forestry plantations, smaller corridors make up an inherent part of the functioning of this production landscape. The conservation value of smaller corridors may also be of value in a landscape which cannot accommodate corridors > 200 m wide, a width accepted as important for maintaining interior species within this landscape (Pryke & Samways 2001).

A key challenge in landscape ecology involves understanding how ecological processes influence species distribution patterns, which is considered important for effective biodiversity conservation (Wiens *et al.* 1993; Hobbs 1997). The fragmentation model approach is considered appropriate in high contrast landscapes such as the ENs currently implemented in the grasslands of KZN (Fischer &

Lindenmayer 2006). Although aiding us in our understanding of spatial processes, the fragmentation model has been criticized for failing to address the challenge of linking animal distribution patterns with ecological processes (Fischer & Lindenmayer 2006). Therefore, the importance of landscape patterns and environmental gradients in driving dung beetle and ant species diversity across the landscape was investigated (Chapter 3). A better understanding of the relative contribution of spatial patterns and environmental gradients in determining species distributions will improve the effectiveness of conservation management within this production landscape. Finally, a general conclusion discusses the overall findings.

Please note, as Chapters 2 and 3 are written as individual manuscripts some repetition was unavoidable.

References

- Aars, J., and R. A. Ims. 1999. The effect of habitat corridors on rates of transfer and interbreeding between vole demes. *Ecology* 80:1648-1655.
- Almeida, S., J. Louzada, C. Sperber, and J. Barlow. 2011. Subtle land-use change and tropical biodiversity: dung beetle communities in cerrado grasslands and exotic pastures. *Biotropica* 43:704-710.
- Andersen, A. N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16:347-357.
- Andersen, A. N. 1995. Classification of Australian ant communities based on functional groups which parallel plant life forms in relation to stress disturbance. *Journal of Biogeography* 22:15-29.
- Andersen, A. N. 1997a. Functional groups and patterns of organisation in North American ant communities: a comparison with Australia. *Journal of Biogeography*. 24:433-460.
- Andersen, A. N. 1997b. Using ants as bioindicators: multiscale issues in ant community ecology. *Conservation Ecology* [online] 1:8.
- Andersen, A. N., and G. P. Sparling. 1997. Ants as indicators of restoration success: relationship with soil microbial biomass in the Australian tropics. *Restoration Ecology* 7:109-114.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat-a review. *Oikos* 71: 355-366.

- Andresen, E. 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography* 26:87-97.
- Armstrong, A. J., and H. J. van Hensbergen. 1996. Impacts of afforestation with pines on assemblages of native biota in South Africa. *South African Forestry Journal* 175:35-42.
- Armstrong, A. J., G. Benn, A. E. Bowland, P. S. Goodman, D. N. Johnson, A. H. Maddock, and C. R. Scott-Shaw. 1998. Plantation forestry in South Africa and its impact on biodiversity. *Southern African Forestry Journal* 182:59-65.
- Bazelet, C. S., and M. J. Samways. 2011. Relative importance of management vs. design for implementation of large-scale ecological networks. *Landscape Ecology* 26:341-353.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241-1252.
- Benett, G., and K. J. Mulongoy. 2006. Review of experience with Ecological Networks, Corridors and Buffer Zones. Secretariat of the Convention on Biological Diversity, Montreal, Technical Series, No. 23, 100 pages.
- Bertzky, B., C. Corridan, J. Kemsey, S. Kenney, C. Ravilious, C. Besançon, and N. Burgess. 2012. Protected Planet Report 2012: Tracking progress towards global targets for protected areas. IUCN, Gland, Switzerland and UNEP-WCMC, Cambridge, UK.
- Bestelmeyer, B. J., and J. A. Wiens. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecological Applications* 6:1225-1240.
- Bieringer, G., and K. P. Zulka. 2003. Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblages of an adjacent dry grassland. *Biodiversity and Conservation* 12:1481-1495.
- Bohac, J. 1999. Staphylinid beetles as bioindicators. *Agriculture, Ecosystems and Environment* 74:357-372.
- Boitani, L., A. Falcucci, L. Maiorano, and C. Rondinini, C. 2007. Ecological networks as conceptual frameworks or operational tools in conservation. *Conservation Biology* 21:1414-1422.
- Braman, S. K., J. G. Latimer, R. D.; Oetting, R. D. McQueen, T. B. Eckberg, and M. Prinster. 2000. Management strategy, shade, and landscape composition effects on urban landscape plant quality and arthropod abundance. *Journal of Economic Entomology* 93:1464-1472.

- Bremer, L. L., and K. A. Farley. 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation* 19:3893-3915.
- Bullock, W. L., and M. J. Samways. 2005. Conservation of flower-arthropod associations in remnant African grassland corridors in an afforested pine mosaic. *Biodiversity and Conservation* 14:3093-3103.
- Burel, F., and J. Baudry. 1995. Farming landscapes and insects. In D. M. Glen, M. P. Greaves, & H. M. Anderson (editors). *Ecology and integrated farming systems*. Wiley, Chichester, UK. Pages 203-220.
- Burel, F., J. Baudry, A. Butet, P. Clergeau, Y. Delettre, D. Le Coeur, F. Dubs, N. Morvan, G. Paillat, S. Petit, C. Thenail, E. Brunel, and J. C. Lefeuvre. 1998. Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica* 19:47-60.
- Chacoff, N. P. and M. A. Aizen. 2006. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *Journal of Applied Ecology* 43: 18–27.
- Chapin F. S., E. S. Zavaleta, V. T. Eviner, L. R. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack and S. Díaz. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.
- Chown, S. L., B. J. van Rensburg, K. J. Gaston, A. S. L. Rodrigues, and A. S. van Jaarsveld. 2003. Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* 13: 1233-1241.
- Collinge, S. K. 2000. Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. *Ecology* 81:2211-2226.
- Cronin, J.T. 2007. From population sources to sieves: the matrix alters host-parasitoid source-sink structure. *Ecology* 88:2966-2976.
- Crooks, K. R., and M. Sanjayan. 2006. Connectivity conservation: maintaining connections for nature. In K. R. Crooks and M. Sanjayan (editors). *Connectivity conservation*. Cambridge University Press, Cambridge, UK. Pages 1–20.
- Crous, C. J., M. J. Samways, and J. S. Pryke. 2013. Exploring the mesofilter as a novel operational scale in conservation planning. *Journal of Applied Ecology* 50:205-214.

Culver, C. D., and A. J. Beattie. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. *Ecology* 64:1983:485-492.

Davis, A. L. V., C. H. Scholtz, and C. Deschodt. 2008. Multi-scale determinants of dung beetle assemblage structure across abiotic gradients of the Kalahari-Nama Karoo ecotone, South Africa. *Journal of Biogeography* 35:1465-1480.

Davis, A. J., Holloway, J. D., H. Huijbregts, J. Krikken, A. H. Kirk-Spriggs, and S. L. Sutton. 2001. Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology* 38:593-616.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14:342-355.

Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies of for the design of natural reserves. *Biological Conservation* 7:129-145.

Didham, R. K., P. M. Hammond, J.H. Lawton, P. Eggleton, and N.E. Stork. 1998. Beetle species response to tropical forest fragmentation. *Ecological Monographs* 68:295-323.

Doube, B. M. 1983. The habitat preference of some bovine dung beetles (Coleptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. *Bulletin for Entomological Research* 73:357-371.

Dudley, N., D. Baldock, R. Nasi, and S. Stolton. 2005. Measuring biodiversity and sustainable management in forest and agricultural landscapes. *Philosophical Transactions of the Royal Society of London B* 360:457-470.

Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic and Applied Ecology* 4:129-138.

Dunning, J. B. Jr., J. R. Borgella, K. Clements, and G. K. Meffe. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9:542-550.

DWAF (Departement of Water Affaris and Forestry). 2006. Abstract of South African forestry facts for the year 2004/2005. Department of Water Affairs and Forestry, Pretoria, South Africa.

Eeley, H. A. C., M. J. Lawes, and D. Macfarlane. 2002. Historical change since 1944 in landscape pattern of indigenous forest in the KwaZulu-Natal Midlands. In A. H. W. Seydack, T. Vorster, W. H. Vermeulen and J. J. van der Merwe (editors). *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, May 2002. Department of Water Affairs and Forestry, Pretoria, South Africa. Pages 68-78.

Escobar, F., G. Halffter, A. Solís, V. Halffter, and D. Navarrete. 2008. Temporal shifts in dung beetle community structure within a protected area of tropical wet forest: a 35-year study and its implications for long-term conservation. *Journal of Applied Ecology* 45:1584-1592.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management* 61: 603-610.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34:487-515.

Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. *Ecology* 66:1762-1768.

Field, L. F. 2002. Consequences of habitat fragmentation for the pollination of wild flowers in moist upland grasslands of KwaZulu-Natal. Dissertation, University of Natal, South Africa.

Fischer, J., and D. B. Lindenmayer. 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos* 112:473-480.

French, K., and R. E. Major. 2001. Effect of an exotic *Acacia* (Fabaceae) on ant assemblages in South African fynbos. *Austral Ecology* 26:303-310.

FSC (Forest Stewardship Council). 1996. FSC international standard: FSC principles and criteria for forest stewardship. FSC-STD-01-001(version 4-0). Forest Stewardship Council A. C., Bonn, Germany.

Gardner, T. A., M. I. M. Hernández, J. Barlow, and C. A. Peres. 2007. Understanding the biodiversity consequences of habitat change, the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology* 45:883-893.

Gaston, K. J., K. Charman, S. F. Jackson, P. R. Armsworth, A. Bonn, R. A. Briers, C. S. Q. Callaghan, R. Catchpole, J. Hopkins, W. E. Kunin, J. Latham, P. Opdam, R. Stoneman, D. A. Stroud, and R. Tratt. 2006. The ecological effectiveness of protected areas: the United Kingdom. *Biological Conservation* 132:76-87.

Gaston, K. J., S. F. Jackson, A. Nagy, L. Cantú-Salazar, and M. Johnson. 2008. Protected areas in Europe: principle and practice. *Annals of the New York Academy of Science* 1134:97-119.

- Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* 281:2045-2047.
- Goodman, P. 2003. Assessing management effectiveness and setting priorities in protected areas in KwaZulu-Natal. *BioScience* 53:843-851.
- Goodman, P. S. 2003. Assessing management effectiveness and setting priorities in protected areas in KwaZulu-Natal. *BioScience* 53:843-851.
- Haas, C. A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* 9:845-854.
- Haddad, N. M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* 9:612-622.
- Haddad, N. M., and K. A. Baum. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* 9:623-633.
- Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* 12: 321-334.
- Hale, M. L., P. W. W. Lurz, M. D. F. Shirley, S. Rushton, R. M. Fuller, and K. Wolff. 2001. Impact of landscape management on the genetic structure of red squirrel populations. *Science* 293:2246-2248.
- Halley, J. M., and J. P. Dempster. 1996. The spatial population dynamics of insects exploiting a patchy food resource: a model study of local persistence. *Journal of Applied Ecology* 33:439-454.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Hanski, I. and M. C. Singer. 2001. Extinction-colonization dynamics and host-plant choice in butterfly metapopulations. *American Naturalist* 158:341-353.
- Harrison, S. and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225-232.
- Hartley, M. J. 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology Management* 155:81-95.
- Hess, G. 1994. Conservation corridors and contagious disease: a cautionary note. *Conservation Biology* 8:256-262.

- Hilty, J. A., W. Z. Jr. Lidicker, and A. Merenlender. 2006. Corridor ecology: the science and practice of linking landscapes for biodiversity conservation. Island Press, Washington.
- Hobbs, R. 1997. Future landscapes and the future of landscape ecology. *Landscape Urban Planning* 37: 1-9.
- Hobbs, R. J. 1992. The role of corridors in conservation: solution or bandwagon? *Trends in Ecology and Evolution* 7:389-392.
- Hoffmann, B. D., and A. N. Andersen. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* 28:444-464.
- Holt, R. D. 2010. Toward a trophic island biogeography: reflections on the interface of island biogeography and food web ecology. In J. B. Losos and R. E. Ricklefs (editors). *The Theory of Island Biogeography*. Princeton University Press, Princeton, USA. Pages 143-185.
- Hunter, M. D. 2002. Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology* 4:159-166.
- Ivanov, K., and J. Keiper. 2010. Ant (Hymenoptera: Formicidae) diversity and community composition along sharp urban forest edges. *Biodiversity and Conservation* 19:3917-3933.
- James, A., K. J. Gaston, and A. Balmford. 2001. Can we afford to conserve biodiversity? *BioScience* 51:43-52.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.
- Jongman, R. H. G. 1995. Nature conservation planning in Europe - developing ecological networks. *Landscape and Urban Planning* 32:169-183.
- Jongman, R. H. G., and G. Pungetti. 2004. *Ecological networks and greenways: concept, design, implementation*. Cambridge University Press, Cambridge, UK.
- Jongman, R. H. G., I. M. Bouwma, A. Griffioen, L. Jones-Walters, and A. M. Doorn. 2011. The pan European ecological network: PEEN. *Landscape Ecology* 26:311-326.
- Joubert, L., J. S. Pryke, and M. J. Samways. 2014. Annual burning drives plant communities in remnant grassland ecological networks in an afforested landscape. *South African Journal of Botany* 92:126-133.

- King, N. L. 1938. Historical sketch of the development of forestry in South Africa. *South African Forestry Journal* 1:4-7.
- Kinvig, R. G., and M. J. Samways. 2000. Conserving dragonflies (Odonata) along streams running through commercial forestry. *Odonatologica* 29:195-208.
- Kirkman, K. E. and R. M. Pott. 2002. Biodiversity conservation in plantation forestry. In S. M. Pierce, R. M. Cowling, T. Sandwith and K. MacKinnon (editors). *Mainstreaming Biodiversity in Development - Case Studies from South Africa*. The World Bank Environmental Department, Washington, DC, USA. Pages 33-42.
- Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70:1715-1725.
- Kreuss, A. and T. Tschardt. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122:129-137.
- Kuussaari, M., R. Bommarco, R. K. Heikinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* 24:564-571.
- Laurance, W. F. 2008. Theory meets reality: how habitat fragmentation research has transcended biogeographic theory. *Biological Conservation* 141:1731-1744.
- Laurance, W. F., and M. A. Cochrane. 2001. Special section: synergistic effects in fragmented landscapes. *Conservation Biology* 15:1488-1489.
- Lawton, J. H., and R. M. May. 1995. *Extinction Rates*. Oxford University Press, Oxford, UK.
- Le Maitre, D. C., D. M. Richardson, and R. A. Chapman. 2004. Alien plant invasions in South Africa: driving forces and the human dimension. *South African Journal of Science* 100:103-112.
- Limolimo, M. V., and D. R. Perault. 2000. Assembly and disassembly of mammal communities in a fragmented temperate rain forest. *Ecology* 81:1517-1532.
- Lindenmayer, D. B. and J. Fischer. 2003. Sound science or social hook - a response to Brooker's application of the focal species approach. *Landscape Urban Planning* 62: 149-158.
- Lindenmayer, D. B., W. Steffen, A. A. Burbidge, L. Hughes, R. L. Kitching, W. Musgrave, M. S. Smith, P. A. Werner. 2010. Conservation strategies in response to rapid climate change: Australia as a case study. *Biological Conservation* 143:1587-1593.

- Lindenmayer, D. B., R. J. Hobbs, and D. Salt. 2003. Plantation forests and biodiversity conservation. *Australian Forestry* 66:62-66.
- Lumaret, J. P., N. Kadiri, and M. Bertrand. 1992. Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology* 29:349-356.
- MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press.
- Madden, K. E., and B. J. Fox. 1997. Arthropods as indicators of the effects of fluoride pollution on the succession following sand mining. *Journal of Applied Ecology* 34:1239-1256.
- Majer, J. D. 1983. Ants: bio-indicators of minesite rehabilitation, land-use and land conservation. *Environmental Management*. 7:375-383.
- Majer, J. D., and A. E. Kock. 1992. Ant recolonization of sand mines near Richards Bay, South Africa. *South African Journal of Science* 88:31-36.
- Majer, J. D., and O. G. Nichols. 1998. Long-term recolonization patterns of ants in western Australian rehabilitated bauxite mines with reference to their use as indicators of restoration success. *Journal of Applied Ecology* 35:161-182.
- Major, R. E., F. J. Christie, G. Gowing, G. Cassis, and C. A. M. Reid. 2003. The effect of habitat configuration on arboreal insects in fragmented woodlands of south-eastern Australia. *Biological Conservation* 113:35-48.
- Manning, A. D., D. B. Lindenmayer, and H. A. Nix. 2004. Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos* 104: 621-628.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.
- McGarigal, K. and S. A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* 12: 335-345.
- McIntyre, S. and R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology* 13: 1282-1292.
- MEA (Millennium Ecosystem Assessment). 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resource Institute, Washington DC, USA. Downloaded from www.unep.org/maweb/documents/document.354.aspx.pdf on 27 March 2014

- Mech, S. G., and J. G. Hallett. 2001. Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology* 15:467-474.
- Menedez, R., and D. Gutierrez. 1996. Altitudinal effects on habitat selection of dung beetles (Scarabaeidae: Aphodiidae) in the northern Iberian peninsula. *Ecography* 19:313-317.
- Mentis, M. T., and B. J. Huntley. 1982. A Description of the Grassland Biome Project. South African National Scientific Programmes Report No. 62. CSIR, Pretoria.
- Mittermeier, R. A., P. R. Gil, M. Hoffman, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux, and G. A. B. da Fonseca. 2004. Hotspots Revisited. CEMEX, Mexico City.
- Mucina, L., and M. C. Rutherford. 2006. The Vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria, South Africa.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. de Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Nasi, R., P. Koponen, J. G. Poulsen, M. Buitenzorg, and W. Rusmantoro. 2008. Impacts of landscape and corridor design on primates in a large-scale industrial tropical plantation. *Biodiversity and Conservation* 17:1105-1126.
- Neke, K. S., and M. A. du Plessis. 2004. The threat of transformation: quantifying the vulnerability of grasslands in South Africa. *Conservation Biology* 18:466-477.
- Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezcútia, and M. E. Favila. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* 141:1461-1474.
- Nichols, E., T. Larsen, S. Spector, A. L. Davis, A., F. Escobar, M. Favila, and K. Vulinec. 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biological Conservation* 137:1-19.
- Nielsen, S. T. 2007. Deforestation and biodiversity: effects of bushland cultivation on dung beetles in semiarid Tanzania. *Biodiversity and Conservation* 16:2753-2769.
- Noss, R. F., A. P. Dobson, R. Baldwin, P. Beier, C. R. Davis, D. A. Dellasala, J. Francis, H. Locke, K. Nowak, R. Lopez, C. Reining, S. C. Trombulak, and G. Tabor. 2012. Bolder thinking for conservation. *Conservation Biology* 26:1-4.

- Noss, R. F., and A. Y. Cooperrider. 2003. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington D.C., USA.
- Numa, C., J. R. Verdú, A. Sánchez, and E. Galante. 2009. Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. *Diversity and Distributions* 15:489-501
- Onstad, D. W.; J. L. Spencer, C. A. Guse, E. Levine and S. A. Isard. 2001. Modeling evolution of behavioural resistance by an insect to crop rotation. *Entomologia Experimentalis et Applicata* 100:195-201.
- Opdam, P., and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* 124:354-362.
- Pardini, R. 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest Landscape. *Biodiversity and Conservation* 13:2567-2586.
- Pardini, R., S. M. de Souza, R. Braga-Neto, and J. P. Metzger. 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biological Conservation* 124:253-266.
- Pereirae, H. M., and G. C. Daile. 2006. Modeling biodiversity dynamics in countryside landscapes. *Ecology* 87:1877-1885.
- Perfecto, I., and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology* 16:174-182.
- Perrings, C., L. Jackson, K. Bawa, L. Brussaard, S. Brush, T. Gavin, R. Papa, U. Pascual, and P. De Ruiter. 2006. Biodiversity in agricultural landscape: saving natural capital without losing interest. *Conservation Biology* 20:263-264.
- Pimentel, D., U. Stachow, D. A. Takacs, H. W. Brubaker, A. R. Dumas, J. J. Meaney, J. A. S. O'Neil, D. E. Onsi, and D. B. Corzilius. 1992. Conserving biological diversity in agricultural/forestry systems - most biological diversity exists in human-managed ecosystems. *BioScience* 42:354-362.
- Pimm, S. L., and P.H. Raven. 2000. Biodiversity: extinction by numbers. *Nature* 403:843-845.
- Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* 269:347-350.
- Pressey, R. L., R. M. Cowling, and M. Rouget. 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation* 112:99-127.

Pryke, S. R., and M. J. Samways. 2001. Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biological Conservation* 101:85-96.

Pryke, S. R., and M. J. Samways. 2003. Quality of remnant indigenous grassland linkages for adult butterflies (Lepidoptera) in an afforested African landscape. *Biodiversity and Conservation* 12:1985-2004.

Pryke, J. S., and M. J. Samways. 2012. Conservation management of complex natural forest and plantation edge effects. *Landscape Ecology* 27:73-85.

Pryke, J. S., and M. J. Samways. 2014. Conserving natural heterogeneity is crucial for designing effective ecological networks. *Landscape Ecology*. DOI: 10.1007/s10980-014-0096-x.

Radeloff, V. C., D. J. Mladenoff, M. A. Boyce. 2000. The changing relation of landscape patterns and jack pine budworm population during an outbreak. *Oikos* 90:417-430.

Reyers, B., D. H. K. Fairbanks, K. J. Wessels, and A. S. van Jaarsveld. 2002. A multicriteria approach to reserve selection: addressing long-term biodiversity maintenance. *Biodiversity and Conservation* 11:769-793.

Reyers, B., J. Nel, B. Egoh, Z. Jonas, and M. Rouget. 2005. National grasslands biodiversity program: grassland biodiversity profile and spatial biodiversity priority assessment. CSIR Report Number: ENV-S-C 2005-102.

Richardson, D. M. 1998. Forestry trees as invasive aliens. *Conservation Biology* 12:18-26.

Rodrigues, A. S. L., S. J. Andelman, M. I. Bakarr, L. Boitani, T. M. Brooks, R. M. Cowling, L. D. C. Fishpool, G. A. B. da Fonseca, K. J. Gaston, M. Hoffmann, J. S. Long, P. A. Marquet, J. D. Pilgrim, R. L. Pressey, J. Schipper, W. Sechrest, S. N. Stuart, L. G. Underhill, R. W. Waller, M. E. J. Watts, X. Yan. 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* 428:640-643.

Rohr, J. R., C. G. Mahan, and K. C. Kim. 2007. Developing a monitoring program for invertebrates: guidelines and a case study. *Conservation Biology* 21:422-433.

Ronce, O. and M. Kirkpatrick. 2001. When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution* 55:1520-1531.

Rosenberg, D. K., B. R. Noon, and E. C. Meslow. 1997. Biological corridors: form, function, and efficacy. *BioScience* 47:677-687.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfeld, R. Dirzo, E. H. Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.

Samways, M. J. 2007a. Insect conservation: a synthetic management approach. *Annual Review of Entomology* 52:465-487.

Samways, M. J. 2007b. Implementing ecological networks for conserving insect and other biodiversity. In A. J. A. Stewart, T. R. New and O. T. Lewis (editors). *Insect Conservation Biology*. CABI, Wallingford, Oxon, UK. Pages 127-143.

Samways, M. J., and K. Kreuzinger. 2001. Vegetation, ungulate and grasshopper interactions inside vs outside an African savanna game park. *Biodiversity and Conservation* 10:1963-1981.

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

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.

Schoeman, F., T. S. Newby, M. W. Thompson, and E. C. Van den Berg. 2013. South African National Land-Cover Change Map. *Journal of Gematics* 2:94-105.

Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1:63-71.

Simberloff, D., J. A. Farr, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6:493-504.

Simberloff, D., M. A. Nuñez, N. J. Ledgard, A. Pauchard, D. M. Richardson, M. Sarasola, B. W. Van Wilgen, S. M. Zalba, R. D. Zenni, R. Bustamante, E. Peña and S. R. Ziller. 2010. Spread and impact of introduced conifers in South America. *Austral Ecol* 35:489-504.

Sloan, S., C. N. Jenkins, L. N. Joppa, D. L. A. Gaveau, and W. F. Laurance. 2014. Remaining natural vegetation in the global biodiversity hotspots. *Biological Conservation* 177:12-24.

Smith, D., and P. Hellmund. 1993. *Ecology of Greenways*. University of Minnesota Press, Minneapolis, USA.

Sodhi, N. S., and P. R. Ehrlich. 2010. *Conservation Biology for All*. Oxford University Press, Oxford.

Solomon, M., A. S. van Jaarsveld, H. C. Biggs, and M. H. Knight. 2003. Conservation targets for viable species assemblages. *Biodiversity and Conservation* 12:2435-2441.

Soulé, M. E., and M. A. Sanjayan. 1998. Ecology - conservation targets: do they help? *Science* 279:2060-2061.

Steffen, W., A. A. Burbidge, L. Hughes, R. Kitching, D. Lindemeyer, W. Musgrave, M. S. Smith, and P. A. Werner. 2009. *Australia's Biodiversity and Climate Change: A Strategic Assessment of the Vulnerability of Australia's Biodiversity to Climate Change*. CSIRO Publishing, Melbourne, Australia.

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

Sutcliffe, O. L., and C. D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperanthus*) between woodland clearings. *Conservation Biology* 10:1359-1365.

Sutherst, R., F. Constable, K. J. Finlay, R. Harrington, J. Luck and M. P. Zalucki. 2011. Adapting to crop pest and pathogen risks under a changing climate. *Wiley-Interdisciplinary Reviews: Climate Change* 2:220– 237.

Terborgh, J. W. 2006. Reserves: How much is enough land and how do we get there from here? In M. J. Groom, G. K. Meffe and C. R. Carroll (editors). *Companion to Principles of Conservation Biology*, 3rd Edition. Sinauer Press, Sunderland, USA.

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

Thiele, H. U. 1977. *Carabid Beetles in their Environments*. Springer, Berlin.

Thomas, C. F. G., L. Parkinson, G. J. K. Griffiths, A. Fernandez Garcia, and E. J. P. Marshall. 2001. Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats. *Journal of Applied Ecology* 38: 100–116.

Thrupp, L. A. 2000. Linking agricultural biodiversity and food security: the valuable role of agrobiodiversity for sustainable agriculture. *International affairs* 76:265-281.

Tscharnkte, T., I. Staffan-Dewenter, A. Kruess, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications* 12:354-363.

Tscharntke, T., A. Gathmann, A. and I Steffan-Dewenter. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology* 35:708–719.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Characteristics of insect populations in habitat fragments: a mini review. *Ecological Research* 17:229-239.

Turner, M. G. 2005. Landscape ecology: what is the state of the science? *Annual Review of Ecology and Systematics* 36:319–344.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. *Landscape ecology in theory and practice: pattern and processes*. Springer, New York.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology letters* 11:1351-1363.

Underwood, A. C., and B. L. Fisher. 2006. The role of ants in conservation monitoring: If, when, and how. *Biological Conservation* 132:166-182.

Varchola, J. M., J. P. Dunn. 2001. Influence of hedgerow and grassy field borders on ground beetle (Coleoptera: Carabidae) activity in fields of corn. *Agriculture, Ecosystems and Environment* 83:153-163.

Walker, B. M., and W. L. Steffen. 1999. Interactive and integrated effects of global change on terrestrial ecosystems. In B. Walker, W. L. Steffen, J. Canadell and J. Ingram (editors). *The Terrestrial Biosphere and Global Change Implications for Natural and Managed Ecosystems*. Book Series 4. Cambridge University Press, Cambridge, UK. Pages 329-375.

Wiens, J. A., N. C. Stenseth, B. Vanhorne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66: 369-380.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607-615.

With, K. A., D. M. Pavuk, J. L. Worchuck, R. K. Oates, and J. L. Fisher. 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications* 12:52-65.

Witt, A. B. R., and M. J. Samways. 2004. Influence of agricultural land transformation and pest management practices on the arthropod diversity of a biodiversity hotspot, the Cape Floristic Region, South Africa. *African Entomology* 12:89-95.

Wittenberg, R., and M. J. W. Cock. 2001. Invasive alien species: a toolkit of best prevention and management practices. CAB International, Wallingford, UK.

Woodcock, B. A., R. Pywell, D. B. Roy, R. Rose, and D. Bell. 2005. Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. *Biological Conservation* 125:192-202.

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

Chapter 2:

All corridors are equal, but some are more equal than others - dung beetle and ant assemblage responses to grassland corridor size within a timber production landscape

Abstract

Ecological networks (ENs) are implemented to lessen the negative impacts of plantation forestry on biodiversity in grasslands within KwaZulu-Natal, South Africa. Optimal design of ENs involves large, good quality corridors. This study investigates the value that smaller corridors have for biodiversity conservation within this system. Ants and dung beetles were sampled in grassland corridors of various sizes, plantation blocks and a nearby protected area (PA). The two taxa differed in their response to fragmentation. Dung beetles showed a decrease in species richness and a corresponding increase in species turnover with increased fragmentation. Dung beetle species composition in corridors was different to that in the PA. Grassland management can play a more important role for dung beetle species composition than fragmentation. In contrast, there were no differences in either species richness or turnover of ants between different biotopes or strong differences in species composition between the corridors and the PA. Smaller corridors contained more unique ant species than larger corridors. This implies that different taxa respond to corridor width differently, and thus the value for smaller corridors is dependent on the taxa concerned. Large corridors provide more ecologically resilient habitats and their conservation effectiveness undoubtedly exceeds that of smaller corridors. But for ants at least, smaller corridors provide valuable additional habitat within this production landscape.

Introduction

To avoid the additional loss of biodiversity and maintain ecosystem functioning, innovative management approaches are necessary (MEA 2005). Apart from setting land aside devoted to the protection and maintenance of nature, connecting large good quality patches of natural habitat that are exposed to natural mimicking disturbances can also provide habitat for a range of species within and across functional groups (Fischer *et al.* 2006; Samways 2007a).

Ecological Networks (ENs) are large scale interconnected natural corridors and patches that connect habitats for organism movement on both evolutionary and ecological timescales (Jongman 1995; Beier & Noss 1998). Although they are implemented in only a few areas in the world, much

conceptual effort has gone into the biodiversity value of ENs (Yu *et al.* 2006; Jongman *et al.* 2011). Increasing the exchange of individuals among local populations facilitates the maintenance of large metapopulations, i.e. groups of local populations where individuals may move between habitat patches (Hanski & Simberloff 1997; Hanski 1998). Movement between distinct habitats is an important part of the ecology of many species. The ability of movement (extent and ease) will be determined by landscape configuration and composition (Damschen *et al.* 2006; Holzschuh *et al.* 2010). Depending on the nature of the matrix, it may facilitate or impede dispersal between habitat patches (Cronin 2007).

In addition to the rescue and (re)colonization effects of movement between local populations, movement may also increase genetic mixing among populations, reducing possible genetic variability erosion and the consequent extinction risks within populations (Baguette *et al.* 2013). Corridors have been found to increase organism movement between patches (Haas 1995; Sutcliffe & Thomas 1996; Gonzalez *et al.* 1998; Haddad 1999; Mech & Hallett 2001), increase gene flow between patches (Aars & Ims 1999; Hale *et al.* 2001; Mech & Hallett 2001), increase population sizes (Fahrig & Merriam 1985; Dunning *et al.* 1995; Haddad & Baum 1999), and maintain biodiversity (Gonzalez *et al.* 1998). Not only is connectivity important for the persistence of certain species, but is also central to many ecosystem processes (Benett & Mulongoy 2006).

From a biodiversity conservation viewpoint, KwaZulu-Natal (KZN) Province, South Africa, is internationally significant (Goodman 2003). It is situated within the biologically rich transition zone between the northern tropical biota and southern subtropical biota on the eastern coast of Africa and forms part of the Maputaland-Pondoland-Albany biodiversity hotspot. The inland area of KZN constitutes part of the distribution of South Africa's grassland biome, the country's most threatened biome. Cultivation, urbanisation, overgrazing and mining, together account for 35% of its transformation (Reyers *et al.* 2005). The effectiveness of PAs in KZN requires more investigation. Invasive alien plants and isolation pose major threats to current PAs and effectiveness is further hindered by problems such as poor design and layout as well as inadequate financial resources, management planning and research efforts (Goodman 2003).

With only 0.02% of land surface areas being covered by the forest biome (Mucina & Rutherford 2006), natural wood sources are scarce in South Africa. To grassland specialists, the timber matrix is inhospitable (Armstrong & van Hensbergen 1996) and acts as a barrier or filter that impedes movement between remnants of natural grassland (Samways & Kreuzinger 2001; Bieringer & Zulka 2003). The high environmental impacts of commercial forestry have led to this industry receiving a great deal of attention from conservation agencies. To date, the timber industry has demonstrated

proactive involvement in attempting to reduce its environmental impact through research related to protecting remnant natural and semi-natural areas within the plantation forestry matrix (see Hartley 2002). On average, one-third of any given plantation remains unplanted to timber, and it is these unplanted areas which form complex ENs of interconnected nodes, corridors and special landscape features (Jongman 1995; Kirkman & Pott 2002; Samways 2007a,b).

Good quality, large habitat corridors and important nodes are considered optimal in EN design, while less confidence is given to smaller, disturbed corridors (Samways *et al.* 2010). The question still remains as to what value the smaller corridors add to the ENs in terms of biodiversity and for maintaining populations within them. The argument on habitat loss versus fragmentation has sometimes concentrated solely on species richness instead of community composition, which tends to show great changes at the cost of endangered and “valuable” species (Tscharnkte *et al.* 2012). Since many species occur in or have at least part of their distributions in semi-natural habitats (such as among urban and agricultural areas), these habitats can potentially provide valuable links between protected areas (PAs) and in this way enhance long term conservation success (Farina 2000; Goodman 2003; Gaston & Spicer 2004; Dudley *et al.* 2005).

A number of studies have found an increase in beta diversity associated with an increase in environmental heterogeneity as a result of fragmentation (see Didham *et al.* 1998; Limolino & Perault 2000; Pardini 2004; Pardini *et al.* 2005). Reasons why beta diversity may increase with fragmentation is the hyper-dynamic nature of smaller habitat fragments (Laurance 2002), the role played by the underlying heterogeneity of the landscape prior to fragmentation (Tscharnkte *et al.* 2012) and organism spill over from the matrix (which may occur if the matrix is not entirely hostile to species, e.g. Pereira & Daile 2006; Holt 2010). Despite the fact that smaller habitat islands contain 1) impoverished communities, 2) involves a lower frequency and strength of biotic interactions (Holt 2010), 3) demonstrates greater extinction probability (Kuussaari *et al.* 2009), and 4) are often devoid of rare, fragment-area-sensitive species, these negative local effects at the patch scale may be numerically overcompensated in terms of total species richness by the higher beta diversity among patches (Tscharnkte *et al.* 2002).

Arthropod biomass and abundance dominate biodiversity in most parts of the world, making them a vital part of ecosystems (Major *et al.* 2003). Arthropods rely almost completely on those resources available locally and contribute significantly to conservation as they play important functional roles, such as improving soil structure, nutrient cycling, pollination, seed dispersal and maintaining plant community composition as well as other animal populations (Majer & Nichols 1998; Stork & Eggleton 1992; Rohr *et al.* 2007). In general, arthropods have also found to be sensitive to a range of

disturbance types (Madden & Fox 1997; Bolger *et al.* 2000; Witt & Samways 2004). Beetles represent a significant part of the grassland fauna in terms of overall abundance, species richness and the range of functional groups that they represent (Thiele 1977; Bohac 1999; Woodcock *et al.* 2005). Dung beetles (Scarabaeidae) have been considered excellent indicator taxa for landscape diversity studies, being ecologically sensitive, and showing compositional responses to small changes in the local environment (Nichols *et al.* 2008). Dung beetles show sensitivity to habitat change (Nielsen 2007; Gardner *et al.* 2007) and subtle land use changes (Almeida *et al.* 2011), as well as to fragmentation and isolation (Klein 1989; Andresen 2003; Nichols *et al.* 2007; Escobar *et al.* 2008). This sensitivity is not restricted to one habitat type or region, and has been shown for different areas of the world and habitats as diverse as the Kalahari Desert (Davis *et al.* 2008), to the rainforests of Borneo (Davis *et al.* 2001) to the scrublands of the Mediterranean (Numa *et al.* 2009)

Since light intensity could determine habitat selection by dung beetles (Doubé 1983; Menezes & Gutierrez 1996), they may be highly sensitive to the impacts of forestry practices. Dung beetles also react quickly to changes in resource availability and the nature of the dung producing ruminants (Lumaret *et al.* 1992). With large herbivores being an important part of grassland systems as well as the livelihoods of the local people in KwaZulu-Natal, dung beetles can provide an important link between different trophic levels.

In many areas of the world ants (Formicidae) have been extensively studied and are often used in studies investigating changes that occur within terrestrial environments (Andersen 1990, 1995, 1997a, b), including impacts of management practices, habitat disturbances and rehabilitation success (Andersen 1990; Majer & Kock 1992; Bestelmeyer & Wiens 1996; French & Major 2001; Perfecto & Vandermeer 2002; Hoffmann & Andersen 2003; Underwood & Fisher 2006). Numerous studies have used ants as bioindicators of ecological processes (Culver & Beattie 1983; Majer 1983; Andersen & Sparling, 1997). Since they are capable of altering habitats and regulating resource distribution to other organisms, ants can often be seen as the terrestrial ecosystem engineers among insects (Jones *et al.* 1994). The variety of ecological roles performed by ants further makes them a suitable group for exploring the effects of edges along fragmented landscapes (Ivanov & Kieper 2010). For these reasons, ants and dung beetles were chosen as study organisms here.

Understanding the degree to which smaller corridors are used by different taxa will allow me to assess their value to the overall ecological network and their ultimate contribution to biodiversity conservation and sustainable land-use (both current and in terms of potential future land-planning). Furthermore, I investigate how biodiversity responds to smaller corridors for determining the potential for implementing ENs in landscapes that cannot accommodate >200 m-wide, a width

considered important for maintaining interior species (Pryke & Samways 2001). Thus, the objective of this study was to determine the contribution of small corridors within the EN framework to the overall conservation of the grassland biome using dung beetles and ants as the target taxa. Specifically, I assess whether there is a difference in dung beetle and ant species richness, composition and beta-diversity variation (as defined by Anderson *et al.* 2011) among grassland corridors of different sizes, a nearby PA and plantation blocks. By decreasing population sizes, habitat loss should increase the influence of stochastic processes and increase extinction rates, leading to decreased alpha diversity in fragmented landscapes (Wilcox & Murphy 1985) and increased beta diversity among them (Loreau 2000; Chase 2003). Alpha diversity is thus expected to decrease as corridor size decreases, and beta diversity is expected to increase.

Methods

Study area and arthropod sampling

This study was undertaken in the Grassland Biome in the KwaZulu-Natal Midlands in South Africa. Sampling took place in two commercial forestry plantations (*Pinus*) and one PA over a maximum linear scale of 14 km. The two plantations were the Good Hope (29° 42 S; 29° 59 E) and Shannon (29° 40 S; 29° 56 E) estates and the PA was the nearby iMpendle Nature Reserve (29° 42 S; 29° 52 E) (see Appendix A for geographical co-ordinates of each site).

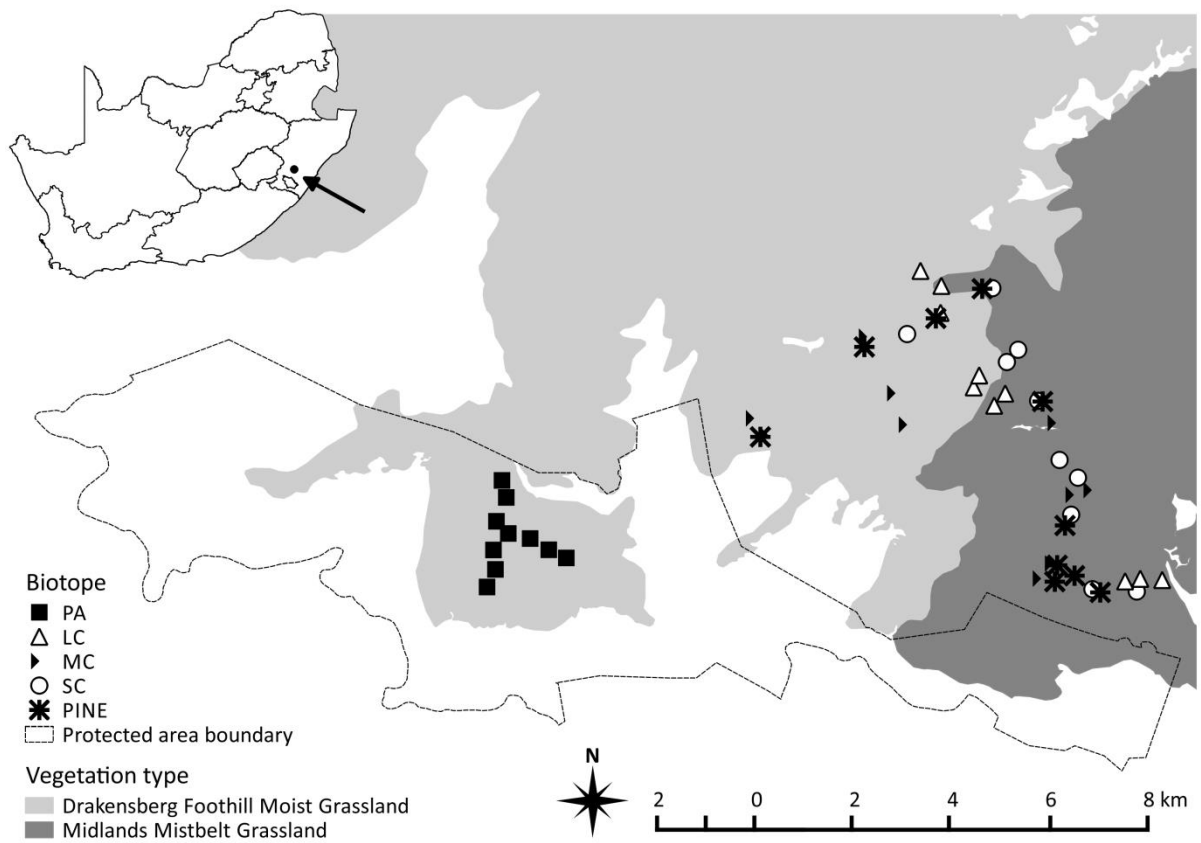


Figure 1 Map of study area. PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor; PINE, plantation blocks. Google Maps link: <https://maps.google.com/maps?ll=-29.68612,29.93102&z=12&t=h&output=classic&dg=brw>

The area experiences summer rainfall with a mean annual precipitation of 730 – 1 280 mm (Mucina *et al.* 2006). Thunderstorms are frequent during summer and autumn. Heavy and frequent mist provides a significant amount of extra moisture (Mucina *et al.* 2006). The area is dominated by threatened Midlands Mistbelt Grassland (MMG, 760-1 400 metres above sea level (m asl)) and Drakensberg Foothill Moist Grassland (DFMG, 880-1 860 m asl) (Mucina *et al.* 2006). The dominant form of land transformation in the area is exotic timber plantations (Kirkman & Pott 2002). Only a

few fragments of the original species-rich MMG remain (Mucina *et al.* 2006). Both these grassland types are forb rich. MMG is dominated by tall, *Themeda triandra* rich grasslands, while DFMG is dominated by short bunch grasses (including *T. triandra* and *Tristachya leucothrix*) (Mucina *et al.* 2006).

Both the plantation blocks and the PA were at a similar elevation (ca 1200 – 1500 m asl). Protected natural areas are surrounded by contrasting landscapes of human modified areas (Hansen & DeFries 2007), making these regions ideal systems for investigating the effects of human activities. The PA was included in the present study to function as a reference of unmodified grassland species richness and composition. It also aided in highlighting the effect different grazing and fire management schemes may have on species composition. While there are some indigenous grazers present in the grassland corridors (such as the southern reedbuck, *Redunca arundinum*), these corridors experience continuous but moderate grazing at varying densities from mostly domestic cattle owned by the local community. The PA on the other hand has been fenced off and is exposed to lighter grazing by various indigenous herbivores. Furthermore, the grassland corridors are burned annually, while the PA is burned biannually. Both the grassland and plantation sites are fairly homogenous, grasslands consisting of a single plant association and plantations being a monospecific stand with minimal shrub undergrowth.

Transects were laid out in grassland corridors of different sizes, plantation blocks and the nearby PA. The edge zone in this system has been estimated to reach 30 m into grassland corridors (Pryke & Samways 2012). This was taken into account when determining corridor size classes. Grassland corridors were categorized into three types according to minimum width: large corridors (>120 m, have more interior area than edge zone), medium corridors (60 – 120 m, interior area is less than edge zone), and small corridors (<60 m, subject to intense edge effects).

The three corridor types, along with the PA and plantation blocks (the five biotopes studied here), had ten replicated sampling transects each, giving a total of 50 transects. All transects were situated parallel to the plantation edge. In plantation blocks and corridors with a minimum width more than 60 m, transects were positioned at least more than 30 m from the edge. All grassland sites were at least 600 m apart.

Each transect consisted of four sampling stations, each 50 m apart. At each station, one dung baited pitfall trap to capture dung beetles and four test-tube traps to capture ants were dug level with the surrounding soil surface. The dung baited pitfall trap consisted of 50 g pig dung hung above a 2 litre (l) bucket. Each bucket was filled with a preservative liquid (water and a small amount of soap to

lessen the effect of surface tension). The four small ant pitfalls (22 mm in diameter) were placed >3 m away from the baited 2 l bucket trap. Ant traps were filled with a 50% ethylene glycol solution (Woodcock 2005). Traps were left open for three days. All insect sampling took place over January-February 2013. Dung beetles were identified to species level where possible. Ants were sorted to recognized taxonomic units (RTUs), and named to genus. For each dung beetle and ant species or morphospecies collected, a voucher specimen was retained at Stellenbosch University.

Data analyses

For each site, data from all four stations were pooled for statistical analysis. As they form part of the same superfamily (Scarabaeoidea) and perform similar functional roles, three Trogidae species that were sampled with baited traps were retained in the data and analysed along with the dung beetle data. It is considered more accurate to refer to estimates of *species density* when working with sample-based data (Samways *et al.* 2010). This study will use the term *species richness*, but it should be kept in mind that these values are relative and not an estimate of the total number of species present.

Presence/absence incidence data are considered more reliable than abundance data for ants (Bestelmeyer & Wiens 2001). Since ants are social insects and dung beetle abundance may be highly sensitive to cattle activity (Lobo *et al.* 1998), using abundance data could result in potential errors due to spatial aggregation. Incidence-based coverage estimator (ICE), Chao2, and second order Jackknife estimators (Jack 2) produce minimum biased estimates (Colwell & Coddington 1994; Chazdon *et al.* 1998). These three estimators were calculated using EstimateS (version 9) with replacement, samples being randomized 999 times. Species accumulation curves were plotted per trap for observed dung beetle and ant species respectively for the different biotopes.

Generalized linear mixed models (GLMM) and linear mixed-effects model (LMM) were used where appropriate (with Tukey post-hoc test) to determine whether significant differences existed between biotopes regarding species richness of dung beetles and ants respectively. GLMMs, LMMs and post-hoc tests were conducted in R (v3.0.3; R Development Core Team 2008) statistical package using the 'lme4' and 'multcomp' packages. Biotope was included as a fixed effect in the model and date of sampling (quantified as a categorical variable), elevation and vegetation type as random effects. To check model quality of fit, residual analyses were performed using Pearson's coefficient. None of the models showed overdispersion of their residuals.

Species data for the different biotopes were used in constructing Venn diagrams for the dung beetles and ants respectively. The Jaccard Index (C_j) of similarity was calculated using the formula:

$$J(A, B) = \frac{|A \cap B|}{|A \cup B|}$$

Permutational multivariate analysis of variance (PERMANOVA) was used to determine whether there were significant differences in dung beetle and ant assemblage structures between the different biotopes (Anderson 2001). By partitioning the variability characterized by a multivariate dissimilarity measure, a PERMANOVA produces a pseudo-F ratio that is compared with a permuted null distribution (Anderson *et al.* 2008). Overall PERMANOVA tests were performed, followed by pairwise tests to investigate which sites differ significantly. Unrestricted permutation of raw data was used, which is considered conservative regarding type I error (Anderson *et al.* 2008). Canonical analyses of principle coordinates (CAP) were used to detect trends in similarity in species assemblage data for the different biotopes. A CAP analysis locates an axis through the multivariate cloud of points which best separates predefined groups (Anderson *et al.* 2008). Data used in the PERMANOVA and CAP routines were fourth-root transformed to reduce the weight of common species and Similarity matrices were derived using Bray-Curtis similarity coefficients (Anderson 2001).

Tests of homogeneity of dispersions (PERMDISP) were used to investigate differences in beta-diversity among biotopes. For the purposes of this study, I define this inter-biotope variation here as “species turnover”. Since beta-diversity is defined in terms of variability in species composition (presence/absence), using compositional data in conjunction with certain resemblance measures (in this case the Jaccard index of similarity), allows the test for homogeneity of multivariate dispersion to be directly interpretable as a test for similarity in beta-diversity among groups (Anderson *et al.* 2006). The PRIMER statistical package (version 6, PRIMER-E 2009; Clarke & Gorley 2006), together with the PERMANOVA add-on (Anderson *et al.* 2008), was used to perform these analyses.

Results

Observed and estimated species richness

A total of 56 dung beetle species (21 056 individuals) representing 22 genera from 9 tribes were sampled. Estimates of total species richness for dung beetles ranged between 57.36 ± 2.32 (ICE) and 59.36 ± 3.07 (Jack2) (Table 1). All three species estimators showed similar trends to observed species richness, with the highest number of dung beetle species present in the PA (46 species, 6 834 individuals), followed by the large corridors (45 species, 4 497 individuals), medium corridors (40 species, 3 624 individuals), small corridors (39 species, 3 624 individuals) and lastly plantation blocks (23 species, 2 428 individuals) (see Appendix B for species list).

Table 1 Total species richness, mean species richness (\pm standard deviation) and species estimates (\pm standard deviation) for overall dung beetle data as well as respective biotopes.

Biotope	Species richness	Mean species richness	ICE	Chao2	Jack2
Overall	56	24.78 (\pm 8.20)	57.36 (\pm 2.32)	57.86 (\pm 4.95)	59.36 (\pm 3.07)
Protected area	46	33.19 (\pm 4.06)	47.81 (\pm 2.41)	49.85 (\pm 5.81)	50.07 (\pm 2.41)
Large corridors	45	29.80 (\pm 4.08)	46.31 (\pm 2.41)	47.51 (\pm 4.67)	48.27 (\pm 4)
Medium corridors	40	24.70 (\pm 4.74)	42.49 (\pm 1.7)	44.24 (\pm 4.57)	45.02 (\pm 3.4)
Small corridors	39	24.00 (\pm 4.81)	42.44 (\pm 2.39)	44.22 (\pm 4.43)	44.12 (\pm 4.77)
Plantation blocks	23	12.30 (\pm 3.02)	25.66 (\pm 1.73)	27.05 (\pm 4.03)	27.16 (\pm 3.65)

A total of 64 ant morpho-species (12 538 individuals) were sampled, representing 23 genera from 14 tribes. For ants, total species estimates ranged between 64.34 ± 2.28 (ICE) and 67.45 ± 4.53 (Jack2) (Table 2). Two of the three species estimators corresponded with the observed trends in species richness between biotopes, with the PAs showing the highest number of ant species (45 species, 3 106 individuals), followed by medium corridors (44 species, 2 553 individuals), large corridors (43 species, 3 106 individuals), small corridors (41 species, 3 438 individuals) and lastly plantation blocks (23 species, 560 individuals). The Chao2 estimator differed only in that it estimated medium corridors as having more ant species than the PA.

Table 2 Total species richness, mean species richness (\pm standard deviation) and species estimates (\pm standard deviation) for overall ant data as well as respective biotopes.

Biotope	Species richness	Mean species richness	ICE	Chao2	Jack2
Overall	64	13.10 (\pm 4.23)	64.34 (\pm 2.28)	64.41 (\pm 4.52)	67.45 (\pm 4.53)
Protected area	45	12.10 (\pm 2.64)	44.8 (\pm 4.05)	45.5 (\pm 4.98)	47.41 (\pm 6.41)
Large corridors	43	15.70 (\pm 3.53)	42.87 (\pm 2.41)	43.43 (\pm 3.36)	43.33 (\pm 5.3)
Medium corridors	44	14.60 (\pm 2.22)	43.54 (\pm 4.54)	46.27 (\pm 7.57)	47 (\pm 6.84)
Small corridors	41	14.60 (\pm 2.95)	39.93 (\pm 2.31)	41.72 (\pm 4.51)	42.13 (\pm 4.51)
Plantation blocks	23	12.30 (\pm 3.02)	22.18 (\pm 4.26)	22.04 (\pm 3.95)	23.04 (\pm 5.13)

Species richness differences between biotopes

The PA had the highest mean number of dung beetle species (Table 3, Fig. 2). Large corridors did not differ significantly from the PA in terms of dung beetle species richness. Medium corridors and small corridors were similar in dung beetle species richness, but showed significantly lower species richness than the PA. Plantation blocks showed significantly lower species richness to all other sites ($P < 0.001$).

There was no significant difference in species richness between the different corridor size types and the PA in terms of ant species richness (Table 3, Fig. 3). Plantation blocks showed significantly lower species richness than all other sites ($P < 0.001$).

Table 3 Differences in dung beetle and ant species richness between the different biotopes as determined by generalized linear mixed models and linear mixed-effects model.

Species richness	Dung beetles ^L	Pearson's coefficient: 13.445			
	PA	LC	MC	SC	
LC	1.449				
MC	3.522**	-2.562			
SC	-3.704**	-2.746*	-0.266		
PINE	-8.022***	-8.453***	-6.365***	6.023***	
	Ants ^G	Pearson's coefficient: 0.513			
	PA	LC	MC	SC	
LC	-0.926				
MC	-0.295	-0.632			
SC	0.295	-0.632	0.000		
PINE	-5.165***	-5.979***	-5.427***	5.427***	

PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

L linear mixed-effects models (used for normally distributed variables); G generalized linear mixed models (used for non-normally).

Figures represent z-values determined by Tukey tests.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

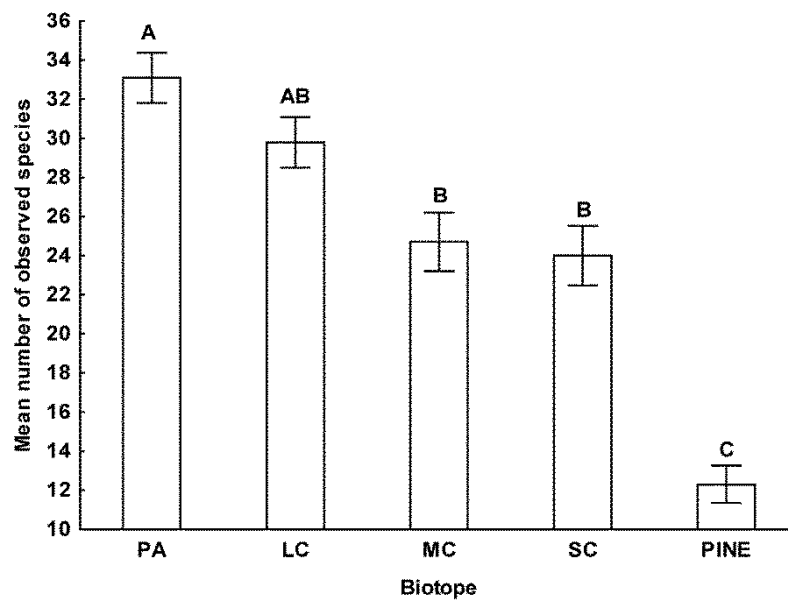


Figure 2 Mean number of observed species richness for dung beetles for each of the different biotopes. Mean (± 1 SE), different letters above the bars represent significantly different means as determined by Tukey tests (5% level). PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

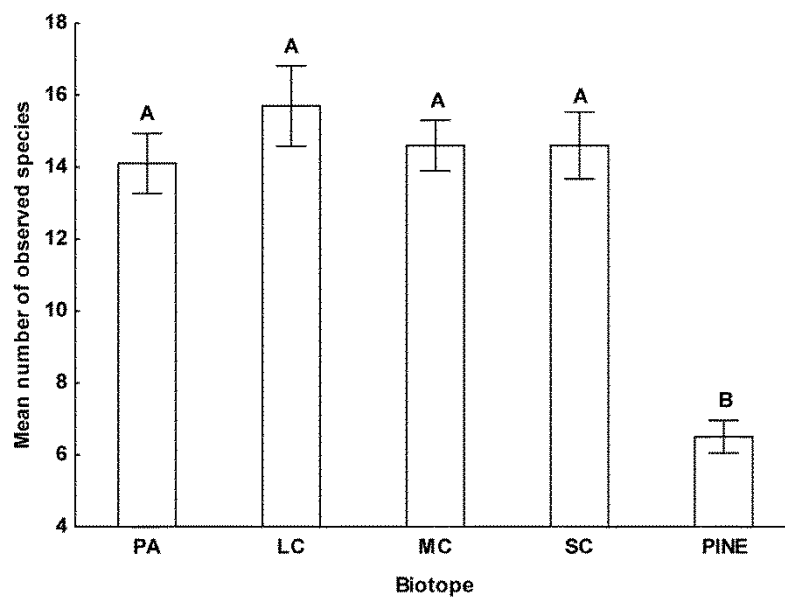


Figure 3 Mean number of observed species richness for ant species for each of the different biotopes. Mean (± 1 SE), with different letters above the bars representing significantly different means as determined by Tukey tests (5% level). PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

Venn diagrams

The Jaccard index of similarity (C_j) was higher between corridors and the PA than between corridors and the plantation blocks for both taxa. Twenty-three (41.07%) dung beetle species were sampled in all sites (Fig. 4). Grassland habitats (corridors and the PA) contained 100% of all dung beetle species sampled. The PA and large corridors each contained four (7.14%) unique dung beetle species, medium corridors contained one (1.79%), and small corridors and plantation blocks both contained no unique dung beetle species. The Jaccard index of similarity was highest between small and medium corridors ($C_j = 0.40$). Plantation blocks had greater similarity to medium and small corridors ($C_j = 0.31$ and 0.30) than to large corridors and the PA ($C_j = 0.28$ and 0.27). Dung beetles in the PA were more similar to those present in the small and medium corridors ($C_j = 0.35$ each), than to those in the large corridors ($C_j = 0.34$).

Twenty (35.71%) ant species were collected in all sites at least once. The PA, medium corridors and small corridors each contained five (8.93%) unique ant species, while the large corridors contained three (5.36%) and the plantation blocks one (1.79%) (Fig. 5). The Jaccard index of similarity was highest between small and medium corridors ($C_j = 0.38$). Ant species present in plantation blocks were most similar to those in small corridors ($C_j = 0.30$), followed by those in either the PA or large corridors ($C_j = 0.29$ each), and least to those present in medium corridors ($C_j = 0.28$). Ant species in the PA were more similar to those present in large corridors ($C_j = 0.35$), than to those present in medium or small corridors ($C_j = 0.33$ each).

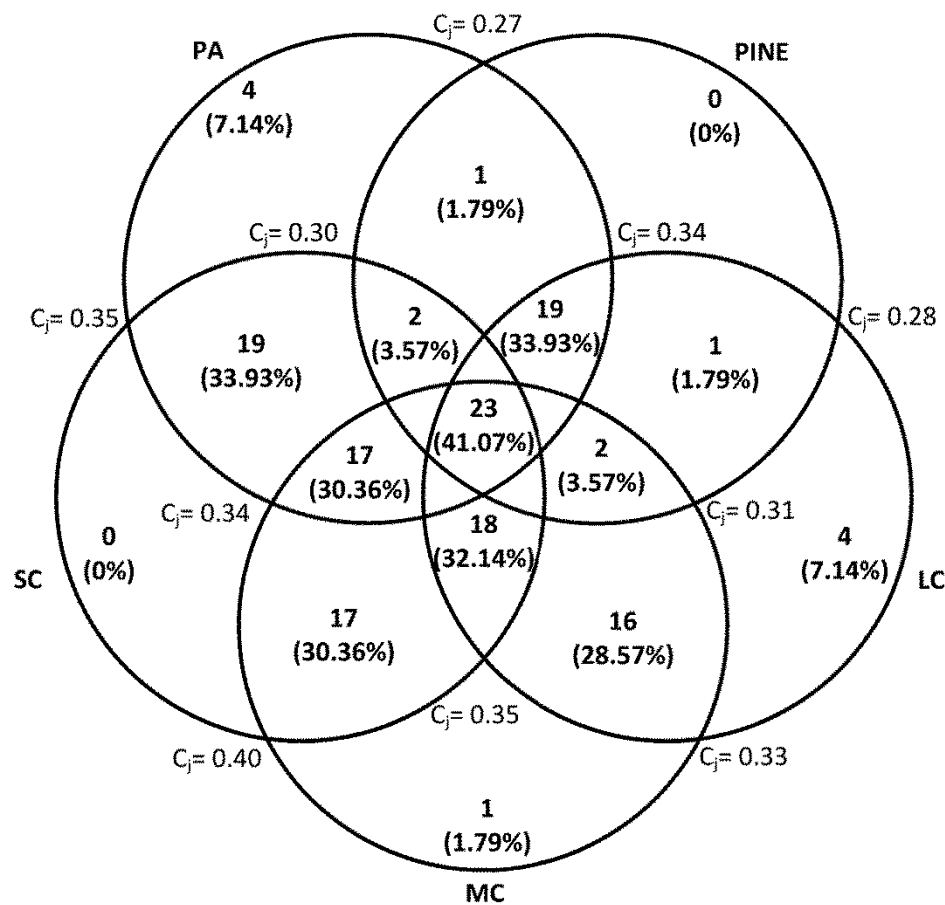


Figure 4 Venn diagram depicting shared species of dung beetles between the different biotopes. Percentages are of total number of species sampled in all habitat types. Jaccard Index (C_j) of similarity is shown between each pair of biotopes. PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

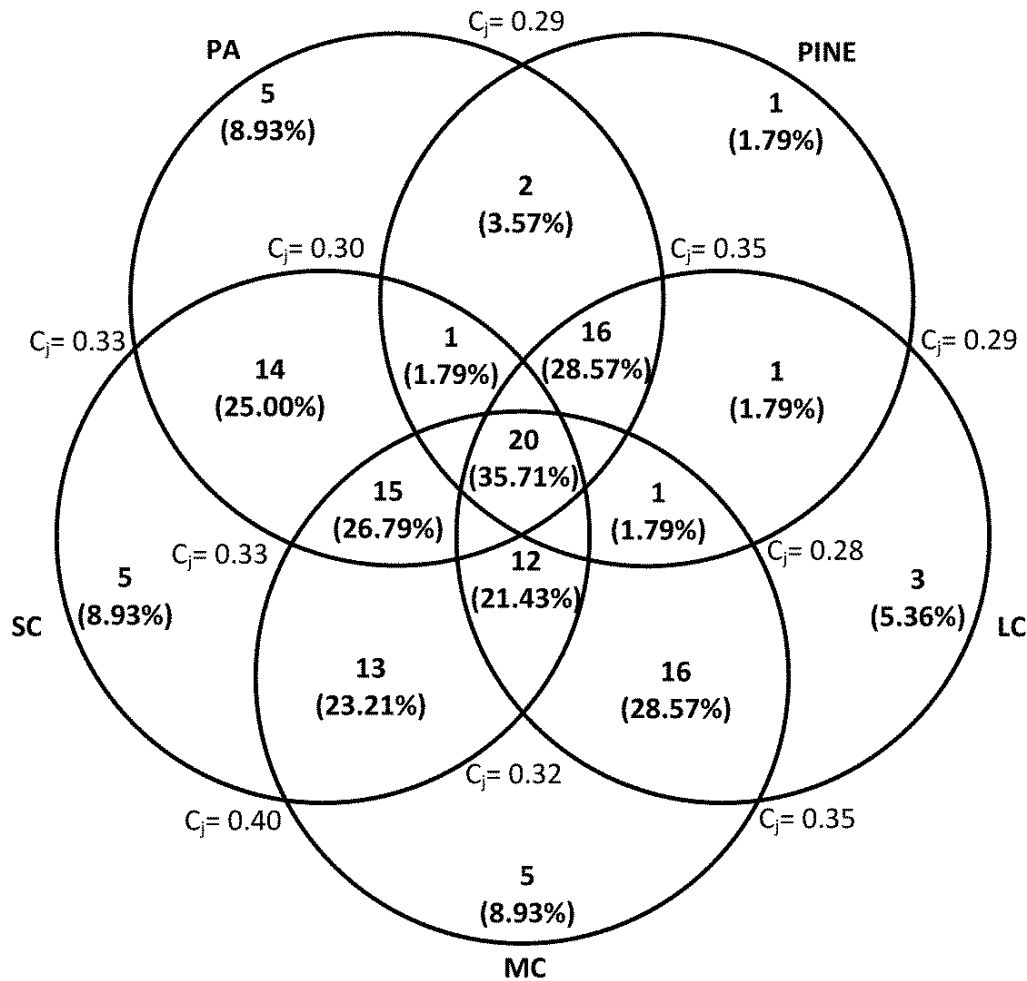


Figure 5 Venn diagram depicting shared species of ants between the different biotopes. Percentages are of total number of species sampled in all habitat types. Jaccard Index (C_j) of similarity is shown between each pair of biotopes. PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

Differences in assemblages between biotopes

Overall PERMANOVA tests indicated significant differences for dung beetle ($F = 8.67$, $P < 0.001$) and ant composition among biotopes ($F = 4.80$, $P < 0.001$). Pairwise t-tests indicated that dung beetle composition in the PA and plantation blocks differed significantly from each other and all other biotopes ($P < 0.001$, Table 4). Corridors did not differ markedly from each other in terms of dung beetle assemblage composition. Ant assemblages in plantation blocks differed significantly from all other biotopes ($P < 0.001$). The PA showed no significant difference from large corridors, a significant difference from medium corridors ($P < 0.01$) and no difference from small corridors. There was no significant difference among the different corridor types in ant assemblage composition.

Table 4 Differences in dung beetle and ant assemblage compositions between the different biotopes as determined by permutational multivariate analysis of variance.

	Dung beetles			
	PA	LC	MC	SC
LC	3.732***			
MC	3.253***	1.392		
SC	3.498***	1.361	0.896	
PINE	4.461***	3.218***	3.036***	2.774***
	Ants			
	PA	LC	MC	SC
LC	1.239			
MC	1.518**	1.171		
SC	1.194	1.214	0.829	
PINE	3.609***	3.122***	3.066***	3.057***

PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

Figures represent t-values determined by pair-wise tests. Number of permutations 999.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

CAP analyses indicated that dung beetle assemblage data showed a lower misclassification error (28%, $m = 15$) than the ant assemblage data (54%, $m = 5$) (Table 5, Fig. 6). Dung beetle assemblage data showed a clear separation of the plantation blocks and the PA from the other biotopes (100% successful allocations each). Large corridors and medium corridors each showed 60% correct allocations, while small corridors only showed 40%. For ant assemblage data, plantation blocks showed the highest percentage successful allocations (100%), followed by the PA (50%). Corridor allocations showed a low percentage correctness, with small and medium corridors being the highest (30% each) and large corridors the lowest (20%).

Table 5 Cross validation of observed groups through 'leave-one-out' allocation in the canonical analyses of principle coordinates.

	Biotope	% correct
Dung beetles	PA	100
Total correct: 72%	LC	60
Misclassification error: 28%	MC	60
M: 15	SC	40
	PINE	100
Ants	PA	50
Total correct: 46%	LC	20
Misclassification: 54%	MC	30
M: 5	SC	30
	PINE	100

Biotope abbreviations: PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

m: number of PCO axes investigated

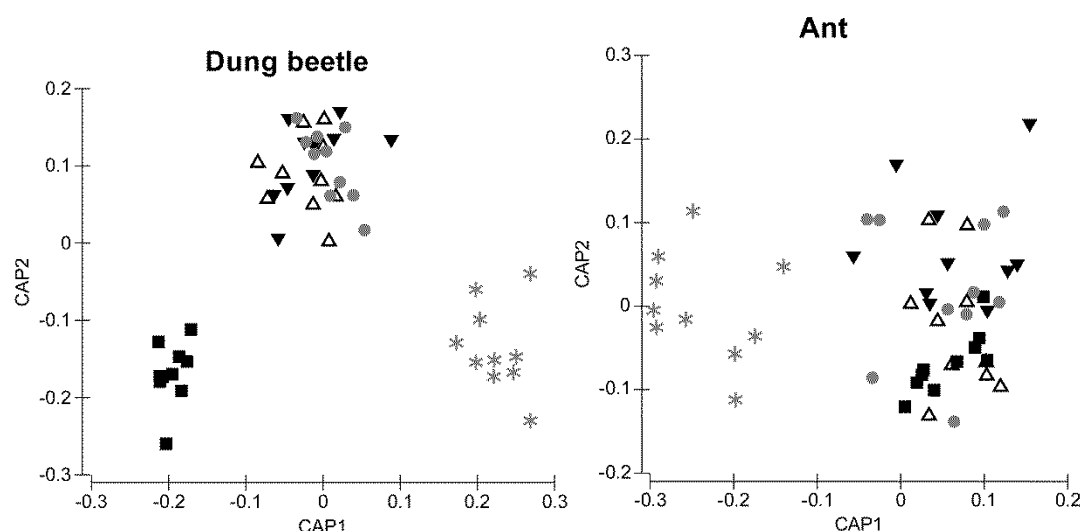


Figure 6 Canonical analysis of principle coordinates ordination plot of dung beetle assemblage data and ant assemblage data. *Squares* represent the protected area, *open triangles* represent large corridors, *black triangles* represent medium corridors, *circles* represent small corridors, and *stars* represent plantation blocks.

Species turnover within biotope

Dung beetles in the PA showed significantly lower species turnover compared to all other biotopes ($P < 0.001$), except large corridors (Table 6, Fig. 7). Medium and small corridors did not show significant differences in dung beetle species turnover from plantation blocks, while large corridors showed significantly lower species turnover compared to plantation blocks ($P < 0.05$). Ants showed no significant difference in species turnover between the different biotopes.

Table 6

Results of the tests of homogeneity of dispersion for dung beetle and ant species data indicating differences in species turnover among the different biotopes.

	Dung beetles			
	PA	LC	MC	SC
LC	1.921			
MC	5.950***	2.204		
SC	4.021***	1.706	0.119	
PINE	5.906***	3.350*	1.903	1.684
	Ants			
	PA	LC	MC	SC
LC	0.15779			
MC	0.95087	0.6896		
SC	0.57089	0.69225	1.5404	
PINE	0.10672	0.22227	0.74858	0.32882

PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

Figures represent the t-values determined by pair-wise comparisons. Number of permutations: 999.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

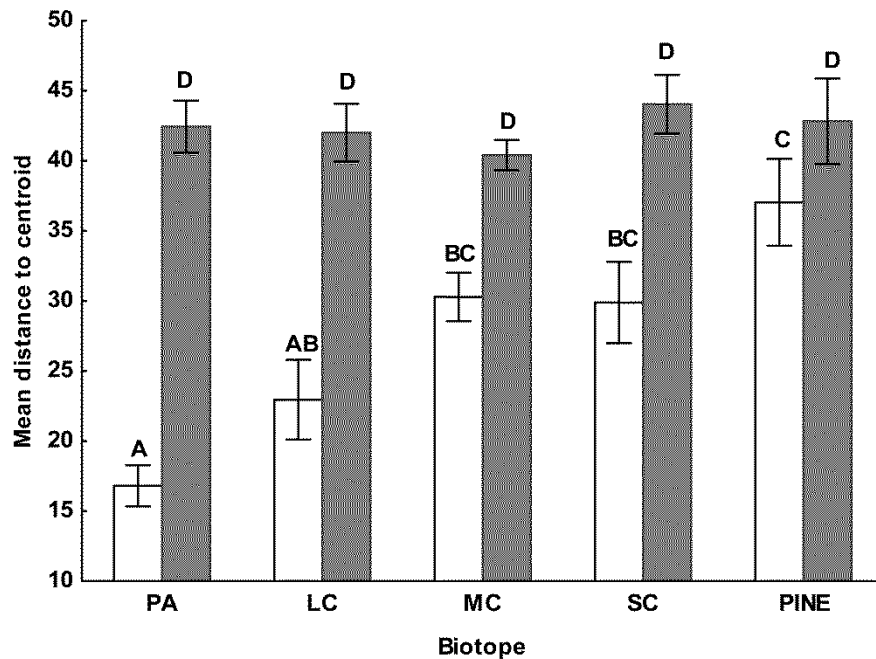


Figure 7 Comparison of dung beetle (open bars) and ant (grey bars) species turnover among the different biotopes. Mean (± 1 SE) with different letters above the bars representing significantly different means (5% level). PA, protected area; LC, large corridors; MC, medium corridors; SC, small corridors; PINE, plantation blocks.

Discussion

Arthropod species richness

Ecosystem processes that can degrade as a result of fragmentation include fragment resistance to species invasion (Collinge 2009) as well as to external disturbances such as hunting and fire (Cochrane & Laurance 2002). By decreasing population sizes, habitat loss should increase the influence of stochastic processes and increase extinction rates, leading to decreased alpha diversity in fragmented landscapes (Wilcox & Murphy 1985). Here, I showed that there were significantly fewer dung beetles at sites subjected to strong edge effects (<120 m wide) compared to the PA. This contrasts with previous work in this area where higher dung beetle diversity in grassland corridors were found along plantation edges (Pryke & Samways 2012). This preference of beetles for edge zones may be due to the high activity of small (Wilson *et al.* 2010) and large (Pryke & Samways 2012) mammals along plantation edges. It should be noted that trapping methods differed between the present study and that of Pryke and Samways (2012) (i.e. baited dung traps versus pitfall traps as well as slightly different sampling periods), and that while I took into account the value of the whole

corridor, Pryke and Samways (2012) measured the edge effect itself within large corridors or at PA boundaries.

While dung beetle species data was found to reflect these expectations, ant species richness, on the other hand, showed no significant differences between grassland corridors of different sizes or the PA. Pitfall catches may be biased by factors such as ground relief as well as species specific differences in locomotion and foraging behaviour, trap avoidance, self-rescue capability and foraging strategy (Greenslade 1973; Marsh 1984; Seifert 1990; Andersen 1997a; Longino 2000; Laeger & Schultz 2005). Yet despite the limitation that these factors place on the ability of pitfall sampling to represent accurate species data, they may also produce more ecologically meaningful information on ant assemblages from the point of view that pitfall traps have roughly equal trappability across different ecosystem types even though not to all species (see Schlick-Steiner *et al.* 2006). Even though pitfall trapping is known to exhibit biases when used to estimate population parameters (Bestelmeyer *et al.* 2000; James 2004), it can be considered useful for comparative studies (Samways 1990; Southwood & Hendersen 2000). Although using a combination of methods for capturing ants (e.g. pitfall trapping along with baiting) may improve the efficiency of sampling and make data more representative of the community, there is no reason why pitfall trapping should not illustrate relative differences between sites in this study, especially considering the homogenous nature of the vegetation.

Work investigating the effects of fragmentation on ant species diversity and composition reports contrasting results. Most studies conducted in tropical forests show a decline in species richness and nest density within fragments relative to continuous habitat (Carvalho & Vasconcelos 1999; Brühl *et al.* 2003), while other tropical forest studies found that edges host higher ant species richness than habitat interiors (Dejean & Gibernau 2000; Vasconcelos 2001). In an urban landscape matrix in Australia, Gibb and Hochuli (2002) found ants in small woodland fragments ($\leq 4 \text{ km}^2$) to contain greater species richness and different ant assemblages to larger woodland fragments ($\geq 80 \text{ km}^2$). This variety of findings may be due to ant responses reflecting complex interactions with other biotic and abiotic factors accompanying fragmentation beyond the scope of most studies (Underwood & Fisher 2006). Previous work on tropical ant fauna has attributed ant distribution patterns to three closely linked underlying factors, namely habitat preference of ants, competition and the influence of weather and climate (e.g. Greenslade 1971). Interaction among species and species exclusion by dominant ants is continuously cited to explain ant distribution patterns. According to Room (1971), the mosaic concept is defined as the distribution of dominant ant species in patches in such a way that their territories do not overlap. Although not tested by the present study, intraspecific

competition may also play an important role in structuring ant assemblages (e.g. the presence of wood ants has been found to negatively impact the ability of carabid beetles to occupy certain habitats (Thiele 1977; Hawes *et al.* 2002)). The results of the present study indicate that ants are unresponsive to corridor width across this landscape, or have been conserved adequately by all the corridors here.

Arthropod species composition

In regions where habitat fragmentation occurred a long time ago, only those species able to cope with fragmented landscapes and thus having a lower susceptibility to edge effects have survived (Balmford 1996). The difference in dung beetle assemblage structure between the PA and the grassland corridors here may be a long term response to fragmentation. In a 800 ha reserve in Costa Rica, a 35 year study on dung beetles revealed a systematic change in species composition, attributed to a loss of habitat in the surrounding landscape and the progressive isolation of the reserve over time (Escobar *et al.* 2008).

Apart from the influence of fragmentation in shaping dung beetle assemblages, current and historic differences in grazing management between the PA and the grassland corridor sites could have contributed to the conspicuous differences in dung beetle assemblage structure. In France, 23 years of grazing abandonment resulted in no change in dung beetle species richness but an evident change in assemblage structure (Fadda *et al.* 2008). While some studies have found dung beetles to utilize a wide variety of faecal matter (Janzen 1983; Kirk & Ridsdill-Smith 1986; Lumaret & Kirk 1987; Lumaret *et al.* 1992), others have found certain species to show a definite local sensitivity to the type and amount of dung resources (Fincher *et al.* 1970; Gittings & Giller 1998; Barbaro *et al.* 1999; Finn & Giller 2002; Loboet *et al.* 2006). Not only do the grassland corridors sometimes experience grazing at a much higher density than which would occur naturally (Samways *et al.* 2010), domestic cattle are the major dung producing ruminants in this system, compared to various natural producers present in the PA. The reduced diversity of dung resources in the grassland corridors could have led to a divergence in dung beetle assemblage structure.

The present study used pig dung as bait, which excludes possible influences from a similar dung source locally available, but it is also limiting in the species it will attract. There may be a number of specialized dung beetle species not sampled since they may not be attracted to the specific bait type used. A more comprehensive survey of dung beetles in this study area should involve using a variety of dung types (including natural variants) as bait in all sites sampled. Nevertheless, some of the same issues arise with these traps as with pitfall traps: methodology was constant and while there may

have been differential responses between species, any differences in assemblages across the landscape are likely attributable to the influence of the various biotopes.

In general, it seems that ants as a taxon are robust to disturbances (Parr *et al.* 2004; Underwood & Fisher 2006). Differences in ant species composition assemblage structure may be more useful in indicating disturbance effects (Fleishman *et al.* 2005). Some studies on the effect of fragmentation on ants found no differences in ant species richness, but did detect significant influences on ant assemblage structure, especially as a result of edge effects (Suarez & Bolger 1998; Carvalho & Vasconcelos 1999; Vasconcelos 2001; Debuse *et al.* 2007; Brandão *et al.* 2011). Edge effects from soy production in the Brazilian Cerrado (savanna) found changes in ant species composition, but not species richness (Brandão *et al.* 2011). Similarly, ant composition has been shown to respond to disturbances such as grazing and fire, with species richness being less responsive (Kotze & Samways 1999; Parr *et al.* 2004). Another study in KwaZulu-Natal, South Africa, on the influence of varying degrees of disturbance (fire and grazing) on arthropod assemblages in naturally fragmented afro-montane forests and the surrounding grassland matrix, found degree of disturbance influenced ant species composition but not species richness (Kotze & Samways 1999).

Here I found no differences in ant assemblage structures between the grassland corridors of different sizes. Previous work on edge effects on ants in a nearby geographical area estimated a 25 m edge zone to road boundaries (Samways *et al.* 1997) and to mesophytic forest urban boundaries (Ivanov & Keiper 2010). In the same area as the present study, Pryke and Samways (2012) found a much smaller edge zone for ants (of 8 m) into grassland corridors. Relative to the 30 m edge zone found for other taxa in this area, this smaller edge zone for ants may make them more resilient to fragmentation.

Another reason why there may have been no detectable difference in ant and dung beetle assemblages present between different sized grassland corridors is that edge effects may stretch much farther into the grasslands than assumed. All sites, even those in the large corridors, may be subject to edge effects. Bieringer *et al.* (2013) studied the influence of plantation block edges on invertebrates in a dry grassland in Austria and conclude that edge influences reach more than 200 m into grasslands. In their study of edge effects on beetles in New Zealand forests, Ewers and Didham (2008) conclude that edge effects function at a kilometre scale. It is possible that considerably larger scale edge effects beyond the influence of the local scale 30 m edge zone could have resulted in the present differences in assemblage structures between the PA and corridors.

The present study did however find a difference in ant assemblages between medium corridors and the PA, but not between small corridors or large corridors and the PA. Large corridors may be similar to the PA due to reduced disturbances associated with fragmentation (e.g. isolation and edge effects). Reasons for similar ant species composition between the small corridors and the PA are uncertain. A possible influence could be due to difference in burning regimes between the different sized corridors. Long term differences in burning regimes have been found to influence ant species composition (but not species richness) in an African Savanna (Parr *et al.* 2004). These differences were only evident for burned versus unburned areas, while the specifics of the burning regimes had little influence on ant assemblage structure. In the system here ants appeared highly resilient and resistant to burning. Parr *et al.* (2004) link changes in ant assemblages to the intensity of differences in habitat cover and structure before and after burning. Other studies investigating the response of ant assemblages to burning have found habitat type (Farji-Brener *et al.* 2002; Ratchford *et al.* 2005; Barrow *et al.* 2007), site aridity (Arnan *et al.* 2006) and post fire habitat modification to be important factors determining the degree of response (Parr *et al.* 2004; Barrow *et al.* 2007). In the present study area, fire management is practiced to simulate natural processes (Samways *et al.* 2010) and maintain fire breaks. The grassland corridors in the study area are burned annually, while the PA is burned biannually. Since burning smaller corridors poses a greater financial risk, controlled grazing and mowing has been suggested as alternative maintenance methods (Samways *et al.* 2010). Smaller corridors may experience less burning than larger corridors and the effect from this disturbance in smaller corridors may be closer to that of the PA. The combined effects of fragmentation as well as differences in burning regimes may be why medium corridors differ more in ant species composition in the PA compared to large and small corridors.

Species turnover within biotope

Ants did not show any differences in species turnover among the different biotopes. Even in the PA, where there is limited influence from fragmentation, ants exhibited beta diversity comparable to that of corridors. The absence of differences in ant species turnover among the different biotopes may either be due to ants exhibiting high heterogeneity in species composition at a very small spatial scale or the spatial arrangement of study sites.

Considering the small size of corridors relative to the estimated size of the edge effect in this study, a reduction in corridor size translates to smaller grassland fragments (i.e. an increase in fragmentation). As expected, with decreasing corridor size, dung beetles showed an increase in species turnover (Loreau 2000; Chase 2003). Pardini *et al.* (2005) found decreasing fragment sizes of

Atlantic forest to result in an increase in spatial variability in small mammal community composition. Pardini *et al.* (2005) suggest that their results are consistent with the concept that fragmented landscapes are hyper-dynamic, i.e. a fragment experiences increased range and/or frequency of the dynamics of most ecological processes (Laurance 2002). Increased hyper-dynamism (an increase in the frequency or amplitude of population, community and landscape dynamics in fragmented habitats (Laurance 2002)) among smaller habitat fragments are considered to be related to an increased vulnerability to 1) stochastic processes and 2) influences coming from the neighboring altered areas, i.e. to increased environmental heterogeneity (Laurance 2002). Although several studies have found an increase in species turnover associated with an increase in environmental heterogeneity caused by fragmentation (Didham *et al.* 1998; Lomolino & Perault 2000; Pardini 2004), higher species turnover among dung beetles in the present study is probably due to other factors, such as isolation.

Species turnover for dung beetles was highest for plantation block sites. The universal structure of this stand throughout the study area removes the role of the matrix in increasing environmental heterogeneity and increasing hyper-dynamism. For dung beetles, less open habitat may restrict dispersal of dung odour cues (Romero-Alcaez & Acila 2000). The high species turnover in plantation blocks could be due, at least partly, to a combined effect of isolation and chance sampling events. In this way, the increase in species turnover associated with decreasing corridor size may also demonstrate an increase in isolation. But since different dung beetle species can show considerable differences in movement patterns, one cannot make sweeping generalizations about dung beetles as a group regarding the dynamics of real world populations (Roslin 2000). Variation in interspecific movement patterns will give rise to a mixture of different spatial population structures, as has been observed for other insects (e.g. Nieminen 1996; Nieminen & Hanski 1998). Another possibility is that these observations are sampling effects due to the distances between sites.

The value of smaller corridors

Species composition is not an entity with its own ecological behaviour. It is comprised of the behaviour of numerous individuals belonging to different species. The present study found dung beetle and ant assemblages to show very different responses to grassland corridor size. While dung beetle species richness was found to decrease with corridors size, corridors of <120 m wide contained ant species richness comparable to that found in larger corridors and the PA. There were more unique ant species present in medium and small corridors compared to large corridors. Ants

appeared more resilient to fragmentation than dung beetles and for them at least smaller corridors may possibly enhance the effectiveness of long term conservation through ENs.

In a study on ant diversity in remnants versus nature reserves in the Cape Floristic Region, Boonzaaier (2006) found remnants to be comparable in overall ant species richness to reserve areas. But Boonzaaier (2006) did not find this to be the case for each of the remnants in the study. Therefore, even though semi natural areas seem promising in contributing to conservation, the variability in disturbance histories and high temporal turnover in species composition prevents assumptions about specific areas and taxa.

Dung beetle species richness in corridors <120 m were not comparable to that of the PA, but still contained many species. Regardless of the fact that species richness of dung beetles and ants in small corridors was comparable to that of larger corridors, community composition differed greatly between the grassland corridors and the PA. Certain species may be highly sensitive to patch area and edge effects and require large contiguous area of natural habitat to avoid high extinction probabilities (Tscharnkte *et al.* 2012). Effective conservation policies require considering these frequently endemic and often flagship species (Sodhi *et al.* 2007; Collinge 2009). Furthermore, smaller corridors may also be temporarily more variable (Hinsley *et al.* 1995; Schmiegelow *et al.* 1997; Terborgh *et al.* 1997), and small, isolated patches would not necessarily guarantee the persistence of species. In the short term, extensively linked systems of core habitats are not essential to the survival of all species, and the island biogeography principle that extinction risk decreases as habitat size increases still holds for a large number of species (Benett & Mulongoy 2006).

Numerous factors may influence the utilization of a grassland fragment by a particular insect species. Fragment preference of butterflies has been found to depend on the level of disturbance within the fragment, fragment size (or corridor width) and species specific characteristics (e.g. mobility and distribution) (Pryke & Samways 2001, 2003). The fact that here, small and medium corridors share more dung beetle and ant species with plantation blocks than do large corridors indicates higher proportions of generalists present in these areas. Effectively, smaller corridors may function as early successional habitats, as has also been found by Bazelet and Samways (2011) for grasshoppers. A number of dung beetle species sampled here in smaller corridors may only be using these areas to feed or move across the landscape. Thus, for many dung beetle species in the plantation matrix, smaller corridors may greatly reduce isolation between large habitat patches. But at a larger scale, dung beetle populations may be more isolated than it would appear. The potential importance of grazing management in shaping dung beetle assemblage structures echoes the work of Bazelet &

Samways (2011) where grassland management was 2-5 times more influential than design in shaping grasshopper assemblages. If grazing management is a key driver in the difference in dung beetle species composition between PA and grassland corridors, fragmentation of the landscape may be more severe for dung beetles than the physical land transformations we as humans can perceive. Dung beetles may not only experience fragmentation from land-use changes that result in distinct habitat transformation, but also effects from more obscure influences such as differences in grazing management regimes. This may be especially true for KwaZulu-Natal, where cattle have significant cultural value and which is South Africa's second highest beef producing province (DAFF 2013).

The effectiveness of conservation management has been found to be highest in landscapes dominated by monocultures (Tscharntke *et al.* 2005; Rundlöf & Smith 2006; Batáry *et al.* 2010). Even though I show that small corridors have biodiversity values as conduits and even as habitat for some taxa, caution should be applied when applying this information to other land transformation scenarios. Nevertheless, considering the important ecological roles played by ants, their effective conservation within smaller corridors may have far reaching ecological benefits within this production landscape.

References

- Aars, J., and R. A. Ims. 1999. The effect of habitat corridors on rates of transfer and interbreeding between vole demes. *Ecology* 80:1648-1655.
- Almeida, S., J. Louzada, C. Sperber, and J. Barlow. 2011. Subtle land-use change and tropical biodiversity: dung beetle communities in cerrado grasslands and exotic pastures. *Biotropica* 43:704-710.
- Andersen, A. N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16:347-357.
- Andersen, A. N. 1995. Classification of Australian ant communities based on functional groups which parallel plant life forms in relation to stress disturbance. *Journal of Biogeography* 22:15-29.
- Andersen, A. N. 1997a. Functional groups and patterns of organisation in North American ant communities: a comparison with Australia. *Journal of Biogeography* 24:433-460.

- Andersen, A. N. 1997b. Using ants as bioindicators: multiscale issues in ant community ecology. *Conservation Ecology* [online] 1:8.
- Andersen, A. N., and G. P. Sparling. 1997. Ants as indicators of restoration success: relationship with soil microbial biomass in the Australian tropics. *Restoration Ecology* 7:109-114.
- Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd, Plymouth, UK.
- Anderson, M. J., K. E. Ellingsen and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683-693.
- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19-28.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.
- Andresen, E. 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography* 26:87-97.
- Armstrong, A. J., and H. J. van Hensbergen. 1996. Impacts of afforestation with pines on assemblages of native biota in South Africa. *South African Forestry Journal* 175:35-42.
- Arnan, X., A. Rodrigo, and J. Retana. 2006. Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. *Journal of Biogeography* 33:1246-1258.
- Baguette, M., S. Blanchet, D. Legrand, V. M. Stevens, and C. Turlure. 2013. Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews* 88:310-326.
- Balmford, A. 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution* 11:193-196.
- Barbaro, E., C. Palestini, and A. Rolando. 1999. Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeidae). *Journal of Insect Conservation* 3:75-84.
- Barrow, L., C. L. Parr, and J. L. Kohen. 2007. Habitat type influences fire resilience of ant assemblages in the semi-arid tropics of Northern Australia. *Journal of Arid Environments* 69:80-95.

Batáry, P., T. Matthiesen, and T. Tschardt. 2010. Landscape-moderated importance of hedges in conserving farmland bird diversity of organic vs. conventional croplands and grasslands. *Biological Conservation* 143:2020-2027.

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

Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241-1252.

Benett, G., and K. J. Mulongoy. 2006. Review of experience with Ecological Networks, Corridors and Buffer Zones. Secretariat of the Convention on Biological Diversity, Montreal, Technical Series, No. 23, 100 pages.

Bestelmeyer, B. J., and J. A. Wiens. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecological Applications* 6:1225-1240.

Bestelmeyer, B. T., and J. A. Wiens. 2001. Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. *Ecological Society of America* 6:1225-1240.

Bestelmeyer, B. T., D. Agosti, L. Alonso, C. R. Brandao, W. L. Jr. Brown, J. H. C. Delabie, and R. Silvestre. 2000. Field techniques for the study of grounddwelling ants: an overview, description, and evaluation. In D. Agosti, J. Majer, L. Alonso, and T. R. Schultz (editors). *Ants: Standard methods for measuring and monitoring biodiversity*. Smithsonian Institution, Washington. Pages 122-144.

Bieringer, G., and K. P. Zulka. 2003. Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblages of an adjacent dry grassland. *Biodiversity and Conservation* 12:1481-1495.

Bieringer, G., K. P. Zulka, N. Milasowsky, and N. Sauberer. 2013. Edge effect of a pine plantation reduces dry grassland invertebrate species richness. *Biodiversity and Conservation* 22:2269-2283.

Bohac, J. 1999. Staphylinid beetles as bioindicators. *Agriculture, Ecosystems and Environment* 74:357-372.

Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. *Ecological Applications* 10:1230-1248.

- Boonzaaij, C. 2006. Conservation in human-influenced areas: epigaeic arthropods in the Cape Floristic Region lowlands. MSc thesis. University of Stellenbosch, Stellenbosch, South Africa.
- Brandão, C. R. F., R. R. Silva, and R. M. Fietosa. 2011. Cerrado ground-dwelling ants (Hymenoptera: Formicidae) as indicators of edge effects. *Zoologia* 28:379-387.
- Brühl, C. A., T. Eltz, and K. E. Linsenmair. 2003. Size does matter - effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. *Biodiversity and Conservation* 12:1371-89.
- Carvalho, K. S., and H. L. Vasconcelos. 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biological Conservation* 91:151-157.
- Chase, J. M. 2003. Community assembly: when should history matter? *Oecologia* 136:489-498.
- Chazdon, R. L., R. K. Colwell, and M. R. Guariguata. 1998. Species richness of woody regeneration in primary and secondary rainforests of northeastern Costa Rica. In F. Dallmeier, and J. A. Comiskey (editors). *Forest biodiversity research, monitoring and modeling: conceptual background and old World cases studies*. Pathenon, Paris.
- Clarke, K. R., and R. M. Warwick. 2001. *Change In Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd Edition. PRIMER-E Ltd, Plymouth.
- Clarke, K. R., and R. N. Gorley. 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E Ltd, Plymouth.
- Cochrane, M. A., and W. F. Laurance. 2002. Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology* 18:311-325.
- Collinge, S. K. 2009. *Ecology of Fragmented Landscapes*. The John Hopkins University Press, Baltimore.
- Colwell, R. K, and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions B* 345:101-118.
- Cronin, J. T. 2007. From population sources to sieves: the matrix alters host-parasitoid source-sink structure. *Ecology* 88:2966-2976.
- Culver, C. D., and A. J. Beattie. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. *Ecology* 64:485-492.

- Damschen, E. I., N. M. Haddad, J. L. Orrock, J. J. Tewksbury, and D. J. Levey. 2006. Corridors increase plant species richness at large scales. *Science* 313:1284-1286.
- Davis, A. L. V., C. H. Scholtz, and C. Deschodt. 2008. Multi-scale determinants of dung beetle assemblage structure across abiotic gradients of the Kalahari-Nama Karoo ecotone, South Africa. *Journal of Biogeography* 35:1465-1480.
- Davis, A. J., Holloway, J. D., H. Huijbregts, J. Krikken, A. H. Kirk-Spriggs, and S. L. Sutton 2001. Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology* 38:593-616.
- DAFF (Department: Agriculture, Forestry and Fisheries). 2013. Trends in the Agricultural Sector. ISSN 1025-5028. Pretoria.
- Debusse, V. J., J. King, and A. P. N. House. 2007. Effect of fragmentation, habitat loss and within habitat characteristics on ant assemblages in semi-arid woodlands of eastern Australia. *Landscape Ecology* 22:731-745.
- Dejean, A., and M. Gibernau. 2000. A rainforest ant mosaic: the edge effect (Hymenoptera: Formicidae). *Sociobiology* 35:385-401.
- Didham, R. K., P. M. Hammond, J. H. Lawton, P. Eggleton, and N. E. Stork. 1988. Beetle species response to tropical forest fragmentation. *Ecological Monographs* 68:295-323.
- Doube, B. M. 1983. The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. *Bulletin for Entomological Research* 73:357-371.
- Dudley, N., D. Baldock, R. Nasi, and S. Stolton. 2005. Measuring biodiversity and sustainable management in forest and agricultural landscapes. *Philosophical Transactions of the Royal Society of London B* 360:457-470.
- Dunning, J. B. Jr., J. R. Borgella, K. Clements, and G. K. Meffe. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9:542-550.
- Escobar, F., G. Halffter, A. Solís, V. Halffter, and D. Navarrete. 2008. Temporal shifts in dung beetle community structure within a protected area of tropical wet forest: a 35-year study and its implications for long-term conservation. *Journal of Applied Ecology* 45:1584-1592.

- Ewers, R. M., and R. K. Didham. 2008. Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences of the United States of America* 105:5426-5429.
- Fadda, S., F. Henry, J. Orgeas, P. Ponel, E. Buisson, T. Dutoit. 2008. Consequences of the cessation of 3000 years of grazing on dry Mediterranean grassland ground-active beetle assemblages. *Comptes Rendus Biologies* 331:532-546.
- Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. *Ecology* 66:1762-1768.
- Farina, A. 2000. *Landscape Ecology in Action*. Kluwer Academic Publishers, Dordrecht.
- Farji-Brener, A. G., J. C. Corley, and J. Bettinelli. 2002. The effects of fire on ant communities in north-western Patagonia: the importance of habitat structure and regional context. *Diversity and Distributions* 8:235-243.
- Fincher, G. T., T. B. Stewart, and R. Davis. 1970. Attraction of coprophagous beetles to faeces of various animals. *Journal of Parasitology* 56:378-383.
- Finn, J. A., and P. S. Giller. 2002. Experimental investigations of colonization by north temperate dung beetles of different types of domestic herbivore dung. *Applied Soil Ecology* 20:1-13.
- Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment* 4:80-86.
- Fleishman, E., R. F. Noss, and B. R. Noon. 2005. Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators* 6:543-553.
- French, K., and R. E. Major. 2001. Effect of an exotic *Acacia* (Fabaceae) on ant assemblages in South African fynbos. *Austral Ecology* 26:303-310.
- Gardner, T. A., M. I. M. Hernández, J. Barlow, and C. A. Peres. 2007. Understanding the biodiversity consequences of habitat change, the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology* 45:883-893.
- Gaston, K. J., K. Charman, S. F. Jackson, P. R. Armsworth, A. Bonn, R. A. Briers, C. S. Q. Callaghan, R. Catchpole, J. Hopkins, W. E. Kunin, J. Latham, P. Opdam, R. Stoneman, D. A. Stroud, and R. Tratt.

2006. The ecological effectiveness of protected areas: The United Kingdom. *Biological Conservation* 132:76-87.

Gaston, K. J., and J. I. Spicer. 2004. *Biodiversity: an Introduction*. Blackwell Publishing Company, Oxford.

Gaston, K. J., S. F. Jackson, A. Nagy, L. Cantú-Salazar, and M. Johnson. 2008. Protected areas in Europe: principle and practice. *Annals of the New York Academy of Sciences* 1134:97-119.

Gibb, H., and D. F. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. *Biological Conservation* 106:91-100.

Gittings, T., and P. S. Giller. 1998. Resource quality and the colonization and succession of coprophagous dung beetles. *Ecography* 21:581-592.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* 281:2045-2047.

Goodman, P. 2003. Assessing management effectiveness and setting priorities in protected areas in KwaZulu-Natal. *BioScience* 53:843-851.

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

Greenslade, P. J. M. 1973. Sampling ants with pitfall traps: digging-in effects. *Insectes Sociaux* 20:343-353.

Haas, C. A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* 9:845-854.

Haddad, N. M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* 9:612-622.

Haddad, N. M., and K. A. Baum. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* 9:623-633.

Hale, M. L., P. W. W. Lurz, M. D. F. Shirley, S. Rushton, R. M. Fuller, and K. Wolff. 2001. Impact of landscape management on the genetic structure of red squirrel populations. *Science* 293:2246-2248.

Hansen, A. J., and R. DeFries. 2007. Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications* 17: 974-988.

Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41-49.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application. In I. Hanski and M. Gilpin (editors). *Ecology, Genetics, and Evolution*. Academic Press, San Diego. Pages 5-26.

Hartley, M. J. 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology Management* 155:81-95.

Hinsley, S. A., P. E. Bellamy, and I. Newton. 1995. Bird species turnover and stochastic extinction in woodland fragments. *Ecography* 18:41-50.

Hoffmann, B. D., and A. N. Andersen. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* 28:444-464.

Holt, R. D. 2010. Toward a trophic island biogeography: reflections on the interface of island biogeography and food web ecology. In J. B. Losos and R. E. Ricklefs (editors). *The Theory of Island Biogeography*. Princeton University Press, Princeton, USA. Pages 143-185.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharnkte. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology* 79:491-500.

Ivanov, K., and J. Keiper. 2010. Ant (Hymenoptera: Formicidae) diversity and community composition along sharp urban forest edges. *Biodiversity and Conservation* 19:3917-3933.

James, C. D. 2004. Trapping intensities for sampling ants in Australian rangelands. *Austral Ecology* 29:78-86.

Janzen, D. H. 1983. Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican deciduous forest and adjacent horse pasture. *Oikos* 41:274-283.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.

Jongman, R. H. G. 1995. Nature conservation planning in Europe - developing ecological networks. *Landscape and Urban Planning* 32:169-183.

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

- Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1:4.
- Kirk, A. A., and T. J. Ridsdill-Smith. 1986. Dung beetle distribution patterns in the Iberian Peninsula. *Entomophaga* 31:183-190.
- Kirkman, K. E., and R. M. Pott. 2002. Biodiversity conservation in plantation forestry. In S. M. Pierce, R. M. Cowling, T. Sandwith and K. MacKinnon (editors). *Mainstreaming biodiversity in development - case studies from South Africa*. The World Bank Environmental Department, Washington, DC, USA. Pages 33-42.
- Klein, B. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70:1715-1725.
- Kotze, D. J., and M. J. Samways. 1999. Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. *Biodiversity and Conservation* 8:1339-1363.
- Kruess, A., and T. Tscharntke. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* 106:293-302.
- Kuussaari, M., R. Bommarco, R. K. Heikinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* 24:564-571.
- Laeger, T., and R. Schultz. 2005. Ameisen (Hymenoptera: Formicidae) als Beifänge in Bodenfallen – wie genau spiegeln sie reale Abundanzverhältnisse wider? *Myrmecologische Nachrichten* 7:17-24.
- Laurance, W. F. 2002. Hyperdynamism in fragmented habitats. *Journal of Vegetation Science* 13:595-602.
- Limolino, M. V., and D. R. Perault. 2000. Assembly and disassembly of mammal communities in a fragmented temperate rain forest. *Ecology* 81:1517-1532.
- Lobo, J. M., J. Hortal, and F. J. Cabrero-Sañudo. 2006. Regional and local influences of grazing activity on the diversity of a semi-arid dung beetle community. *Diversity and Distributions* 12:111-123.
- Lobo, J. M., J. -P. Lumaret, and P. Jay-Robert. 1998. Sampling dung beetles in the French Meddeiterranean area: effects of abiotic factors and farm practices. *Pedobiologia* 42:252-266.

- Lomolino, M. V., and D. R. Perault. 2000. Assembly and disassembly of mammal communities in a fragmented temperate rain forest. *Ecology* 81:1517-1532.
- Longino, J. T. 2000. What to do with the data. In D. Agosti, J. D. Majer, L. E. Alonso and T. R. Schultz (editors). *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. Smithsonian Institution Press, Washington, London, 2000. Pages 186-203.
- Loreau, M. 2000. Are communities saturated? On the relationship of alpha, beta and gamma diversity. *Ecological Letters* 3:73-76.
- Lumaret, J. -P., and A. A. Kirk. 1987. Ecology of dung beetles in the French Mediterranean region (Coleoptera: Scarabaeinae). *Acta Zoológica Mexicana* 24:11-55.
- Lumaret, J. -P., N. Kadiri, and M. Bertrand. 1992. Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology* 29:349-356.
- Madden, K. E., and B. J. Fox. 1997. Arthropods as indicators of the effects of fluoride pollution on the succession following sand mining. *Journal of Applied Ecology* 34:1239-1256.
- Majer, J. D. 1983. Ants: bio-indicators of minesite rehabilitation, land-use and land conservation. *Environmental Management* 7:375-383.
- Majer, J. D., and A. E. Kock. 1992. Ant recolonization of sand mines near Richards Bay, South Africa. *South African Journal of Science* 88:31-36.
- Majer, J. D., and O. G. Nichols. 1998. Long-term recolonization patterns of ants in western Australian rehabilitated bauxite mines with reference to their use as indicators of restoration success. *Journal of Applied Ecology* 35:161-182.
- Major, R. E., F. J. Christie, G. Gowing, G. Cassis, and C. A. M. Reid. 2003. The effect of habitat configuration on arboreal insects in fragmented woodlands of south-eastern Australia. *Biological Conservation* 113:35-48.
- Marsh, A. C. 1984. The efficacy of pitfall traps for determining the structure of a desert ant community. *Journal of the Entomological Society of South Africa* 47:115-120.
- MEA (Millennium Ecosystem Assessment). 2005. *Ecosystems and human well-being: biodiversity synthesis*. World Resource Institute, Washington DC, USA. Downloaded from www.unep.org/maweb/documents/document.354.aspx.pdf on 27 March 2014.

- Mech, S. G., and J. G. Hallett. 2001. Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology* 15:467-474.
- Menedez, R., and D. Gutierrez. 1996. Altitudinal effects on habitat selection of dung beetles (Scarabaeidae: Aphodiidae) in the northern Iberian peninsula. *Ecography* 19:313-317.
- Mucina, L., and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria, South Africa.
- Mucina, L., D. B. Hoare, M. C. Lotter, P. J. du Preez, M. C. Rutherford, C. R. Scott-Shaw, G. J. Bredenkamp, L. W. Powrie, L. Scott, K. G. T. Camp, S. S. Cilliers, H. Bezuidenhout, T. H. Mostert, S. J. Siebert, P. J. D. Winter, J. E. Burrows, L. Dobson, R. A. Ward, M. Stalmans, E. G. H. Oliver, F. Siebert, E. Schmidt, K. Kobisi, L. Kose. 2006. Grassland biome. In L. Mucina and M. C. Rutherford (editors). *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia* 19. South African National Biodiversity Institute, Pretoria, South Africa.
- Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezcútia, and M. Favila. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* 141:1461-1474.
- Nichols, E., T. Larsen, S. Spector, A. L. Davis, F. Escobar, M. Favila, K. Vulinac. 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological Conservation* 137:1-19.
- Nielsen, S. T. 2007. Deforestation and biodiversity: effects of bushland cultivation on dung beetles in semiarid Tanzania. *Biodiversity and Conservation* 16:2753-2769.
- Nieminen, M. 1996. Migration of moths in a network of small islands. *Oecologia* 108:643-651.
- Nieminen, M., and I. Hanski. 1998. Metapopulations of moths on islands: a test of two contrasting models. *Journal of Animal Ecology* 67:149-160.
- Numa, C., J. R. Verdú, A. Sánchez, and E. Galante. 2009. Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. *Diversity and Distributions* 15:489-501.
- Pardini, R. 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest Landscape. *Biodiversity and Conservation* 13:2567-2586.

- Pardini, R., S. M. de Souza, R. Braga-Neto, and J. P. Metzger. 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biological Conservation* 124:253-266.
- Parr, C. L., H. G. Robertson, H. C. Biggs, and S. L. Chown. 2004. Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* 41:630-642.
- Pereira, H. M., and G. C. Daile. 2006. Modeling biodiversity dynamics in countryside landscapes. *Ecology* 87:1877-1885.
- Perfecto, I., and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology* 16:174-182.
- Pryke, J. S., and M. J. Samways. 2012. Conservation management of complex natural forest and plantation edge effects. *Landscape Ecology* 27:73-85.
- Pryke, S. R., and M. J. Samways. 2001. Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biological Conservation* 101:85-96.
- Pryke, S. R., and M. J. Samways. 2003. Quality of remnant indigenous grassland linkages for adult butterflies (Lepidoptera) in an afforested African landscape. *Biodiversity and Conservation* 12:1985-2004.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Ratchford, J. S., S. E. Wittman, E. S. Jules, A. M. Ellison, N. J. Gotelli, and N. J. Sanders. 2005. The effects of fire, local environment and time on ant assemblages in forests and fens. *Diversity and Distributions* 11:487-497.
- Reyers, B., J. Nel, B. Egoh, Z. Jonas, and M. Rouget. 2005. National Grasslands Biodiversity Program: Grassland Biodiversity Profile and Spatial Biodiversity Priority Assessment. CSIR Report Number: ENV-S-C 2005-102.
- Rohr, J. R., C. G. Mahan, and K. C. Kim. 2007. Developing a monitoring program for invertebrates: guidelines and a case study. *Conservation Biology* 21:422-433.

- Romero-Alcaez, E., and J. M. Acila. 2000. Landscape heterogeneity in relation to variations in epigaeic beetle diversity of a Mediterranean ecosystem. Implications for conservation. *Biodiversity and Conservation* 9:985-1005.
- Roslin, T. 2000. Dung beetle movements at two spatial scales. *Oikos* 91:323-335.
- Rundlöf, M., H. G. Smith. 2006. The effect of organic farming on butterfly diversity depends on landscape context. *Journal of Applied Ecology* 43:1121-1127.
- Samways, M. J. 2007a. Insect conservation: a synthetic management approach. *Annual Review of Entomology* 52:465-487.
- Samways, M. J. 2007b. Implementing ecological networks for conserving insect and other biodiversity. In A. J. A. Stewart, T. R. New and O. T. Lewis (editors). *Insect Conservation Biology*. CABI, Wallingford, Oxon, UK. Pages 127-143.
- Samways, M. J. 1990. Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. *Oecologia* 84:482-490.
- Samways, M. J., and K. Kreuzinger. 2001. Vegetation, ungulate and grasshopper interactions inside vs outside an African savanna game park. *Biodiversity and Conservation* 10:1963-1981.
- Samways, M. J., C. S. Bazelet, and J. S. Pryke. 2010. Provision of ecosystem services by large scale corridors and ecological networks. *Biodiversity and Conservation* 19:2949-2962.
- Samways, M. J.; M. A. McGeoch, and T. R. New. 2010. *Insect Conservation: A Handbook of Approaches and Methods*. Oxford University Press, Oxford.
- Samways, M. J., R. Osborn, and F. Carliel. 1997. Effect of a highway on ant (Hymenoptera: Formicidae) species composition and abundance, with a recommendation for roadside verge width. *Biodiversity and Conservation* 6:903-913.
- Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? *Ecology* 78:1914-1932.
- Seifert, B. 1990. Wie wissenschaftlich wertlose Fangzahlen entstehen - Auswirkungen artspezifischen Verhaltens von Ameisen an Barberfallen direk beobachtet. *Entomologische Nachrichten Berichte* 34:21-28.
- Sodhi, N. S., B. W. Brook, and C. J. A. Bradschaw. 2007. *Tropical Conservation Biology*. Blackwell Publishing, Oxford.

- Southwood, T. R. E., and P. A. Hendersen. 2000. *Ecological Methods*. Blackwell Science, Oxford.
- Stork, N. E., and P. Eggleton. 1992. Invertebrates as determinants and indicators of soil quality. *American Journal of Alternative Agriculture* 7:38-47.
- Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effect of fragmentation and invasion on native ant communities in coastal Southern California. *Ecology* 79:2041-2056.
- Sutcliffe, O. L., and C. D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology* 10:1359-1365.
- Terborgh, J., L. Lopez, and J. Tello. 1997. Bird communities in transition: the Lago Guri islands. *Ecology* 78:1494-1501.
- Thiele, H. U. 1977. *Carabid beetles in their environment. A study on habitat selection by adaptation in physiology and behaviour*. Springer-Verlag, NY.
- Tscharnkte, T., I. Staffan-Dewenter, A. Kruess, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications* 12:354-363.
- Tscharnkte, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, J. Brngtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Fründ, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews* 87:661-685.
- Tscharntke, T., A. M. Klein, A. Kreuss, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* 8: 857-874.
- Underwood, A. C., and B. L. Fisher. 2006. The role of ants in conservation monitoring: If, when, and how. *Biological Conservation* 132:166-182.
- Vasconcelos, H. L. 2001. Landscape modifications and ant communities. In R. O. Bierregaard Jr., T. E. Lovejoy and R. Mesquita (editors). *Lessons from Amazonia: the ecology and conservation of a fragmented forest*. Yale University Press, New Haven. Pages 199-207.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: effects of fragmentation on extinction. *The American Naturalist* 125:879-887.

Wilson, J. W., R. L. Stirnemann, Z. S. Shaikh, and M. Scantlebury. 2010. The response of small mammals to natural and human altered edges associated with Afromontane forests of South Africa. *Forest Ecology and Management* 259:926-931.

Witt, A. B. R., and M. J. Samways. 2004. Influence of agricultural land transformation and pest management practices on the arthropod diversity of a biodiversity hotspot, the Cape Floristic Region, South Africa. *African Entomology* 12:89-95.

Woodcock, B. 2005. Pitfall trapping in ecological studies. In S. Leather (editor). *Insect Sampling in Forest Ecosystems*. Blackwell Science, Oxford, UK. Pages 37-57.

Woodcock, B. A., R. Pywell, D. B. Roy, R. Rose, and D. Bell. 2005. Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. *Biological Conservation* 125:192-202.

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

Chapter 3:

Beyond corridor size - a continuum model approach to dung beetle and ant assemblage structures in a fragmented grassland

Abstract

Effective conservation management of transformed landscapes may benefit from the use of conceptual landscape models. The present study is aimed at improving the landscape model currently employed in a timber production landscape in KwaZulu-Natal, South Africa. The effects of landscape patterns and environmental gradients on dung beetle nesting guilds and ant assemblages within grassland corridors and a nearby protected area were investigated. Within grassland corridors, tunnelling dung beetle species richness were sensitive to landscape level fragmentation and elevation, especially large species, while ant species richness were influenced by elevation and vegetation type. Differences in management (grazing and fire) may be a strong driver of the dung beetle assemblage differences between the grassland corridors and the protected area. Other variables that explained some of the variation in dung beetle species composition were elevation, vegetation type, and soil hardness. Elevation was the only environmental variable explaining some of the variation in ant species composition. Incorporating elevation into the current management scheme may improve the conservation effectiveness within this transformed landscape.

Introduction

As the human population and its demand for resources continues to expand, the conservation of biodiversity is becoming ever more challenging (Chown *et al.* 2003). Demand for land, especially for activities such as farming, housing, plantation forestry, transport infrastructure and urbanisation, inevitably reduces and fragments natural habitats globally. Habitat fragmentation is a catch-all term for a multi-scale process (Keitt *et al.* 1997; Olff & Rithcie 2002) that changes habitat arrangement, isolation, quality, and connectivity (Fahrig 2003). As has been shown in a range of environments and for an array of different taxa, habitat loss and fragmentation entails negative consequences to different aspects of biodiversity (Fahrig 2003). Understanding habitat fragmentation's role in ecological processes is increasingly being seen as a prerequisite for sound science, policy and management (Hunter 2002).

An important structural approach to the conservation of local, regional and global biodiversity entails setting aside land formally devoted to the protection and maintenance of nature (Gaston *et al.* 2006, 2008). Apart from this, connecting large good quality patches of natural habitat that are

exposed to natural mimicking disturbances can also provide habitat for a range of species within and across functional groups (Fischer *et al.* 2006; Samways 2007a). The conservation management of transformed landscapes entails a sound understanding of how organisms are distributed through space (Fischer & Lindenmayer 2006; Pryke & Samways 2014). From this regard, conceptual landscape models may be helpful tools (McIntyre & Hobbs 1999; Lindenmayer & Fischer 2003; Manning *et al.* 2004). The landscape model most frequently used in fauna research and conservation in human-transformed landscapes is the “fragmentation model”, which distinguishes natural patches spread throughout a transformed “matrix” (Saunders *et al.* 1991; Harrison & Bruna 1999; Debinski & Holt 2000; Haila 2002; Fahrig 2003). The fragmentation model approach stems from the theory of island biogeography (MacArthur & Wilson 1967). Three key assumptions of the fragmentation model include: 1) a clear contrast exists between human defined patches and the rest of the landscape, 2) numerous organisms view these human-defined patches as suitable “habitat patches”, and 3) the relationship between landscape patterns (e.g. patch size, patch isolation, patch shape) and species distribution patterns is of interest and is a sensible surrogate for the ecological processes causally connected to species distribution patterns (Fischer & Lindenmayer 2006).

Apart from the fragmentation model, several other models exist. One of these is the “continuum model” (as proposed by Fischer and Lindenmayer 2006), which is based on continuum theory. Although widely accepted in vegetation ecology, continuum theory has received relatively far less attention from animal ecologists. Continuum theory states that “...vegetation has a gradually changing species composition along environmental gradients, with each species having an individualistic...distribution” (Austin 1999, p. 170-171). Environmental gradients may be direct (e.g. temperature), indirect (e.g. latitude) and resource related (e.g. nutrients) (Austin & Smith 1989). The continuum model is centred on species specific differences and gradual changes through space, thus broad conservation strategies based on this model include: 1) landscape scale (e.g. mix of patch sizes and vegetation types, topography) and microhabitat scale (e.g. structural complexity) heterogeneity should add additional niches and enhance species richness (e.g. Tews *et al.* 2004). 2) Unchanged habitats are probably beneficial for the majority of native and endemic species which have co-evolved with these habitats. However, altered habitats may also be utilised by native species. Conservation enhancement may therefore be effective throughout the entire landscape. 3) Because of species-specific differences, no particular conservation action could be beneficial to all species (Fischer & Lindenmayer 2006).

The continuum model is considered an improvement on the fragmentation model in landscapes with distinct ecological gradients, while the fragmentation model approach is considered sensible in high

contrast landscapes (Fischer & Lindenmayer 2006). An example of such a high contrast landscape would be the Ecological Networks (ENs) currently implemented in the grasslands of KwaZulu-Natal (KZN) Province, South Africa, where plantation forestry is considered a significant driver of the critically endangered status of the vegetation types found within this region (Mucina *et al.* 2006). Fortunately, as a commercial operation, plantation forestry is required to be environmentally sensitive. On average, one-third of any given plantation remains unplanted to timber, and it is these unplanted areas which form complex ENs of interconnected nodes, corridors and special landscape features (Jongman 1995; Kirkman & Pott 2002; Samways 2007a, b) that connect habitats for organism movement on both evolutionary and ecological timescales (Beier & Noss 1998; Jongman 1995).

Insects make up the majority of diversity in terrestrial ecosystems and are environmentally sensitive at point localities (Pryke & Samways 2010). Dung beetles (Scarabaeidae) and ants (Formicidae) were chosen as study organisms in the present study. Dung beetles play well understood ecological roles (Hanski & Cambefort 1991), have proven to be sensitive to changes in their local environment (Chown & Steenkamp 1996) and to be useful in monitoring habitat changes (see McGeoch 1998). Due to their dependence on vertebrate dung, dung beetle communities are likely to be influenced by changes in mammal communities (Estrada *et al.* 1999), which are themselves often affected by synergistic effects such as habitat modification and fragmentation. Ants often dominate insect assemblages and form an important part of biodiversity, influencing other organisms and soil processes (Dauber & Wolters 2000; Lenoir *et al.* 2001). They can affect the composition and diversity of plant species (King 1977; Dean *et al.* 1997) as well as each other and other arthropod predators by means of interference or intraguild predation (Laakso & Setälä 2000; Hawes *et al.* 2002). In other words, ants are capable of affecting the overall biodiversity of a particular habitat or site. Ants are increasingly being employed to monitor the effects of climate change (Botes *et al.* 2006), habitat fragmentation as well as conservation success (Mitrovich *et al.* 2010).

Fragmentation-related ecological processes are not deemed irrelevant by the continuum model. Instead, it emphasizes the possibility of additional ecological complexity in transformed landscapes that is not effectively included in the fragmentation model (Fischer & Lindenmayer 2006). The present study aims at improving the understanding of the current landscape model employed within the ENs in KwaZulu-Natal by investigating the importance of landscape patterns and environmental gradients in driving dung beetle and ant species diversity across the landscape. A better understanding of the relative contribution of spatial patterns and environmental gradients in

determining species distributions will improve the effectiveness of conservation management within this production landscape.

Methods

Study area

This study was undertaken in the Grassland Biome in the KwaZulu-Natal Midlands in South Africa (Fig. 1). Sampling took place in two commercial forestry plantations (*Pinus spp*) and one protected area (PA) over a maximum linear scale of 14 km. The two plantations were Good Hope (29° 42 S; 29° 59 E) and Shannon (29° 40 S; 29° 56 E) estates and the PA was the nearby iMpendle Nature Reserve (29° 42 S; 29° 52 E) (see Appendix A for geographical co-ordinates of each site).

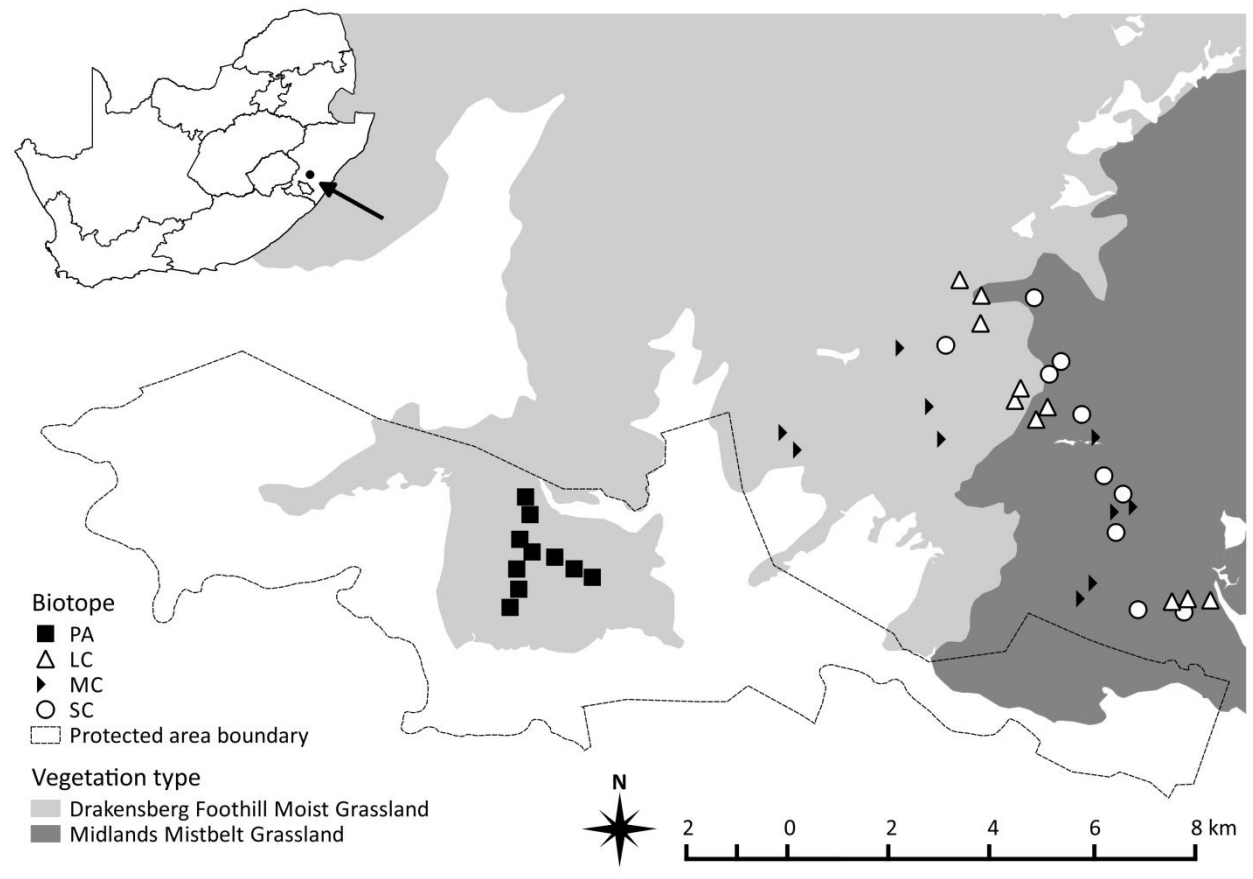


Figure 1 Map of study area. PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor. Google Maps link: <https://maps.google.com/maps?ll=-29.68612,29.93102&z=12&t=h&output=classic&dg=brw>

The area experiences summer rainfall with a mean annual precipitation of 730 – 1 280 mm (Mucina *et al.* 2006). Thunderstorms are frequent during summer and autumn. Heavy and frequent mist provides a significant amount of extra moisture (Mucina *et al.* 2006). The area is dominated by threatened Midlands Mistbelt Grassland (MMG, 760-1 400 metres above sea level (m asl)) and Drakensberg Foothill Moist Grassland (DFMG, 880-1 860 m asl) (Mucina *et al.* 2006). The dominant form of land transformation in the area is exotic timber plantations (Kirkman & Pott 2002). Only a few fragments of the original species-rich MMG remain (Mucina *et al.* 2006). Both these grassland types are forb rich. MMG is dominated by tall *Themeda triandra* rich grasslands, while DFMG is dominated by short bunch grasses (including *T. triandra* and *Tristachya leucothrix*) (Mucina *et al.* 2006). Both the grassland and plantation sites are fairly homogenous, grasslands consisting of a single plant association and plantations being a monospecific stand with minimal shrub undergrowth, resulting in high contrast between natural and transformed habitats.

Transects were laid out in grassland corridors of different sizes and the nearby PA. Protected natural areas are surrounded by contrasting landscapes of human modified areas (Hansen & DeFries 2007), making these regions ideal systems for investigating the effects of human activities. The PA was included in the present study to function as a reference of unmodified grassland species richness and composition. It also aided in highlighting the effect different grazing and fire management schemes may have on species composition. While there are some indigenous grazers present in the grassland corridors (such as the southern reedbuck, *Redunca arundinum*), these corridors experience continuous but moderate grazing at varying densities from mostly domestic cattle owned by the local community. The PA on the other hand has been fenced off and is exposed to lighter grazing by various indigenous herbivores. Furthermore, the grassland corridors are burned annually, while the PA is burned biannually. Corridors were classified into three different classes according to minimum width. Since the edge zone for plantation blocks has been estimated to reach 30 m into grassland corridors (Pryke & Samways 2012), the three classes were: large corridors (> 120 m, should have more interior area than edge area), medium corridors (60 – 120 m, interior area becomes less than edge zone), and small corridors (< 60 m, subject to intense edge effects).

The three corridor types, along with the PA (the four biotopes studied here), had ten replicated sampling transects each, giving a total of 40 transects. All corridor transects were situated parallel to the plantation edge. In corridors with a minimum width more than 60 m, transect were positioned at least more than 30 m from the edge. All sites were at least 600 m apart.

Arthropod sampling

Each transect consisted of four sampling stations, each 50 m apart. At each station, one dung baited pitfall trap to capture dung beetles and four test-tube traps to capture ants were dug level with the surrounding soil surface. The dung baited pitfall trap consisted of 50 g pig dung hung above a 2 litre (l) bucket. Each bucket was filled with a preservative liquid (water and a small amount of soap to lessen the effect of surface tension). The four small ant pitfalls (22 mm in diameter) were placed at least >3 m away from the baited 2 l bucket trap. Ant traps were filled with a 50% ethylene glycol solution (Woodcock 2005). Traps were left open for three days. All insect sampling took place over January - February 2013. Dung beetles were identified to species level where possible. Ants were sorted to recognized taxonomic units (RTU's), and named to genus.

Biomass is thought to reflect the negative effects of habitat modification on dung beetle communities more clearly than abundance (Vulinec 2002; Larsen *et al.* 2005). Thus, for each dung beetle species a mean adult body length was determined by measuring five randomly chosen adults. From this a weighted mean body length was calculated for each site, using the formula:

$$\bar{x} = \frac{\sum_{i=1}^n L_i n_i}{\sum_{i=1}^n n_i}$$

Where n_i is the density (abundance) of the i th species and L_i is the mean length of the i th species (Woodcock *et al.* 2009).

While the most common method employed to evaluate the impact of habitat alteration on biodiversity is species richness, this method does not take into account complementary information regarding ecosystem functioning, such as the diversity of the ecological roles of the species (Chapin *et al.* 2000; Purvis & Héctor 2000; Tilman 2001; Díaz & Cabido 2001; Perrings *et al.* 2010). One of the characteristics usually used to identify functional groups or guilds of beetle species belonging to the subfamily Scarabaeinae is related to food relocation and involves three groups: telecoprids, paracoprids and endocoprids (Spector 2006). Telecoprids (or rollers) arrive at the dung and shape a ball which they roll away and either bury or leave on the soil surface. Paracoprids dig tunnels straight down or at an oblique angle to the dung deposition site, where in they bury portions of the dung. Endocoprids live and nest within the dung. Since not all sampled dung beetles could be identified to species level and a lack in species specific nesting behaviour for some species, paracoprids and endocoprids were grouped together in the following analyses as simply tunnelling dung beetles. Dung beetle species data were thus split into two groups for statistical analyses, namely tunnelling

dung beetles (TDBs) and rolling dung beetles (RDBs). For each dung beetle and ant species or morphospecies collected, a voucher specimen was retained at Stellenbosch University.

Environmental variables

A useful focus when applying continuum theory to animal ecology would be on gradients that are expected to be relevant to an array of animal species, such as food, shelter, space and climate (Fischer & Lindenmayer 2006). Elevation (m asl) and rockiness were included in the present study as surrogates to approximate ecologically relevant gradients as these variables have been found to influence invertebrate species richness in a similar system (see Crous *et al.* 2013). Percentage rockiness was determined for each site using 2x50 m transects, each being 15 cm away from each other. Every meter a one centimetre diameter pole was held perpendicular to the soil surface and noted as rock when any rocky surface greater than 10 cm in diameter was encountered. This was then divided by the total number of measures (100) to obtain a percentage of rockiness for each site. Since soil hardness can give an indication of compaction due to grazer trampling (Cingolani *et al.* 2003), it was also included in the present study as a surrogate of grazing intensity. Four measurements of soil hardness (kilogram-force) were made at every site by pushing a penetrometer (Lang Penetrometer, Inc.) into the soil to a depth of 13 cm. These readings were added and averaged to give one reading of soil hardness per site. Apart from these variables, other environmental variables noted for each site include vegetation type (MMG or DFMG) and minimum corridor width.

Statistical analyses

Since obvious significant differences existed between dung beetle and ant assemblage structures in corridors and the PA (see Chapter 2), analyses involving measured environmental variables potentially influencing species richness were conducted only on data for corridor grassland sites. Using generalized linear mixed models (GLMMs) and linear mixed-effects model (LMMs), each of the response variables describing TDB, RDB and ant species richness were correlated against the explanatory variables minimum corridor width (m), mean soil hardness (kg-force), rockiness(%), elevation (m asl), and vegetation type (DFMG or MMG), while date of sampling (quantified as a categorical variable) was included as a random effect. This was repeated with TDB - and RDB weighted mean body length as response variables. To check model quality of fit, residual analyses were performed using Pearson's coefficient. None of the models showed overdispersion of their residuals. To further explore potential relationships between species response variables and

measured environmental variables, scatter plots were constructed for those variables found to have significant influences on species response data. GLMMs, LMMs and post-hoc tests (Tukey tests) were conducted in the *R* (v3.0.3; R Development Core Team 2008) statistical package using the ‘lme4’ and ‘multcomp’ packages.

Canonical correspondence analyses (CCAs) were used to investigate the potential effect of measured environmental variables may have on ant and dung beetle species composition across grassland study sites. Partial Monte Carlo permutation tests were used to determine the environmental variables that explained a significant amount of variation TDB, RDB and ant species data respectively. As this test is inclined to judge too many variables significant, significant values were adjusted using Holm’s correction. Biotope type and vegetation type were included as factors in the analyses, while rockiness, mean soil hardness and elevation were included as continuous variables. Species richness of TDBs, RDBs and ants were overlaid on CCA ordinations of sampled sites as supplementary variables. Species data were square root transformed to decrease the importance of abundant species. Number of permutations was 999. CCAs and ordination plots were conducted in CANOCO v5.02 (Ter Braak & Smilauer 2012).

Results

A total of 43 TDB species (15 040 individuals) representing 15 genera from five tribes, and ten RDB species (3 433 individuals) representing seven genera from four tribes were sampled. A total of 63 ant morpho-species (11 971 individuals) were sampled, representing 23 genera from 14 tribes (see Appendix B for species list).

Environmental variables important for univariate species data

Environmental variables which influence univariate species response data in grassland corridors were minimum width, elevation and vegetation type (Table 2 & 3, Figs 2-4). None of the significant relationships between species response data and the continuous variables were found to be linear. TDB species richness increased as minimum corridor width increased to a point (300m) after which it decreased slightly (Fig 2a). Increase in elevation was associated with an increase in TDB species richness to about 1400 m asl, after which TDB species richness decreased in increasing elevation (Fig 2b). Ant species richness showed an opposite relationship than this to elevation, with ant species richness decreasing with increasing elevation to about 1400 m asl, after which ant species richness increased with increasing elevation (Fig 2c). Vegetation type had a significant influence on ant species richness. According to post-hoc tests, MMG contained significantly less ant species

compared to DFMG (Fig 3). The weighted mean body length of TDBs was significantly influenced by corridor width, elevation and vegetation type. Both corridor width and elevation seemed to have a positive influence on TDB weighted mean body length (Figs 2d & 2e), while the average weighted mean body length for TDBs in DFMG was significantly higher than that of MMG (Fig 4).

Table 2: Summary results of the Generalized Linear Models and Linear Mixed-effect Models for correlations between environmental variables and ant, tunnelling and rolling dung beetle species richness within grassland corridors.

	Variable	Minimum corridor width	Soil hardness	Rockiness (%)	Elevation	Vegetation type	Pearson's coefficient
Species richness	TDB ^G	5.336*	0.482	0.392	4.466*	3.457	0.653
	RDB ^G	0.306	0.001	1.846	0.002	0.001	0.631
WMBL	Ants ^G	0.16	0.05	0.001	5.509*	5.037*	0.406
	TDB ^L	15.829***	0.013	0.014	17.337***	11.351***	0.005
	RDB ^L	0.525	0.766	2.493	0.088	1.05	0.022

TDB, tunnelling dung beetle; RDB, rolling dung beetle; WMBL, weighted mean body length.

L linear mixed-effects models (used for normally distributed variables); G generalized linear mixed models (used for non-normally).

Figures represent chi-square values.

* P<0.05, ** P<0.01, *** P<0.001

Table 3 Differences in ant species richness and tunnelling dung beetle weighted mean body length (WMBL_{tun}) between the different vegetation types as determined by Tukey tests

	z-value	p-value
Ant species richness	-2.22	0.026
WMBL _{tun}	-2.95	0.003

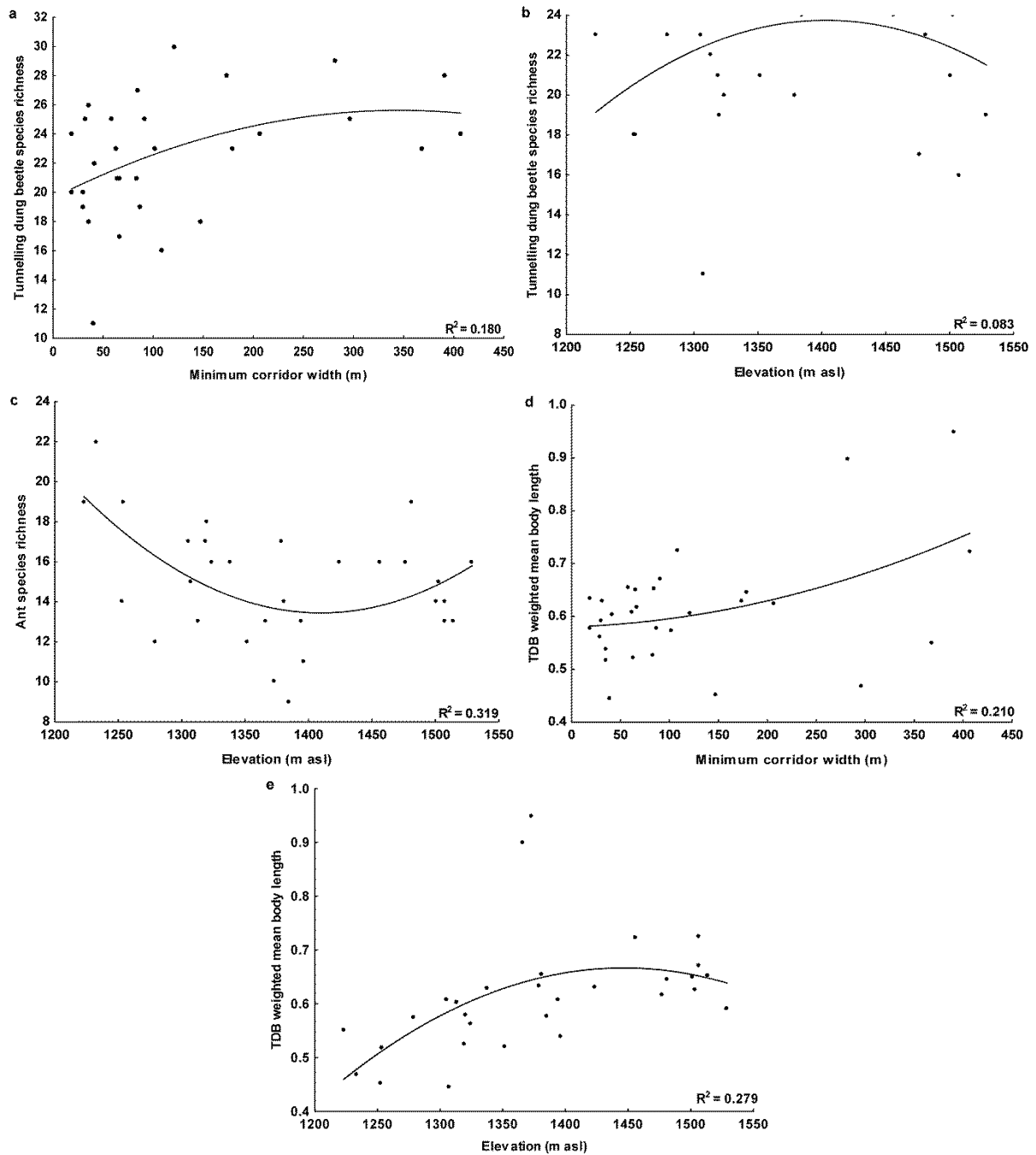


Figure 2 Scatter diagrams of a) TDB species richness and minimum corridor width (m), b) TDB species richness and elevation (m asl), c) ant species richness and elevation d) TDB weighted mean body length and minimum corridor width, and e) TDB weighted mean body length and elevation. Lines represent quadratic polynomial regressions. R^2 , R-squared values. TDB, tunnelling dung beetle. M asl, metres above sea level

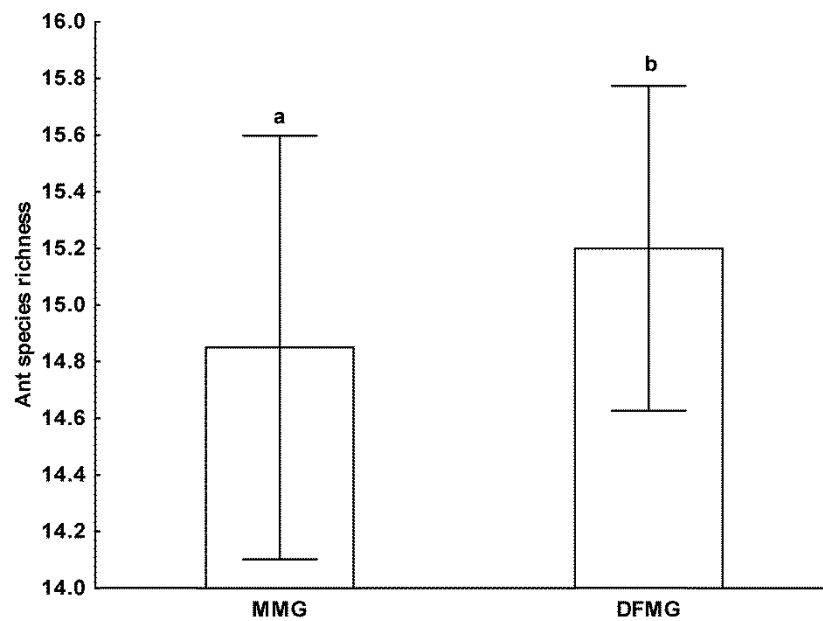


Figure 3 Mean ant species richness by vegetation type (± 1 SE). Different letters above the bars represent significantly different means as determined by Tukey tests (5% level). MMG, Midlands Mistbelt Grasslands; DFMG, Drakensberg Foothill Moist Grassland.

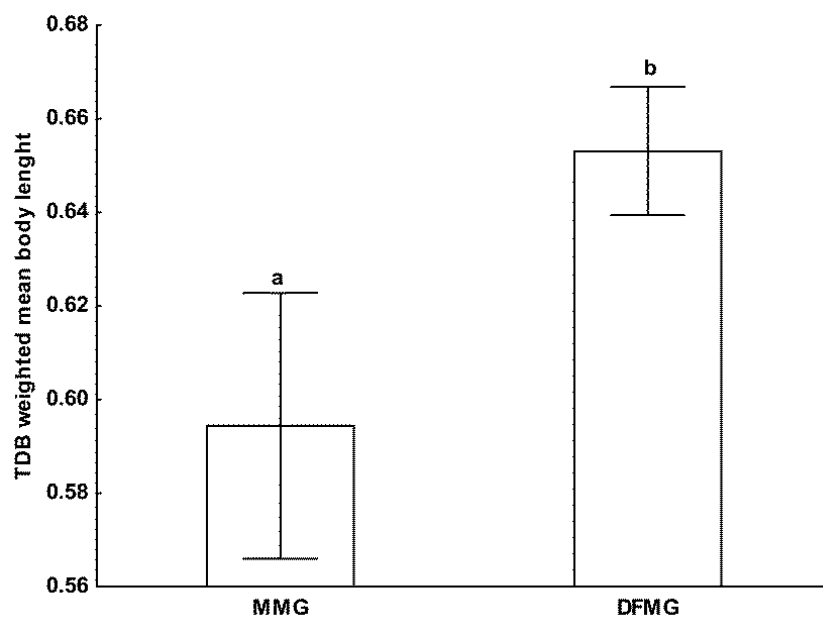


Figure 4 Average weighted mean body length for tunneling dung beetle species by vegetation type (± 1 SE). Different letters above the bars represent significantly different means as determined by Tukey tests (5% level). TDB, tunneling dung beetle; MMG, Midlands Mistbelt Grasslands; DFMG, Drakensberg Foothill Moist Grassland.

Environmental variables affecting species composition

TDB and RDB species composition was significantly influenced by biotope type, vegetation type, elevation as well as soil hardness (Table 4, Fig 5). The two primary axes explained 29.05% of the cumulative variation of TDB species data and 36.82% of RDB species data. Ant species composition was significantly influenced only by elevation (Table 4, Fig 6). For ants, the two primary axes explained 12.67% of the cumulative variation of species data. (See also Appendix E & F for influence of measured variables on specific dung beetle and ant species).

Table 4 Summary of simple effects of environmental variables on species response data as determined by canonical correspondence analyses.

Variable	Explains %		
	Tunnelling dung beetles	Rolling dung beetles	Ants
Biotope			
PA	20.0**	20.7**	3.1
LC	5.4*	12.0**	4.2
MC	4.1	2.1	3.4
SC	5.4*	4.8	2.6
Vegetation type	10.7**	20.3**	3.1
Elevation	10.1**	19.9**	4.8*
Soil hardness	6.9*	7.3*	3.8
Rockiness	2.4	0.8	2.2

PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor

Values express % of variation in species data explained

DFMG, Drakensberg Foothill Moist Grassland; MMG, Midlands Mistbelt Grassland

* P<0.05, ** P<0.01, *** P<0.001 (Holm correction)

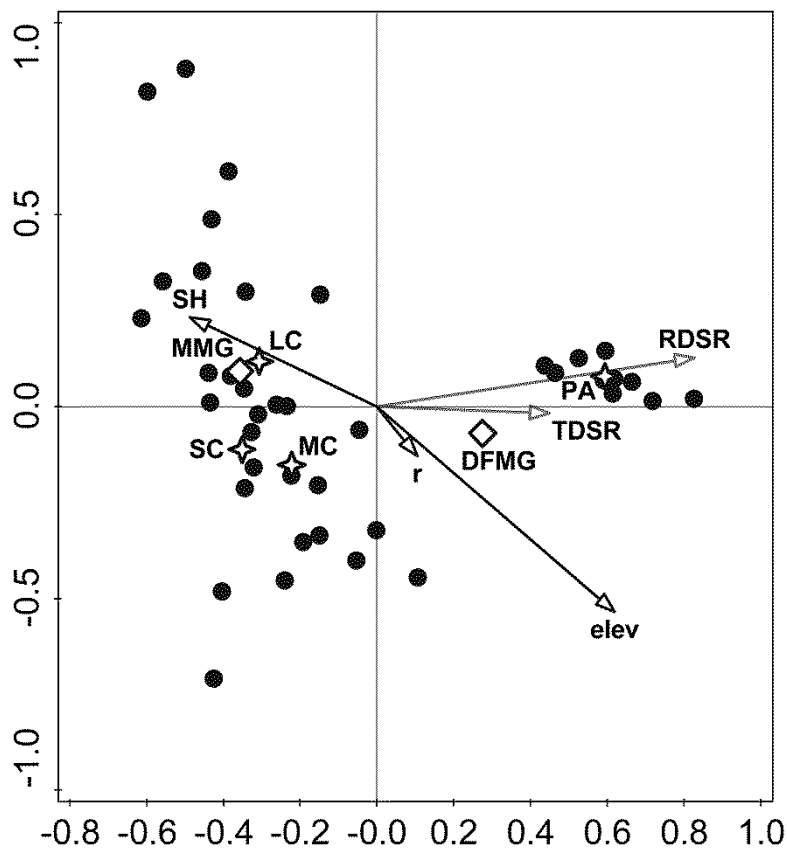


Figure 5 Canonical correspondence analysis (CCA) ordination for dung beetle species data across grassland sites and measured environmental variables. Tunnelling dung beetle species richness (TDSR) and rolling dung beetle species richness (RDSR) are added as supplementary variables. Biotope (PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor) and vegetation type (DFMG, Drakensberg foothill moist grassland; MMG, midlands mistbelt grassland) are included as factors. Other variables included are elevation (elev), mean soil hardness (SH) and rockiness (r).

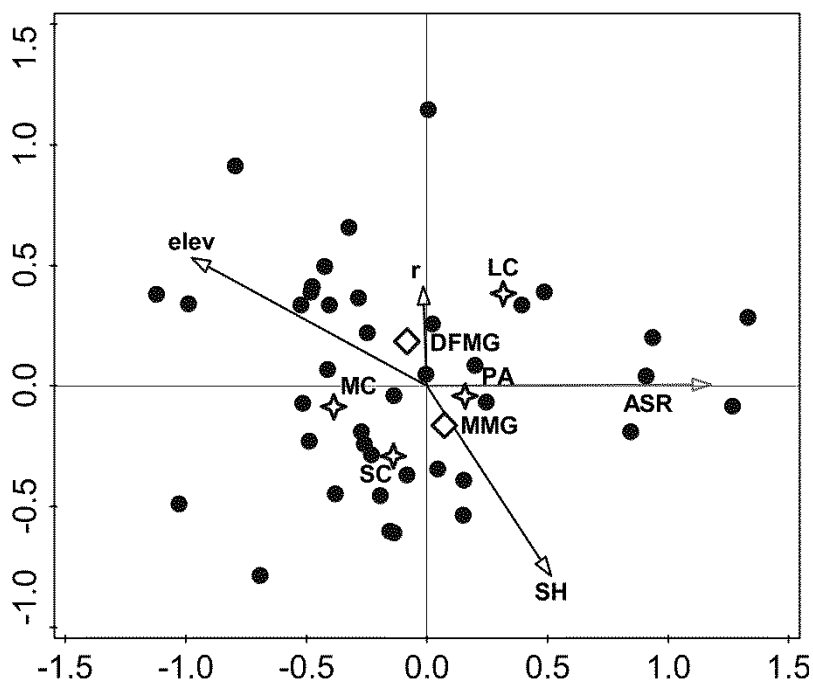


Figure 6 Canonical correspondence analysis (CCA) ordination for ant species data across grassland sites and measured environmental variables. Ant species richness (ASR) is added as a supplementary variable. Biotope (PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor) and vegetation type (DFMG, Drakensberg foothill moist grassland; MMG, midlands mistbelt grassland) are included as factors. Other variables included are elevation (elev), mean soil hardness (SH) and rockiness (r).

Discussion

The influence of corridor width

Within grassland corridors, corridor width was found to be an important variable influencing tunnelling dung beetle (TDB) species richness. This is in agreement with conservation recommendations arising from the fragmentation model, which considers larger natural patches to be more important than smaller patches (Diamond 1975). Lower TDB species richness in smaller corridors could be due to the increased influence of stochastic processes on populations within fragmented landscapes, resulting in increased extinction rates and decreased alpha diversity (Wilcox & Murphy 1985), or due to a lower diversity of dung producing elements within these corridors (see discussion further down). The present study found TDB weighted mean body length to show a reduction with reduced corridor width. This is in accordance with other studies that found larger bodied dung beetle species to be more reactive to disturbance than smaller bodied species (Larsen *et al.* 2005; Gardner *et al.* 2008; Nichols *et al.* 2007).

Larger sized dung beetles bury disproportionately more dung, and are therefore more functionally efficient relative to smaller species (Doubé 1990; Larsen *et al.* 2005; Nichols *et al.* 2007).

Furthermore, dung burial rates have been found to decrease as dung beetle species richness decreases in the community (Larsen *et al.* 2005). Considering the non-random loss in TDB species richness (less larger bodied species with a reduction in corridor size) and the differential influence of habitat modification on different functional guilds (Escobar 2004), the consequences for ecological functioning within these grassland corridors are far reaching (see Larsen *et al.* 2005; Nichols *et al.* 2007). In this regard, corridor width may not only be a sensible proxy of TDB species richness, but also ecological functioning.

The resilience shown by ants to corridor width is in agreement with other studies in grassland remnants in which smaller patches had equal or more ant species compared to larger patches (Dauber *et al.* 2006; Gibb and Hochuli 2002). Previous work on tropical ant fauna has attributed ant distribution patterns to three closely interlinked underlying factors: habitat preference of the ants, competition and the influence of weather and climate (e.g. Greenslade 1971). One hypothesis continuously cited to explain distribution patterns of ants involves interaction among species, and species exclusion by dominant ants. According to Room (1971), the mosaic concept is defined as the distribution of dominant ant species in patches in such a way that their territories do not overlap. Considering the sensitivity of ants to interspecific competition (see Andersen 1992; Andersen & Patel 1994; Morrison 1996; Retana & Cerdá 2000), intraspecific competition may also be an important factor in structuring ant assemblages (e.g. the presence of wood ants has been found to negatively

impact the ability of carabid beetles to occupy certain habitats (Thiele 1977; Hawes *et al.* 2002)). A potential reduction in other invertebrate taxa with decreasing corridor width may contribute to the success of less competitive ant species, explaining the surprising amount of unique species within smaller grassland corridors (see Chapter 2) and the limited effect that corridor size has on ant species richness. This statement was not tested by the present study and remains to be proven. Mapping the distribution of ants within the present study area and identifying dominant species (see Majer *et al.* 1994) may shed light on the importance of competition in determining ant distribution patterns within the current study area. Furthermore, ants have been referred to as being more stationary than other insects groups, due to their perennial nests and restricted foraging ranges, and future studies focused on microscale heterogeneity within the landscape may detect great sensitivity of ants to their spatial distribution (Verdú *et al.* 2011).

Important environmental gradients

Since greater elevational range will undoubtedly span a greater range of environmental variation, increasing heterogeneity in the landscape and microhabitat scale, elevation may function as a surrogate of important underlying ecological processes. Elevation was the only environmental variable explaining some of the observed variation in ant species composition among the grassland biotopes. Elevation also explained some of the variation in dung beetle species composition. The significant effect of elevation on dung beetle and ant species data should be approached with caution. Species abundances are typically positively autocorrelated, so that points situated close to each other in space tend to have more similar values than what would be expected by random chance (Lichstein *et al.* 2002). This pattern is driven by numerous causes that could be either exogenous (e.g. autocorrelated environment, disturbance) and/or endogenous (e.g. dispersal limitation, conspecific attraction, demography) (Sokal & Oden 1978; Legendre 1993). Elevation is a highly spatially structured environmental variable, itself being highly autocorrelated. The effect of elevation on dung beetle and ant species distribution in the present study may thus be highly exaggerated. However, studies in other parts of South Africa have also found elevation to influence invertebrate species composition (see Pryke & Samways 2010; Munyai & Foord 2012) and these results support Crous *et al.* (2013) in suggesting it as a possible mesofilter. Numerous other studies have assessed the effect of elevation on insect assemblages (Samways 1989; McCoy 1990; Olson 1994; Romero-Alcaraz & Avila 2000; Axmacher *et al.* 2004; Pryke & Samways 2008), a general trend being decreasing species diversity with increasing elevation. Lower productivity at higher elevations has been proposed as a cause of decreasing abundance and diversity at higher elevations (Lawton *et al.* 1987). The relationship between elevation and TDB and ant species richness in the present study

was not a simple linear relationship. This may be due to the relatively smaller elevational range of the present study (relative to climatic conditions) and/or complex biological interactions (such as intra- and interspecific competition).

Within grassland corridors, vegetation type was found to have a significant influence on ant species richness and TDB weighted mean body length. These results should be interpreted with caution since the study design was biased (of the 30 sites included in the analyses of grassland corridors, 20 were classified as MMG and ten as DFMG). Still, since the two grassland vegetation types are classified according to underlying abiotic variables, vegetation type may function as a surrogate of those underlying variables. Soils between the two vegetation types differ in origin, with the epedal and plinthic soils of MMG derived from shale and sandstone, and the well-drained soils of DFMG derived from mudstone, sandstone and dolerite (Mucina *et al.* 2006). Since soil type has been found to be an important determinant of dung beetle distribution (Doubé 1983; Davis 1987), differences in soil types between the two vegetation types may also explain its influence on dung beetle species composition.

The role of fire and grazing management

Although the present study found corridor width to be significant for TDB species richness and biomass within grassland corridors, it was not the only environmental variable influencing dung beetle species across the landscape. Biotope type was found to explain the highest amount of the variation in dung beetle species composition, particularly in terms of whether the biotope formed part of the PA or part of the grassland corridors. Since fire and grazing are considered to be the most common large-scale disturbances occurring in seasonally dry grasslands and major factors structuring these communities (Noy-Meir 1995), differences in fire and grazing management between the two land-uses could be contributing to the strong differences in dung beetle assemblages. In South African grasslands, fire has been found to be an important driver of arthropod and plant assemblage structures (Little *et al.* 2013; Joubert *et al.* 2014). In the present study area, fire management is practiced to simulate natural processes (Samways *et al.* 2010) and maintain fire breaks. Since most feeding galleries are within the first 30 cm of the soil surface (Bang *et al.* 2005), factors such as fire intensity may affect dung beetle species composition although this remains to be tested.

Grazing is regarded as an ecosystem scale disturbance (Dupre & Dlekman 2001; Díaz *et al.* 2007) and has been found to influence species richness, assemblage structure as well as competition among species (Dupre & Dlekman 2001; Mucina *et al.* 2006; Bilyeu *et al.* 2007). In the present

study, grazing management in the grassland corridors differ from that in the PA in that corridors experienced much higher grazing densities than would occur naturally (Samways *et al.* 2010) and domestic cattle form the major dung producing ruminants (compared to various natural producers in the PA). There are three complementary mechanisms attributable to dissimilarity in grazing management which may explain the strong differences in dung beetle assemblage structures between the corridors and the PA. First, since many dung beetle species have been found to show some degree of specialisation to dung type (Fincher *et al.* 1970; Davis 1994), a reduction in the heterogeneity of food resources would result in a reduction of those species specialized for particular dung types. Second, a higher density of domestic cattle would result in a competitive advantage for those species good at exploiting this food source (e.g. Louzada & Silva 2009). Competition has been hypothesized to play an important role in organizing dung beetle communities (Hanski & Cambefort 1991). In the present study, much fewer rolling dung beetle (RDB) species were sampled and in far fewer numbers than TDBs. This is not surprising as most tropical dung beetle communities show high proportions of tunnelers (Davis 1994a), and this has also been found for other regions in KwaZulu-Natal below 1900 m asl (Davis *et al.* 1999). Yet despite this presumably inherent low RDB diversity for this region, RDB species were distinctly greater in PA sites, suggesting that the low RDB diversity in corridors can at least partly be influenced by differences in grazing management. In a study investigating the biogeographical boundaries of dung beetles in Northern KwaZulu-Natal, Davis *et al.* (1999) found an increase in RDB species at higher elevations. Davis *et al.* (1999) compare this to a similar community trend in the winter rainfall region of South Africa (see Davis 1994b, 1997). Davis *et al.* (1999) attribute this trend to the faster dung removal ability of RDBs compared to most TDB tribes, and relate this to the lower density of droppings and shorter periods for dung colonization and burial in a cool highland, high rainfall ecosystem. Even though the PA sites were all at higher elevations than the grassland corridors, the elevational range of the present study was not large enough for there to be major differences in climate between the different sites. Since the PA contains mostly pellet dropping elements, compared to the large pat producing cattle in the corridors, fast removal of small amounts of dung may provide RDBs with a competitive advantage in the PA compared to the corridors. This can be related to a study in France, where a transition from pellet producing sheep farming to pat producing cattle farming led to a decrease in RDBs and an increase in TDBs (Lumaret *et al.* 1992). Thirdly, higher bovine densities in corridors should result in soil compaction due to livestock trampling, advancing the few species that can cope with the hardest soils (Halffter *et al.* 1992). There were no significant differences in soil hardness between the different biotopes, but the PA did have the lowest mean soil hardness. This may be due to differences in soil type and/or trampling. While the present study did not find soil hardness to affect

species richness in the corridors, it did have an influence on dung beetle species composition. Arellano *et al.* (2008) studied the effect of landscape features on the abundance and movement patterns of a common scarab beetle (*Canthon cyanellus cyanellus*) in Southern Mexico through mark-release-recapture techniques. The only local scale environmental variables significantly affecting beetles was soil hardness, with beetles preferring less hard soils. It is thus not surprising that differences in management between these two different land-uses would result in very different assemblages of dung beetles, although further studies are needed to investigate the relative importance of the proposed complementary mechanisms. Considering the importance of management in driving dung beetle species composition within this system, the fragmentation model assumption that human-defined patch boundaries should correspond closely with animal-perceived patch boundaries should be relaxed and the influence of management for dung beetles given more weight.

Improving the fragmentation model

Numerous studies have addressed how fragmentation influences biodiversity (reviewed by Fahrig 2003). Landscape features considered important for population and community ecology include: patch area (Kruess & Tscharntke 2000), patch quality (Hanski & Singer 2006), the ratio of habitat edge to interior (Radeloff *et al.* 2000), isolation of habitat fragments (Collinge 2000), patch diversity (Varchola & Dunn 2001), as well as microclimate (Braman *et al.* 2000). Recent additions to our understanding of the spatial ecology of insects include differential reactions of predators and prey (With *et al.* 2002), genetic change in insect populations (Ronce & Kirkpatrick 2001), as well as temporal changes in the landscape structure (Onstad *et al.* 2001). Despite this increase in awareness of the landscape features that drive insect population and community variation, the links between landscape change and insect dynamics is still riddled with clear knowledge gaps (see Hunter 2002). Although aiding us in our understanding of spatial processes, the fragmentation model fails to address the challenge of linking animal distribution patterns with ecological processes (Fischer and Lindenmayer 2006), which is considered key for effective biodiversity conservation (Hobbs 1997). It has been stated that an over-reliance on this model can lead to a 1) limited predictive ability of animal distribution patterns (Lindenmayer & Fischer 2003) and 2) simplistic conservation advice which does not take threatening processes into account (Manning *et al.* 2004). At the opposite end of the complexity spectrum, the continuum model stresses species specific difference, making it impossible for any particular conservation action to benefit all species. The fragmentation model allows a foundation from which to work without being overwhelmed by the vast complexity that

constitutes natural ecosystems. Its simplicity allows space for improvement. By plugging into it more detailed models such as the continuum model, it can be customized to definite systems.

By including potential surrogates of environmental gradients, the present study emphasizes the fact that there is room for improvement regarding the fragmentation model currently employed in this timber production landscape. Since dung beetles may be more reactive at a scale corresponding to human defined “habitat patches” (see Kirkman & Pott 2002; Numa *et al.* 2009), and ants may be responsive at more local scales (Andersen 1997; Graham *et al.* 2009; Verdú *et al.* 2011; Munyai & Foord 2012), it is not surprising that the former taxa conforms to the assumptions of the fragmentation model, while the latter more to the continuum model. But dung beetles were also found to be responsive to other environmental gradients, adding to our knowledge of potential surrogates of ecological processes important for dung beetle distribution and relaxing those assumptions about what constitutes a “habitat”. The importance of management in structuring community composition of dung beetles underpins the importance of management over design in this system, as was found by Bazelet and Samways (2011) for grasshoppers, and highlights the value of including complementary information (such as nesting guilds for dung beetles) in understanding compositional responses to different management regimes. Furthermore, elevation was found to be important for both dung beetle nesting guilds as well as ant species composition, which supports the suggestion of Crous *et al.* (2013) of elevation as a possible mesofilter.

References

- Andersen, A. N. 1992. Regulation of “momentary” diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *The American Naturalist* 140:401-420.
- Andersen, A. N. 1997. Using ants as bioindicators: multiscale issues in ant community ecology. *Conservation Ecology* 1: 8.
- Andersen, A. N., and A. Patel. 1994. Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia* (Berlin) 98:15-24.
- Arellano, L., J. L. León-Cortés, and O. Ovaskainen. 2008. Patterns of abundance and movement in relation to landscape structure: a study of the common scarab (*Canthon cyanellus cyanellus*) in Southern Mexico. *Landscape Ecology* 23:69-78.

- Austin, M. P. 1999. A silent clash of paradigms: some inconsistencies in community ecology. *Oikos* 86: 170-178.
- Austin, M. P. and T. M. Smith. 1989. A new model for the continuum concept. *Vegetatio* 83: 35-47.
- Axmacher, J. C., G. Holtmann, L. Scheuermann, G. Brehm, K. Muller-Hohenstein, and K. Fiedler. 2004. Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distributions* 10:293-302.
- Bang, H. S., J. Lee, O. S. Kwon, Y. E. Na, Y. S. Jang, and W. H. Kim. 2005. Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. *Applied Soil Ecology* 29:165-171.
- Bazelet, C. S., and M. J. Samways. 2011. Relative importance of management vs. design for implementation of large-scale ecological networks. *Landscape Ecology* 26:341-353.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241-1252.
- Bilyeu, D. M., D. J. Cooper, and N. T. Hobbs. 2007. Assessing impacts of large herbivores on shrubs: tests of scaling factors for utilisation rates from shoot-level measurements. *Journal of Applied Ecology* 44:168-175.
- Botes, A., M. A. McGeoch, H. Robertson, A. Van Niekerk, H. Davids, and S. L. Chown. 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* 33:71-90.
- Braman, S. K., J. G. Latimer, R. D., Oetting, R. D. McQueen, T. B. Eckberg, and M. Prinster. 2000. Management strategy, shade, and landscape composition effects on urban landscape plant quality and arthropod abundance. *Journal of Economic Entomology* 93:1464-1472.
- Chapin F. S., E. S. Zavaleta, V. T. Eviner, L. R. Naylor, P. M. Vitousek, H. L. Reynolds, D.U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack and S. Díaz. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.
- Chown, S. L., and H. Steenkamp. 1996. Body size and abundance in a dung beetle assemblage: optimal mass and the role of transients. *African Entomology* 4:203-212.
- Chown, S. L., B. van Rensburg, K. Gaston, A. Rodrigues, and A. van Jaarsveld. 2003. Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* 13: 1233-1241.

- Cingolani, A., M. Cabido, D. Renison, and V. Neffa. 2003. Combined effects of environmental and grazing on vegetation structure in Argentine granite grasslands. *Journal of Vegetation Science* 14:223-232.
- Collinge, S. K. 2000. Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. *Ecology* 81:2211-2226.
- Crous, C., M. J. Samways, and J. S. Pryke. 2013. Exploring the mesofilter as a novel operational scale in conservation planning. *Journal of Applied Ecology* 50:205-214.
- Dauber, J., J. A. N. Bengtsson, and L. Lenoir. 2006. Evaluating effects of habitat loss and land-use continuity on ant species richness in seminatural grassland remnants. *Conservation Biology* 20:1150-1160.
- Dauber, L., and V. Wolters. 2000. Microbial activity and functional diversity in the mounds of three different ant species. *Soil Biology & Biochemistry* 32:93-99.
- Davis, A. L. V. 1987. Geographical distribution of dung beetles (Coleoptera: Scarabaeidae) and their seasonal activity in south-western Cape Province. *Journal of the Entomological Society of Southern Africa* 50:275-285.
- Davis, A. L. V. 1994. Associations of afrotropical Coleoptera (Scarabaeidae, Aphodiidae, Staphylinidae, Hydrophilidae, Histeridae) with dung and decaying matter: implications for selection of fly- control agents for Australia. *Journal of Natural History* 28:383-399.
- Davis, A. L. V. 1994a. Compositional differences between dung beetle (Coleoptera: Scarabaeidae s. str.) assemblages in winter and summer rainfall climates. *African Entomology* 2:45-51.
- Davis, A. L. V. 1994b. Community organization in a South African, winter rainfall, dung beetle assemblage. *Acta Oecol* 15:727-738.
- Davis, A. L. V. 1997. Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae s. str.). *African Journal of Ecology* 35:10-38.
- Davis, A. L. V. , C. H. Scholtz, and S. L. Chown. 1999. Species turnover, community boundaries and biogeographical of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography* 26:1039-1055.
- Dean, W. R. J., S. J. Milton, and S. Klotz. 1997. The role of ant-mounds in maintaining small-scale patchiness in dry grasslands in central Germany. *Biodiversity and Conservation* 6:1293-1307.

- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14:342-355.
- Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies of for the design of natural reserves. *Biological Conservation* 7:129-145.
- Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16: 646–655.
- Díaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. Casanoves, D. G. Hilchunas, C. Skarpe, G. Rusch, M. Sternberg, I. Noy-Meir, J. J. Landsberg, W. Zhang, H. Clark, and B. D. Campbell. 2007. Plant trait responses to grazing: a global synthesis. *Global Change Biology* 13:313-341.
- Doube, B. M. 1983. The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve South Africa. *Bulletin of Entomological Research* 73:357-371.
- Doube, B. M. 1990. A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology* 15:371-383.
- Dupré, C., and M. Dlekman. 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. *Ecography* 24:275-286.
- Escobar, F. 2004. Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. *Tropical Zoology* 17:123-136.
- Estrada, A., A. Anzures, and R. Coates-Estrada. 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*) and dung beetles at Los Tuxtlas, Mexico. *American Journal of Primatology* 48:253-262.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34:487-515.
- Fincher, G. T., T. B. Stewart, T. and R. Davis. 1970. Attraction of coprophagous beetles to feces of various animals. *Journal of Parasitology* 56:378-383.
- Fischer, J., and D. B. Lindenmayer. 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos* 112:2.
- Fischer, J., D. B. Lindenmayer, and A. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment* 4:80-86.

- Gardner, T. H., J. Barlow, and C. Peres. 2008. The value of primary, secondary and plantation forests for a neotropical dung beetle fauna. *Journal of Applied Ecology* 45:883-893.
- Gaston, K. J., K. Charman, S. F. Jackson, P. R. Armsworth, A. Bonn, R. A. Briers, C. S. Q. Callaghan, J. Hopkins, W. E. Kunin, J. Latham, P. Opdam, R. Stoneman, D. A. Stroud and R. Tratt. 2006. The ecological effectiveness of protected areas: The United Kingdom. *Biological Conservation* 132:76-87.
- Gaston, K. J., S. F. Jackson, A. Nagy, L. Cantú-Salazar, and M. Johnson. 2008. Protected areas in Europe: principle and practice. *Annals of the New York Academy of Science* 1134:97-119.
- Gibb, H. and D. F. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. *Biological Conservation* 106:91-100.
- Graham, J., A. J. Krzysik, D. A. Kovacic, J. J. Duda, D. C. Feeman, J. M. Emlen, J. C. Zak; W. R. Long, M. P. Wallace, C. Chamberlin-Graham, J. P. Nutter and H. E. Balbach. 2009. Species richness, equitability, and abundance of ants in disturbed landscapes. *Ecological Indicators* 9:866-877.
- Greenslade, P. J. M. 1971. Interspecific competition and frequency changes among ants in Solomon Islands cocoa plantations. *Journal of Applied Ecology* 8:323-52.
- Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* 12: 321-334.
- Halffter, G., M. E. Favila, and V. Halffter. 1992. A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. *Folia Entomológica Mexicana* 84:131-156.
- Hansen, A. J., and R. DeFries. 2007. Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications* 17: 974–988.
- Hanski, I. and M. C. Singer. 2001. Extinction-colonization dynamics and host-plant choice in butterfly metapopulations. *The American Naturalist* 158:341-353.
- Hanski, I., and Y. Cambefort. 1991. *Dung beetle ecology*. Princeton University Press, New Jersey.
- Harrison, S. and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225-232.
- Hawes, C., A. J. A. Stewart, and H. F. Evans. 2002. The impact of wood ants (*Formica rufa*) on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in a Scots pine plantation. *Oecologia* 131:612-619.

- Hobbs, R. 1997. Future landscapes and the future of landscape ecology. *Landscape and Urban Planning* 37: 1 -9.
- Hunter, M. D. 2002. Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology* 4:159-166.
- Jongman, R. H. G. 1995. Nature conservation planning in Europe - developing ecological networks. *Landscape and Urban Planning* 32:169-183.
- Joubert, L., J. S. Pryke, and M. J. Samways. 2014. Annual burning drives plant communities in remnant grassland ecological networks in an afforested landscape. *South African Journal of Botany* 92:126-133.
- Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes [online]. *Ecology and Society* 1: <http://www.consecol.org/vol1/iss1/art4/> .
- King, T. J. 1977. The plant ecology of ant-hills in calcareous grasslands. I Patterns of species in relation to ant-hills in southern England. *Journal of Ecology* 65:235-256.
- Kirkman, K. E. and R. M. Pott. 2002. Biodiversity conservation in plantation forestry. In S. M. Pierce, R. M. Cowling, T. Sandwith and K. MacKinnon (editors). *Mainstreaming biodiversity in development - case studies from South Africa*. The World Bank Environmental Department, Washington, DC, USA. Pages 33-42.
- Kreuss, A. and T. Tschardt. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122:129-137
- Laakso, J. and H. Setälä. 2000. Impacts of wood ants (*Formica aquilonia* Yarr.) on the invertebrate food web of the boreal forest floor. *Annales Zoologici Fennici* 37:93-100.
- Larsen, T. H., N. M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8:538-547.
- Lawton, J. H., M. MacGarvin, and P. A. Heads. 1987. Effects of altitude on the abundance and species richness of insect herbivores on bracken. *The Journal of Animal Ecology* 56: 147-160.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- Lenoir, L., T. Persson, and J. Bengtsson. 2001. Wood ants as potential hot spots for carbon and nitrogen mineralisation. *Biology and Fertility of Soils* 34:235-240.

- Lichstein, W. J., T. R. Simons, S. A. Shriver, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* 72:445-463.
- Lindenmayer, D. B. and J. Fischer. 2003. Sound science or social hook-a response to Brooker's application of the focal species approach. *Landscape and Urban Planning* 62: 149-158.
- Little, I. T., P. A. R. Hockey, and R. Jansen. 2013. A burning issue: Fire overrides grazing as a disturbance driver for South African grassland bird and arthropod assemblage structure and diversity. *Biological Conservation* 158:258-270.
- Louzada, J. N. C. and P. R. C. Silva. 2009. Utilisation of introduced Brazilian pastures ecosystems by native dung beetles: Diversity patterns and resource use. *Insect Conservation and Diversity* 2:45-52.
- Lumaret, J. P., N. Kadiri, and M. Bertrand. 1992. Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology* 29:349-356.
- MacArthur, R. H. and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press.
- Manning, A. D., D. B. Lindenmayer, and H. A. Nix. 2004. Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos* 104: 621-628.
- McCoy, E. D. 1990. The distribution of insects along elevational gradients. *Oikos* 58: 313-322.
- McGeoch, M A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews of the Cambridge Philosophical Society* 73:181-201.
- McIntyre, S. and R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology* 13: 1282-1292.
- Mitrovich, M. J., T. Matsuda, K. Pease and R. N. Fisher. 2010. Ants as a measure of effectiveness of habitat conservation planning in Southern California. *Conservation Biology* 24:1239-1248.
- Morrison, L. W. 1996. Community organization in a recently assembled fauna: the case of Polynesian ants. *Oecologia* 107:243-256.
- Mucina, L., D. B. Hoare, M. C. Lotter, P. J. du Preez, M. C. Rutherford, C. R. Scott-Shaw, G. J. Bredenkamp, L. W. Powrie, L. Scott, K. G. T. Camp, S. S. Cilliers, H. Bezuidenhout, T. H. Mostert, S. J. Siebert, P. J. D. Winter, J. E. Burrows, L. Dobson, R. A. Ward, M. Stalmans, E. G. H. Oliver, F. Siebert, E. Schmidt, K. Kobisi, L. Kose. 2006. Grassland biome. In L. Mucina and M. C. Rutherford (editors).

- The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria, South Africa.
- Munyai, T. C., and S. H. Foord. 2012. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. *Journal of Insect Conservation* 16:677-695.
- Nichols, E., T. Larsen, S. Spector, A. L. Davis, A., F. Escobar, M. Favila, and K. Vulinec. 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biological Conservation* 137:1-19.
- Noy-Meir, I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. *Journal of Vegetation Science* 6:701-710.
- Numa, C., J. R. Verdú, A. Sánchez, and E. Galante. 2009. Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. *Diversity and Distributions* 15:489-501.
- Oloff, H., and M. E. Rithcie. 2002. Fragmented nature: Consequences for biodiversity. *Landscape and Urban Planning* 58:83-92.
- Olson, D. M. 1994. The distribution of leaf-litter invertebrates along a Neotropical altitudinal gradient. *Journal of Tropical Ecology* 10: 129-150.
- Onstad, D. W.; J. L. Spencer, C. A. Guse, E. Levine and S. A. Isard. 2001. Modeling evolution of behavioural resistance by an insect to crop rotation. *Entomologia Experimentalis et Applicata* 100:195-201.
- Perrings C, S. Naeem, F. Ahrestani, D. E. Bunker, P. Burkill, G. Canziani, T. Elmqvist, R. Ferrati, J. Fuhrman, F. Jaksic, Z. Kawabata, A. Kinzig, G. M. Mace, F. Milano, H. Mooney, A. H. Prieur-Richard, J. Tschirhart, and W. Weisser. 2010. Ecosystem services for 2020. *Science* 330: 323–324.
- Pryke, J. S., and M. J. Samways. 2008. Conservation of invertebrate biodiversity on a mountain in a global biodiversity hotspot, Cape Floral Region. *Biodiversity and Conservation* 17:3027-3043.
- Pryke, J. S., and M. J. Samways. 2010. Significant variables for the conservation of mountain invertebrates. *Journal of Insect Conservation* 14:247-256.
- Pryke, J. S., and M. J. Samways. 2012. Conservation management of complex natural forest and plantation edge effects. *Landscape Ecology* 27:73-85.

- Pryke, J. S., and M. J. Samways. 2014. Conserving natural heterogeneity is crucial for designing effective ecological networks. *Landscape Ecology*. DOI: 10.1007/s10980-014-0096-x.
- Purvis, A., and A. Héctor. 2000. Getting the measure of biodiversity. *Nature* 405: 212–219.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Radeloff, V. C., D. J. Mladenoff, M. A. Boyce. 2000. The changing relation of landscape patterns and jack pine budworm population during an outbreak. *Oikos* 90:417-430.
- Retana, J., and X. Cerdá. 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. *Oecologia* 123:436-444.
- Romero-Alcaraz, E., and J. M. Avila. 2000. Effect of elevation and type of habitat on the abundance and diversity of Scarabaeoid dung beetle (Scarabaeoidea) assemblages in a Mediterranean area from Southern Iberian Peninsula. *Zoological Studies* 39:351-359.
- Ronce, O. and M. Kirkpatrick. 2001. When sources become sinks: migrational meltdown in heterogenous habitats. *Evolution* 55:1520-1531.
- Room, P. M. 1971. The relative distributions of ant species in Ghana's cocoa farms. *Journal of Animal Ecology* 40:735–751.
- Samways, M. J. 1989. Taxon turnover in Odonata across a 3000 m altitudinal gradient in southern Africa. *Odonatologica* 18:263-274.
- Samways, M. J. 2007a. Insect conservation: a synthetic management approach. *Annual Review of Entomology* 52:465-487.
- Samways, M. J. 2007b. Implementing ecological networks for conserving insect and other biodiversity. In A. Stewart, T. New and O. Lewis (editors). *Insect conservation biology*. CABI, Wallingford, Oxon, UK. Pages 127-143.
- Samways, M. J., C. S. Bazelet, and J. S. Pryke. 2010. Provision of ecosystem services by large scale corridors and ecological networks. *Biodiversity and Conservation* 19:2949-2962.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.

- Sokal, R. R., and N. L. Oden. 1978. Spatial autocorrelation in biology: 2. Some biological implications and four applications of evolutionary and ecological interest. *Biological Journal of the Linnean Society* 10:229–249.
- Spector, S. 2006. Scarabaeinae dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *Coleopterists Bulletin* 60: 71–83.
- ter Braak C. J. F. and P. Smilauer. 2012. Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power, Ithaca, USA.
- Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*: 31: 79-92.
- Thiele, H. U. 1977. Carabid beetles in their environments. Springer, Berlin.
- Tilman, D. 2001. Functional diversity. In S. A. Levin (editor). *Encyclopedia of biodiversity*, Vol. 3. Academic Press, San Diego. Pages 109–120.
- Varchola, J. M., J. P. Dunn. 2001. Influence of hedgerow and grassy field borders on ground beetle (Coleoptera: Carabidae) activity in fields of corn. *Agriculture, Ecosystems and Environment* 83:153-163.
- Verdú, J. R., C. Numa, and O. Hernández-Cuba. 2011. The influence of landscape structure on ants and dung beetles diversity in a Mediterranean savanna-Forest ecosystem. *Ecological Indicators* 11:831-839.
- Vulinec, K. 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. *Biotropica* 34:297-309.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: effects of fragmentation on extinction. *The American Naturalist* 125:879-887.
- With, K. A., D. M. Pavuk, J. L. Worchuck, R. K. Oates, and J. L. Fisher. 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications* 12:52-65.
- Woodcock, B. A. 2005. Pitfall trapping in ecological studies. In S. R. Leather (editor). *Insect sampling in forest ecosystems*. Blackwell Science, Oxford, UK. Pages 37-57.

Woodcock, B. A., S. G. Potts, T. Tscheulen, E. Pilgrim, A. J. Ramsey, J. Harrison-Cripps, V. K. Brown, and J. R. Tallwin. 2009. Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. *Journal of Applied Ecology* 46:920-929.

Chapter 4

Conclusion

Anthropogenic induced habitat loss and fragmentation is a major threat to biodiversity (Ewers & Didham 2006). Transformation by plantation forestry poses a serious threat to South African grasslands (Mucina & Rutherford 2006), one of the country's once common vegetation types. Mitigating measures are needed to lessen the environmental impacts of this land-use type. Approximately one third of each plantation (500 000 ha nationally) has been set aside for biodiversity conservation (Kirkman & Pott 2002), forming large scale interconnected natural corridors and nodes that connect habitats for organism movement on both evolutionary and ecological timescales, i.e. ecological networks (ENs) (Jongman 1995; Beier & Noss 1998).

A good understanding of how organisms are distributed through space will improve the conservation management of transformed landscapes (Fischer & Lindenmayer 2006; Pryke & Samways 2014). Knowledge of the importance of spatial patterns (i.e. corridor width) and environmental gradients (natural heterogeneity) in influencing grassland species can guide our focus on those variables important for optimized conservation management and planning within ENs. The present study was aimed at exploring the role of corridor width in driving invertebrate assemblages across a transformed landscape and to investigate other possible environmental variables significant for species distributions. Using dung beetles and ants as focal taxa, I investigated the contribution of smaller grassland corridors in KwaZulu-Natal, South Africa to overall conservation within a timber production landscape by comparing them to a nearby protected area (PA) (Chapter 2). Furthermore, the applicability and possible improvement of the fragmentation model approach to conservation management within this high contrast production landscape was explored by examining environmental gradients other than corridor width as possible drivers of dung beetle and ant species distribution patterns across this landscape (Chapter 3). Dung beetle nesting behaviour (tunnelling and rolling species) and size were also employed in the analyses as that functionality may aid in understanding the underlying drivers of differences in species assemblage structures.

Narrow corridors are considered to be less suitable habitats due to stronger edge effects from the surrounding timber matrix (Samways & Moore 1991; Samways *et al.* 2010; Pryke & Samways 2012a). Here, corridor size was found to be an important factor for dung beetle species richness, with dung beetle assemblages present in smaller corridors housing significantly fewer species compared to the PA. Thus for dung beetles, the recommended minimum width of 250 m for biodiversity conservation within this production landscape (Pryke & Samways 2001) is applicable. While dung beetles showed a high sensitivity to landscape level fragmentation, ants seemed unaffected by corridor width, with

smaller corridors even containing more unique ant species than larger corridors. For ants at least, smaller corridors seem to add significantly to their overall conservation within this specific system.

As was found by Pryke and Samways (2012b), I showed large corridors to be comparable in arthropod species richness to a PA, once again illustrating the conservation value of investing in ENs, provided they are wide enough. Still, the total amount of species utilizing smaller grassland corridors was surprising. Although smaller corridors may function more like early successional habitats (Bazelet & Samways 2011; see also Chapter 2) than optimal habitat, these areas may provide additional foraging areas as well as increasing connectivity across the landscape, at least for the majority of dung beetle and ant species within the present study, and in this way permanently enhance populations within larger corridors (Haddad 1999; Fahrig 2001; Benett & Mulongoy 2006). Smaller remnants of natural patches are an integral spatial component of many transformed landscapes worldwide. The surprisingly high species richness for dung beetles and ants within smaller corridors may also be found for other taxa and in other production landscapes, implying that active conservation planning and management may also be valuable within landscapes restricted to retaining only smaller areas of natural patches.

There were marked differences between the dung beetle assemblages present in the PA and the grassland corridors. This was largely due to rolling dung beetles showing a close association with PA sites. I attribute this to differences in grazing management between these land-uses, with the PA holding a larger variety of pellet producing, natural grazers and the grassland corridors mostly pat producing, domestic cattle. For grasshoppers within this system, management has been found to be more important than design (Bazelet & Samways 2011). However, when including a much broader range of taxa, importance for many species lies in both design and management (which links to maximal heterogeneity) (Pryke and Samways 2014). For dung beetles in my study, both variables appeared important, but the relative importance of design and management for dung beetle species was not specifically tested, and is likely also determined by nesting guild. Although assemblages of dung beetles may be actively managed by including certain grazers not currently in these grassland corridors, the large grassland corridors contained the same number of unique dung beetle species as the PA. The current grazing management scheme does not seem to be detrimental to the overall conservation effectiveness of these ENs.

Dung beetles not only exhibited a higher sensitivity to landscape level fragmentation than ants, but dung beetle assemblages also showed a higher sensitivity to environmental variables (as variation in dung beetle assemblages was explained by more environmental variables and to a greater degree than that of ant assemblages). The differential response of dung beetles and ants to both fragmentation and environmental variables once again emphasizes the importance of taking a multi-

taxa approach when investigating species responses to their environment. Communities consist of species that relate to the landscape on a broad range of spatial scales (Holt 1996; Debinsky & Holt 2000). The anthropocentric view (often employed in landscape planning) of what constitutes a suitable habitat does not take species specific differences in response to the influence of specific mesofilters/microhabitats (Hunter 2005; Crous *et al.* 2013), or differences in the scale at which these influences are perceived, into account.

Apart from using a multi-taxa approach, including additional information other than species data can also highlight the limitations of the anthropocentric “habitat” patch. Including nesting functional guild in the analyses of dung beetle species data showed that even when a taxon views the landscape in a way similar that of the human-defined habitat patch, including additional information other than species data (i.e. functional information) can improve our understanding of additional factors important in determining habitat suitability. Including supplementary information in the analyses of ant species data (such as dominance, see Majer *et al.* 1994) may also advance our knowledge of factors important for ant distribution patterns across this landscape. Furthermore, since larger dung beetle species were more sensitive to landscape level fragmentation than smaller species, functional information (i. e. size) may also be useful in circumstances where taxonomic expertise are lacking.

For both dung beetles and ants, elevation was found to significantly influence species richness within grassland corridors. It is difficult to separate the influence of elevation on species distribution patterns from the inherent variation due to geographical differences among sites (since elevation itself is spatially autocorrelated), but considering the interrelatedness of elevation, vegetation type and soil type in the present study area (see Appendix C), it seems safe to consider elevation as a proxy for environmental heterogeneity. Similarly, other studies near and within the study region have found habitat heterogeneity to be significant for biodiversity conservation planning within these grasslands (Crouse *et al.* 2013; Pryke & Samways 2014).

Whenever agricultural intensification enters a landscape, habitat heterogeneity becomes greatly reduced at a variety of spatial scales (Brenton *et al.* 2003). My study was conducted in endangered remnant grasslands within a timber production landscape, a land-use which has contributed to the threatened status of this vegetation type. As outlined in Chapter 1, conservation outside of formally protected areas can contribute to biodiversity conservation and is essential to lessen the detrimental effects that intensive land-use types (such as timber production in this study) have on biodiversity and ecological functioning. My study showed that larger corridors were comparable in dung beetle and ant species richness to a nearby PA, once again illustrating the effectiveness of ENs in biodiversity conservation and stressing the importance of corridor size in achieving this

effectiveness. Apart from corridor width, environmental variables associated with environmental heterogeneity were found to be important for both taxa, pointing to the possible improvement of the present fragmentation model approach to conservation management within this system. Future planning for biodiversity conservation within production landscapes should take the natural variation within the landscape into account (Benton *et al.* 2003; Pryke & Samways 2014). My study illustrates that this is true whether an organism conforms to the human centred perspective of what constitutes a suitable habitat patch or not.

References

- Bazelet, C. S., and M. J. Samways. 2011. Relative importance of management vs. design for implementation of large-scale ecological networks. *Landscape Ecology* 26:341-353.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241-1252.
- Benett, G., and K. J. Mulongoy. 2006. Review of experience with ecological networks, corridors and buffer zones. Secretariat of the Convention on Biological Diversity, Montreal, Technical Series, No. 23, 100 pages.
- Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18:182-188.
- Crous, J. C., M. J. Samways, and J. S. Pryke. 2013. Exploring the mesofilter as a novel operational scale in conservation planning. *Journal of Applied Ecology* 50:205-214.
- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14:342-355.
- Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81:117-142.
- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100: 65-74.
- Fischer, J., and D. B. Lindenmayer. 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos* 112:2.
- Haddad, N. M., and K. A. Baum. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* 9:623-633.
- Holt R. D. 1996. Food webs in space: an island biogeographic perspective. In G. A. Polis and K. O. Winemiller (editors). *Food Webs*. Chapman & Hall, New York. Pages 313-323.

- Hunter, M. L. 2005. A mesofilter conservation strategy to complement fine and coarse filters. *Conservation Biology* 19:1025–1029.
- Jongman, R. H. G. 1995. Nature conservation planning in Europe - developing ecological networks. *Landscape and Urban Planning* 32:169-183.
- Kirkman, K. E. and R. M. Pott. 2002. Biodiversity conservation in plantation forestry. In S. M. Pierce, R. M. Cowling, T. Sandwith and K. MacKinnon (editors). *Mainstreaming Biodiversity in Development - Case Studies from South Africa*. The World Bank Environmental Department, Washington, DC, USA. Pages 33-42
- Majer, J. D., J. H. C. Delabie, and M. R. B. Smith. 1994. Arboreal ant community patterns in Brazilian cocoa farms. *Biotropica* 26:73-83.
- Mucina, L., and M. C. Rutherford. 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute, Pretoria, South Africa.
- Pryke, S. R., and M. J. Samways. 2001. Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biological Conservation* 101:85-96.
- Pryke, J. S., and M. J. Samways. 2012a. Conservation management of complex natural forest and plantation edge effects. *Landscape Ecology* 27:73-85.
- Pryke, J. S., and M. J. Samways. 2012b. Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. *Journal of Applied Ecology* 49:591–600.
- Pryke, J. S., and M. J. Samways. 2014. Conserving natural heterogeneity is crucial for designing effective ecological networks. *Landscape Ecology*. DOI: 10.1007/s10980-014-0096-x.
- Samways, M. J., C. S. Bazelet, and J. S. Pryke. 2010. Provision of ecosystem services by large scale corridors and ecological networks. *Biodiversity and Conservation* 19:2949-2962.
- Samways, M. J., and S. D. Moore. 1991. Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. *Biological Conservation* 57:205–219.

Appendix A

Global positioning co-ordinates and elevation of sampled sites in Good Hope – and Shannon estates and iMpendle Nature Reserve in KwaZulu-Natal, South Africa. PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor; PINE, plantation block; m asl, metres above sea level.

Site	Latitude	Longitude	Biotope	Elevation (m asl)	Vegetation type
1	S29.67069°	E029.96797°	LC	1366	Midlands Mistbelt Grassland
2	S29.70994°	E030.00108°	LC	1223	Midlands Mistbelt Grassland
3	S29.65370°	E029.95434°	LC	1503	Drakensberg Foothill Moist Grasslands
4	S29.71023°	E029.99326°	LC	1253	Midlands Mistbelt Grassland
5	S29.66939°	E029.96132°	LC	1456	Drakensberg Foothill Moist Grasslands
6	S29.66688°	E029.96248°	LC	1481	Drakensberg Foothill Moist Grasslands
7	S29.67323°	E029.96564°	LC	1373	Midlands Mistbelt Grassland
8	S29.64487°	E029.95010°	LC	1424	Drakensberg Foothill Moist Grasslands
9	S29.64802°	E029.95451°	LC	1394	Midlands Mistbelt Grassland
10	S29.70968°	E029.99646°	LC	1233	Midlands Mistbelt Grassland
11	S29.67062°	E029.94481°	MC	1477	Drakensberg Foothill Moist Grasslands
12	S29.69203°	E029.98245°	MC	1305	Midlands Mistbelt Grassland
13	S29.70648°	E029.97807°	MC	1319	Midlands Mistbelt Grassland
14	S29.70965°	E029.97552°	MC	1320	Midlands Mistbelt Grassland
15	S29.67943°	E029.91797°	MC	1501	Drakensberg Foothill Moist Grasslands
16	S29.67591°	E029.91502°	MC	1507	Drakensberg Foothill Moist Grasslands
17	S29.67725°	E029.94727°	MC	1507	Drakensberg Foothill Moist Grasslands
18	S29.69102°	E029.98623°	MC	1279	Midlands Mistbelt Grassland
19	S29.65872°	E029.93883°	MC	1514	Drakensberg Foothill Moist Grasslands
20	S29.67688°	E029.97867°	MC	1352	Midlands Mistbelt Grassland
21	S29.68898°	E029.86183°	PA	1423	Drakensberg Foothill Moist Grasslands
22	S29.70530°	E029.87540°	PA	1426	Drakensberg Foothill Moist Grasslands
23	S29.69257°	E029.86274°	PA	1435	Drakensberg Foothill Moist Grasslands
24	S29.69759°	E029.86066°	PA	1449	Drakensberg Foothill Moist Grasslands
25	S29.70015°	E029.86316°	PA	1455	Drakensberg Foothill Moist Grasslands
26	S29.70362°	E029.86003°	PA	1470	Drakensberg Foothill Moist Grasslands
27	S29.70772°	E029.86045°	PA	1463	Drakensberg Foothill Moist Grasslands
28	S29.71142°	E029.85868°	PA	1456	Drakensberg Foothill Moist Grasslands
29	S29.70121°	E029.86777°	PA	1451	Drakensberg Foothill Moist Grasslands
30	S29.70359°	E029.87170°	PA	1435	Drakensberg Foothill Moist Grasslands
31	S29.69847°	E029.98058°	PINE	1338	Midlands Mistbelt Grassland
32	S29.64863°	E029.96311°	PINE	1405	Midlands Mistbelt Grassland
33	S29.70685°	E029.97893°	PINE	1325	Midlands Mistbelt Grassland
34	S29.71030°	E029.97843°	PINE	1349	Midlands Mistbelt Grassland
35	S29.70904°	E029.98259°	PINE	1341	Midlands Mistbelt Grassland
36	S29.71256°	E029.98802°	PINE	1308	Midlands Mistbelt Grassland
37	S29.67237°	E029.97585°	PINE	1371	Midlands Mistbelt Grassland
38	S29.67982°	E029.91633°	PINE	1511	Drakensberg Foothill Moist Grasslands
39	S29.66088°	E029.93826°	PINE	1517	Drakensberg Foothill Moist Grasslands

40	S29.65487°	E029.95334°	PINE	1516	Drakensberg Foothill Moist Grasslands
41	S29.67223°	E029.97491°	SC	1379	Midlands Mistbelt Grassland
42	S29.69620°	E029.98188°	SC	1324	Midlands Mistbelt Grassland
43	S29.71189°	E029.98636°	SC	1307	Midlands Mistbelt Grassland
44	S29.65817°	E029.94728°	SC	1529	Drakensberg Foothill Moist Grasslands
45	S29.71237°	E029.99572°	SC	1254	Midlands Mistbelt Grassland
46	S29.64852°	E029.96526°	SC	1381	Midlands Mistbelt Grassland
47	S29.68468°	E029.97943°	SC	1338	Midlands Mistbelt Grassland
48	S29.68841°	E029.98331°	SC	1313	Midlands Mistbelt Grassland
49	S29.66406°	E029.96832°	SC	1396	Midlands Mistbelt Grassland
50	S29.66147°	E029.97070°	SC	1385	Midlands Mistbelt Grassland

Appendix B

Species list of recorded flora in this study (compiled by family scientific names) and abbreviations used for CANOCO analysis. Assigned nesting guilds included for Scarabaeidae.

Family	Scientific name	Abbreviation	Nesting guild
Formicidae	<i>Aenictus 1</i>	Aenic1	
	<i>Aenictus 2</i>	Aenic2	
	<i>Anoplolepis 1</i>	Anopl1	
	<i>Anoplolepis 2</i>	Anopl2	
	<i>Camponotus 1</i>	Campo1	
	<i>Camponotus 2</i>	Campo2	
	<i>Camponotus 3</i>	Campo3	
	<i>Camponotus maculatus</i>	Campos	
	<i>Cardiocondyla 1</i>	Cardi1	
	<i>Crematogaster 1</i>	Crema1	
	<i>Crematogaster 2</i>	Crema2	
	<i>Crematogaster 3</i>	Crema3	
	<i>Crematogaster 4</i>	Crema4	
	<i>Dorylus 1</i>	Doryl1	
	<i>Hypoconera 1</i>	Hypop1	
	<i>Hypoconera 2</i>	Hypop2	
	<i>Lepisiota 1</i>	Lepis1	
	<i>Meranoplus 1</i>	Meran1	
	<i>Meranoplus 2</i>	Meran2	
	<i>Meranoplus 3</i>	Meran3	
	<i>Monomorium 1</i>	Monom1	
	<i>Monomorium 2</i>	Monom2	
	<i>Monomorium 3</i>	Monom3	
	<i>Monomorium 4</i>	Monom4	
	<i>Monomorium 5</i>	Monom5	
	<i>Monomorium 6</i>	Monom6	

	<i>Monomorium</i> 7	Monom7	
	<i>Ocymyrmex</i> 1	Ocymy1	
	<i>Ocymyrmex</i> 2	Ocymy2	
	<i>Pachycondyla</i> 1	Pachy1	
	<i>Pheidole</i> 1	Pheid1	
	<i>Pheidole</i> 2	Pheid2	
	<i>Pheidole</i> 3	Pheid3	
	<i>Plagiolepis</i> 1	Plagi1	
	<i>Plagiolepis</i> 2	Plagi2	
	<i>Plagiolepis</i> 3	Plagi3	
	<i>Plagiolepis</i> 4	Plagi4	
	<i>Plagiolepis</i> 5	Plagi5	
	<i>Plagiolepis</i> 6	Plagi6	
	<i>Plectotena</i> 1	Plect1	
	<i>Polyrhachis</i> 1	Polyr1	
	<i>Rhoptromyrmex</i> 1	Rhopt1	
	<i>Solenopsis</i> 1	Solen1	
	<i>Strumigenys</i> 1	Strum1	
	<i>Tapinolepis</i> 1	Tapin1	
	<i>Tapinoma</i> 1	Tapina1	
	<i>Technomyrmex</i> 1	Techn1	
	<i>Technomyrmex</i> 2	Techn2	
	<i>Tetramorium</i> 1	Tetra1	
	<i>Tetramorium</i> 10	Tetra10	
	<i>Tetramorium</i> 11	Tetra11	
	<i>Tetramorium</i> 12	Tetra12	
	<i>Tetramorium</i> 13	Tetra13	
	<i>Tetramorium</i> 14	Tetra14	
	<i>Tetramorium</i> 15	Tetra15	
	<i>Tetramorium</i> 16	Tetra6	
	<i>Tetramorium</i> 2	Tetra2	
	<i>Tetramorium</i> 3	Tetra3	
	<i>Tetramorium</i> 4	Tetra4	
	<i>Tetramorium</i> 5	Tetra5	
	<i>Tetramorium</i> 6	Tetra6	
	<i>Tetramorium</i> 7	Tetra7	
	<i>Tetramorium</i> 8	Tetra8	
	<i>Tetramorium</i> 9	Tetra9	
Scarabaeidae	<i>Caccobius</i> A	CaccoA	Tunnelling
	<i>Caccobius</i> B	CaccoB	Tunnelling
	<i>Caccobius</i> C	CaccoC	Tunnelling
	<i>Caccobius</i> D	CaccoD	Tunnelling
	<i>Caccobius</i> E	CaccoE	Tunnelling
	<i>Catharsius</i> A	CathaA	Tunnelling
	<i>Catharsius</i> B	CathaB	Tunnelling
	<i>Cleptocaccobius</i> A	CleptA	Tunnelling

	<i>Copris A</i>	CopriA	Tunnelling
	<i>Copris B</i>	CopriB	Tunnelling
	<i>Copris C</i>	CopriC	Tunnelling
	<i>Drepanellus laticollis</i>	DrepaLa	Tunnelling
	<i>Drepanocerus A</i>	DrepaA	Tunnelling
	<i>Drepanocerus C</i>	DrepaC	Tunnelling
	<i>Drepanocerus kirbyi</i>	DrepaKi	Tunnelling
	<i>Epirinus A</i>	EpiriA	Rolling
	<i>Epirinus relictus</i>	EpiriRe	Rolling
	<i>Epirinus validus</i>	EpiriVa	Rolling
	<i>Euoniticellus A</i>	EuoniA	Tunnelling
	<i>Garreta A</i>	GarreA	Rolling
	<i>Gymnopleurus A</i>	GymnoA	Rolling
	<i>Helicopris A</i>	HelioA	Tunnelling
	<i>Neosisyphus B</i>	NeosiB	Rolling
	<i>Odontoloma peckorum</i>	OdontPe	Rolling
	<i>Oniticellus A</i>	OniticA	Tunnelling
	<i>Onitis A</i>	OnitisA	Tunnelling
	<i>Onthophagus A</i>	OnthoA	Tunnelling
	<i>Onthophagus B</i>	OnthoB	Tunnelling
	<i>Onthophagus C</i>	OnthoC	Tunnelling
	<i>Onthophagus D</i>	OnthoD	Tunnelling
	<i>Onthophagus E</i>	OnthoE	Tunnelling
	<i>Onthophagus F</i>	OnthoF	Tunnelling
	<i>Onthophagus G</i>	OnthoG	Tunnelling
	<i>Onthophagus H</i>	OnthoH	Tunnelling
	<i>Onthophagus I</i>	OnthoI	Tunnelling
	<i>Onthophagus J</i>	OnthoJ	Tunnelling
	<i>Onthophagus K</i>	OnthoK	Tunnelling
	<i>Onthophagus L</i>	OnthoL	Tunnelling
	<i>Onthophagus M</i>	OnthoM	Tunnelling
	<i>Onthophagus N</i>	OnthoN	Tunnelling
	<i>Onthophagus O</i>	OnthoO	Tunnelling
	<i>Onthophagus Q</i>	OnthoQ	Tunnelling
	<i>Onthophagus R</i>	OnthoR	Tunnelling
	<i>Onthophagus S</i>	OnthoS	Tunnelling
	<i>Pedaria A</i>	PedarA	Tunnelling
	<i>Proagoderus A</i>	ProagA	Tunnelling
	<i>Proagoderus B</i>	ProagB	Tunnelling
	<i>Sarophorus costatus</i>	SaropCo	Tunnelling
	<i>Scarabaeus B</i>	ScaraB	Rolling
	<i>Sisyphus A</i>	SisypA	Rolling
	<i>Sisyphus B</i>	SisypB	Rolling
	<i>Xinidium dentilabrus</i>	XinidDen	Tunnelling
	<i>Xinidium dewitzi</i>	XinidDew	Tunnelling
Trogidae	<i>Trox A</i>		

*Trox C**Trox D*

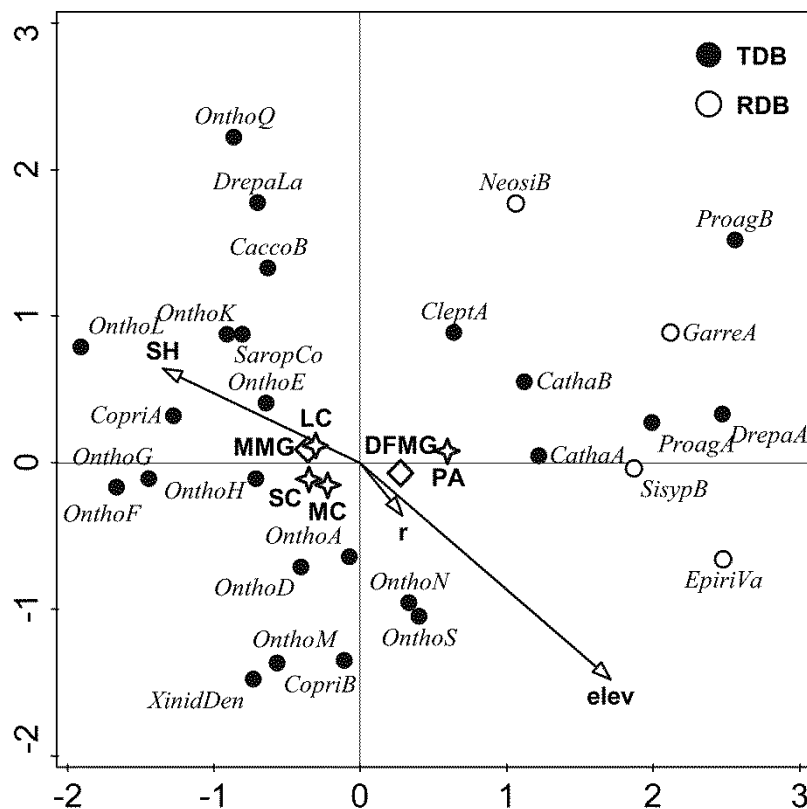
Appendix C

Spearman rank order correlations for environmental variables, biotope types and vegetation types. Significant correlations in bold font ($p < 0.05$). PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor; MMG, Midlands Mistbelt Grassland; DFMG, Drakensberg Foothill Moist Grassland; SH, soil hardness (kilogram-force); elev, elevation (metres above sea level); r, rockiness (%).

	PA	LC	MC	SC	MMG	DFMG	SH	elev
LC	-0.333							
MC	-0.333	-0.333						
SC	-0.333	-0.333	-0.333					
MMG	-0.577	0.115	0.000	0.462				
DFMG	0.577	-0.115	0.000	-0.462	-1.000			
SH	-0.315	-0.135	0.165	0.285	0.492	-0.492		
elev	0.308	-0.148	0.100	-0.260	-0.866	0.866	-0.501	
r	-0.151	0.082	0.236	-0.168	-0.083	0.083	0.088	0.106

Appendix D

Canonical correspondence analysis (CCA) ordination for 30 best fitting of the 53 dung beetle species (outliers removed) and measured environmental variables. Biotope (PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor) and vegetation type (DFMG, Drakensberg foothill moist grassland; MMG, midlands mistbelt grassland) are included as factors. Other variables included are elevation (elev), mean soil hardness (SH) and rockiness (r). TDB, tunnelling dung beetles; RDB, rolling dung beetles. See Appendix B for list of species abbreviations.



Appendix E

Canonical correspondence analysis (CCA) ordination for 30 best fitting of the 64 ant species and measured environmental variables. Biotope (PA, protected area; LC, large corridor; MC, medium corridor; SC, small corridor) and vegetation type (DFMG, Drakensberg foothill moist grassland; MMG, midlands mistbelt grassland) are included as factors. Other variables included are elevation (elev), mean soil hardness (SH) and rockiness (r). See Appendix B for list of species abbreviations.

