The effect of commercial forestry plantations and roads on southern Afrotemperate forest arthropod diversity

by
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I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

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“Die Knysna-Bos is 'n lewende entiteit wat ons moet respekteer en bewaar”

“The Knysna Forest is a living entity which we should respect and conserve” - Dalene Matthee

General summary

With only about 12% of the Earth's surface under some form of official protection and the human population on the rise exponentially, production landscapes can and should contribute significantly towards biodiversity conservation in the future. Globally, management practices that balance production and conservation are important for creating sustainable agriculture and timber production landscape. This study aims to determine how a heterogeneous, unfenced national park in South Africa, containing a mosaic of commercial plantations, natural forests and fynbos is affected by land transformation. This was achieved by focussing on artificially created and natural edges found in this landscape, through analysing and comparing the composition and species richness of arthropods across linear transects. Specifically I determined if natural edges next to southern Cape Afrotemperate forests are altered by anthropogenic influences such as forestry plantations, and their felling, as measured by epigaeic arthropod diversity. The effects of different road types, and directions that these roads dissect the forest, were also assessed. I found that pine plantations provide little suitable habitat for either forest or fynbos arthropods. The natural fynbos-forest ecotone harbours a unique composition of arthropod assemblages, with the smallest edge effect into the forest. Once this is replaced by commercial pine plantations, an edge effect up to 30 m into the forests from the plantation edge is detected. When plantations bordering natural forests are felled, the edge effect increases to 50 m into natural forests. Research on edge effects created by roads showed that both wider, arterial roads as well as secondary roads affected the diversity of forest arthropods up to 50 m into the natural forest. These effects are therefore similar to that observed after clear felling of plantations except that, in contrast to possible regeneration of natural edge habitat after clear felling, these edges are now permanent fragmentary features in the forest with little chance of recovery. Even hiking trails affected overall arthropod assemblages in the adjacent forests up to 10 m. Although this likely does not lead to forest fragmentation due to an in-tact forest canopy, these areas alter natural assemblages with unknown population dynamic consequences. I also show that east-west directed roads have

stronger fragmentary effects as determined by arthropod diversity, along their southern edge than north-south directed roads, with east and west facing edges. Increased sunlight penetration, with its accompanying changes in microclimatic conditions is put forward to explain these differences. Habitat loss due to the establishment of commercial plantation forestry in the region not only leads to a decrease in suitable fynbos habitat, but also impacts adjacent natural forest arthropod diversity. The remaining southern Cape Afrotemperate forests are greatly fragmented by a network of roads. Due to the uniqueness of these forests, special management is needed to ensure that the biodiversity in the region is optimally conserved without adversely affecting production yields. Some possible mitigation actions are put forward. However, these should be assessed for their effectiveness in future research studies before they are implemented.

Opsomming

Met slegs sowat 12% van die Aardoppervlak tans amptelik beskerm en die aanhoudende, eksponensiële groeikoers van die mens, het die tyd ryp geword vir die mens om te besef dat landskappe wat nie amptelik beskerm word nie kan en sal moet bydra tot biodiversiteitsbewaring. Wêreldwyd is bestuurspraktyke rakende volhoubare landskappe, wat poog om 'n balans te handhaaf tussen bewaring en produksie, bewys om suksesvol by te dra tot bewaring. Hierdie studie het beoog om te bepaal hoe 'n heterogene, onomheinde nasionale park in Suid-Afrika, met kommersiële plantasies, natuurlike woude en fynbos wat groot areas binne die grense van die park bedek, geraak word deur die rande van hierdie aangrensende habitat-tipes te bestudeer. Dit was gedoen deur na beide die natuurlike en versteurde woudrand te kyk. Spesifiek het ek bepaal of natuurlike woudrande se grondlewende arthropoda beïnvloed word deur kommersiële denne-plantasies en hul verwydering. Die moontlike effekte van verskillende pad-tipes en padrigtings op woudfragmentasie is ook bepaal. Ek het bevind dat denne-plantasies min geskikte habitat vir beide woud- en fynbos-arthropoda bied. Ook, sodra plantasies aangrensend aan natuurlike woude kaalgekap word, vergroot die afstand wat effekte penetreer tot sowat 50 meter binne woude. Die resultate in verband met paaie wat deur die woud loop toon aan dat wyer, hoofpaaie sowel as sekondêre paaie arthropoda gemeenskappe tot 50 meter in die woud in affekteer. Hierdie rand-effek afstand is vergelykbaar met dié van kaalkap-plantasie areas, alhoewel dit verskil in die feit dat die paaie permanente fragmentasie veroorsaak en kaalkap areas moontlik gerehabiliteer kan word. 'n Interessante bevinding was dat ook staproetes die diversiteit van arthropoda beïnvloed tot en met 10 meter langs die roetes. Alhoewel dit nie tot fragmentasie lei nie, aangesien die blaredak steeds onbeskadig is, verander die natuurlike gemeenskappe met onbekende gevolge rakende hul populasie dinamika. Resultate toon ook aan hoe paaie wat in 'n oos-wes rigting loop meer invloed uitoefen op woude aan die suiderkant van hierdie paaie, teenoor noord-suid paaie wat minder invloed uitoefen. Verhoogde vlakke van sonlig-penetrasie, met gepaardgaande mikro-klimatiese veranderings, kan moontlik hierdie

bevindings verduidelik. Die verlies van habitat vanweë die plant van grootskaalse plantasies lei nie net tot ‘n vermindering in geskikte fynbos habitat nie, maar dit affekteer ook die aangrensende woude se natuurlike arthropoda diversiteit. Ter opsomming is gevind dat paaie wel die oorblywende Suid-Kaapse woude fragmenteer. Vanweë die uniekheid van hierdie woude, word spesiale bestuur vereis om te verseker dat die groter area se biodiversiteit optimaal bewaar word sonder om opbrengste te danke aan produksie te beïnvloed. ‘n Aantal moontlike versagtings-aksies word ter tafel gesit. Dit word egter aangeraai om die sukses van hierdie metodes eers te bepaal voordat dit geïmplementeer word.

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1.1) General Introduction

1.1.1) The biodiversity crisis and defining state of landscape disturbance

As the human population and its effects on the landscape increases, natural ecosystems are becoming increasingly under pressure. Globally, natural landscapes are being transformed on a daily basis; a stark reality of the ever growing human population and its growing requirements. The price paid is often loss of biodiversity that result in severe negative effects on ecological functions (Loreau *et al*. 2001). Attempts to counter biodiversity loss have been made, with most governments recognising the need for healthy, functional ecosystems. At the World Summit for Sustainable Development in 2002 (WSSD), world leaders agreed to significantly decrease the loss of biodiversity by the year 2010 (Hanski 2005), indicating at least an interest by world leaders in global environmental issues. However, the implementation of these targets is often difficult or non-existent (Veitch *et al*. 2012). Accountability seems to be lacking, although there has been a steady increase in areas under protection since the dawn of the green revolution, starting in the 1960's (Pingali 2012). During the 1970's, approximately 4 000 000 km^2 of terrestrial land was considered protected. By 2003 this figure rose to more than 16 000 000 km^2 (Chape *et al*. 2005). Today, between 8.85 and 11.5% of Earth's surface is under some form of protection (IUCN 1998; Rodrigues *et al*. 2004), with more recent figures estimating it at around 12.2% (Chape *et al*. 2005). The need to assess the effectiveness of these areas in protecting biodiversity arises. Viewed from a landscape level, protected areas can often be seen as islands of biodiversity surrounded by a matrix of land-uses that are hostile environments for most biodiversity. Habitat transformation, fragmentation, harvesting of species, limited migration both into and out of reserves, edge effects and climate change are just some of the potential challenges often, but not exclusively, experienced by areas under protection (Newmark 1987; Liu *et al*. 2002; Berger 2003). Habitat transformation is currently the single greatest threat to biodiversity within large tracts of land getting converted to agricultural and urban environments (Brooks *et al.* 2002), yet these transformed areas may also effect neighbouring natural areas through edge effects and the breakdown of the metapopulation (i.e. through fragmentation) (see Fahrig 1997; Hanski 1998) Therefore, it is important to understand that anthropogenic threats to biodiversity are not confined to areas outside of reserves only and that ecosystems face on-going disturbances even under formal protection. Failure to effectively conserve biodiversity in areas already protected could render our attempts in maintaining sustainable landscapes futile.

A big task and responsibility of 21st century ecologists is to properly define and measure landscape transformation and habitat loss and the resulting disturbance on ecosystems, first and foremost, where after solutions and mitigation strategies can be formulated. However, a single disturbance is often multiple in its effect, possibly leading to a cascade of effects in the ecosystem as a whole (Pace *et al*. 1999). A well-studied example of cascades in ecosystems is from the Costa Rican wet forests, where the presence of a top predator (Clerid beetle) is associated with lower amounts of intermediate predators (specialized ants), and in turn linked to greater herbivory and less abundance of plants (Letourneau & Dyer 1998). These indirect effects, of species on one another through a series of linked biotic interactions, could eventually completely alter ecological integrity if disturbed (Wootton 1994). Moreover, these effects are often difficult to measure by the researcher due to the fact that the ideal state to which we are working towards is often poorly understood. Ecological intactness without a comparative ecological reference state is immeasurable (Rykiel 1985). The concept of an ecological reference in ecosystems remains widely discussed and ever-evolving and could possibly provide useful information on future monitoring as well as current status, if attainable (Hawkins *et al*. 2010). More often than not, an ecological reference condition is lacking. Ecological reference typically refers to a natural ecological condition with minimal or no human disturbances or alterations, or alternatively a condition from the past that serves as a comparable benchmark of biodiversity for a certain area (Stoddard *et al*. 2006). Several categories of reference conditions have been put forward, including minimally disturbed condition (MDC), historical condition (HC), least disturbed condition (LDC) and best attainable condition (BAC) (Stoddard *et al*. 2006). These have been suggested due to the disparity in what a reference condition is defined to be and the difficulty of finding a true natural state. Natural fluctuations in time and space are difficult to separate from unnatural disturbances, and the limited time scale in which many studies are performed further hinder the possible correct quantification of an ecological reference (Willis & Birks 2006). Therefore, it is not always easy to truly monitor protected areas, or identify a disturbance unless it is conspicuous.

1.1.2) Indicators of ecological health

Even with an ideal ecological reference state mostly lacking or difficult to gather, gateway has been made towards defining and measuring ecological disturbance with the advancement of use of bioindicators. Indicative of the state of a given environment, these indicators provide the researcher with a tool to assess ecological integrity as a whole, and importantly, indicate the presence of a disturbance (McGeoch 1998). Ecological integrity, defined as the intactness of an ecosystem with all its natural species assemblages and processes, is measurable given that appropriate indicators are identified (Karr 1991). Indicators should be measurable surrogates for larger environmental conditions, or end-points, and therefore need to be 1) sensitive towards stress, 2) widely distributed, 3) easy to collect, 4) distinguishable in their reaction between natural and human-induced stress and 5) relevant to the phenomenon in question (Noss 1990). *Ecological indicators* are defined as characteristic taxa that responds in a predictable manner towards disturbance, also indicating stress on other taxa in the ecosystem (McGeoch 1998). It may take many forms, for example witnessing changes in the spatial distribution of species in assessing landscape level disturbance, monitoring population sizes in assessing disturbance in a particular species or comparing species richness through space and time in measuring ecosystem-level disturbance (Karr 1991). Another form of indication of disturbance in ecological systems are environmental indicators. *Environmental* *indicators*, as defined by McGeoch (1998), are those indicative of a change in a given environment. They are species or a set of species that respond in predictable, measurable ways towards stress of whichever form (see Spellerberg 1991). They are used to detect and monitor specific changes in the environment, whereas ecological indicators differ by demonstrating the impact, usually in long term monitoring (McGeoch 1998). A third form of indication is that of biodiversity indicators. *Biodiversity indicators* refer to measurable parameters in an ecosystem, such as species richness and endemism, genetic variables in populations, landscape parameters (which may include variables such as the shape of an ecosystem and dispersal between viable areas, for example), parameters pertaining to species and the community compositions they form part of and also community-ecosystem parameters (referring to how diversity is spread across a certain geographical range). An umbrella term encompassing most indicators of ecological integrity, as used by most authors, is the term ‘bioindicator’. Bioindicators are single species or alternatively a group of species indicative of a larger interactive system, which with its presence, absence or community-level changes could indicate disturbance in an ecosystem (McGeoch 1998). It needs to be able to reflect not only the state of a system, but also be indicative of the impact of the disturbance on the habitat, larger species communities and the whole ecosystem by being intricately connected to a subset of taxa or diversity in general (McGeoch 1998). For example, bioindicators could indicate the diversity of other species, an important tool when considering indirect, cascading effects that a disturbance might have on ecosystems (Rainio & Niëmela 2003). In ecosystems facing anthropogenic disturbances, the use of any of these sets of indicators reflective of the system’s status is much needed and can be used to make important managerial decisions. This is especially true in areas already protected, or ecosystems where restoration of disturbed areas is a key priority. Important is the selection of taxa for indication, and countless studies have been done using, and in effect testing, a wide array of possibilities. Whereas vegetation surveys are often used in restoration ecology and biodiversity monitoring (Keenan *et al*. 1997; Moore *et al*. 1999; Seabloom & van Der Valk 2003), arthropods remain one of the most widely used indicators of ecological health. Due to their abundance, ecological role, unique life history and diversity in behaviour, arthropods are regarded as the epitome of bioindication (McGeoch 2007). Also, having short reproductive spans and being able to show rapid responses to micro-environmental change, they further fit the bill in terms of indication (McGeoch 2007). Capturing arthropods is also not too difficult a task, with numerous trapping methods in existence, each one specializing on a certain guild or niche of arthropods. Furthermore, arthropods provide us with vital ecosystem services, furthering their importance in ecosystems and value in biodiversity surveys (Longcore 2003). Examples of studies where arthropod bioindicators are used in monitoring restoration are plentiful (Longcore 2003; Nakamura *et al*. 2003; Gratton & Denno 2005; Moreira *et al*. 2007; Zeppelini *et al*. 2009). Biological indication, whichever taxa is used, may take many forms, including species compositional changes, species richness changes and changes in abundance of certain taxa (Uehara-Prado *et al*. 2009). An example of where a specific arthropod taxon is used as indicators include the Dragonfly Biotic Index, or DBI, where the sensitivity of Odonata species to their environments may be used as a tool to measure the health of the environment, and especially water bodies, in question (Simaika & Samways 2011). How we define indicators and their role in research though, should be kept in mind. The purpose of bioindicators will always be limited to indication, whether it be indication towards disturbance, successful restoration or indication of ecological health, remaining largely unconcerned with the countless mechanisms driving these outcomes. The outcomes are variable and largely depend on the focal taxa used. For example, studies done in the Atlantic Forests in Brazil showed a difference in restoration success outcomes when using gall insects compared to ants as bioindicators (Moreira *et al*. 2007). In using vegetation survey data compared to spider diversity in measuring restoration success on limestone quarries, Wheater *et al*. (2000) found dissimilarities between restored and natural sites, indicating the importance of using more than one focal group. It also highlights the differences in sensitivity towards disturbance by different taxa. The choice of bioindicator could also be area specific, in the sense that certain species are better equipped as bioindicators than others for a given area (Latha & Thanga 2010). It is commonly advised that different taxa should be included in monitoring studies in order for the researcher to gather a wider perspective on the ecological interactions possibly affected by disturbance, and to better measure successful restoration (Di Castri *et al*. 1992; Solbrig 1991; Hammond 1994; Gardner *et al*. 2010; Feest *et al*. 2011). In fact where feasible a multi taxon approach is considered vitally important for studies monitoring biodiversity responses to ecological factors (Gerlach *et al*. 2013).

1.1.3) Arthropods as indicators of forest ecosystem health

Forests are unique ecosystems. With at least half of all species on earth found in tropical forests, it is important to note that tropical forests are being depleted at unparalleled rates compared to other biomes (Myers 1988). Globally, the ecosystem services provided by tropical forests are irreplaceable and humanity is directly and indirectly dependent on these areas for our wellbeing (Daily 1997). Therefore, we need to continually assess global forest integrity, working with the biological tools available indicative of healthy forest ecosystems. The abundance of arthropods in especially tropical forests, and their micro-niche specifications, adds credence to their use in bioindication (Erwin 1982). They play vital roles in upholding forest ecosystems (see Seastedt & Crossley 1984). Forest invertebrates in general also prefer cooler temperatures and higher humidity compared to non-forest species, and are sensitive to even the smallest changes in their preferred niches (Pearce & Venier 2006). It is this sensitivity of many specialized arthropods that indicate the smallest environmental change that makes them valuable as bioindicators (Gerlach *et al*. 2013).

In terms of disturbance indicators, ants, ground beetles, dung beetles and spiders are among the most often used taxa in forests when assessing human altered landscapes (Maleque *et al*. 2009). Ground beetles (Coleoptera: Carabidae) have been proven for example to be good indicators of forest fragmentation due to their biology. Carabid beetles are, with a few exceptions, large and conspicuous, easily sampled by use of pitfall trapping (New 2010). Also, their assemblages readily change in relation to habitat modifications or – characteristics, holding implications for ecological studies across landscapes (i.e. reserve design) (Baker *et al*. 2006). Being one of the larger families of Coleoptera, with estimates ranging from 25 000 – 40 000 species (Thiele 1977; Lovei & Sunderland 1996), they hold large variety and have very high local endemism (New 2010). In New Zealand, for example, a total of 50 genera of ground beetles are endemic out of a known total of 78 (Larochelle & Lariviere 2007). Due to ground beetles being ‘abundant, speciose and ecologically well-known’ (Niëmela 1996), they are important in conservation planning and evaluating human-altered landscapes (Holland & Luff 2000). Dung beetles (Coleoptera: Scarabaeidae) as well are excellent indicators of disturbance in forests and useful in overall biodiversity monitoring (Klein 1989; Koivula *et al*. 2002; Magura 2002; Spector 2006). Their close association with their host species, mostly herbivores, makes them useful as indicators of the diversity of other species (Koch *et al*. 2000). Not only limited by dung presence, the habitat structure and soil type also largely influence the occurrence of dung beetles (Hill 1996). Davis *et al*. (2000) found lower dung beetle species diversity in plantations compared to rain forest, with plantations containing generalist and some natural forest species and virtually no forest-interior endemics. Ground moisture could also influence dung beetle diversity, with a study showing increases in dung from an increased deer population in Japan did not manifest in a higher dung beetle turnover; instead, higher exposure due to tree mortality altered soil moisture levels, limiting increases in dung beetle numbers (Kanda *et al*. 2005). The close association of dung beetles to their hosts and habitat, coupled with the fact that as a family they are well-described, makes them useful as tools of indication in conservation studies. Ants (Hymenoptera: Formicidae) is another taxonomic group often used as bioindicator (Samways 1983; Samways *et al*. 1996; Andersen 1997; Andersen *et al*. 2002; Nakamura *et al*. 2007). Their abundance, use of habitats, easy identification and easy sampling makes them useful tools of indication (Schmidt *et al*. 2013). Spiders in forests, another possible indicator of ecological health, are abundant and react readily to altered systems (Coddington *et al*. 1996; Churchill 1998), and have been used in their capacity as indicators of ecosystem health (Bromham *et al*. 1999; Willet 2001).

1.1.4) Threats to forests: Habitat loss and the forest edge

The loss of natural landscapes is one of the major contributors towards species extinction (Groombridge 1992; Burkey 1995; Didham *et al*. 1996; Niemelä 1997). Of all the factors leading to losses of natural ecosystems, anthropogenically caused habitat destruction contributes the most towards this phenomenon (Pimm & Raven 2000). The effects of habitat loss are countless and found to be more severe than habitat fragmentation (Fahrig 1997). The major cause of forest loss globally is the clearing of forests for production landscapes in order to supply for a growing human demand (Sharma & Rowe 1992). Although the most observable effect of forest loss is the extinction of species, as mentioned, the important role of forests in providing us with vital ecosystem services are equally relevant when assessing the effects of forest loss. Global hydrologic and carbon cycles are important regulatory processes performed by forests, which in turn contribute meaningful feedback to global changes (Laurance 1999). Forest loss is therefore not only a local catastrophe, but a global problem with wide-reaching effects. On top of this, human activities in and around forests usually tend to increase the amount of forest edge, often transforming the natural landscape's 'soft edges' into 'hard edges', referring to the permeability of an edge (Stamps *et al*. 1987). Edge permeability is the concept ascribed to the flow of energy and matter across an edge, with 'hard' edges referring to a starker contrast in vegetative characteristics than 'soft' edges (Laurance *et al*. 2002; Strayer *et al*. 2003; Lopez-Barrera *et al*. 2006). Ecotones, defined as the interface between two differing ecological communities (Kark 2013), is an important field of study in ecology as human altered landscapes tend to increase ecotonal areas in natural ecosystems. In mosaic landscapes, where we find natural areas occurring amidst human-altered areas, the interface between natural versus altered habitats and how species perceive it could play significant roles in the success of conserving optimal biodiversity (Pryke & Samways 2012). Viewed on a landscape-level, ecotones serve either as barriers for certain species, or as corridors between habitats (Magura 2002), with the permeability of the edge being an important factor. For example, forest dung and carrion beetles have been found to be severely affected by clear cut areas in Central Amazonia, perceiving a clear cut edge as an impenetrable barrier, thereby hindering dispersal to other forest fragments (Klein 1989). Furthermore, altered areas amidst native forests often fail to serve as stepping stones between forest fragments for arthropod species, limiting their possible dispersal and associated gene flow (Magura *et al*. 2001). Hard edges have been proven to impact ground beetle dispersal compared to soft edges, in a study done by radiotracking individuals, by serving as a barrier for dispersal (Charrier *et al*. 1997). The composition of taxa found at the undisturbed, natural ecotone is often unique too, having conservation value in itself as edge specialists (Magura 2002). Their role in forest succession and acting as source populations for recovering habitats should not be overlooked (Molnár *et al*. 2001).

The edges of forests and how species perceive it are thus as crucial as the intact habitat itself in optimal forest protection. Not only are there significant changes in species compositions and abundances at the edge, the micro-climatic changes encountered at the edge might have significant effects penetrating deeper into the forest interior. Whereas an intact forest canopy serves as a buffer, protecting the interior from external factors, a degraded edge allows for severe micro-climatic changes (Laurance *et al*. 1998). These micro-climatic changes often reach deep into the forest interior, altering natural ecological functioning and species compositions (Ferreira & Laurance 1997). These effects, termed edge effects, are measured by the distance the effect penetrates into a natural ecosystem (Murcia 1995), or alternatively the magnitude of the effect at any given distance into an ecosystem (Laurance & Yensen 1991). The effect of the edge into natural ecosystems is variable, depending on the habitat type and bordering land-use (Bieringer & Zulka 2003; Baker *et al*. 2007; Pryke & Samways 2012). The magnitude and distance of the edge effect are directly related to the differences in composition and structure of the two bordering communities (Didham & Lawton 1999; Harper *et al*. 2005). Importantly, unprotected landscapes have potential to contribute towards biodiversity conservation, and could be incorporated in conservation planning to assist protected areas towards this purpose (Bhagwat *et al*. 2008). For example, soft edges, i.e. selective logging instead of total deforestation around natural forested areas could aid biodiversity conservation in the remaining forest, by having less of an edge effect (Broadbent *et al*. 2008). Also, edges being left to naturally regenerate and not being exposed to fire have been found to be 2-5 times less severe in their penetrating effect in central Amazonia (Didham & Lawton 1999). Land-uses such as commercial plantations will predictably thus have less of an edge effect than clear cut areas, for example, being similar in structure and vegetation height than natural forests (Peyras *et al*. 2013).

Due to differences in responses by different species, the edge effect will predictably not be similar for any two taxa (Matlack 1994; Murcia 1995). An edge effect, in definition, is a broad term with many encompassing factors possibly affecting biodiversity. These factors include any abiotic changes, for example wind increases, sunlight increases and temperature increases, indirectly facilitating biotic changes, such as tree diameter changes, species compositional changes and changes in species richness (Foggo *et al*. 2001). Therefore, each study conducted on edge effects will possibly harbour different results, depending on the vegetative characteristics of both the natural habitat and the bordering altered area. In a Tasmanian wet *Eucalyptus* forest, bordering a regenerating natural forest edge, beetle assemblages have been found to be similar to interior assemblages only at 22 m into the natural forest (Baker *et al*. 2006). Whereas most edge effects in forests are found to stop at around 20-50 m (Murcia 1995), some research suggests edge effects of more than 1 kilometre, depending on forests type and taxa used in assessments (Ewers & Didham 2008). In the Amazon, the world's largest tropical forest, the median edge effect is approximately 100 metres, when comparing a multitude of affected taxa across 146 literature reviews (Broadbent *et al*. 2008). Studies using ants as bioindicator of a possible edge effect in tropical forests bordering human altered areas, were dissimilar in outcome when comparing the distance of the penetrating effect: From zero edge effect (Majer *et al*. 1997) to 200 m (Carvalho & Vasconcelos 1999; Wirth *et al*. 2007). Laurance *et al*. (1997) proposed a penetration effect of 80 m, in terms of changes in the forest structure and microclimate, into natural forests. In general, for forest invertebrates, species richness and abundances are usually affected in the first 100 m from the forest edge, with assemblages showing significant changes at 200-300 m (Ries *et al*. 2004; Laurance *et al*. 2002; Ewers & Didham 2008). There seem to be no general pattern regarding the distance of an edge effect and taxa affected, with much disparity from the literature. It is clear though that altered edges influence the occurrence and dispersal of native forest arthropods. The extent to which this is happening though is specific to multiple local conditions and extrapolation from previous studies should be done with caution.

1.1.5) Threats to forests: Habitat fragmentation and roads in forests

Throughout the world, and especially in the tropics, forest fragmentation is having significant effects on forest integrity and species dispersal (Turner 1996). For example, it has been found that carabid assemblages are more species rich in smaller forest patches than larger, unfragmented forests due to the increasing influx of generalist species from the surrounding matrix with decreasing forest patch size (Niëmela & Halme 1992; Halme & Niëmela 1993; Pihlaja *et al*. 2006). Homogenization of species compositions often tends to increase as fragmented areas become more abundant, and edge specialist species often flourish in areas altered by human activities, predictably to the demise of deep forest specialists (Didham *et al*. 1998). For example, species occurring at forest edges have been proven to be positively affected by increases in fragmentation (Cappuccino & Root 1992; Didham *et al*. 1998). Considering their provision of vital ecosystem services and role in maintaining forest health, changes in arthropod diversity due to fragmentation could have devastating cascading effects on forest ecosystems. Human activities, such as forest clear-cutting, road construction or fire, often result in the removal of the forest canopy, indirectly impacting forest specialists. Without an intact forest canopy, increases in wind flow, temperatures and drier soil conditions directly impact forest arthropods by altering their preferred niche-zones (Pearce & Venier 2006). This makes forests especially vulnerable to fragmentation. A similar principle of forest edge effects applies for forest roads. From the literature it is evident that the edge effect created by roads in forests is unique to every situation. In natural landscapes, we find edges where two habitat types, or biomes, border, with species naturally adapted to these areas. In forests, temporal gaps in the canopy occur naturally, whether it is due to fire, windfall trees or floods. Roads, on the other hand, are unnatural in their creation of a permanent edge, and in forests, contribute towards networks of linear canopy gaps creating unnatural abiotic changes (Coffin 2007). By doing this, roads increase the amount of edge in a forest and could result in a fragmented landscape as opposed to a continuous habitat (Reed *et al*. 1996). Many studies from around the globe indicate a negative response from indigenous forest biodiversity towards the establishment of roads (Reed *et al*. 1996; Tinker *et al*. 1998; Coffin 2007). Microclimatic changes caused by roads could affect leaf litter and vegetation composition, soil macro-invertebrates and overall species richness with variable effects in time (Coffin 2007). The edge effect created by roads might be even greater than clear cut areas, dissecting larger forest areas into smaller patches (Reed *et al*. 1996). Also serving as an unnatural edge as perceived by the bordering forest's species, roads may severely alter ecological intactness several metres into a forest (Avon *et al*. 2010). Research conducted in the Chequamegon National Forest, Wisconsin, have found an edge effect of 15 metres into the forest based on plant assemblages, with most invasive species being found at the road verge (Watkins *et al*. 2003). The facilitation of invasive species by roads is not uncommon (Forman *et al*. 2003; Gelbard & Belnap 2003). Other studies found the effect of roads on plants to be less than 5 metres (Avon *et al*. 2010), while road effects of up to 200 metres have also been reported (Angold 1997). Arthropods are also affected by roads dissecting forests. Roads could also serve as physical barriers for specialized forest beetles, limiting their dispersal abilities (Koivula & Vermeulen 2005). For example, Keller & Largiader (2003) found that roads are absolute barriers for gene flow in *Carabus violaceus,* a species of ground beetle found in Europe and Japan, causing a loss in genetic variability. On the other hand, it has been suggested that roads can act not only as corridors, facilitating species dispersal, but also serve as unique habitats hosting mostly generalist open habitat species (Koivula 2005). In the Netherlands, roads with broad verges have been found to contribute towards ground beetle dispersal between heathland fragments, with the width of the roadside verge influencing dispersal success (Vermeulen & Opdam

1995). Again, the edge effect created by roads in forests is unique to every situation. Road type, -width, -age, amount of traffic and forest type will all influence how species perceive roads (Coffin 2007).

1.2) Study Area

1.2.1) Forests in South Africa: the southern Cape forest complex

In South Africa, forests cover only 0.56% of the total land area, making it the smallest biome in the country (Low & Rebello 1996; Mucina & Rutherford 2006). Compared to other forests situated in temperate regions across the globe, South Africa's forests are highly diverse regions with tropical features (Phillips 1931; Berliner 2011). Naturally, the indigenous forests of South Africa are patchy in their distribution, with most forest patches being less than 1 km^2 in size (Cooper 1985; Geldenhuys 1989; Low & Rebello 1996). In total, about 20 000 forest patches are found in South Africa (Berliner *et al*. 2006). The discontinuity of South Africa's forest biome is a result of historic climatic fluctuations and disturbance regimes, especially during the last 180 000 years (Partridge *et al*. 1990; Eeley *et al*. 1999; Lawes *et al*. 2000). From lignite deposits, it has been revealed that the southern Cape region supported subtropical vegetation with Restionaceae, palms and forest elements (Thiergart & Frantz 1962; Helgren & Butzer 1977; Coetzee *et al*. 1983). These tropical elements have been in existence before the development of the circum-Antarctic ocean system, the cold Benguela current on the west coast of South Africa and the enlarged Antarctic ice sheet (Shackleton & Kennet 1975; Van Zinderen Bakker 1975; Vail & Hardenbol 1979). During the Late Miocene, a shift from subtropical forests to typical fynbos and strandveld elements occurred (Coetzee & Rogers 1982; Hendey 1984; Scott 1995). Today, forests are confined to kloofs, large screes and zones safe from fire, especially in the Western Cape Province. However, even with its small size and fragmented nature, these forest relics contain much biodiversity worthy of conserving (Geldenhuys 1989). In terms of plant species richness per unit area, South African forests are second only to the highly diverse fynbos biome (Gibbs Russel 1985; Gibbs Russel 1987). On a global scale, these forests have the highest tree diversity of any warm-temperate forest on earth and are unrivalled in the southern Hemisphere despite its small surface area (Silander 2001). Also, the diversity of genera and families are unmatched globally (Silander 2001; Cowling 2002). The conservation of the biodiversity within these forests becomes increasingly important as approximately 42.5% have been transformed and continue to be transformed (Eeley *et al*. 2001).

In Southern Africa today, two major forest types exist: Afrotemperate forests and Indian Ocean coastal belt forests (Moll & White 1978; Berliner 2011). The indigenous forests of the southern Cape are considered as the largest forest complex in South Africa (Phillips 1931; Acocks 1988), comprising approximately 60 561 hectares (Geldenhuys 1991). The Southern Cape Afrotemperate Forest complex, stretching roughly from Mossel Bay in the West to Humansdorp in the East, can be subdivided into three categories based on species composition: Firstly, the mountain forests, which is typical Afromontane forest (White 1978); secondly the coastal escarpment forests, which in terms of species composition largely coincides with the Indian Ocean coastal belt forests more to the north (Moll & White 1978); and lastly the plateau forests which includes many species associated with Afromontane forests (Geldenhuys 1982). Within the mountain forests, *Cunonia capensis* and *Ocotea bullata* are the most abundant tree species, whereas the most common species within the plateau forest are *Olea capensis* subsp. *macrocarpa*, *Podocarpus latifolius*, *Pterocelastrus tricuspidatus* and *Gonioma kamassi* (Geldenhuys 1982). Since the discovery of the forest by Europeans in 1750, the forests have been utilized with associated anthropogenic disturbances due to the high timber value of many of these species (Geldenhuys 1991). From 1778 to 1939, conservation policies gradually developed, with a practical conservation system being implemented in 1874 (Phillips 1931). By 1939 the forests were closed for exploitation (Geldenhuys 1991). Re-opened in 1965, due to sufficient recovery of the indigenous forests, the state controlled exploitation from there on through scientific measures (von Breitenbach

1974). In the area of the southern Cape, stands of alien trees were planted by the government from 1876 onwards (Phillips 1931). These trees, mostly of *Pinus*, *Eucalyptus* and *Acacia*, were planted on native fynbos bordering the natural forests, as well as areas of unnaturally opened forests (Phillips 1931). Since 2009, with the formation of the Garden Route National Park, the southern Cape forests are officially protected, with the only exploitation of indigenous timber being limited to individually identified trees. Today, the landscape is typically in a patchwork mosaic. The forests have been fragmented historically by fire (Geldenhuys 1994), grazing, exploitation and clearing, and today are limited physically by rainfall (Geldenhuys 1991). Ongoing commercial forestry practices further limit natural forest establishment in the area, but plantations show the potential of encouraging the establishment of forest species (Geldenhuys 1991). In 1991, exotic plantations of mainly pine and eucalypts occupied a total area of 76 750 hectares (compared to 60 561 ha of forest) with few major changes since. The landscape is continually changing, due to the commercial forestry practices occurring within the area. Clear felled plantation areas cover extensive land, often bordering indigenous forests, and these open areas take years to recover to either exotic plantation trees or, if left to recover, to natural veld. Naturally, forests in the southern Cape would border fynbos, a very diverse, fire-adapted biome consisting of low- to medium sized shrubs. Different subdivisions of fynbos bordering the forests of Knysna are found in the southern Cape. This includes South Outeniqua Sandstone Fynbos, Tsitsikamma Sandstone Fynbos and most importantly, Garden Route Shale Fynbos (Mucina & Rutherford 2006). The latter occurs within the study range of the present study, with wide belts of *Virgilia oroboides* occurring at the interface between fynbos and forest (Mucina & Rutherford 2006). This fynbos vegetation type is classified as endangered, with more than half of the area already transformed due to crop cultivation and the establishment of pine and eucalypt plantations (Mucina & Rutherford 2006).

1.2.2) Climate

The climate of the southern Cape, coupled with the topography of the area, enables the persistence of the large southern Cape forest complex. The southern Afrotemperate forest vegetation unit is mostly determined by high rainfall throughout the year (Mucina & Rutherford 2006), persisting in areas with a mean annual precipitation of 863 mm. Whereas a high average rainfall is a definite determinant of forest persistence, the extent of southern Cape forests are locally driven intensely by fires which in turn are driven by dry mountain winds (Geldenhuys 1994). The endemic fynbos naturally bordering the forests of the region is in fact a fire-prone biome even though fires rarely penetrate the Afrotemperate forest (van Wilgen *et al*. 1990). This is partially due to the unique topography of the southern Cape, with a mountain shadow effect of particular importance in the area, allowing for much of the precipitation received whilst excluding fires to penetrate the forests. The Fynbos bordering the southern Cape forests receives a mean annual rainfall of 700mm (310-1 120mm) (Mucina & Rutherford 2006).

1.2.3) Geology of the study area

The larger southern Cape region has a range of substrates with a unique geographical history. The fynbos soils are mostly acidic, moist clay-loam, prismacutanic and pedocutanic soils derived from Caimans Group and Ecca (Mucina & Rutherford 2006). The southern Afrotemperate Forest are found on soils varying from shallow Mispah, Glenrosa and Houwhoek forms to sandy Fernwood form. These soils are derived from the Table Mountain sandstone group and shales from the Cape Supergroup. These soils are also partly derived from Cape Granite.

1.3) Problem statement, aim and thesis outline

The forest biome of South Africa is unique, not only locally, but globally. Whereas by far the most studies on the southern Cape forest complex focused on trees and optimal forest management, today little is known regarding especially arthropods within this area. Previous studies focusing on birds included some monitoring of invertebrate numbers (re: Koen 1988;

Koen 1992). There is a lack of data pertaining to the native arthropods (Fynbos and Afrotemperate forests) and their role in upholding these ecosystems which are in a constant battle for space at the fynbos-forest interface. Also, forestry production areas cover vast tracts of land in the region, often established on areas where Fynbos naturally bordered the forests. The effect of mature pine stands (some being up to 30 years old before being felled) and their clear felling on the ecological integrity of forests bordering these areas remains unknown. The main aim of this thesis is to determine whether or not edge zones, as measured in epigaeic arthropod diversity, exist in the broader southern Cape region as a cause of human-induced disturbance. Chapter 2 of this thesis focuses on the different major land-uses / biotopes in the southern Cape forest complex, namely fynbos, natural forests, mature pine plantations and clear felled plantations, and how they differ and interact with one another with regards to their respective epigaeic arthropod biodiversity. Specifically, I determine the effect of alteration of the natural fynbos-forest ecotone on the arthropod assemblages associated within natural Afrotemperate forests. I determine this effect in terms of the penetrating distance into forests, compared between fynbos, pine blocks and clear felled areas bordering forests. In Chapter 3 I investigate the effect of different road types and road direction on forest arthropod assemblages by using forest arthropod biodiversity as indicators of the existence of forest edge zones. In Chapter 4 I summarize my main findings and give indication of management implications of this research for optimal forest conservation.

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2) Chapter 2

The response of epigaiec arthropods to the edge effect of natural Afrotemperate forest edges created by alien timber plantations and their removal

2.1) Abstract

Landscape mosaics are diverse, interacting areas characterised by patches of different biotopes occupying spaces in close proximity to each other. Most landscapes today however have vast areas of production occurring throughout natural ecosystems, impacting species dispersal and occurrence. I determined whether, and to what extent, commercial plantations and their felling affect the natural arthropod biodiversity associated with the Afrotemperate forest edge. Forest arthropods are excellent indicators of overall forest integrity and have been used in their capacity as bioindicators across the globe. This study was done in the southern Cape Afrotemperate forest complex of South Africa, the largest continuous forest in South Africa. In this landscape, natural forests and –fynbos co-occur with exotic plantations to form a heterogeneous landscape where production and biodiversity conservation interlink. I use the natural edge between forest and fynbos as a reference for natural edges. Pine plantations directly bordering natural forests had a larger edge effect than the forest-fynbos ecotone. Once plantations are clear felled, arthropods in the adjoining forest were affected the most severely. Responses in terms of species richness and assemblage compositions were mostly taxon specific. The results emphasise the need for effective restoration of clear felled areas, with ongoing monitoring being conducted in both the disturbed patch as well as in the adjoining natural forest. The results also show that pine plantations are not effective in conserving native forest arthropod diversity, and that a stark edge exists between these two structurally similar vegetation communities.

2.2) Introduction

Natural forests world-wide are faced with anthropogenic disturbances that threaten their long term sustainability (Laurance *et al*. 2012). To mediate this loss of timber there has been a great increase in surface area covered by exotic plantations (Andersson *et al*. 2015). Totalling about 34% of the world's timber production, plantations today produce more timber than any other form of forestry (Sedjo & Botkin 1997) and may directly result in even greater reduction of natural forests (Clapp 1995; Smith-Ramirez 2004; Wilson *et al*. 2005; Echeverria *et al*. 2006). In South Africa, commercial timber plantations cover about double the 0.56% surface area covered by indigenous forests (Low & Rebelo 1996; Shackleton 2004; Berliner 2011). Although indigenous forests are rarely commercially utilised for timber in South Africa, these are under threat from resource extraction by rural communities (von Maltitz & Grundy 2000; Shackleton *et al*. 2007) and the transformation of adjacent land-uses, for example timber production areas occurring within natural landscapes (Pryke & Samways 2012).

Indigenous forests in South Africa have a natural patchy distribution, with the largest continuous complex situated in the southern Cape occupying an area of approximately 60 651 hectares (Geldenhuys 1991). These forests are unique; although being typically temperate in nature, they contain many tropical features due to their unique evolutionary history and location (Geldenhuys 1992). As a result, these forests are surprisingly high in biodiversity when compared to other temperate forests across the globe (Phillips 1931; Silander 2001).

The southern Cape region today is characterized by the native fynbos- and forest biomes intermingled with human settlement and agricultural- and forestry production areas, creating a mosaic landscape of different land-uses. Fynbos is an evergreen, sclerophyllous and fire-adapted veld-type that naturally borders forest edges in this region (Geldenhuys 1994). This vegetation is highly diverse in terms of its floral diversity (Holmes & Cowling 1997), but differs substantially in composition to forests as it is dominated by shrubs and grassy, leafless plants (Holmes & Cowling 1997). In the southern Cape, fynbos both surround indigenous forests and naturally occur as fynbos ‘islands’ within forests (Midgley & Bond 1990). However, many areas previously covered by fynbos have been converted to commercial forestry plantations to supply for a growing timber need (Geldenhuys 1994). Exotic plantations in this region occupy a total area of approximately 76 750 hectares (Geldenhuys 1991), some of which have recently been clear-felled for restoration purposes.

Although it is apparent that stands of timber plantation trees have a relatively less adverse impact on the ecological health of native forests compared to other land-uses, or serve as alternative habitat for some species (Geldenhuys et al. 1986; Knight et al. 1987; Bonham et al. 2002; Hartley 2002), they still impoverish biodiversity, and as such contribute little to native biodiversity conservation (Samways & Moore 1991; Wood & Samways 1991; Pryke & Samways 2009). In plantations globally, 94% of studies report a decrease in biodiversity when compared to natural forests (Stephens & Wagner 2007). Also, the risk of losing specialist ecotonal species found at the fynbos-forest border increases with the establishment of exotic stands of trees, regardless of the possible beneficial aspects to the natural forest interior. For example, studies on forest arthropods have shown that anthropogenically-created edges, such as those created by commercial plantations bordering native forests, have significant negative effects on assemblages of native arthropods occurring within the natural landscape (Ingham & Samways 1996; Malcolm 1997; Ozanne et al. 1997; Didham et al. 1998; Magura 2002; Baker et al. 2006; Pryke & Samways 2009). However, research conducted on arthropods in the southern Cape forests are sparse and of little conservation value (re: Koen & Breytenbach 1988).

Modification of landscapes for production purposes not only effects the patch that is transformed, but can also lead to changes in neighbouring patches through the altering of edge effects (Donovan *et al*. 1997; Magura 2002; Ries *et al*. 2004). Edge effects are naturally found in most pristine landscapes and occur between structurally different vegetation types. These edges are important for biodiversity as many species use these transition zones as habitat (Kotze and Samways 2001). In transformed landscapes, there is much more edge than would naturally occur and there may be fundamental differences between these transformed edges compared to natural edges (Pryke and Samways 2012).

Edge effects can be measured by the distance that the effect penetrates into a natural ecosystem (Murcia 1995), or alternatively by the magnitude of the effect at any given distance into an adjoining ecosystem (Laurance & Yensen 1991). The magnitude and distance of the effect are directly related to the differences in composition and structure of the two bordering biotic communities (Harper *et al*. 2005). Mechanisms that drive edge effects are diverse but include factors such as increased predation levels (Batary & Baldi 2004) as well as differences in wind speed, temperature and radiation levels (Chen *et al*. 1995). Moreover, unnatural alterations in the abiotic parameters at the forest edge could lead to a variety of edge effects, including decreases in leaf litter decomposition (Didham 1999), altered tree recruitment (Laurance *et al*. 1998) and influxes of alien species (Vitousek *et al*. 1997; Cadenasso & Pickett 2001). In turn, these effects could impact the natural biodiversity of the edge and how native species interact (Alverson *et al*. 1988; Fagan *et al*. 1999; Batary *et al*. 2014).

Forest arthropods make up an important component of forest biodiversity (Taylor & Doran 2001, Oxbrough *et al*. 2010). They occupy all areas from soil and leaf litter layers, to herbaceous understory layers as well as the canopy (Taylor & Doran 2001; Oxbrough *et al*. 2010). Arthropods also play an important role in many ecosystem processes such as nutrient cycling and pollination (Taylor & Doran 2001; Lawes *et al*. 2005; Lencinas *et al*. 2008; Oxbrough *et al*. 2010). Furthermore, arthropods have a vital role in food webs acting as herbivores, predators and also serving as the main food source for many vertebrates (Taylor & Doran 2001; Oxbrough *et al*. 2010). Understanding the ecological interactions that exist between arthropod communities and vegetation characteristics is essential for indigenous forest management. Predictably, the transformed ecosystems and land-uses that surround and occur within the southern Cape forests will influence and have influenced arthropod communities within the forest itself (Kotze & Samways 1999), possibly with an effect on the natural ecological functioning of the forest. Studies from other forests in South Africa indicate that transformed landscapes, especially those under commercial plantations stands, do impact native arthropod assemblages (Kotze & Samways 1999; Pryke & Samways 2009, 2012). Plantations have also been found to be less species rich in terms of ant biodiversity compared to fynbos (Donnelly & Giliomee 1985; Manders 1989). However, the effects of transformation and/or restoration efforts on arthropod assemblages have not been evaluated in the southern Cape Afrotemperate forest complex, or any forest that is associated with endemic South African fynbos vegetation.

Terrestrial invertebrates serve as excellent indicators of the health of many ecosystems, and have become an increasingly important tool for biological surveys over the last three decades due to their importance in ecological processes (Oliver & Beattie 1996; Whitmore *et al*. 2002; McGeoch *et al*. 2011). Given their high value as indicators of ecological integrity, I use ground dwelling arthropods to get a better understanding of the anthropogenic disturbances faced by the bordering indigenous forests of the southern Cape. The aim of this study is to use arthropod diversity in Fynbos, pine plantations and natural forest to determine the impact of the different land-uses on the edge effects around natural southern Cape Afrotemperate forests. Specifically I determined whether exotic timber plantation blocks alter the distance of the edge effect between natural forest/fynbos boundaries and how the removal of these plantations affects arthropod assemblages in the forest. I hypothesize that plantation blocks bordering natural Afrotemperate forest will have less of an edge effect than clear cut areas, due to the shading effect provided by mature pine trees favouring forest species. Fynbos, forming a soft edge due the thickness of the vegetation associated with the natural fynbos-forest ecotone, will predictably have the least amount of edge effect.

2.3) Materials and methods

2.3.1) Study area and site selection

The study area ranged from Bergplaas in the West (33.912116 S, 22.736818 E) to Harkerville in the East (34.02456 S, 23.17470 E), southern Cape, South Africa in the Garden Route National Park (GRNP) and surrounds (Appendix 1). The GRNP is an unfenced reserve encompassing a mosaic of different habitats, including indigenous Afrotemperate forests and fynbos, as well as extensive protected wetlands. Incorporated within and surrounding the national park are large tracts of commercial pine and eucalypt plantations, cattle pastures and human settlements. The southern Cape Afrotemperate forest complex comprises about 60 651 hectares, contains 465 vascular plant species, with 206 species reaching their distribution limit within this area (Geldenhuys 1992). The study area has a moderate climate and receives rain all year round, with March being the wettest month. Little difference in both average rainfall and temperature was recorded during the sampling period (Appendix 2). The greater southern Cape forest complex, stretching roughly from Mossel Bay in the West to Humansdorp in the East, can be subdivided into three landscape zones with an own distinct plant species composition: Firstly, the mountain forests, which is typical Afromontane forest (White 1978); secondly the coastal escarpment forests, which in terms of species composition largely coincides with the Indian Ocean coastal belt forests more to the north (Moll & White 1978); and lastly the plateau forests which includes many species associated with Afromontane forests (Geldenhuys 1982). Within the mountain forests, *Cunonia capensis* and *Ocotea bullata* are the most abundant tree species, whereas the most common species within the plateau forests are *Olea capensis* subsp. *macrocarpa*, *Podocarpus latifolius*, *Pterocelastrus tricuspidatus* and *Gonioma kamassi* (Geldenhuys 1982).

Since 1750 the forests have been utilized for the high value of the timber of these species for construction and furniture (Geldenhuys 1991). By 1939 the forests were closed for exploitation due to perceived degradation of forest structure. By 1965 they were re-opened for controlled timber harvesting because of sufficient recovery of the indigenous forests (von Breitenbach 1974; Geldenhuys 1991). Stands of alien trees (*Pinus*, *Eucalyptus* and *Acacia*) were planted in the fynbos bordering the natural forests, as well as in areas of unnaturally opened forests from 1876 onwards (Phillips 1931). These stands still exist today with pine being the most dominant and the focus of this study. Since 2009, with the formation of the Garden Route National Park, the forests are officially protected, with the only exploitation of indigenous timber being limited to individually identified trees. Today, the landscape is typically a mosaic of natural forest, fynbos, timber plantations and agriculture, with the forests fragmented historically by fire, grazing and clearing (Geldenhuys 1991, 1994). Clear felled plantation compartments cover extensive areas, often bordering indigenous forests. These areas are either under rotation (i.e. to be replanted) or the blocks are being removed and restored for conservation purposes. Once plantations are clear felled, these areas transform to even harder edges as vegetation that remains is very sparse and there is no protection effect on the edge by the remaining adjoining vegetation (Appendix 3, fig. 5.1). Here, the age of the clear felled areas varied between 5 and 156 months. Naturally, forests in the southern Cape would border fynbos with the ecotone gradually changing from forest to a vegetation type comprising of both forest and fynbos species, then into pure fynbos, creating a closed edge.

2.3.2) Arthropod sampling

Sampling was conducted over two seasons; late autumn (April-May) and late spring (October-November) 2014. Six line transects were established from the interior of the indigenous forest and into the interior of each of the three adjacent habitat types (pine blocks, clear felled areas or fynbos). In total, 18 line transects were established across the study area. Ten stations were established on each line transect, with five stations situated at 5 m, 10 m, 20 m, 30 m and 50 m distances from the forest edge, running into the natural forest and five stations at the same distances into the adjoining habitat type. The forest edge was defined as the area directly below the canopy edge of the first indigenous forest tree. In addition, another six stations were established at deep forest locations which were at least 100 m from any forest edge or trail, to serve as natural reference sites for comparative purposes. At each station, four pitfall traps were placed at the corners of a 0.5 m × 0.5 m square, with the ten stations forming a line parallel to the edge during both sampling occasions. Each pitfall trap consisted of a plastic cup (7.5 cm in diameter and 9.5 cm in depth) that was buried so that its rim was flush with the ground and was left open for 7 days. One trap per station was baited with a pig-dung and chicken liver mix (Pryke *et al*. 2013) to attract dung and carrion feeders (Appendix 3, fig. 5.5). All traps contained one-quarter ethylene glycol and water (1:1 ratio) as preservative. All captured arthropods were preserved in 70% ethanol until identification. Each individual arthropod was assigned to a morphospecies (a taxonomic unit based on morphological differences) and identified to order and family level. Voucher specimens are housed in the Entomology Museum, Department of Conservation Ecology and Entomology, Stellenbosch University.

2.3.3) Data analyses

Data from the two collection seasons were pooled. Species estimates (Chao2 and Jacknife2) for the different habitat types were calculated in Estimate S, for each habitat type, after all stations per habitat type were pooled. The Coleoptera (beetles), Scarabaeidae (scarab beetles), Orthoptera (crickets, grasshoppers, and locusts), Arachnida (spiders, scorpions, and harvestmen), Diptera (flies) and Formicidae (ants) were selected as focal taxa due to their high collection rates here. Scarabaeidae were also included in the focal group Coleoptera.

The seven biotopes included in this study are deep forest, forest bordering pine, forest bordering clear felled areas, forest bordering fynbos, pine plantations, clear felled areas and fynbos. To test the influence that each of the seven biotopes had on arthropod species richness, Generalized Linear Mixed Models (GLMM’s) were calculated for the overall arthropods collected and for arthropods in the different focal taxonomic groups respectively.

The GLMM's were performed by using the *lme4* package (Bates & Sarkar 2007) in R (R Development Core Team 2007). The overall model incorporated the fixed effects of transect and habitat type, as well as the random effect of elevation and season. Further analyses use the GLMM's to determine the differences in species richness between the 10 stations and deep forest stations. For all analyses, a GLMM fit by Laplace approximation and with a Poisson distribution was used (Bolker *et al*. 2009). Post-hoc analyses were performed only on the factors significantly affecting species richness using a Tukey post-hoc test in R in the *multcomp* package (Hothorn *et al*. 2008).

To determine differences in arthropod assemblage composition between the seven different biotopes, I calculated Permutational multivariate analyses of variance (PERMANOVA) in PRIMER 6 (PRIMER-E 2008) for the habitat type and then again for each station along the transect compared to the deep forest sites. Bray-Curtis similarity measures were performed, after the data were square-root transformed to reduce the weight of common species (Anderson 2001). These analyses were performed for the overall arthropod assemblage composition as well as the compositions of specific focal arthropod taxa. The arthropod assemblage data of the different biotopes data were also investigated by means of a canonical analysis of principal coordinates (CAP) (Anderson & Willis 2003). This analysis is performed to effectively delineate certain aspects of interest within a dataset with high background variance. CAP analyses were only conducted for overall arthropod similarities.

2.4) Results

2.4.1) Arthropod assemblages in the different biotopes

A total number of 7 306 individual specimens were sampled, comprising 484 morphospecies from 17 arthropod orders. Overall, fynbos had the highest number of species sampled (n=217,

Table 2.1). Chao2 estimated clear felled alpha diversity at 405.75 and Jacknife2 estimated 333.3, the highest estimates of all the habitats. Coleoptera was found to be the most species rich order, followed by Diptera and Orthoptera (Table 2.1). The taxonomic group Arachnida and the families Scarabaeidae and Formicidae also had relatively high species richness. Fynbos as a habitat had a significantly higher mean species richness compared to four of the other six habitat types (Fig. 2.1). Biotopes that were significantly less species rich compared to fynbos were pine plantations, clear felled areas, forests bordering fynbos and forests bordering clear felled areas. Lower percentages of arthropods shared between the biotopes and deep forest stations are artefacts of lower sampling effort at deep forest stations (n = 6 stations for deep forest sites vs. n = 30 stations for the respective biotopes).

Table 2.1: Summarised results of sampled species richness with Chao2 and Jacknife2 diversity estimates included for each of the seven biotopes. P-Forest = natural forests bordering pine blocks, F-Forest = natural forests bordering fynbos, C-Forest = natural forests bordering clear felled areas.

Taxa	Diversity index	Pine	Fynbos	Clear felled	P - Forest	F - Forest	C - Forest	Deep Forest
Overall	Sampled	194	217	211	172	175	199	90
	Chao2	234,4 (SD±22.9)	285,68 (SD±26.51)	405,75 (SD±65.73)	255,18 (SD±32.74)	296,83 (SD±47.54)	290,24 (SD±34.54)	110,39 (SD±15.52)
	Jacknife2	253,53	308,3	333,3	253,27	263,4	292,07	122,93
Coleoptera	Sampled	53	61	71	43	45	55	21
	Chao2	61,05 (SD±9.83)	89,04 (SD±18.09)	205,6 (SD±86.16)	67,66 (SD±19.55)	109,22 (SD±48.94)	73 (SD±18.3)	56,2 (SD±16.81)
	Jacknife2	67,23	92,16	116,36	62,86	73,4	70,33	39,43
Scarabaeidae	Sampled	14	21	23	11	14	15	9
	Chao2	14,2 (SD±0.64)	23 (SD±5.48)	66,83 (SD±29.15)	11,83 (SD±1.93)	29 (SD±19.75)	15,87 (SD±2.88)	19,41 (SD±14.34)
	Jacknife2	14,43	25,4	37,5	14	22,46	17,43	15,96
Formicidae	Sampled	15	16	11	12	12	12	3
	Chao2	25,2 (SD±11.04)	17,66 (SD±2.27)	11,83 (SD±1.6)	12,75 (SD±1.27)	28,4 (SD±14.43)	25,33 (SD±13.82)	3,41 (SD±1.13)
	Jacknife2	24,43	19,86	13,93	13,83	21,5	22,93	3,96
Orthoptera	Sampled	13	17	17	13	11	16	6
	Chao2	13,55 (SD±1.13)	17,41 (SD±0.9)	37,41 (SD±25.99)	28 (SD±19.75)	11,41 (SD±1.13)	29,33 (SD±13.82)	6,2 (SD±0.64)
	Jacknife2	14,4	17,86	26,96	21,46	11,96	26,93	6,43
Diptera	Sampled	31	29	30	31	27	26	17
	Chao2	47,3 (SD±12.08)	39,08 (SD±8.21)	47,77 (SD±12.23)	46 (SD±12.09)	50,47 (SD±19.41)	31,62 (SD±5)	18,73 (SD±2.16)
	Jacknife2	49,33	42,83	43,33	46,86	44,9	36,3	21,3
Arachnida	Sampled	25	36	28	25	21	29	14
	Chao2	45 (SD±16.93)	60,08 (SD±16.63)	38,73 (SD±8.78)	48,47 (SD±19.41)	25,08 (SD±4.12)	104,2 (SD±63.99)	20,66 (SD±6.32)
	Jacknife2	41,4	58,83	43,3	42,9	28,83	56,43	23,86

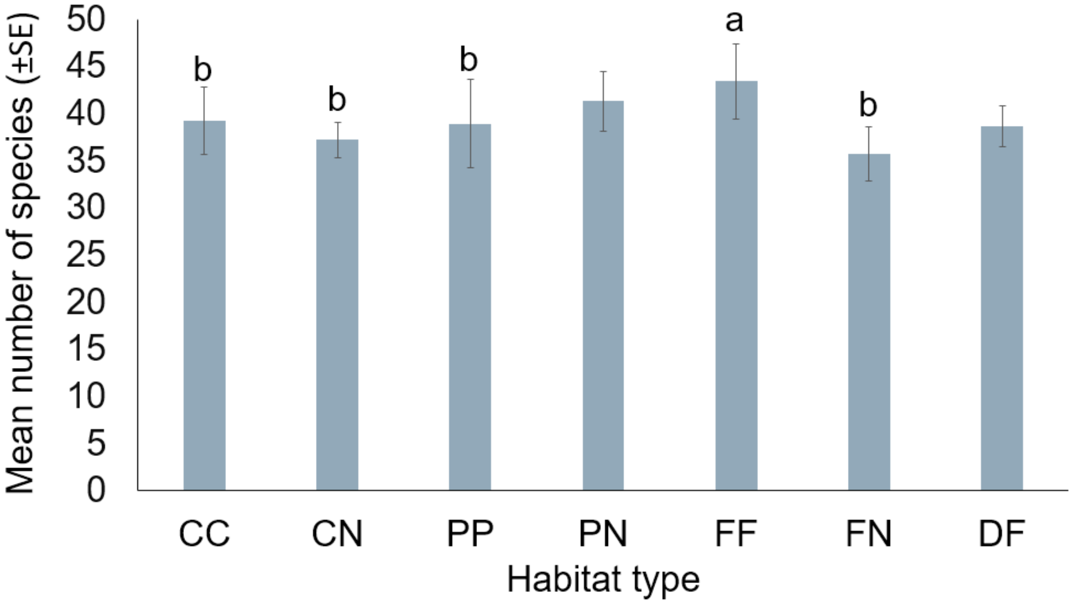

Figure 2.1: Between habitat comparisons of overall alpha diversity. Mean (±1 SE); different letters above bars indicate significantly different means (5% level). *PP*: Pine plantation. *FF*: Fynbos. *CC*: Clear felled areas. *PN*: Forest bordering pine blocks. *FN*: Forest bordering fynbos. *CN*: Forest bordering clear felled areas. *DF*: Deep forest reference stations.

Forests bordering clear felled and pine areas shared the highest number of species between them than any other two biotopes, both in the number of species shared (n=120) and the percentage shared between them (Table 2.2). Deep forest reference stations shared the fewest number of species with fynbos and clear felled areas respectively (n=63 and 61) with less than 45% of deep forest species found in these biotopes. Clear felled areas shared high numbers of species with most of the biotopes, although most were shared with fynbos (n=115 or 75.65%). Fynbos had the highest observed species richness as well as the highest number of unique species (n=53).

Table 2.2: The total number of unique species per habitat type* and number of species shared between the respective habitat types (Rare species (n≤4) excluded)

	Unique spp.	CN	PN	FN	CC	PP	FF	DF
CN	36	*						
PN	28	120 (**81.63%**)	*					
FN	30	103 (**72.02%**)	103 (**73.57%**)	*				
CC	49	107 (**71.33%**)	110 (**73.82%**)	96 **(63.57%)**	*			
PP	33	109 (**72.66%**)	109 (**75.17%**)	98 (**65.33%**)	110 (**73.82%**)	*		
FF	53	90 (**57.69%**)	110 (**72.36%**)	109 (**73.15%**)	115 (**75.65%**)	119 (**78.81%**)	*	
DF	9	65 (**49.61%**)	67 (**54.03%**)	66 (**53.65%**)	61 (**44.52%**)	65 (**48.87%**)	63 (**43.75%**)	*

*CN-forest bordering clear felled; PN-forest bordering pine; FN-forest bordering fynbos; CC-clear felled; PP-pine; FF-fynbos; DF-deep forest

All habitat types differed significantly in terms of overall arthropod assemblage compositions (Table 2.3; Fig. 2.2). Forests bordering clear felled areas significantly differed from deep forest locations for beetles, scarab beetles and flies. Forest bordering pine, however, revealed no significant differences for these focal groups compared to deep forest locations (Table 2.3; Fig. 2.2). Also, forests bordering fynbos were also similar to the reference stations for both the scarab beetles and flies. Arthropod assemblages showed a definite clustering pattern into the respective habitat types (Fig. 2.2). Clear felled assemblage compositions had little resemblance to fynbos or forest, but did overlap with pine areas to some extent (Fig. 2.2). Fynbos and forests yielded different arthropod assemblages with little overlap.

Table 2.3: Permutational multivariate analysis of variance (PERMANOVA) of the selected focal taxon's assemblage compositions compared between the different habitats.

Beta diversity **Taxa**	**df**	**Pseudo - F**	**p-value**	**Post-hoc***
Overall	6	08.1919	0.001**	All biotopes different
Beetles	6	15.037	0.001**	All biotopes different except: PN=DF
Scarabs	6	24.709	0.001**	All biotopes different except: DF=FN, PN
Arachnida	6	02.2166	0.001**	CC≠CN, FF,FN,; CC≠PN,PP; CN≠FF, FN; FF≠FN, PN, PP, PN, PP
Dipterans	6	08.2038	0.001**	All biotopes different except: DF=FN, PN; FN=PN
Orthoptera	6	03.7591	0.001**	All biotopes different except: CC=PP; CN=DF, PN; DF=FN, PN; FN=PN, PP
Ants	6	06.7727	0.001**	All biotopes different except: CC=CN, PP; CN=PN, PP; FN=PP

CC=Clear felled; PP=Pine; FF=Fynbos; CN=Forest bordering clear felled; PN=Forest bordering pine; FN=Forest bordering fynbos; DF=Deep Forest

*P < 0.05, **P < 0.001, ***P < 0.0001

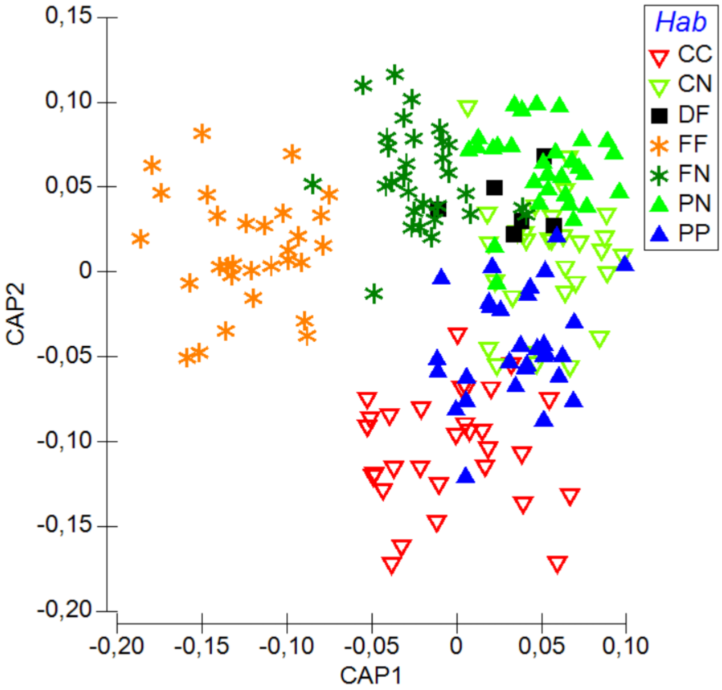

Figure 2.2: Canonical analysis of principal coordinates (CAP analysis) indicating similarity of arthropod assemblage compositions between the six different habitats (with Deep Forest reference sites included). *CC*: Clear felled areas; *CN*: Forests bordering clear felled; *DF*: Deep forest; *FF*: Fynbos; *FN*: Forests bordering fynbos; *PN*: Forests bordering pine; *PP*: Pine plantations.

2.4.2) Edge effects on indigenous forest arthropod assemblages

Overall, arthropods did not show a significant difference in species richness along the Pine-Forest and Clear felled-Forest transects, but showed for the Fynbos-Forest transect (Fig. 2.3). There were significantly more species occurring at 10 m, 20 m, and 30 m in the fynbos from the forest edge than 20 m into the forest.

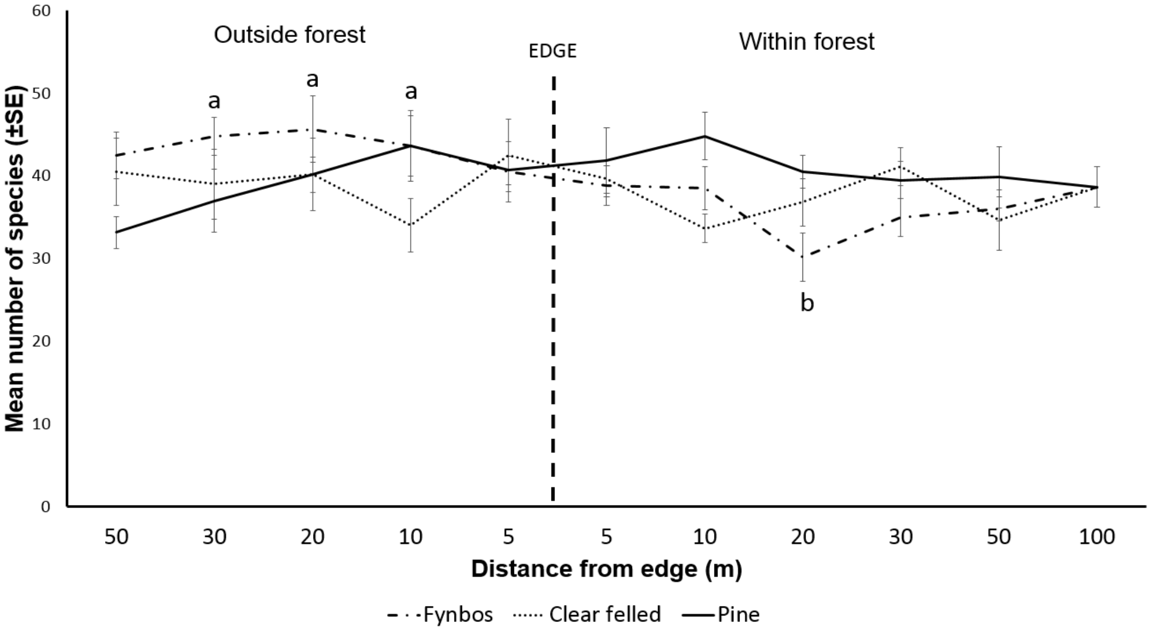

Figure 2.3: Overall species richness (mean±1SE) across transects for different land-uses bordering indigenous Afrotemperate forest at differing distances from the forest edge. Different letters above bars represent significantly different means (5% level).

Selected focal taxa had different responses to the forest edge in terms of species richness. Ant species richness was significantly higher at the 50 m clear felled sites than 50 m into the forest on the same transect. The FN-transect (fynbos-forest) also showed significant differences in ant species richness, with the fynbos boasting overall higher species richness than the bordering natural forest (Fig. 2.4). The PN-transect did not have differences in species richness for ants (Fig. 2.4). Beetles (Coleoptera) had a general similarity along transects in terms of species richness, although a decrease in species richness was observed along the

Clear felled-Forest (CN) transect, with the forest being less species rich than the clear felled areas bordering it. Scarab beetles followed a similar trend, although significant differences in species richness were also found along the Pine-Forest (PN) transect. For scarab beetles, significantly more species were found in general in the pine and clear felled areas than in the natural forests bordering it. Fynbos and the forests bordering it had similar species richness of both scarab beetles as well as all beetles. For both the CN- and PN-transects, Diptera increased in species richness along the transect towards the deep forest stations, with significantly lower species richness found on stations furthest away from the natural forest edge within the clear felled and pine land-use areas. Diptera species richness reaches its peak in deeper forest sites bordering pine and clear felled areas. Along the natural forest-fynbos ecotone (FN-transect), Diptera species richness remained similar. The Orthoptera and arachnids did not show any significant differences in species richness for any of the three transects.

Overall, species assemblage composition showed significant differences between all stations outside of the natural forest compared to deep forest reference sites. Along the FN-transect, overall forest arthropod compositions are significantly different up to 20 m into the natural forest. Forest stations bordering clear felled areas are significantly different in species assemblage compositions compared to deep forest reference stations up to 50 m into the natural forest. Along the PN-transect, natural forest stations were significantly different in species assemblage compositions compared to the deep forest reference stations up to 30 m from the forest edge (Table 2.4, Fig. 2.5).

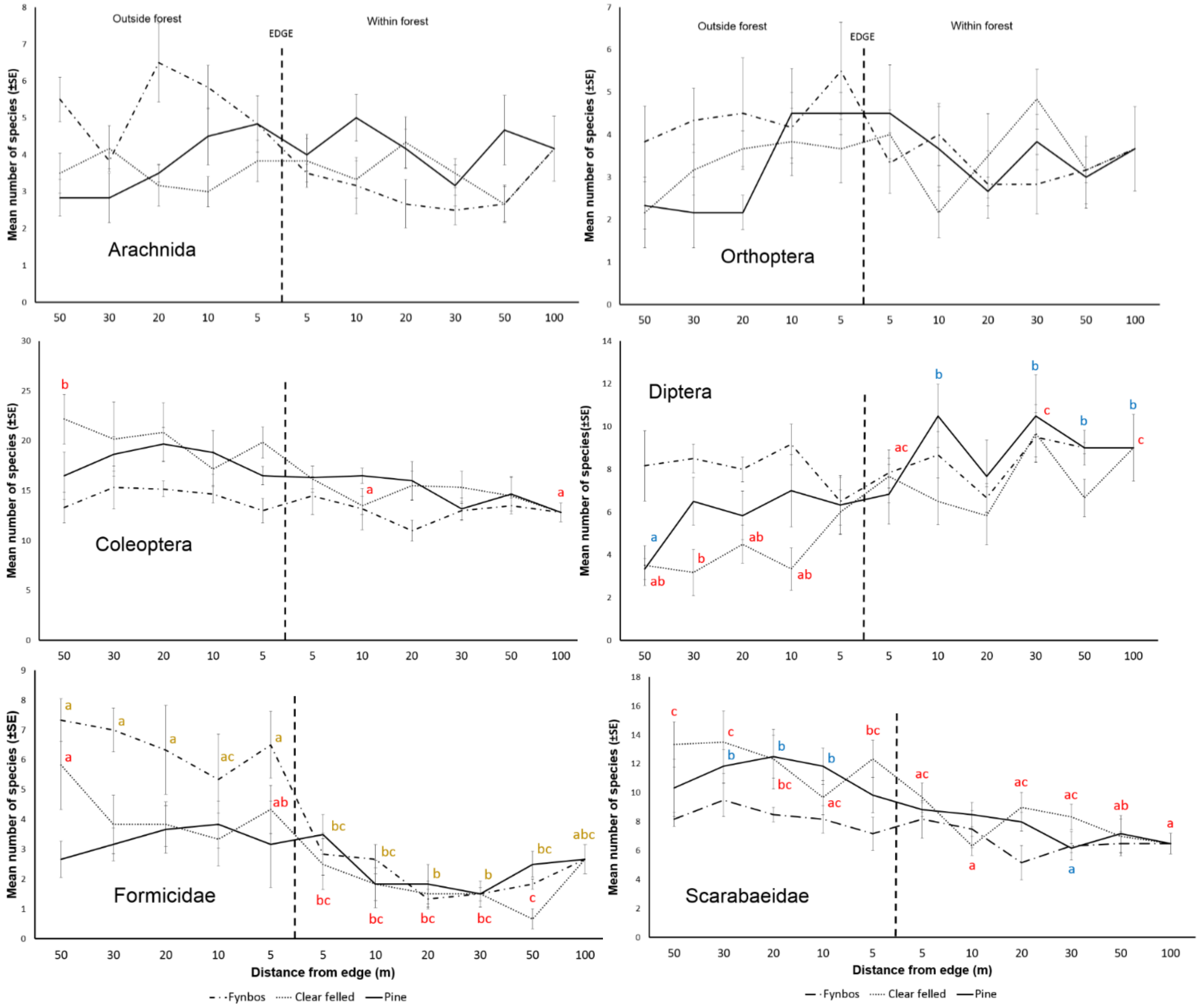

Figure 2.4: Species richness (mean±1SE) for selected focal taxa across the respective transects. Different letters represent significantly different means (5% level). Red letters: Clear felled-Forest. Blue letters: Pine-Forest. Golden letters: Fynbos-Forest.

Diptera species composition on natural forest/fynbos transects was generally similar to deep forest station up to 20 m into the natural fynbos (Table 2.4). However, when bordering pine plantations or clear felled areas, assemblages generally differed up to five meters into the natural forest. Ant assemblage composition from all stations was generally similar to deep forest reference sites, but differed significantly from all fynbos sites in natural fynbos / forest transects (Table 2.4). Both pine and clear felled areas significantly changed this pattern with numerous stations outside of forests having similar assemblages to those at deep forest stations and numerous forest stations hosting significantly different ant assemblages than reference deep forest stations (Table 2.4). Orthoptera assemblage composition was generally unaffected by station position, except in deep pine plantation sites (30 m and 50 m) that differed significantly from deep forest reference sites. All three land-uses showed little effect on arachnid assemblage composition within forests. The coleopteran (Scarabaeidae included) and the Scarabaeidae showed little variation in assemblage composition between different natural forest stations and the deep forest reference sites, but significantly differed from natural fynbos sites. The same was true for transects between pine plantations and natural forest. However, for these two taxa, forests bordering clear felled areas were significantly different in species composition compared to the deep forest reference stations up to 30 m into the natural forest (Table 2.4).

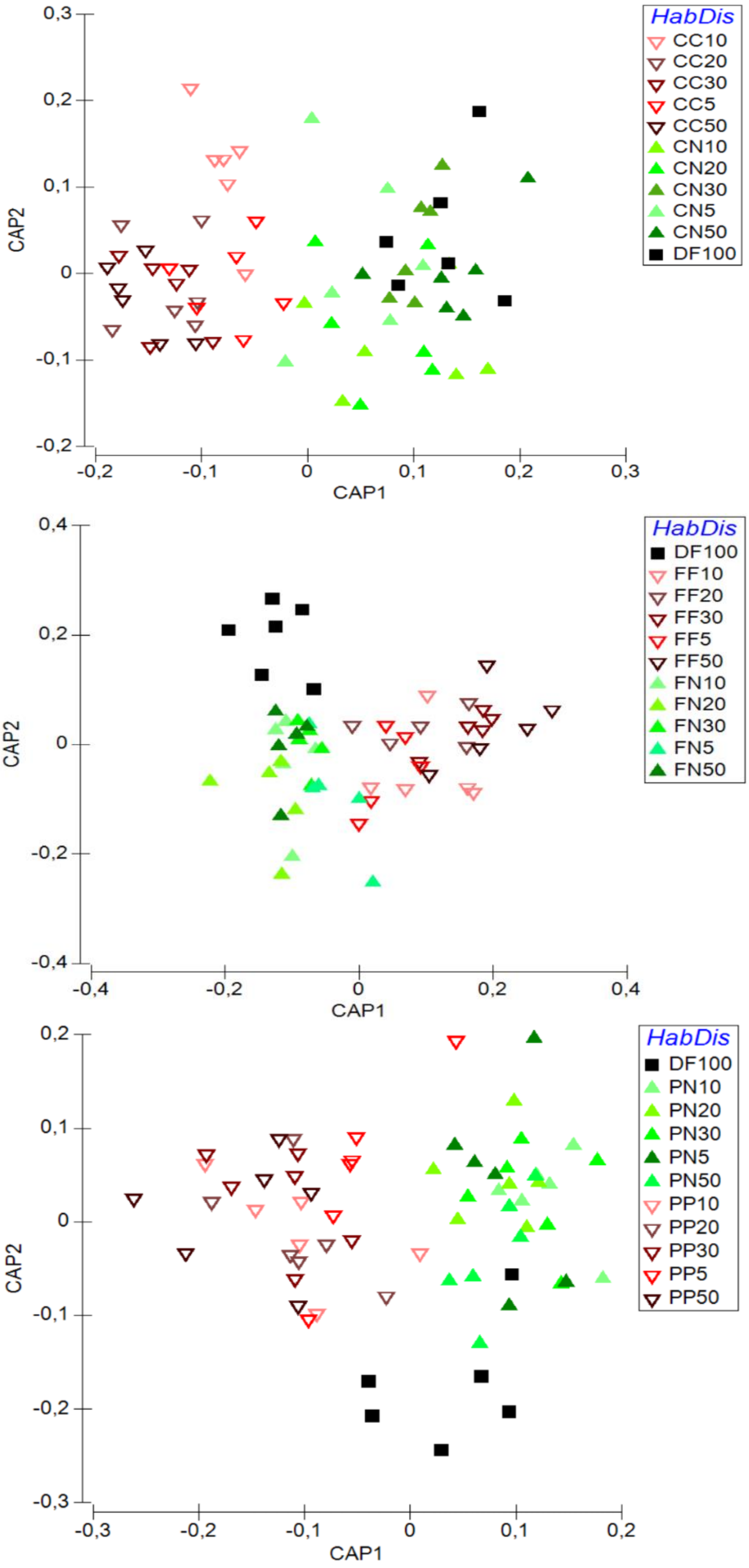

Figure 2.5: Canonical analysis of principal coordinates (CAP analysis) indicating similarity of arthropod assemblage compositions between the 10 different stations (in metres) along the ecotone (with Deep Forest (DF) reference sites included). FF: Fynbos. FN: Forest bordering fynbos. CC: Clear felled. CN: Forest bordering clear felled. PP: Pine. PN: Forest bordering pine.

Table 2.4: Permutational multivariate analysis of variance (PERMANOVA) of arthropod assemblage compositions for selected focal taxa across the different land-use transects compared to deep forest reference compositions (>100 m from a forest edge) (reported pairwise t-values).

Focal taxa	Land-use type	Outside forest (m)					Within forest (m)				
		50	**30**	**20**	**10**	**5**	**5**	**10**	**20**	**30**	**50**
Diptera	Fynbos	2.43**	2.09**	1.37	1.28	1.67*	0.90	1.19	1.19	0.90	1.35
	Clear felled	2.61**	1.81**	1.89**	1.85*	1.59*	1.38*	1.07	1.36	1.28	1.35
	Pine	2.06**	1.49*	1.23	1.15	1.65**	1.56*	1.15	1.07	1.48*	1.37
Formicidae	Fynbos	2.64**	2.62**	2.45*	2.16**	2.08*	1.46	1.30	1.51	2.18**	1.19
	Clear felled	1.59	1.40	1.75*	1.25	1.31	1.91*	1.38	1.66*	1.66*	3.26*
	Pine	1.16	0.96	1.89*	1.24	1.37	1.02	1.64*	2.02**	1.91**	1.36
Orthoptera	Fynbos	1.27	1.01	1.38	1.51	1.55	1.42	0.87	1.54	0.80	1.23
	Clear felled	1.68	1.62	1.54	1.38	1.70	1.12	0.83	1.52	1.36	1.15
	Pine	1.71*	1.69*	1.32	0.65	1.23	1.45	1.02	1.08	0.47	0.69
Arachnida	Fynbos	1.30	1.68**	1.15	1.39	1.01	1.04	1.35	1.15	1.54	0.84
	Clear felled	1.50*	1.44*	1.86**	1.21	1.23	1.37	1.53*	0.70	1.04	1.08
	Pine	1.51*	1.12	0.91	1.30	1.21	1.24	1.28	0.74	1.01	1.14
Scarabaeidae	Fynbos	2.73**	2.40**	1.92*	2.2*	1.86*	1.37	0.5	1.17	1.16	0.94
	Clear felled	3.09**	3.25**	3.16**	2.3**	3.18**	1.78*	1.28	2.23*	1.83*	1.08
	Pine	2.59**	2.98**	2.31*	2.81**	2.90**	1.14	1.35	1.53	0.69	0.96
Coleoptera	Fynbos	2.21**	2.00**	1.58*	2.02**	1.82**	1.37	1.00	1.28	1.12	0.86
	Clear felled	2.48**	2.56**	2.63**	2.07**	2.41**	1.49*	1.18	1.73**	1.56*	1.06
	Pine	0.98**	2.29**	1.84*	2.14**	2.18**	1.25	1.36	1.17	0.99	0.98
Overall	Fynbos	2.22***	1.85***	1.70**	1.8***	1.66**	1.33*	1.19	1.33*	1.25	1.1
	Clear felled	2.52***	2.23***	2.35***	1.79***	1.93***	1.59***	1.07	1.52**	1.32*	1.3*
	Pine	1.86**	2.03***	1.72**	1.64**	1.67***	1.35**	1.28*	1.24*	1.29*	1.06

* P < 0.05, **P < 0.001, ***P < 0.0001

2.5) Discussion

2.5.1) Arthropod assemblages in the different habitat types

Here, I show that the open habitat types, fynbos and clear felled areas, were the most species rich. Other studies support these findings, which have shown that clear felled areas support both open-habitat species and forest generalists (Niëmela *et al*. 1993; Koivula *et al*. 2002; Pawson *et al*. 2008). Interestingly, the highest species estimates were in the clear felled areas, typically containing a mixture of alien invasive species, fynbos and scattered logs (Appendix 3, fig. 5.4). These findings support the view by Pryke & Samways (2009), in that the naturalness of an area does not always result in a higher alpha diversity of arthropods. It is known that open, mixed areas provide habitat for generalist species that opportunistically colonise areas previously unsuitable for their persistence (Didham *et al*. 1996; Kaila, Martikainen & Punttila 1997). Also, these findings lend evidence towards the co-existence of species under the Intermediate Disturbance Hypothesis (IDH). The high number of species shared between clear felled areas and fynbos, and to a lesser extent forest (competetively superior species) together with the large number of unique species (rapid colonizers), does indeed fit well in to the IDH (Shea *et al*. 2004). The large number of species that were unique to these clear felled areas in our study may therefore be a mixture of such opportunistic generalist species and non-native species usually associated with pine plantations. The latter is supported by results of assemblage composition analyses that showed that pine plantations and clear felled areas have more similar composition to each other than either of these have with natural fynbos sites. This also indicates that areas cleared from pine are less beneficial in sustaining native arthropods and that these assemblages have not yet been restored to a more natural state. Pine stands, although being less species rich, do support at least some native arthropod assemblages, compared to recovering fynbos (previously pine plantation) that harbours many unique species, from a study by Pryke & Samways (2009). However, once clear felled areas are fully restored given adequate time (to either fynbos or forest depending on the historic biome and vegetational succession), the scenario will predictably change towards favouring historically clear felled areas instead of mature pine stands with regards to sustaining viable populations of native arthropods (Butterfield 1997; Magura *et al*. 2003; Pawson 2006).

Arthropod assemblages sampled from the three respective natural forest types overlapped to some extent with the bordering habitats that differ in land-use type. In fact, all transect types shared more than a hundred species (over 70% of all taxa collected per transect type) between bordering habitat types. There is therefore some degree of movement, or spill-over, of arthropods between bordering habitats and any change that leads to altered arthropod assemblages in one of these habitats would result in a change in the other. The spill-over of insects from one habitat / land-use into the bordering habitat is not uncommon (Rand *et al*. 2006). The fact that between-biotope movement is readily witnessed in the southern Cape forest complex, makes restoration of disturbed areas a key priority. Influxes of foreign arthropods into natural systems could vastly alter insect food web dynamics (Rand *et al*. 2006; Tscharntke *et al*. 2005), and, in turn, forest integrity (Maleque *et al*. 2006). Alternatively, the movement of forest arthropods into adjacent land-uses / habitats indicates that strong, viable source populations are able to recolonize disturbed areas. Edges do act as source areas for species dispersal (Molnár *et al*. 2001) and the high movement of species across edges found here highlights their conservation value. However, the extent to which they do this is limited and will predictably remain limited unless areas are adequately restored (Barnes *et al*. 2014).

2.5.2) Edge effects on indigenous forest arthropod assemblages

Fynbos boasts the highest diversity of arthropod species across the ecotone. Both plantation blocks and clear cut areas shared uniformly low species richness with natural forests when compared to fynbos. The significantly higher overall species richness found in the fynbos bordering forests could be ascribed to natural patterns in species richness, as these two biomes are very different in their structure, composition and abiotic parameters (van Wilgen *et al*. 1990). Previous work found similar results, with fynbos being more species rich in terms of arthropod diversity compared to afrotemperate forests (Pryke & Samways 2009). These differences are reflected in the composition of species as well, with the fynbos and forest harbouring significantly different overall arthropod assemblage compositions. Fynbos do not border the forest as a hard edge; instead, the forest-fynbos ecotone often form a continuous clump of mixed vegetation with a gradual decrease in canopy height moving away from the forest (Appendix 3, fig. 5.3). The Keurboom (*Virgilia oroboides*) are typically found at the interface of these two biomes, but are usually absent from production areas where pine trees were clear cut. These ecotonal areas have a unique floristic composition, acting as a buffer zone around the natural forest protecting the forest from penetrating sunlight, dust, water run-off and exotic arthropod influxes (Mucina & Rutherford 2006; Delgado *et al*. 2007). The 20 m edge effect reported in forests bordering fynbos though could be explained as a natural adaptation of arthropod species to the forest-fynbos ecotone. Specialization of species at the ecotone of two biomes is not uncommon (Molnár et al. 2001; Ribeiro *et al*. 2008). Natural edge adapted species are vital components of any ecosystem, and could significantly contribute towards ecological intactness by acting as source populations for dispersal (Molnár *et al*. 2001).

When pine trees replace the natural forest-fynbos border, non-forest arthropod assemblages penetrate deeper into these forests (up to 30 m) indicating that pine stands allow for less buffering of natural forest assemblages against the surrounding assemblages. Deep forest arthropods decrease the extent of their range in forests bordering pine plantations. Pine plantations do however provide a buffer against abiotic and biotic influxes into the natural forest; (Norton 1998; Brockerhoff *et al*. 2001; Hartley 2002; Denyer *et al*. 2006; Campbell *et al*. 2011) when pines are felled non-forest arthropod assemblages could penetrate at least to

50 m into natural forest. This indicates that this action creates more suitable habitat for arthropod taxa not normally associated with forests. The gradual increase in height of vegetation associated with natural borders deteriorates completely with the formation of plantation forestry. Once clear felled, environmental factors acting on the forest edge will increase in their penetrating ability due to the removal of any bordering vegetation (Peyras *et al*. 2013), thus supporting Peyras *et al*. (2013) in the existence of a gradient of hardness.

The Orthoptera did not perceive the forest edge as a barrier for dispersal as it was equally species rich both sides of the forest edge and did not generally differ in species composition. Contrasting research from the KwaZulu-Natal Midlands in South Africa, where forests, grasslands and timber plantations interlink to create a mosaic landscape, revealed a strong relationship between habitat edge and distance from edge on both grasshopper richness as well as compositions (Pryke & Samways 2012). The variety of biologies found in orthopterans and the fact that different trapping methodologies attract different functional types could explain these differences (Bidau 2014). The methodology used in this study (pitfall trapping) is not especially favourable for trapping most orthopterans (compared to sweep nets, re: Larson *et al*. 1999). However, these results highlight the fact that extrapolation of results must be done with caution, and that species in different regions or with different biologies may have different responses towards different forms of disturbance.

At the natural fynbos-forest ecotone, no significant differences in Diptera species richness were witnessed. However, the Diptera species richness was lowest at the clear felled and pine stations furthest away from the forest. Similar results were obtained by Helle & Muona (1985), where Diptera species richness were significantly higher in mature forest in Finland than clear cut areas bordering the forest. In the tropical Australian countryside, Diptera species richness decreased significantly moving from larger forest sites to pasture lands (Smith & Mayfield

2015). This indicates a lack of dipterans to adapt to these disturbed areas. Suggestions have been made by Smith & Mayfield (2015) that significant decreases in diptera species richness and compositions could result in ecosystem services mediated by dipterans to be lost (services such as pollination and pest control). The demise of dipterans is alarming and the monitoring of these species could provide useful insights into restoration success. Edge effects reaching into the natural forest for diptera were not severe, although significant differences in assemblage compositions did occur at individual forest stations bordering clear felled and pine areas.

At the open habitats (fynbos and clear felled) there was an increase in ant species richness moving out from the forest edge into these open areas, yet no significant differences across the pine-forest interface and species richness remained uniformly low. The assemblage composition of ants was also significantly different between fynbos and forest stations, suggesting that these two biomes harbour different species assemblages as expected (Koen & Breytenbach 1988). Fynbos were the only biotope bordering forests that showed a significant difference in this regard towards deep forest stations. Also, the concentration of resources at forest edges should be considered when explaining the increases in ant species richness (Banschbach *et al*. 2012). The fact that ant species richness were significantly higher in only the two habitats with low- to medium growing vegetation in this study, compared to the mature pine stands and indigenous forests, suggests that sunlight availability and/or temperature might be the causal factor leading to an increase in species numbers. Recent findings support the view that temperature are in fact more influential on ant species richness, independent of tree canopy cover or macro-habitat (Werenkraut *et al*. 2014). The increase in ant species richness in the clear felled areas and fynbos, together with the natural forest ant species assemblage shift outward from the natural forest into the clear felled and pine areas, suggest that ants of this area prefer open habitat.

Deep forest arachnids utilize the immediate forest edge where forests border clear felled areas; however, they lack the ability to disperse deeper into clear cut areas due to a possible lack of prey availability, suitable shelter or an altered micro-climate (Larrivée *et al*. 2008). At least some spiders have a tendency for forest edges, with increased species richness found at the immediate forest edge (Pajunen *et al*. 1995; Horvath *et al*. 2002). Here, I found that spider species richness was uniform across transects for all three land-uses. However, a recent study by Larriveé *et al*. (2008) found no relation between edge zones and species richness, rather a change in community assemblages. Their study strongly suggests the abruptness of the forest edge, i.e. soft versus hard, to play a significant role in spider assemblage changes across the habitat interface (Larriveé *et al*. 2008). In their comparison of clear cut edges versus wildfire edges, the latter being a softer edge relative to the clear cut edge, spider assemblage changes is more abrupt at the clear cut edges. The present study support their results in that clear felled areas were the only land use to affect interior forest stations at 10 m in, whereas stations within the clear felled zones had significantly different spider assemblages. Fynbos and pine stands, both being categorized as softer edges relative to clear felled areas in this study, had no edge effect on spider compositions. This study strongly suggests that ground-dwelling forest spiders readily utilise fynbos as well as the soft forest edge linking fynbos with natural forests. Also, few species specialize on the natural forest-fynbos ecotonal niche, as the spider assemblages at edge stations did not differ from either interior forest or fynbos stations. Pine plantations also harboured spider assemblages similar to those found in native forests, however; once clear felled, the composition of spider assemblages changed significantly. Their role in food webs (Atlegrim & Sjoberg 1995; Nyffeler 2000) and nutrient recycling in the early stages of natural forest succession (Hodkinson *et al*. 2001) highlights their importance in restoration monitoring.

For the Coleoptera, including Scarabaeidae, all fynbos stations differed significantly in their assemblage compositions from deep forest reference stations; however, all forest stations bordering fynbos were similar in their assemblage compositions. The fact that both the pine and fynbos habitats did not have any edge effect on both beetle and scarab beetle assemblages within the forest, compared to the severe edge effect found in forests bordering clear felled areas, provides strong evidence towards altered micro-climatic changes associated with the hard forest edge. Both the order Coleoptera and the family Scarabaeidae was more species rich and had different assemblage compositions in the clear felled areas than the forests bordering these areas, similar to a study on carabid beetles in boreal forest fragments, where clear cut areas boasted significantly higher species richness (Heliola *et al*. 2001). The hard edge associated with clear felled areas could allow increased sunlight, -water runoff and an influx of foreign species usually unable to penetrate natural forests (Laurance 2002). Beetles are very sensitive towards anthropogenic disturbances (Klein 1989; Nichols *et al*. 2007). Plantation forestry, characterised by regular harvesting and replanting, could severely impact native beetle diversity, even 27 years after disturbance (Spence *et al*. 1996). Dung beetles have been found to be strongly affected by altered vegetation characteristics, a different than normal micro-climate (Davis *et al*. 2001) as well as dung availability produced by native mammals (Estrada & Coates-Estrada 2002), all which are possibly affected by the hard edge associated with clear felled-forest interfaces. A combination of these factors is typically used to explain edge effects as severe as found here. Encouraging though is recent findings that dung beetles rapidly respond to vegetation restoration efforts in Afromontane forest patches in Nigeria, with a 53% increase in dung beetle abundances after only three years of passive restoration of disturbed forest areas (Barnes *et al*. 2014). No edge effects are reported for forests bordering pine plantations, as beetle assemblages were similar to deep forest stations in all natural forest stations bordering pine stands, although the edge between forest and pine plantations are stark for beetles. This indicates that natural forest beetle assemblages do not utilise commercial plantations as corridors for dispersal. However, other studies show that pine plantations could provide important alternative habitats for typical forest beetles (Pawson *et al*. 2008). This is not the case here as forest beetles did not use the commercial plantation blocks. The structure of pine plantations, with a high tree canopy and a general cooling effect, could explain the fact that beetles associated with deep forest stations could utilise forests up to 5m from the pine edge due to the blocking out of sunlight at the natural forest edge (Tabor *et al*. 2007). Shading effects have been proven to significantly influence beetle compositions (Spence *et al*. 1996; Namakura *et al*. 2009). However, within pine stands few natural understory floral species persisted, and the drastic difference in vegetation characteristics between pine stands and afrotemperate forests could explain the absence of deep forest beetle assemblages within the pine stands (Appendix 3, fig. 5.2).

2.6) Conclusion

The southern Cape forest complex does have both natural and artificial edge effect, with the fynbos-forest ecotone comprising of a unique zone, effectively displaced once commercial forestry commences at the forest edge. A loss of fynbos specialist species occurs as a result of the establishment of plantations on former fynbos areas and an increase in edge effect occurs once the fynbos-forest ecotone gets displaced by plantations. This edge effect reaches up to 30 m into the bordering natural forest. Furthermore, once pine stands are clear felled, the edge effect increases, penetrating up to 50 m into the adjacent forest. The impact of these changes on arthropod responses could alter forest integrity. This suggests that not only fynbos and forest should be conserved in this landscape, but conservation should also consider the edge between the two biotopes as critically important. Thus, these two biotopes should be conserved as a single conservation unit, retaining both fynbos and natural forest, as well as the edge between them. Arthropod diversity, too, should be monitored throughout the duration of restoration in both the clear felled areas as well as the adjacent forest. The high-use value of arthropods in monitoring ecosystem health should be incorporated in the Garden Route National Park’s management plans together with vegetation restoration to insure sufficient recovery of disturbed areas.

2.7) References

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3) Chapter 3

How road size and direction fragments ancient Afrotemperate forest arthropod assemblages

3.1) Abstract

Forests are sensitive ecosystems naturally characterised by a closed canopy with a unique micro-climate to which forest species have adapted. In pristine forests, these conditions alter in areas with sun flecks or where trees have fallen over, as well as on forest edges. However, roads through forests may lead to permanent fragmentation by increasing the amount of edge as perceived by forest biota. I determined how different types of roads and their direction affect forest arthropod biodiversity in the southern Cape Afrotemperate forest complex of South Africa. This was achieved by focussing on different types of road running through the forest, through analysing and comparing the composition and species richness of selected arthropod groups across linear transects. Results show changes in arthropod species richness, abundance and assemblage composition due to differences in road type in especially the Diptera, Coleoptera, Formicidae and dung associated arthropods. Edge effects of up to 50 m were reported for both the wide arterial roads and the narrower, secondary roads. Hiking trails affected arthropod assemblages only up to 10 m into the forest. Roads directed east-west affected forest arthropods more negatively than roads directed north-south. These results suggest that the largest continuous forest in South Africa is highly fragmented by roads in terms of arthropod biodiversity which could lead to cascading effects on overall forest integrity.

3.2) Introduction

Ecosystem edges naturally occur where two biotopes converge. Forests are usually characterised by a closed high canopy, but often have areas of naturally opened gaps in the canopy caused by treefall (Bouget & Duelli 2004). This affects the dynamics of the forest as well as the radiation energy penetrating to the forest floor, altering the micro-climate and various biological processes (Falinski 1978). Schowalter (1994), for example, found an increase in sap-sucking arthropods and a decrease in Lepidopterans, predaceous beetles and decomposers in newly formed canopy gaps in Puerto Rico. However, these areas play a vital role in forest succession and are only temporal in nature (Bouget & Duelli 2004). Also, many forest tree species are reliant on these openings to reach canopy status (Canham 1989).

Of special concern are the effects of human-caused, permanent gaps in the forest canopy. Road construction and -utilisation are widely reported to have adverse effects on environments, especially in sensitive forest habitats, mainly due to the opening of the tree canopy. This allows for influxes of unnatural environmental factors (Delgado *et al*. 2007), creating access to remote areas for logging (Nagendra *et al*. 2003; Fearnside 2007) and facilitating the influx of alien plant species (Arévalo *et al*. 2005). Reported adverse impacts on ecosystem functioning further include, amongst others, altered air quality, -soil properties, -vegetation and –wildlife abundances and occurrences (Forman & Alexander 1998; Coffin 2007). The effect of roads on vertebrates, especially birds and mammals, are well studied (Benitez-Lopez *et al*. 2010; McGregor *et al*. 2008; Gryz & Krauze 2008). However, exactly how insects are affected by roads that penetrate natural environments remains understudied (Muñoz, Torres & Megías 2015) especially in Africa. Previous findings have shown that roads impact insect diversity, with studies reporting an increase in insect abundance and diversity moving away from the roadside into the habitat interior (Haskell 2000; Dunn & Danoff-Burg 2007). Most importantly, roads often act as barriers for forest species that perceive these as forest edges (Kolasa & Zalewski 1995; Murcia 1995). Roads could also assist the movement of generalist, open-habitat arthropods along road corridors through forests (Koivula 2005). Due to the open canopy above roads, they exposed the adjacent forest with limiting factors such as drier conditions, increased light and altered nutrient levels (Coffin 2007), making roads ideal spaces for the influx of foreign species (Parendes & Jones 2000; Gelbrad & Belnap

2003). Importantly, the effects of roads regularly penetrate the surrounding habitat several metres in (Forman *et al*. 2003), often causing changes in micro-climatic conditions (Haskell 2000; Godefroid & Koedam 2004). As a result, roads affect the ecological functioning and dynamics of the system, creating 'road-effect zones' that may vary in time and space (Coffin 2007). An understudied concept is that the impact of a road through natural forest may also depend on the direction of the road. Differences in road direction will relate the angle of the sun and how far into the forest sunlight will penetrate these forest edges (Matlack 1993). Sunlight in turn dries leaf litter and increases surface temperature in naturally cool forests (Kapos 1989), while also deterring the naturally photonegative forest species. In the southern hemisphere it is expected that, due to the constant more northerly position of the sun during the entire day, the southern edges of roads running in an east-west direction will receive more sunlight penetrating into the forests than the edges of roads running in a north-south direction. The forest edges next to north-south directed roads will receive penetrating sunlight (sunlight angled into the forest edges) only during the morning or afternoon, depending on which side of the road. It is therefore likely that forests next to roads in an east-west direction (and particularly their southern side) would be more prone to desiccation and have larger edge effects into the forest than forests next to north-south direction.

Differences in the size of a canopy gap can have different effects on arthropod assemblages (Phillips & Shure 1990). The effect of road width on arthropods in forests is still a relatively understudied field of research (Muñoz, Torres & Megías 2015). Traffic volume has received far greater attention in assessing the impact of roads penetrating natural environments (McKenna *et al*. 2001; Roa & Girish 2007; Seshardi & Ganesh 2011). In the southern Cape forest complex, which has a long history of forestry road creation and -utilisation, roads are predicted to have significant effects on forest biodiversity due to the creation of permanent forest canopy gaps (Phillips & Shure 1990; Schowalter 1994). In the Knysna forest, observations on vegetation regrowth along forest roads and canopy gaps above 0.1 hectare in size revealed a micro-climate that deteriorate forest communities. For example, few seedlings establish in these areas due to unnatural drier soil conditions (Geldenhuys 1982). The impact of forestry roads on forest arthropod biodiversity in the southern Cape forest complex is still unknown.

The high value of arthropods for assessing ecological integrity is well-documented (Magura 2002; McGeoch 2007; Maleque *et al*. 2009). In forests, with its unique micro-climate that is sustained by a closed tree canopy, arthropods are especially sensitive towards disturbance and provide good indicator taxa for assessing changes in forest systems (Klein 1989; Koivula *et al*. 2002; Magura 2002; Spector 2006; Maleque *et al*. 2009). Within the southern Cape forest complex, the largest continuous forest in South Africa, forestry roads form a network of linear gaps, creating permanent and continuous areas with unnaturally high levels of light and other environmental variables penetrating the forest interior. The aim of this study was to determine how roads of different width and orientation through the Southern Cape Afrotemperate forests affect the magnitude of the edge effect into the forest as measured by the diversity of different epigaiec arthropod groups.

3.3) Materials and Methods

3.3.1) Study area and site selection

The study area in the southern Cape, South Africa, ranged from Bergplaas in the West (33.912116 S; 22.736818 E) to Diepwalle in the East (33.94058 S; 23.16141 E), in the Garden Route National Park (GRNP) (Table 3.1). The GRNP contains a suite of different biomes, with indigenous Afrotemperate forests occupying 60 651 ha of the park (Geldenhuys 1991). Forestry roads occur throughout the GRNP, with many of these roads being accessible to the public (Fig. 3.1). Initially being created as trails by which early woodcutters transported timber out of the forest, today these roads are permanent gravel roads dissecting large parts of the forest. The widest gravel road running through the forest is the R339, a public road that connects Uniondale in the north with Knysna in the south. This road is a relatively wide two lane gravel road, which on a daily basis is used by commercial timber trucks transporting mostly exotic timber (Appendix 3, fig.5.6). The majority of the wood is harvested from the commercial plantations dominating large tracts of the landscape around the natural forest. Furthermore, many secondary roads form a network of canopy gaps throughout the forest. These roads are not as often utilized as the R339 and receive far less traffic volumes (Appendix 3, fig.5.6). For recreational purposes, hiking trails are abundant within the forest, and often penetrate deep into undisturbed forest (Appendix 3, fig.5.6). All arterial sites were selected off the R339, with sites being at least one kilometre apart to reduce pseudo-replication. Secondary road and hiking trail sites were selected across the study area at random, with secondary roads also at least one kilometre apart.

Table 3.1: Location of sampling sites. Sites in bold were those sites selected to test for the influence of road direction on arthropod assemblages. Along all east-west roads only the southern edges were sampled.

Transect	Road Type	Road Direction	Latitude	Longitude
1	**Arterial**	**North-South**	**-33.94058**	**23.16141**
2	Arterial	Diagonal	-33.945960	23.155617
3	**Arterial**	**North-South**	**-33.95135**	**23.14805**
4	**Arterial**	**East-West**	**-33.95465**	**23.15156**
5	**Arterial**	**East-West**	**-33.958028**	**23.156155**
6	**Arterial**	**East-West**	**-33.96256**	**23.15738**
7	Arterial	Diagonal	-33.96976	23.14793
8	Arterial	Diagonal	-33.973524	23.147332
1	Secondary	Diagonal	-33.920287	22.958593
2	**Secondary**	**North-South**	**-33.906888**	**22.963660**
3	**Secondary**	**North-South**	**-33.95153**	**23.15332**
4	Secondary	Diagonal	-33.94550	23.09763
5	**Secondary**	**East-West**	**-33.94400**	**23.10210**
6	**Secondary**	**East-West**	**-33.94614**	**23.12980**
7	**Secondary**	**North-South**	**-33.94928**	**23.05733**
8	Secondary	Diagonal	-33.95331	23.05652
1	Hiking trail		-33.915149	22.735434
2	Hiking trail		-33.914001	22.737021
3	Hiking trail		-33.916405	22.956244
4	Hiking trail		-33.913965	22.95383
5	Hiking trail		-33.94303	23.05279
6	Hiking trail		-33.94486	23.05327
7	Hiking trail		-33.94750	23.14162

8	Hiking trail	-33.94794	23.14214
1	**Deep Forest**	**-33.912116**	**22.736818**
2	**Deep Forest**	**-33.913965**	**22.95383**
3	**Deep Forest**	**-33.943455**	**23.05389**
4	**Deep Forest**	**-33.945394**	**23.102132**
5	**Deep Forest**	**-34.075695**	**23.22961**
6	Deep Forest	-33.948844	23.141793
7	Deep Forest	-33.976461	23.191346
8	Deep Forest	-33.94898	23.166639

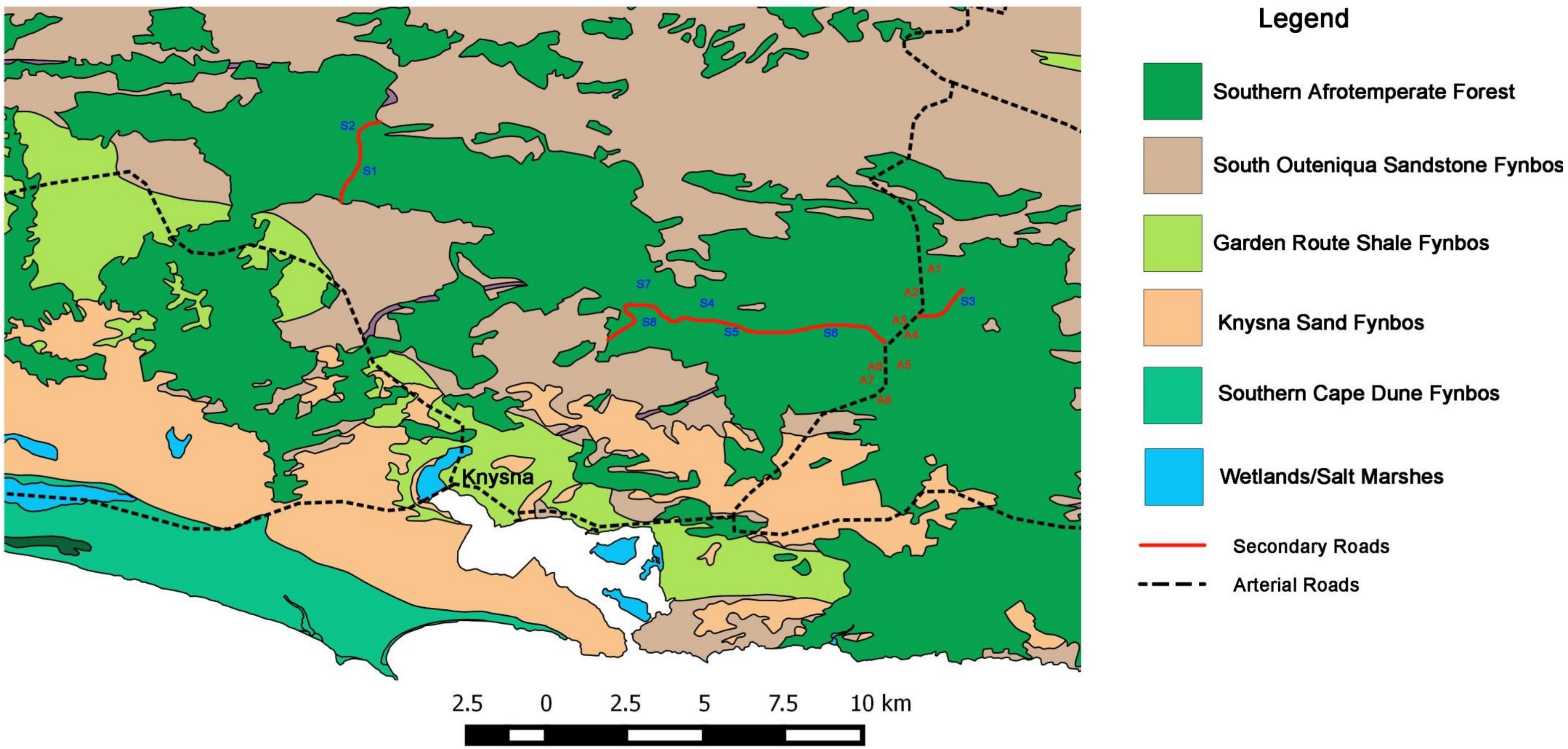

Figure 3.1: Map indicating location of road sites. Sites labelled in blue are transects next to secondary roads. Sites labelled in red are transects next to arterial roads.

3.3.2) Arthropod sampling

Sampling was conducted over two seasons; late autumn (April-May) and late spring (October-November) 2014. Eight line transects per road type were erected perpendicularly to each of the three categories of road (arterial, secondary, hiking) (Appendix 3, Fig. 5.6). A subset of ten transects were used to test for the effect of road direction on arthropod assemblages (Table 3.1; Figure 3.1). Five of these were selected for east-west running roads (transects directed southwards from these roads) and five for north-south running roads (transects directed eastwards and westwards from these roads) (Table 3.1). On each line transect, five stations were established at 5 m, 10 m, 20 m, 30 m and 50 m from the edge of the road into the forest. The 5 m stations were placed directly next to the road, underneath the edge of the canopy of the first indigenous forest tree. An additional 8 reference stations were selected at randomly chosen deep forest locations that were at least 100 m from any road or anthropogenic disturbance. For analyses of the effect of road direction on arthropod assemblages, five deep forest stations were selected at random from the eight deep forest stations to avoid possible biases created by unbalanced sampling design (Anderson & Walsh 2013). At each station, four pitfall traps were placed at the corners of a 0.5 m × 0.5 m square during both sampling occasions. Each pitfall trap consisted of a plastic cup (7.5 cm in diameter and 9.5 cm in depth) that was buried so that its rim was flush with the ground and was left in the field for 7 days. One trap per station was baited with a pig-dung and chicken liver mix (Pryke *et al*. 2013) to attract dung and carrion feeders. All traps contained one-quarter ethylene glycol and water (1:1 ratio) as preservative. All captured arthropods were preserved in 70% ethanol until identification. Each individual arthropod was assigned to a morphospecies and identified to order and family level. Voucher specimens are housed in the Entomology Museum, Department of Conservation Ecology and Entomology, Stellenbosch University.

3.3.3) Statistical procedures

Data from the two respective collection seasons were pooled. Species estimates (Chao2 and Jacknife2; Hortal *et al*. 2006) were calculated in EstimateS v.7.5.2 (Colwell 2009) with 999 randomizations of samples for each of the road type (arterial, secondary, hiking). These non-parametric species estimators provide the best overall species estimates when many rare species are present (Novotny & Basset 2000; Hortal *et al*. 2006) and when working with relatively small sample sizes (Colwell & Coddington 1994). The Coleoptera (beetles), Orthoptera (grasshoppers, crickets, and locusts), Arachnida (spiders, scorpions, and harvestmen), Diptera (flies) and Formicidae (ants) were selected as focal taxa due to their high abundances in this study. Arthropods were also classified according to their functional feeding guild based on the dominant feeding behaviour of the particular life stage collected (juvenile or adult) of the particular family (Scholtz & Holm 1985) and as indicated by their mouthparts (Labandeira 1997). These included the herbivores, predators (including parasites), detritivores (including fungivores, scavengers and omnivores) and dung associated species. Ants were treated as a separate taxonomic and functional group due to their wide range of feeding habits. Dung associated species mostly comprised of dung beetles and flies that were attracted to the dung bait and were not included in the detritivores due to their specialised feeding habits.

To test the influence of road type and direction on arthropod species richness and abundance, data from the 5 stations per transect were compared to the deep forest reference stations, Generalized Linear Mixed Models (GLMM's) were calculated for the overall arthropods collected and for arthropods in the different focal taxonomic- and functional groups respectively. The GLMM's were performed by using the *lme4* package (Bates & Sarkar 2007) in R (R Development Core Team 2007). The overall models incorporated the fixed effects of road type or road direction, as well as the random effects of elevation and season. For all analyses, a GLMM fit by Laplace approximation and with a Poisson distribution was used (Bolker *et al*. 2009). Post-hoc analyses were performed only on factors found to significantly affect species richness and abundance using a Tukey post-hoc test in R in the *multcomp* package (Hothorn *et al*. 2008).

To test the influence of road type and direction on arthropod assemblage composition, data from the 5 stations respectively were compared to deep forest reference stations using Permutational multivariate analyses of variance (PERMANOVA) in PRIMER 6 (PRIMER-E 2008). Data were square-root transformed to reduce the weight of abundant species (Anderson 2001) where after Bray-Curtis similarity measures were calculated. These analyses were performed for the overall arthropod assemblage composition as well as the compositions of specific focal arthropod taxa and functional groups. Arthropod assemblages were further compared by means of canonical analysis of principal coordinates (CAP) which can effectively delineate aspects of interest within a dataset with high background variance (Anderson & Willis 2003).

3.4) Results

3.4.1) Road type

A total number of 4 507 individuals were sampled, comprising 209 morphospecies from 17 orders. The Coleoptera was the most species rich order (57 species) overall, followed by the Diptera (34 species), Arachnida (31 species), Orthoptera (15 species) and Formicidae (14 species). The most species rich functional group was the predators (60 species), followed by the herbivores (43 species), dung associated arthropods (33 species) and detritivores (32 species). Overall, sampled species richness was similar between forests bordering the three different types of road for all taxa and functional groups (Table 3.2). Chao2 and Jacknife2 diversity indices however estimated higher species richness in forests bordering arterial roads.

Table 3.2: Summarised results of sampled species richness with Chao2 and Jacknife2 diversity estimates included for each of the types of road.

	Diversity index	Arterial	Hiking	Secondary
Overall	Sampled	132	130	131
	Chao2	187.46 (SD±20.42)	168.51 (SD±15.32)	162.81 (SD±13.38)
	Jacknife2	204.96	188.33	181.85
Arachnida	Sampled	21	25	21
	Chao2	22.56 (SD±1.96)	30.6 (SD±5.24)	23.33 (SD±3.09)
	Jacknife2	24.62	34.78	25.57
Coleoptera	Sampled	36	37	33
	Chao2	64 (SD±20.49)	46 (SD±6.89)	38.9 (SD±5.21)
	Jacknife2	59.42	52	43.76
Scarabaeidae	Sampled	10	11	9
	Chao2	11.31 (SD±2.04)	11.21 (SD±0.65)	9.43 (SD±1.18)
	Jacknife2	12.94	11.33	9.98
Diptera	Sampled	23	24	25
	Chao2	25.73 (SD±3.25)	27.64 (SD±4.32)	35.71 (SD±11.56)
	Jacknife2	28.55	30.19	35.08
Formicidae	Sampled	9	10	10
	Chao2	12.93 (SD±6.33)	11.75 (SD±2.36)	17 (SD±10.24)
	Jacknife2	13.23	13.92	15.85
Orthoptera	Sampled	14	10	11
	Chao2	19.46 (SD±6.65)	11.31 (SD±2.3)	11.43 (SD±1.18)
	Jacknife2	20.83	14.23	11.96
Predators	Sampled	42	45	38
	Chao2	50.21 (SD±6.03)	52.39 (SD±5.44)	40.67 (SD±2.77)
	Jacknife2	57.33	59.69	44.24
Herbivores	Sampled	26	22	23
	Chao2	82 (SD±49.07)	35.23 (SD±10.98)	28.6 (SD±5.24)
	Jacknife2	50.71	37.30	32.78
Detritivores	Sampled	14	13	20
	Chao2	49.44 (SD±43)	34.43 (SD±27.26)	41 (SD±17.74)
	Jacknife2	27.98	23.73	37.57
Dung associated	Sampled	28	25	26
	Chao2	31.06 (SD±3.12)	25.87 (SD±1.67)	33 (SD±10.24)
	Jacknife2	34.87	26.96	31.85

High numbers of species were shared between forests adjoining the different road types (Table 3.3). Lower percentages of arthropods shared between roads and deep forest stations are artefacts of lower sampling effort at deep forest stations (n = 8 stations for deep forest sites vs. n = 40 stations for forests next to roads). However, compared to arterial and secondary roads, hiking trails still shared a slightly higher percentage of arthropod species with deep forest reference stations.

Table 3.3: Number of species shared between forests bordering the different road types (rare species (n ≤ 4) excluded).

Road type	Arterial	Secondary	Hiking
Arterial	*		
Secondary	83 (**89.25%**)	*	
Hiking	83 (**90.22%**)	86 (**92.47%**)	*
Deep Forest	63 (**70.79%**)	65 (**70.65%**)	64 (**72.22%**)

Overall species assemblage compositions differed significantly between all forest types (forest bordering arterial, secondary and hiking roads) (Table 3.4). Overall, arthropod composition of forest sampling points along hiking trails did not differ from the deep forest reference stations, even if sampling effort in deep forest stations were smaller (Table 3.4, Fig 3.2). Reference stations were dissimilar to forests bordering arterial- and secondary roads and stations in the latter two tended to separate in the CAP analysis (Table 3.4, Fig 3.2).

Table 3.4: Permutational multivariate analysis of variance (PERMANOVA) of the selected focal taxon's assemblage compositions compared between the different forest types based on the bordering road type.

Arthropod group	**df**	**Pseudo - F**	**p-value***	**Post-hoc**
Overall	3	3.5251	0.0001***	DF=H
Arachnida	3	1.8024	0.0157*	DF=H, S, A
Coleoptera	3	5.1309	0.0001***	DF=H
Diptera	3	3.7293	0.0001***	DF=H, S, A
Formicidae	3	1.6618	0.0918	DF=H, S, A
Orthoptera	3	3.3487	0.0001***	DF=none

DF=Deep Forest; A=Arterial road; S=Secondary road; H=Hiking trail
$^*P < 0.05$, $^{**}P < 0.001$, $^{***}P < 0.0001$

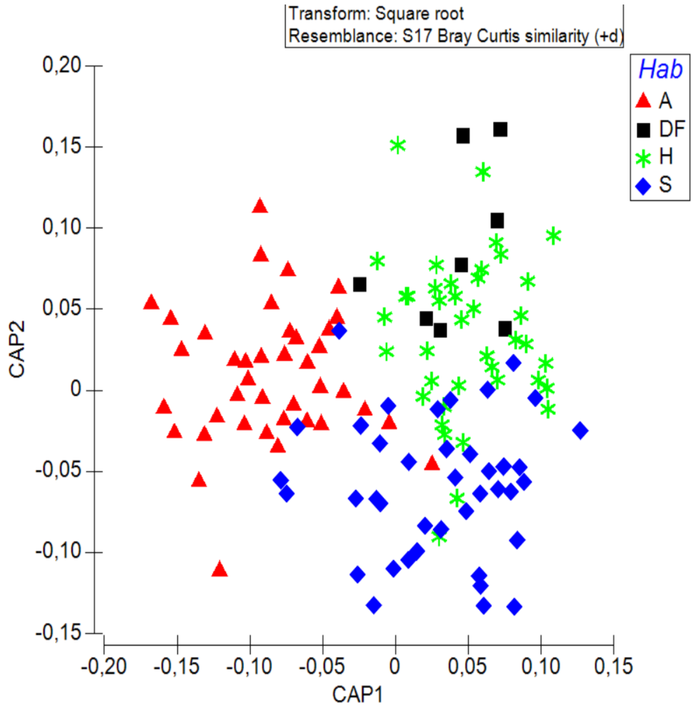

Figure 3.2: Canonical analysis of principal coordinates (CAP) indicating similarity of arthropod assemblages between forests bordering different road types with deep forest reference sites included (A-arterial road; DF-deep forest; H-hiking trail; S-secondary road).

Hiking trails generally had the highest number of species per station along transects and was always statistically similar to deep forest stations (Fig. 3.3). Secondary roads generally had intermediate species richness per station although their numbers never differed significantly from deep forest stations. Arterial roads, in contrast, generally contained the least number of species and their overall, Diptera and dung associated groups were significantly lower compared to deep forest stations (Fig. 3.3). More than 40 arthropod species were found at the deep forest stations, compared to less than 30 species encountered at stations directly next to arterial roads. Diptera species richness were highest at deep forest stations (11±1.9) and stations directly next to hiking trails (11.63±0.86), but was lowest at stations 5 m from arterial roads (5±0.8). Dung associated arthropods showed a similar trend (Fig. 3.3) with highest species richness at deep forest stations (16.75±1.69) and directly next to hiking trails (18.75±1.08), whereas stations 5 m from arterial roads harboured the lowest species richness (9.38±0.71).

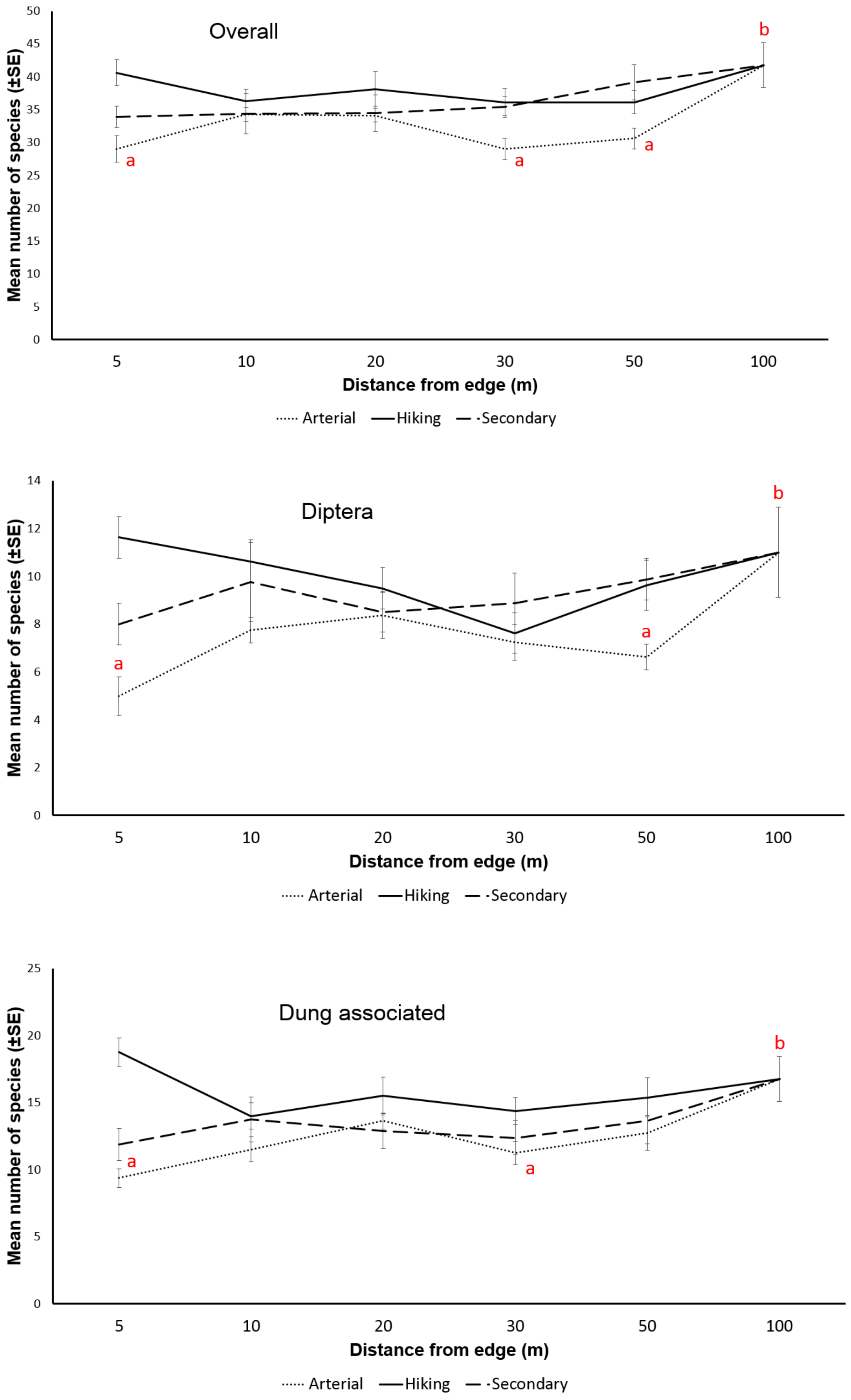

Figure 3.3: Species richness (mean ± SE) along transects next to three different road types at different distances from the road edge compared to deep forest reference stations. Different letters represent significantly different means (5% level).

Overall, arthropod abundance decreased from deep forest stations moving towards both secondary and arterial roads (Table 3.5). The most significant drop in overall species abundance was found at stations directly bordering arterial roads (71.88±8.36) compared to deep forest reference stations (212.75 ±41.42). Secondary roads, however, were significantly different at all stations along transects with regards to overall arthropod abundance. Hiking trails had lowest impact on overall arthropod abundance as all stations were statistically similar to deep forest stations (Table 3.5). Secondary roads had a greater effect on Coleoptera abundance compared to arterial roads, with significant decreases at all stations along transects compared to deep forest stations. In forests bordering arterial roads, only the 5 m station were significantly lower in species abundances compared to deep forest stations for Coleoptera. Diptera abundance was lowest at stations 5 m from arterial roads and differed significantly from deep forest reference stations. Both the Arachnida and Orthoptera showed little response to roads with regards to abundance. Formicidae were less abundant at stations 5 m from hiking trails and stations 30 m and 50 m from secondary roads compared to deep forest stations. Road type also had seemingly little effect on arthropod functional groups (Table 3.5). Herbivores were unaffected by roads in terms of abundance (Table 3.5). However, a variety of responses were found for the predators, detritivores and dung associated arthropods with arterial roads showing the greatest responses (Table 3.5).

Table 3.5: Abundance of arthropod taxa along transects bordering different road types. Stations that significantly differ from deep forest stations are indicated in bold.

Taxa	**Road type**	**Distance from road edge (m)**					
		5	10	20	30	50	100
Overall	Arterial	**71.88 (SE±8.36)*****	124.125 (SE±15.41)	**109.13 (SE±6.85)***	**107.13 (SE±9.6)***	120.63 (SE±14.6)	212.75 (SE±41.42)
	Secondary	**99.13 (SE±7.53)****	**107.88 (SE±13.83)***	**100 (SE±10.82)****	**92.25 (SE±4.97)*****	**106.75 (SE±12.06)***	
	Hiking	142.13 (SE±16.45)	115.63 (SE±10.88)	153.25 (SE±26.36)	129.63 (SE±16.9)	134.88 (SE±24.15)	
Coleoptera	Arterial	**37.625 (SE±5.07)****	61.13 (SE±14.33)	59.75 (SE±4.69)	53 (SE±6.94)	68.5 (SE±12.88)	105.88 (SE±22.52)
	Secondary	**40.38 (SE±5)****	**38.5 (SE±4.49)****	**37.75 (SE±6.06)****	**36 (SE±4.8)*****	**36.88 (SE±7.61)****	
	Hiking	66.63 (SE±11.44)	49.12 (SE±7.04)	63.38 (SE±17.96)	60.38 (SE±10.91)	71.38 (SE±22.38)	
Arachnida	Arterial	3.38 (SE±0.56)	3.29 (SE±0.6)	4.25 (SE±0.73)	2.88 (SE±0.44)	3.5 (SE±0.82)	6 (SE±1.63)
	Secondary	4.25 (SE±0.59)	3.5 (SE±0.68)	3.86 (SE±0.32)	5.25 (SE±0.59)	4.75 (SE±0.81)	
	Hiking	4.5 (SE±0.87)	3.5 (SE±0.6)	4.63 (SE±0.98)	**2 (SE±0.41)***	4.63 (SE±1.02)	
Diptera	Arterial	**11.25 (SE±2.3)*****	29.63 (SE±4.36)	24.63 (SE±3.08)	26.75 (SE±5.13)	25.5 (SE±3.51)	51.5 (SE±18.49)
	Secondary	28.5 (SE±4.45)	34.63 (SE±10.29)	26.25 (SE±3.78)	21 (SE±3.42)	30.63 (SE±5.55)	
	Hiking	35.88 (SE±4.16)	28.25 (SE±2.64)	43.5 (SE±11.47)	18.13 (SE±3.39)	26.5 (SE±7.99)	
Orthoptera	Arterial	5.63 (SE±1)	9.5 (SE±0.93)	5.5 (SE±0.82)	6.25 (SE±1.73)	5.38 (SE±1.21)	7.75 (SE±2.86)
	Secondary	8 (SE±1.05)	8.63 (SE±1.86)	6.5 (SE±1.21)	6.5 (SE±1.21)	9.75 (SE±1.33)	
	Hiking	6.57 (SE±1.64)	7.13 (SE±1.52)	7.75 (SE±1.64)	7.13 (SE±2.26)	6.38 (SE±1.13)	
Formicidae	Arterial	2.13 (SE±0.9)	3.88 (SE±0.79)	2.13 (SE±0.91)	3.5 (SE±1.45)	4.13 (SE±1.43)	6.5 (SE±1.68)
	Secondary	3.13 (SE±0.4)	3.75 (SE±1.19)	4.29 (SE±0.6)	**2.57 (SE±0.35)***	**2.14 (SE±0.59)****	
	Hiking	**1.75 (SE±0.53)***	2.38 (SE±0.32)	3.75 (SE±1.13)	5.5 (SE±1.55)	4 (SE±1.2)	

*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$

Table 3.5 continued:

Functional group	**Road type**	**Distance from road edge (m)**					
		5	10	20	30	50	100
Dung associated	Arterial	**31.63 (SE±6.2)*** **	64.88 (SE±15.13)	58.38 (SE±5.91)	**57.88 (SE±8.52)***	67.5 (SE±11.12)	121.38 (SE±33.71)
	Secondary	**41.25 (SE±5.78)***	43.5 (SE±11.26)	42.38 (SE±6.67)	**31.63 (SE±6.11)****	44.5 (SE±9.59)	
	Hiking	77.75 (SE±9.06)	55.13 (SE±8.09)	83.5 (SE±17.4)	61.88 (SE±8.87)	71.75 (SE±21.65)	
Predators	Arterial	**18.5 (SE±2.51)*****	26.5 (SE±3.41)	29 (SE±2.48)	**24 (SE±2.88)***	29.13 (SE±5.19)	40.38 (SE±6.81)
	Secondary	30.25 (SE±4.5)	31.63 (SE±3.2)	24.38 (SE±4.9)*	25 (SE±3.42)	25.5 (SE±3.43)	
	Hiking	28.38 (SE±4.6)	24.88 (SE±1.44)	27.38 (SE±5.06)	**17.63 (SE±3.53)*****	30 (SE±5.82)	
Herbivores	Arterial	6.75 (SE±1.1)	9.75 (SE±1.03)	5.88 (SE±1.2)	5.75 (SE±1.43)	5.25 (SE±1.83)	8.25 (SE±2.9)
	Secondary	8.63 (SE±1.21)	9.5 (SE±2.15)	11.25 (SE±2.45)	8.63 (SE±1.58)	11.13 (SE±1.43)	
	Hiking	5.75 (SE±1.69)	7.13 (SE±1.44)	7.88 (SE±1.63)	6.88 (SE±1.64)	6.88 (SE±1.01)	
Detritivores	Arterial	2.13 (SE±0.58)	2.25 (SE±0.65)	**0.63 (SE±0.26)***	1 (SE±0.38)	**0.75 (SE±0.41)***	3.25 (SE±0.86)
	Secondary	2.63 (SE±0.65)	1.63 (SE±0.32)	2.5 (SE±0.85)	3.25 (SE±0.94)	1.5 (SE±0.5)	
	Hiking	1.75 (SE±0.45)	1.38 (SE±0.6)	1.63 (SE±0.56)	1.63 (SE±0.38)	1.63 (SE±0.56)	

*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$

Along transects, both arterial roads and secondary roads affected the overall arthropod assemblage composition in forests up to 50 m (Table 3.6). Stations bordering hiking trails were only affected at the 5 m and 10 m zones; thereafter all stations were statistically similar to deep forest stations. Formicidae assemblages were significantly different along the total length of both the arterial- and secondary road transects, but only up to the 5 m station on hiking trails. Diptera, detritivores and dung associated arthropod assemblage composition were only affected when close to arterial roads. Coleoptera assemblage composition was significantly different to deep forest reference stations along transects bordering secondary roads. Arterial roads and hiking trails however had little overall impact on Coleoptera assemblage composition. The Orthoptera, Arachnida, herbivores and predators were little influenced by any road type.

Table 3.6: Permutational multivariate analysis of variance (PERMANOVA) of arthropod assemblage composition for selected focal taxa and functional groups along transects bordering different road types compared to deep forest reference stations (>100 m from a forest edge). T-values are reported.

Taxa	**Road type**	**Distance from road edge**				
		5	10	20	30	50
Overall	Arterial	__1,43**__	__1,38**__	__1,25*__	__1,25*__	__1,23*__
	Secondary	__1,31*__	__1,37**__	__1,39**__	__1,29*__	__1,28*__
	Hiking	__1,26*__	__1,32*__	1,09	1	0,88
Diptera	Arterial	__1,78**__	0,85	1,17	0,61	1,42
	Secondary	1,16	1,04	1,10	1,01	1,14
	Hiking	1,09	0,84	0,75	0,79	0,57
Formicidae	Arterial	__2,55**__	__1,68*__	__1,99*__	__1,63*__	__1,74*__
	Secondary	__1,66*__	1,34	__1,53*__	__2,04**__	__2,08**__
	Hiking	__2,31**__	1,33	1,32	0,72	1,41
Coleoptera	Arterial	1,36	1,32	1,15	1,23	0,68
	Secondary	__1,57*__	__1,79**__	1,27	__1,4*__	__1,47*__
	Hiking	1,35	__1,76*__	0,77	0,84	0,85
Orthoptera	Arterial	1,29	__2,44***__	1,48	1,64	1,51
	Secondary	1,11	1,34	__1,84*__	1,13	1,58
	Hiking	1,46	1,56	__2,23**__	1,42	1,10
Arachnida	Arterial	0,56	0,80	1,21	0,78	0,98
	Secondary	1,08	1,16	__1,62*__	1,05	0,50
	Hiking	0,94	0,88	0,55	1,01	0,92
Detritivores	Arterial	__1,54**__	__1,52*__	1,42	0,99	1,08
	Secondary	1,34	1,31	1,21	1,37	1,24
	Hiking	0,72	0,75	0,97	0,89	1,04

Predators	Arterial	1,10	1,06	**1,37***	1,22	1,28
	Secondary	1,21	**1,39***	**1,59****	1,08	1,21
	Hiking	1,10	1,21	0,83	1,18	0,69
Herbivores	Arterial	1,26	**2,10****	1,20	1,52	0,94
	Secondary	1,12	**1,61***	1,49	1,13	1,44
	Hiking	1,34	1,28	**1,91****	1,19	1,33
Dung associated	Arterial	**1,57***	1,24	0,91	0,81	1,20
	Secondary	1,23	1,35	1,03	1,06	0,83
	Hiking	1,18	1,50	0,53	0,62	0,29

*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$

3.4.2) Road direction

Overall arthropod species richness along transects in forests bordering roads that differ in direction was only significantly different along east-west directed roads (i.e. forests to the south of these roads, northern exposed forest edge) (Fig. 3.4). Stations up to 30 m into the forests from these roads had significantly less species compared to deep forest reference stations. For the selected focal taxa and functional groups, only the Diptera and dung associated species revealed significantly lower species richness, and only at 5 m stations into forests along transects of east-west directed roads (Fig. 3.5).

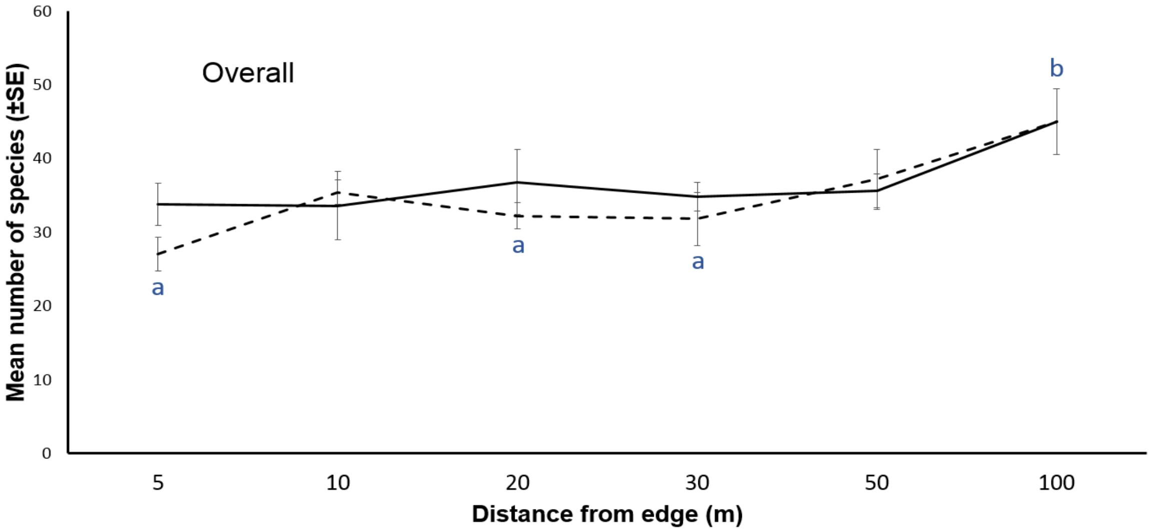

Figure 3.4: Species richness (mean ± SE) along transects for roads of different direction at different distances from the road edge. Different letters represent significantly different means (5% level). Transects perpendicular to roads in the north-south direction are indicated by the solid line while transects perpendicular to roads in the east-west direction are indicated by the broken line.

Compared to deep forest stations, overall arthropod numbers were significantly less up to 30 m next to both the north-south directed roads (east / west facing forest edge) as well as east-west (north facing forest edge) directed roads (Fig. 3.6). The Diptera, Arachnida, dung associated arthropods and predators were significantly less abundant compared to deep forest stations only next to the east-west directed roads at individual stations. The Coleoptera were significantly less abundant next to both east-west directed roads as well as north-south directed roads (Fig. 3.6).

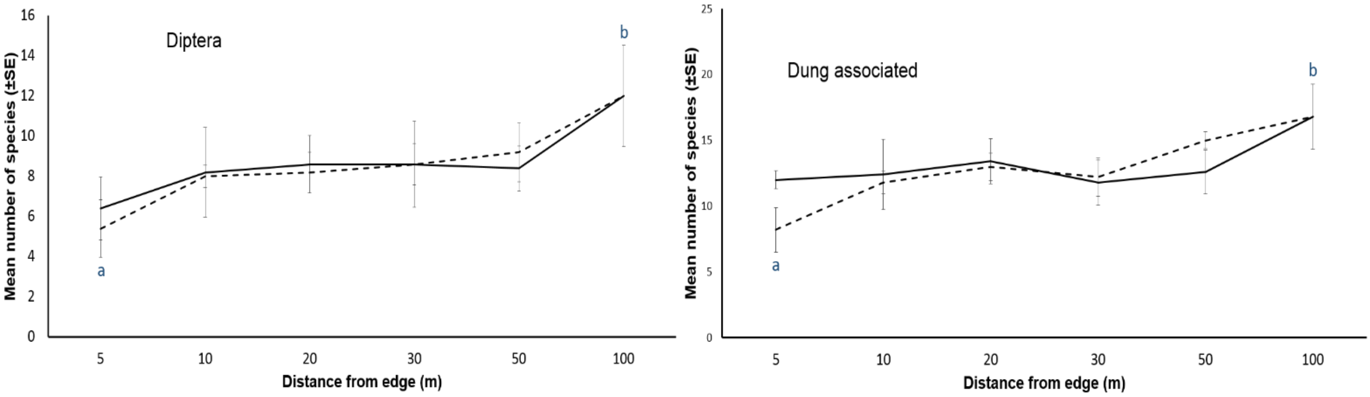

Figure 3.5: Species richness (mean ± SE) of Diptera and dung associated arthropods along transects for the two road direction categories at differing distances from the forest edge. Different letters represent significantly different means (5% level). Transects perpendicular to roads in the north-south direction are indicated by the solid line while transects perpendicular to roads in the east-west direction are indicated by the broken line.

In terms of species assemblage composition, arthropods were overall significantly different at the 5 m and 10 m stations next to east-west directed roads compared to deep forest reference stations (Table 3.7). For transects next to north-south directed roads the effect was only evident up to 5 m from the road. The Coleoptera, Arachnida, detritivore, herbivore and dung associated groups were little affected by road direction in terms of assemblage composition (Table 3.7). The Diptera was influenced up to 5 m next to roads in both directions. The Orthoptera and Formicidae showed significant different assemblages mostly associated with roads in the east-west direction. The Formicidae however also revealed statistically significant differences next to north-south directed roads at the 5 m and 10 m stations (Table 3.7). North-south directed roads also had a significant influence on predaceous arthropod assemblages when compared to deep forest stations.

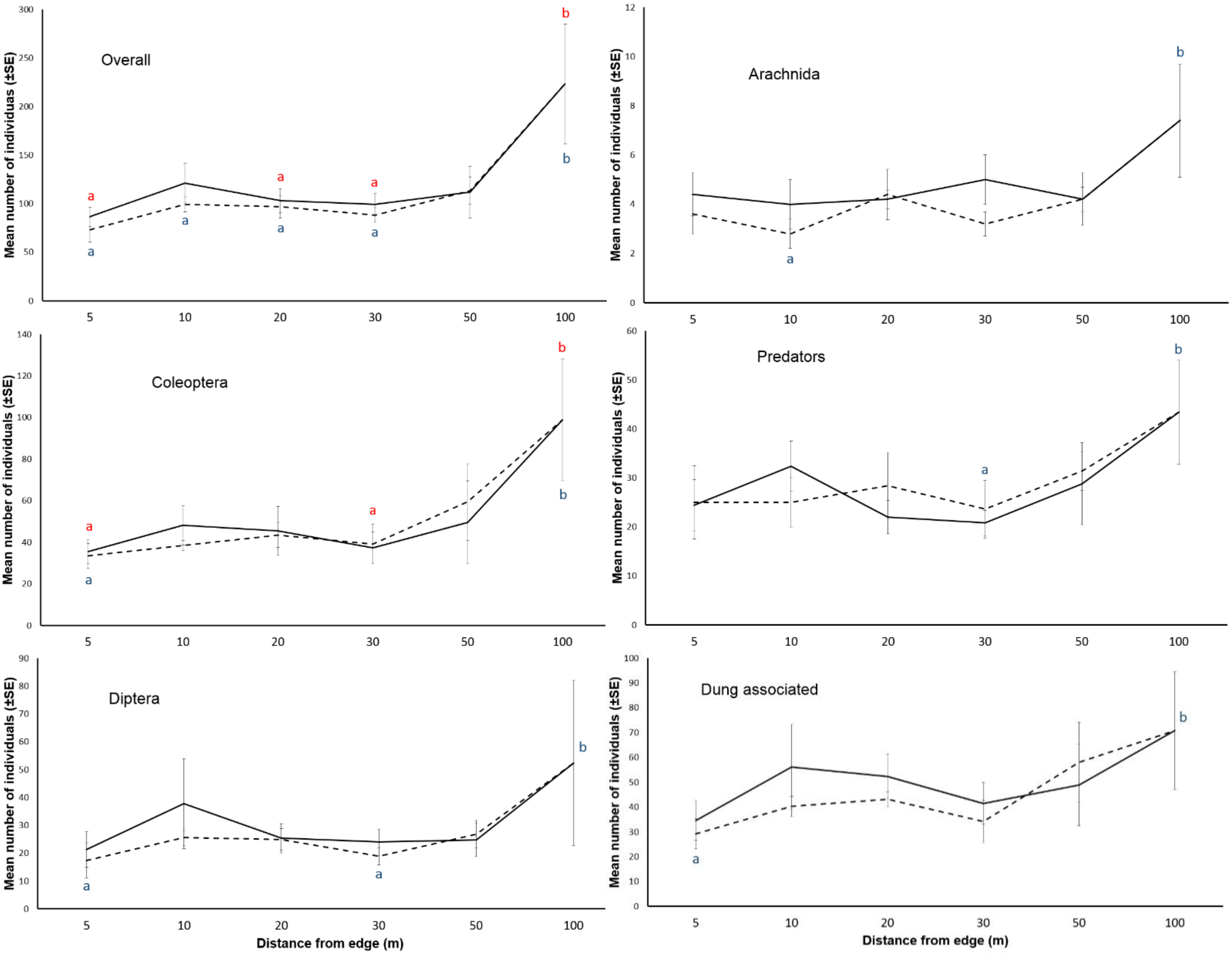

Figure 3.6: Abundance (mean ± SE) of overall arthropods and selected arthropod groups along transects for the two road direction categories at differing distances from the forest edge. Different letters near bars represent significantly different means (5% level). Transects perpendicular to roads in the north-south direction are indicated by the solid line while transects perpendicular to roads in the east-west direction are indicated by the broken line.

In a CAP analysis, the five randomly selected deep forest stations grouped closely together (Fig. 3.7). Except for the 50 m and 5 m stations, stations next to the north-south directed roads grouped fairly closely together. These forests were pooled, regardless of edges facing east / west. The 50 m stations on transects next to north-south and east-west directed roads were the closest in resembling deep forest stations. Stations at 5 m on the north-south directed roads revealed little similarities with deep forest stations and grouped close to the 5 m and 10 m stations next to the east-west directed roads (Fig. 3.7).

Table 3.7: Permutational multivariate analysis of variance (PERMANOVA) of arthropod assemblage composition for selected focal taxa and functional groups along transects perpendicular to roads that are directed in different directions. Arthropod assemblage composition of each station is compared to that of deep forest reference stations (>100 m from a forest edge). Pairwise t-values are reported.

Taxa	**Road direction**	**Distance from road edge**				
		5	10	20	30	50
Overall	east-west	**1.27***	**1.21***	1.12	1.18	0.97
	north-south	**1.32***	1.11	1.14	1.08	1.15
Coleoptera	east-west	0.96	1.11	0.82	0.96	0.82
	north-south	1.21	0.93	0.99	1.04	1.24
Diptera	east-west	**1.64***	0.86	0.87	0.79	0.89
	north-south	**1.54***	0.96	0.97	0.9	1.12
Orthoptera	east-west	1.09	**2.05****	**1.69***	1.08	0.8
	north-south	1.17	1.16	1.48	1.55	1.03
Formicidae	east-west	**1.73***	1.31	1.72	**2.78****	1.58
	north-south	**1.84***	**1.53***	1.73	1.29	1.42
Arachnida	east-west	1.23	1.12	1.13	1.29	1.03
	north-south	1.55	1.17	**1.47***	0.91	1.29
Detritivores	east-west	1.33	1.06	1.28	0.92	1.06
	north-south	1.29	0.99	1.12	1.39	1.1
Predators	east-west	1.12	1.31	1.1	1.32	0.93
	north-south	**1.45***	1.21	**1.42***	1.03	**1.5****
Herbivores	east-west	1.13	**1.85****	1.38	1.16	0.94
	north-south	1.22	1.33	1.42	1.65	1.1
Dung associated	east-west	1.38	0.95	0.81	0.8	0.74
	north-south	1.14	0.88	0.63	0.52	0.7

*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$

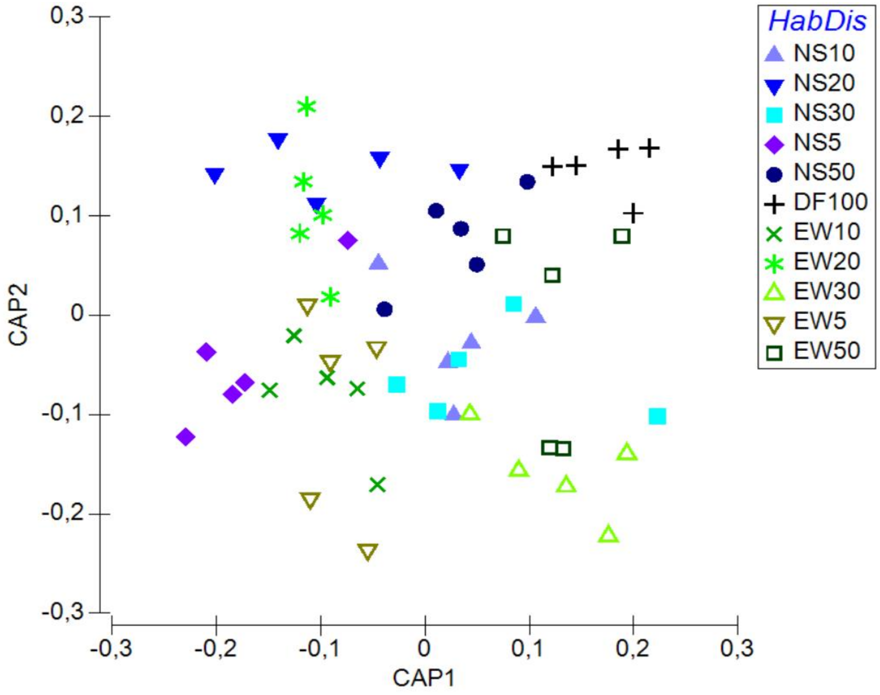

Figure 3.7: Canonical analysis of principal coordinates (CAP analysis) indicating similarity of arthropod assemblage composition between the 5 different stations (in metres) in transects perpendicular to east-west directed roads (EW; along the southern edge only) and north-south directed (NS) roads respectively (with Deep Forest (DF) reference sites included).

3.5) Discussion

In this study, I show that the southern Cape forest complex is fragmented by roads dissecting these ancient Afrotemperate forests. Edge effects were present along both major road types investigated. The impact of increased edge habitat (i.e. fragmentation) in natural ecosystems is known to alter ecological integrity of forest systems by allowing for foreign abiotic and biotic parameters to enter the system (Matlack & Litvaitis 1999; Tscharntke *et al*. 2002). These harder edges prevent movement and can lead to metapopulation break through inbreeding depression and reduced rescue effects (Hanski 1998). The impact of changes in arthropod species assemblages due to increased edge habitat in Afrotemperate forests remains unknown. However, Roland & Taylor (1995) showed that forest fragmentation in Canada alters the interaction between forest herbivore populations and their natural enemies, with increased fragmentation leading to unnatural outbreak durations of forest defoliators. Fragmentation that lead to a decline in abundance of insectivorous birds (Stouffer & Bierregaard 1995; Stratford

& Stouffer 1999) and bats (Kalko 1998) near forest edges decreased predation on litter dwelling and foliage insects, which lead to increases in herbivory (Benitez-Malvido *et al*. 1999). Although no increase in herbivore abundance was detected in this study, the composition of herbivore assemblages were altered at near-road stations. Therefore it seems as if alterations in vegetation characteristics near roads may cause assemblages to change rather than decreased predation. Furthermore, whereas previous work found an increase in predatory arthropods near forest edges (Didham *et al*. 1998), I found a significant drop in predator abundance next to arterial roads. Importantly these vegetation changes do not necessarily infer differences in plant species composition. For example, trees growing at forest edges can produce higher concentrations of nitrogen and soluble-sugars than trees in deep forest, which affect insect populations (Fortin & Mauffette 2001). Alterations to the phenology of the forest vegetation at the exposed edges can also lead to changes in nutrient availability for forest floor arthropods that cause changes in herbivorous arthropod assemblages (Restrepo *et al*. 1999)

The magnitude of edge effects next to arterial and secondary roads in these Afrotemperate forests were up to 50 m from the road edge as measured in altered assemblage composition of arthropods. Significantly altered assemblages were also detected up to 50 m into natural forests from arterial roads for some groups (e.g. Formicidae). The magnitude of the edge effects created by arterial and secondary roads is comparable to the large edge effects created by forestry plantations and clear felling of these on adjoining forest arthropod biodiversity in these same forests (Chapter 2). This supports findings from previous work that showed that, rather than creating a fairly soft edge, the effect of roads on forests are more similar to clear cut areas and effectively increases the amount of hard forest edge (Reed *et al*. 1996). Another South African study estimated an edge zone of 25 m bordering a highway in grassland savannah in KwaZulu-Natal (Samways *et al*. 1997). The reason for approximately double the width of the road edge zone here indicates that natural forest is predictably much more sensitive towards increases in penetrating light and other factors than a grassland savannah (Forman & Alexander 1998; Spellerberg 1998; Trombulak & Frissell 2000).

Most previous studies on road edge effects were conducted in the tropics (e.g. Lovejoy *et al*. 1986; Carvalho & Vasconcelos 1999; Laurance *et al*. 2002; Laurance 2004; Wirth et al. 2007; Broadbent *et al*. 2008) and the penetrating effects reported are often far greater than 100 m. A study of road edge effects on litter invertebrate communities by Delgado *et al*. (2013), found a road edge zone of only 10 m into the adjoining forest. Their study was conducted in both laurel forests and natural pine forests. Edge effects on soil macroinvertebrate fauna were restricted to the first 100 m from the road edge in mixed-mesophytic deciduous forests in the USA (Haskell 2000). Road edge effects of ca. 10 m are found in the southern Appalachian forests in North Carolina Jackson *et al*. (2014). The temperate forests of the southern Cape therefore seems to be more comparable with forests occurring on relatively similar latitudes across the globe in terms of road edge effects as perceived by forest invertebrates. However, extrapolation from previous work needs to be done with caution as results seem fairly localised due to differences in a range of factors.

Increased road width is known to contribute towards road-induced ecosystem disturbance. For example, Dunn & Danoff-Burg (2007) found that paved two-lane roads and highways running through a New York forest caused a lower diversity and abundance of some arthropod taxa compared to a one-lane unpaved road. These results are similar to a study by Bohac *et al*. (2004) that found a higher diversity of beetles bordering a small road compared to a highway in a cultural landscape in the Czech Republic. The greater width of and higher traffic loads on arterial roads in this study should then, according to previous work, be more detrimental to forest arthropod diversity (e.g. Koivula & Vermeulen 2005). However, even though the arterial road had a greater effect across multiple taxa studied, secondary roads were not much different in terms of overall edge effects. It should be noted here that both roads were unpaved and thus were not influenced by the presence of asphalt. It therefore seems that in general, the creation of the canopy gap has a more significant influence on arthropod diversity than the actual road width and/or traffic volume, here. Therefore any road that creates a gap in the forest canopy would be detrimental to forest biodiversity and function.

Light availability is predicted to increase in forests as one moves closer to a road (Delgado *et al*. 2007). Coupled with an increase in temperature, it is suggested that altered micro-climatic conditions associated with light and temperature causes arthropod compositional changes (Murcia 1995; Werenkraut *et al*. 2014). In the present study both overall arthropod species richness and –abundance significantly decreased next to roads when compared to deep forest sites. This likely indicates a loss of forest specialist species that are sensitive to microclimatic changes such as light and temperature, with little influx of open-habitat generalists. Forest interiors have been shown to contain rare and specialist species of various taxonomic groups which are absent from road edge zones (Koivula 2005; Carpio *et al*. 2009; Delgado *et al*. 2013). For example, Carpio *et al*. (2009) assessed the effect of a newly constructed road on dung beetle diversity and showed that specialist dung beetles were much less common next to roads. In the current study dung associated species were also greatly affected in terms of both species richness and assemblage composition in forests bordering arterial roads. Flies associated with deep forest stations ignored the arterial road edges zone in this study likely due to altered micro-climatic conditions (Kapos 1989; Murcia 1995). Although the Diptera are not often used as bioindicators compared to more well-known groups such as carabid beetles, scarab beetles, ants and Arachnida, this study indicates that flies could be good indicators of forest disturbance due to their diverse life-cycles and environmental requirements (Durska 2013; Delgado *et al*. 2013).

As expected, hiking trails affected arthropod assemblages the least of the three road types studied. They shared numerous arthropod species with deep forest reference stations, they had similar numbers of arthropod species richness and abundance, and had similar arthropod assemblage composition for nearly all taxonomic and functional groups. However, even these seemingly benign recreational pathways created an edge effect when assemblage composition of all taxa collected are collectively compared to deep forest reference stations. Hiking trails affected arthropod assemblage composition up to 10 m into the adjoining forest. Despite the lack of disturbance of the forest canopy and its associated microclimatic changes, arthropods therefore still seemed to respond to these as a low magnitude edges. Recreational trails are prone to soil erosion (Hinckley *et al*. 1983; Deluca *et al*. 1998), soil compaction and root exposure (Li *et al*. 2005), factors that could impact epigaeic arthropod assemblages. However, few previous studies focused on the effects of recreational trails on biodiversity. A study on arthropods revealed how ski trials are barriers to the movement of flightless and short-winged forest beetles due to changes in plant composition near the edges (Strong *et al*. 2002). In forest and mixed-grass prairie ecosystems, specialist bird species were less common near recreational trails (Miller *et al*. 1998). In the Rocky Mountain forests, hiking trails were found to be conduits for the movement of certain plant species along trails (Benninger-Truax *et al*. 1992). Similarly, certain arthropods such as dipterans could also increase in activity along hiking trails as these areas increase ease of dispersal and opportunities for prey searching (Delgado *et al*. 2013). Here, the Diptera were also more abundant and species rich near hiking trails again emphasising their possible use as indicators of disturbances in forests.

In this study I have shown that road direction could influence the magnitude of edge effects in natural forests. East-west directed roads had a greater edge effect along their southern edge (with a northern exposure of the forest edge) in terms of arthropod species richness and assemblage composition, when compared to north-south directed roads. This is likely due to forests to the south of east-west directed roads experiencing a higher level of sunlight penetration relative to forests bordering north-south directed roads which in turn creates a bigger edge (Matlack 1993; Murcia 1995; Didham & Lawton 1999). Other studies focusing on the aspect of edges found results similar to those obtained here. Matlack (1993) showed how north-facing edges in the United States were unaffected by variables such as litter moisture, temperature and radiation, whereas south-, west- and east facing edges showed strong gradients linked to edge orientation. This strongly suggests that variables dependent on sunlight penetration, in turn dependent on edge orientation, to have significant effects on the forest micro-environment. It has also been revealed how edge zones could have higher air temperature and decreased humidity (Kapos 1989). Kapos (1989) showed how photosynthetically active radiation increased in the understory up to 40 m from the edge into a natural forest in Brazil, whereas soil moisture was found to be depleted up to 20 m from the edge. Increased stomata conduction in plants near edges was also found. Owing to these altered edge zones and the effects thereof on edge vegetation, it is suggested that the increased levels of sunlight penetration to not only directly, but also indirectly, affect arthropod diversity. Whereas multiple taxa showed a decrease in abundance moving towards east-west directed roads, only a single taxonomic group, Coleoptera, revealed such decreases moving towards north-south directed roads. These significant declines could be indicative of phototactic organisms, adapted to shaded forest environments, responding negatively towards increases in sunlight penetration (Xiang-Feng & Chao-Liang 2004). Diptera, along with dung associated arthropods, revealed the strongest response, being both less species rich and less abundant at stations bordering east-west directed roads. They also revealed different assemblage compositions next to both road direction categories.

Apart from flies, Formicidae assemblages seemed particularly good as indicators of habitat disturbance in this study as also recognised in previous studies (Dauber & Wolters 2004; Chen *et al*. 2011; Majer & Beeston 1996; Kaspari & Majer 2000; Andersen *et al*. 2006; Nakamura *et al*. 2007; Palladini *et al*. 2007). These results also echo those of previous work in other forest types (e.g. Brühl *et al*. 2003) where ants were found to be good indicators of forest fragmentation. In the present study ant assemblages indicated edge effects of up to 50 m for both arterial and secondary roads, and up to 5 m for hiking trails. Interestingly, a study on ant species richness and compositional changeover in the forests of Brazil also detected an edge effect of 50 m (Sobrinho & Schoereder 2007). Ant compositional changes were also evident next to roads in both directions evaluated. However, when overall effects of fragmentation on forest biota are studied, it is evident that a multitude of different taxa should be considered as different taxa responded differently towards disturbances created by the various road types assessed here. Where feasible, a multi-taxon approach is considered critically important for studies that monitor biodiversity responses to ecological factors (Gerlach *et al*. 2013).

This study is the first of its kind in the greater southern Cape region of South Africa and provides evidence that a distinct edge effect of up to 50 m is detectable for arthropods bordering both arterial- and secondary roads. The 10 m effect penetrating forests bordering hiking trails is likely due to the creation of unique zones with slightly different biotic (e.g. cleared plant communities) and abiotic (e.g. compaction and increased erosion) effects whilst the effects of the larger roads seems to be directly related to the creation of canopy gaps rather than factors associated with increased road width ad traffic volumes. Sunlight penetration and its cascading effects on other variables seems to play a major role in these perceived edge effects as it was shown that road direction was an important factor in explaining arthropod assemblage compositional changes. Further studies are however needed to evaluate differences in specific microclimatic variables and their impact on arthropod assemblages. It is possible that other forest biota, apart from arthropods, might also be influenced by the increase in forest edge, and that the southern Cape forests are much more fragmented than previously believed. This baseline research shows that forest integrity needs active management to be maintained. Ecosystem services mediated by dipterans especially are at risk of being lost from arterial road verges if not mitigated. These services include pollination and pest control, key services within any natural ecosystem (Smith & Mayfield 2015).

3.6) References

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4) Chapter 4

General conclusions and management recommendations

The transformation of natural landscapes into production areas is a major cause of biodiversity loss (Ewers & Didham 2006). Little doubt exist that there is a need for production and biodiversity conservation to co-exist, rather than being mutually exclusive. With a rapidly growing human population and an increase in demand for natural resources, we are yet to achieve true ecological sustainability coupled with socio-economic growth.

Attempts towards creating sustainable landscapes have been made though. Ecological networks (ENs) that act as large scale, interconnected corridors between habitats for species dispersal and movement can alleviate some pressures associated with habitat fragmentation (Jongman 1995; Samways, Bazelet & Pryke 2010; Pryke & Samways 2012). Research on ENs in South Africa has shown that it is possible for species to use set-aside corridors in landscape mosaics in a grassland matrix (Pryke & Samways 2012). Although not empirically tested, the same may be true for arthropods in the southern Cape Afrotemperate forest complex that contain a mosaic of commercial plantations, Afrotemperate forests and fynbos over large tracts of land. The establishment of ENs in this research area has received little attention and needs ongoing research to carefully select priority areas (Blasi *et al*. 2008). Understanding biotic responses to edge effects will go a large way in providing vital information for the selection and implementation of effective ENs (Sala *et al*. 2002; Pryke & Samways 2012).

In the southern Cape, exotic plantations cover wide tracts of land effectively replacing the natural fynbos-forest ecotone as well as large areas once covered by fynbos and some natural forests (Phillips 1931). I have shown that forest arthropod assemblages do not perceive pine plantations as alternative forest habitat. Pine plantations, as expected, also fail to provide habitat for fynbos species and these affect natural forest assemblages up to 30 meters into adjacent forests (Chapter 2). It is however possible to manage plantations in such a way that these contribute significantly towards sustaining natural biota with little loss in timber production (Norton 1998). It should therefore in theory be possible that plantations in the southern Cape could be specifically managed in order to alleviate their effect on natural forests and even increase regional biodiversity (Gjerde & Saetersdal 1997) without incurring large economic costs (Hartley 2002). Most importantly a strong correlation exists between biodiversity and the amount of native vegetation left within plantations (Staines 1983; Parker *et al*. 1994). Therefore habitat loss should be minimised and movement between patches should be encouraged (Fig. 4.1; Pryke & Samways 2012). To provide ecological stepping stones some practices include having large-diameter, native trees scattered throughout a plantation (dispersed retention), in linear strips or alternatively in clumps (aggregated retention) (Franklin *et al*. 1997). Alternatively, remnant patches of indigenous trees, covering between 5% and 10% (Woodley & Forbes 1997; Hartley 2002) should be conserved within large plantation blocks (Franklin *et al*. 1997).

My research shows that plantations, and especially their periodic removal (felling), have enormous effects on the edges of forests bordering these. Pine plantations open the naturally denser fynbos-forest edges and allow conditions to change up to 30 meters into the forests. Felling these (e.g. for harvesting) opens the edge up to even greater negative influences that penetrate these forests up to 50 meters. The preservation and possibly restoration of the natural fynbos-forest ecotone should therefore be prioritised (Fig. 4.1). This would especially be important in small remnant forest patches as, if one considers that edge effects penetrate forests up to 50 meters, patches of ca. 150 meters in diameter and smaller would essentially be entirely altered in terms of arthropod assemblages. Future research should aim to determine the width of the edge effect on the fynbos side in order to make management recommendations on the size of natural vegetation tracts next to forests patches that are needed to effectively buffer these from unnatural influences.

Natural ecotones along the edges of natural forests comprise a unique zone of arthropod diversity with overlap between taxa from both biotopes (Chapter 2). Their preservation would therefore go a long way in protecting both forest arthropod diversity and some natural fynbos arthropods. This is important since most plantations in the region occupy land previously covered by e.g. Garden Route Shale Fynbos (Mucina & Rutherford 2006) and, as I have shown here (Chapter 2), fynbos house numerous specialised arthropod taxa. This veld type today is considered endangered, with more than half of it lost to cultivation and the establishment of plantations (Mucina & Rutherford 2006). More research is needed on the effect of plantations, and their edge effects on fynbos arthropod communities in order to make sound management recommendations with regards to the implementation of effective ENs (Fig 4.1). This would be an essential first step in identifying priority areas for the establishment of ENs. Work on other systems such as grasslands in South Africa indicates that corridor width should be a minimum of 64 m (Pryke & Samways 2012), reaching widths of up to 250 m wide (Pryke & Samways 2001).

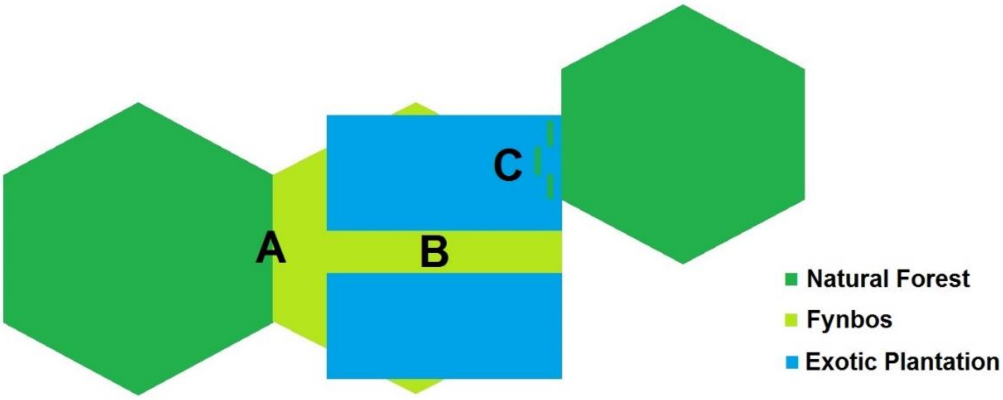

Figure 4.1: Proposed optimal biodiversity conservation could include the protection of the natural forest-fynbos edge to alleviate unnatural edge effects (A), creating fynbos corridors through production areas (B) and, where plantations and natural forest directly border without the possibility of restoring a natural edge zone, incorporate indigenous floral components at the edge inside the plantation (C).

Human induced edge zones into forests are not confined to production landscapes. I have shown that the multitude of arterial and secondary roads that pass through large tracts of indigenous forests create edge effects similar in magnitude to those created by clear felling of plantations (Chapter 3). These roads therefore permanently fragment these forests and lead to a retraction in forest specialist species, the consequences of which are still largely unknown. The creation of any road accessible for a motor vehicle would open the forest canopy and would be detrimental to forest biodiversity and function. In the plantation forestry areas, roads are often constructed between plantation edges and natural forests. The effect of these on forest biota is likely just as large as public roads if the natural fynbos-forest edge is not left intact. Roads in such areas should therefore preferentially be constructed as far away from the natural forest edge as possible. Road verges are often incorporated into ecological corridors in grasslands (Tanghe & Godefroid 2000; Hopwood 2008) However, if roads also affect lower growing vegetation types (e.g. grasslands and fynbos) by creating large edge effects, the effectiveness of these corridors for biodiversity conservation could be compromised (Samways *et al*. 1997). Fairly large edge effects in these vegetation types seems very likely as even seemingly benign recreational paths had effects on arthropod biodiversity of up to 10 meters into the adjoining forest in this study (Chapter 3). It has to be mentioned that it is unlikely that these recreational paths would lead to forest fragmentation but rather that arthropods respond to changes in a variety of biotic and abiotic variables such as altered soil properties and understory plant assemblage composition. Any creation of additional roads should be carefully planned in line with these results. However much research still need to be conducted on this topic, as factors here not previously considered to be important (e.g. road direction) impact arthropod diversity.

The typical landscape is driven by numerous factors, including the economic climate of a region, political decision-making and the socio-economic status of its people, with biodiversity conservation being an aspect thereof (Antrop 2005). The Garden Route National Park is a heterogeneous national park and unique in South Africa due to it firstly being unfenced and secondly by having large tracts of land not currently set aside for conservation but rather production. Because of this, the park should enjoy special management treatment balancing both production and conservation, working with major plantation owners in the region. Mankind today face a rather difficult task in balancing its priorities and needs. Research pertaining to sustainable landscapes, where both biodiversity conservation and production co-occur should receive more attention globally. It is becoming more and more relevant, and even more necessary.

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Appendices

Appendix 1: Location of sampling sites with additional information for the forestry production areas

Deep Forest	**Latitude**	**Longitude**	**Approximate age**	**Species**	**Cut down date**
Beervlei	-33.912116	22.736818			
Millwood	-33.913965	22.95383			
Gouna	-33.943455	23.05389			
Kom-se-Bos	-33.945394	23.102132			
Diepwalle	-33.948844	23.141793			
Rabbet	-33.94898	23.166639			
Fynbos					
Fisantehoek	-34.00315	23.22357			
Gouna	-33.98647	23.04413			
Ysternek	-33.92887	23.16090			
Dal van Varings	-33.91406	23.14294			
Rabbet 1	-33.946404	23.166475			
Rabbet 2	-33.946653	23.168235			
Clear felled					
Karatara 1	-33.91070	22.81273	5 months	*Pinus radiata*	01-01-2014
Karatara 2	-33.89618	22.78257	24 months	*Pinus radiata*	01-05-2012
Farleigh	-33.893618	22.884537	8 months	*Pinus radiata*	01-09-2013
Millwood	-33.89961	22.97584	73 months	*Pinus pinaster*	01-04-2008
Gouna	-33.964514	23.051484	156 months	*Pinus radiata*	01-05-2001
Greenfern	-34.02456	23.17470	Recently replanted	*Pinus eliotti*	
Pine					
Bergplaas 1	-33.89646	22.72569	23 years	*Pinus radiata*	
Bergplaas 2	-33.89606	22.74831	>30 years	*Pinus radiata*	01-04-2015
Karatara	-33.91124	22.80313	27 years	*Pinus radiata*	
Beervlei	-33.91750	22.73464	17 years	*Pinus radiata*	
Spruitbos	-33.94481	23.08410	20 years	*Pinus radiata*	
Gouna	-33.962458	23.05481	>30 years	*Pinus radiata*	01-04-2015

Appendix 2: Climatic data for the sampling periods

Season 1: Late Autumn					**Season 2: Late Spring**				
Month	**Day**	**Average minimum temperature**	**Average maximum temperature**	**Total rainfall (mm)**	**Month**	**Day**	**Average minimum temperature**	**Average maximum temperature**	**Total rainfall (mm)**
April	11	19	29	0,0	October	31			0,0
	12	15	30	0,0	November	1	14	16	1,0
	13	9	30	0,0		2	16	17	0,0
	14	18	25	11,2		3	16	19	30,0
	15	15	20	6,6		4	11	20	27,6
	16	15	22	0,0		5	15	19	0,0
	17	14	24	0,0		6	15	19	0,0
	18	17	22	0,0		7	15	21	0,0
	19	18	22	0,0		8	16	19	0,0
	20	18	21	0,0		9	17	20	0,0
	21	18	19	6,8		10	14	16	10,2
	22	16	19	17,6		11	16	20	1,4
	23	12	14	45,8		12	15	19	8,8
	24	14	20	0,8		13	13	19	3,4
	25	16	20	0,0		14	13	19	4,8
	26	15	17	26,2		15	8	16	23,2
	27	14	19	1,4		16	9	17	1,2
	28	16	21	0,0		17	13	20	0,0
	29	17	20	9,6		18	12	19	0,0
	30	14	19	0,0		19	13	19	0,0
May	1	14	21	0,0		20	11	19	5,0
	2	15	25	0,0		21	14	20	0,0
	3	17	20	0,0		22	16	21	0,0
	4	15	24	8,6		23	15	18	23,0
	5	9	18	0,2		24	15	19	3,4
	6	13	20	0,0		25	16	20	0,0

	7	11	29	0,0		26	17	21	0,0
	8	16	19	14,8		27	14	23	0,0
	9	15	21	0,2		28	17	20	2,6
Total				149,8					145,6
Mean		15	21,72413793	5,165517241			14,14285714	19,10714286	5,020689655

Appendix 3: Supporting photos of study area and trap methodology

Figure 5.1: Examples of the three forest edge types included in this study. Top: Clear felled area. Middle: Mature pine stand. Bottom: Natural fynbos / forest ecotone.

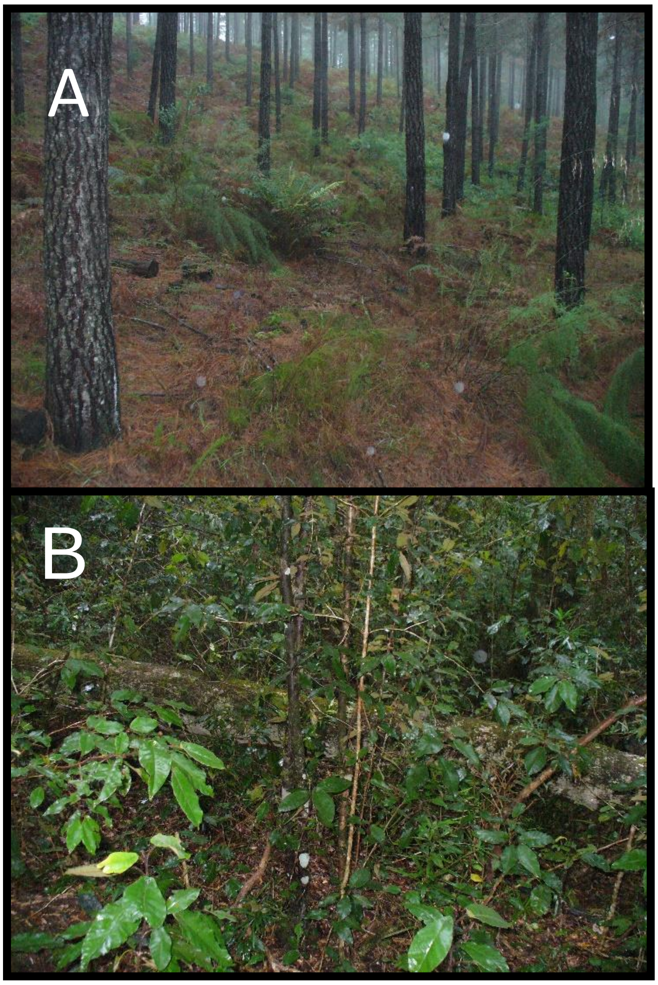

Figure 5.2: A comparison of the typical understory vegetation between mature pine blocks (A) and natural afrotemperate forests (B).

Figure 5.3: Photos that illustrate the typical fynbos-forest ecotone. A - Fynbos site 1 at Fisantehoek, B - Fynbos site 6 at Rabbet Island (Diepwalle). Notice the abundance of Keurboom.

Figure 5.4: Evidence of alien invasive species colonising areas that have been clear cut for relatively longer periods of time, with scattered logs. A – Clear felled site 4 at Millwood. B – Clear felled site 5 at Gouna.

Figure 5.5: Examples of both unbaited (top) and baited (bottom) pitfall traps used in this study.

Figure 5.6: Examples of arterial roads (top left) and secondary roads (top right). Hiking trails are exposed to trampling (bottom left) as well as increased water run-off (bottom right).