Disturbance factors related to conservation of biodiversity in large-scale ecological networks

by

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Declaration

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Overall Summary

Globally, habitat transformation causes biodiversity loss, with the transformed matrix often affecting the disturbance regime in remnant natural patches. In South Africa, significant parts of the Indian Ocean coastal belt and grassland biomes have been transformed into commercial forestry plantations of alien trees, which are detrimental to local biodiversity. Consequently, large scale ecological networks (ENs) of remnant natural vegetation, maintained areas (e.g. firebreaks) and special landscape features (e.g. rocky outcrops and wetlands) have been implemented among forestry compartments to offset the negative effect of this land use on biodiversity. Different grassland areas, which constitute a major portion of ENs, were managed in different ways, as governed by their primary purpose (e.g. fire protection or conservation). The overall aim of this study was to determine how grassland floral and grasshopper herbivore communities responded to different disturbances (mowing, burning and grazing), and how we can adjust management of the major disturbances to effectively conserve these major components of biodiversity in ENs.

Sampling was carried out in the commercial forestry ENs in the lower-elevation Zululand area and adjacent reserve area iSimangaliso Wetland Park, as well as in the forestry ENs in the higher-lying Midlands and adjacent iMpendle Nature Reserve. Both the reserves or protected areas (PAs) acted as reference sites, while other sites were chosen to represent the predominant disturbances in ENs at each locality: mowing, annual vs. longer-rotation burning, time since last fire, and domestic cattle grazing.

In the Zululand subtropical grassland (chapter 2), I explored the effect of frequent mowing on firebreaks, and the effect of patch size and isolation on plant communities in non-firebreak natural areas of the EN. Frequent mowing resulted in plant species loss and a shift in species composition of firebreaks. Furthermore, small, isolated patches in the EN far away from the PA border had lower plant species richness and greater species turnover than wide, interconnected corridors near the PA border, which, in turn, was similar to reference sites in the PA. As plant species were lost from frequently-mown firebreaks and small, isolated patches in the EN, I recommend that this management practice should be confined to demarcated areas (e.g. forestry compartment edges and firebreaks) and that creation of wide, interconnected corridors should be prioritized when designing ENs.

In higher elevation Afromontane grassland (chapter 3), I investigated the effect of annual burning on plant communities in firebreaks by comparing them to less frequently burned grassland in the EN and PA, respectively. Grazing by domestic cattle was taken as an

embedded factor for firebreak and less frequently burned sites in the EN. There were three firebreak types: annually-burned with heavy cattle grazing (plantation firebreaks), annually-burned with light cattle grazing (peripheral firebreaks), and annual burning without cattle grazing (PA firebreaks). Burned reference grassland in the EN and PA hosted plant communities that were similar in species richness, composition and turnover. This was also the case for lightly-grazed peripheral EN firebreaks and PA firebreaks. However, species composition and turnover of plantation EN firebreaks with heavy cattle grazing differed from that in the other two firebreak types. Although not significant ($P<0.1$), plantation EN firebreaks had less plant species than reference burned grassland in the EN, and all firebreak types had less plant species, lower species turnover and different species composition when compared to reference burned grassland in the PA. Annual burning of firebreaks, with and without cattle grazing, caused a significant shift in plant species composition and a reduction in plant species turnover. When annual burning was combined with heavy cattle grazing, plant species were lost, as was the case in plantation EN firebreaks. Therefore, I recommend that this management practice should be confined to firebreaks, and that cattle access to firebreaks should be strictly controlled.

In Chapter 4, I considered the effect of cattle grazing (presence vs. absence, as well as intensity) on Afromontane grassland against the natural backdrop of variation caused by time since last fire in grassland with longer fire-return intervals (excluding all firebreaks). Lowest plant species richness and turnover occurred in unburned (i.e. burned >12 months prior to sampling), ungrazed grassland in the PA. Burning and grazing both caused a change in plant species composition that went hand in hand with an increase in plant species richness and turnover. However, burning (burned vs. unburned) only affected plant communities in ungrazed grassland in the PA. Similarly, the presence of large mammalian grazers (EN vs. PA) only affected plant communities in unburned grassland. Unburned plant communities grazed by domestic cattle in the EN were similar to those in the PA grazed by indigenous black wildebeest, indicating that cattle grazing simulates, at least to some degree, the effect of indigenous ungulate grazing. Nevertheless, heavily-grazed grassland had less plant species than moderately-grazed grassland in the EN. I recommend that burning and grazing should continue in grassland ENs, as these natural disturbances are necessary to maintain diverse and dynamic ecosystems. Nevertheless, managers should instigate cattle grazing with caution, as high intensity grazing can be detrimental to conservation efforts.

In Chapter 5, I examined the effect of annual burning, cattle grazing (presence vs. absence) and time since last fire on grasshopper assemblages in Afromontane grassland. In

general, grasshoppers benefitted from disturbance, and were remarkably resilient to different disturbance regimes. Grasshopper species richness and their abundance were both greatest in annually-burned firebreaks with light cattle grazing, and lowest in moribund grassland in the PA which had not been burned for several years. Yet, time since last fire only affected grasshopper communities in the absence of large grazers (in the PA). None of the individual disturbances had an effect on the grasshopper assemblage. Rather, these insects responded to the combined effect of annual burning with cattle grazing. Sites were similar in grasshopper species richness, composition and abundance whenever either annual burning or cattle were absent, which suggests that these two disturbances drive changes in the grasshopper assemblage in these grasslands. Although grasshoppers benefited from annual burning with light cattle grazing, I would not recommend this disturbance regime outside firebreaks. Rather, management of other grassland areas in the EN should adapt longer fire-return intervals with a rotational cattle grazing system, so that undisturbed habitat is provided for other sensitive taxa.

In conclusion, grassland plants and grasshoppers benefited from some form of disturbance, but were lost from small, isolated patches in the EN, as well as from areas with high disturbance frequency and intensity. Simulation of natural disturbances (moderate levels of fire and grazing) in wide, interconnected corridors is necessary for maintaining diverse and dynamic grassland ecosystem in ENs among commercial forestry plantations.

Samevatting

Omskepping van natuurlike habitat na lande of plantasies veroorsaak biodiversiteitsverlies wêreldwyd. Boonop het sulke veranderinge dikwels ′n effek op die versteurings binne-in oorblywende kolle natuurlike plantegroei wat verreikende gevolge kan hê. Groot gedeeltes van die Suid-Afrikaanse grasveldbioom is omskep in bosbou plantasies wat bestaan uit uitheemse bome wat ′n baie groot nadelige effek op plaaslike biodiversiteit het. Daarom is grootskaalse ekologiese netwerke (EN’e), wat bestaan uit oorblywende kolle natuurlike plantegroei, brandbane en spesiale habitattipes in die landskap (bv. rotsriwwe en vleilande), tussen bosbouplantasies geïmplimenteer met die doel om die negatiewe effek van plantasies op plaaslike biodiversiteit te verlig. Bestuur van grasvelde, wat ′n groot gedeel van EN’e uitmaak, wissel dikwels en hang af van hulle primêre doel (bv. beskerming van plantasies teen wegholveldbrande of natuurbewaring). Die doel van hierdie projek was om vas te stel hoe plant- en springkaangemeenskappe in grasvelde reageer op verskillende versteurings (grassny, brand en beweiding), en die optimale bestuur van die versteurings om die biodiversiteit in grasvelde beter te bewaar.

Steekproewe is geneem in EN’e tussen bosbouplantasies in die laagliggende Zululand en langsliggende wêrelderfenisgebied, iSimangaliso Wetland Park, asook in die hoërliggende Midlands en langsliggende iMpendle Natuurreservaat (NR). NR’e het as verwysing gedien waarteen die effek van grassny, frekwensie van brande, tydsverloop vanaf die laaste brand, en beweiding deur beeste, wat tipiese versteuringe in EN’e is, gemeet is.

In hoofstuk 2 het ek vasgestel wat die effek van grassnyfrekwensie op plantgemeenskappe in brandbane is, en hoe plantgemeenskappe in subtropiese grasveld in die res van die EN reageer op die grootte en strukturele isolasie van oorblywende kolle natuurlike plantegroei. ′n Hoë grassnyfrekwensie het ′n verandering in die spesiesamestelling van plantgemeenskappe in brandbane veroorsaak wat gepaard gegaan het met spesiesverlies. Terselfdertyd was daar minder plant spesies in klein, geïsoleerde kolle natuurlike plantegroei as wat daar in wyer, aaneenskakelende gange nader aan die natuurreservaatgrens was. Laasgenoemde het plantgemeenskappe bevat wat baie soortgelyk aan die in die natuurreservaat was. Daarom stel ek voor dat die skep van wye, aaneengeskakelde natuurlike habitat prioriteit moet geniet wanneer nuwe EN’e ontwerp word, en dat gras slegs gereeld gesny moet word in spesifieke, afgebakende areas (bv. brandbane). Die rede hiervoor is dat hierdie bestuurspraktyk nie bevorderlik was vir die bewaring van plantdiversiteit in EN’e nie.

In hoofstuk 3 het ek gekyk hoe die plantgemeenskappe in brandbane daarop reageer om elke jaar gebrand te word deur hulle te vergelyk met Afrikaberg grasveld in die EN en NR wat minder gereeld gebrand word. Beweiding deur beeste is gesien as ′n integrale deel van die EN. Ek het onderskei tussen plantasiebrandbane met swaar beweiding, randbrandbane met ligte beweiding en brandbane in die NR sonder beweiding. Die plantspesiesamestelling van brandbane, met ligte of geen beweiding nie, het verskil van grasvelde wat minder gereeld gebrand word. Tog is die hoeveelheid plantspesies nie geraak nie. Alhoewel die plantgemeenskappe in ligbeweide brandbane soos die in onbeweide brandbane in die NR was, het die plantspesiesamestelling van beide verskille getoon wanneer hulle vergelyk is met plantasiebrandbane wat swaarder deur beeste bewei is. Plantspesierykheid in plantasiebrandbane was boonop heelwat laer as wat in NR grasvelde gevind is, en daar was heelwat meer kaal grond in plantasiebrandbane as in enige van die ander areas. Oor die algemeen het plantspesiesrykheid van brandbane nie daaronder gely om elke jaar gebrand te word nie, maar kwesbare plantgemeenskappe in brandbane het wel daaronder gely om swaar bewei te word. Daarom stel ek voor dat jaarlikse brande tot brandbane beperk word en dat beeste se toegang tot brandbane streng beheer word.

In die hoofstuk 4 ondersoek ek die effek van beweiding deur beeste (teenwoordigheid teenoor afwesigheid, sowel as beweidingsintensiteit) op die plantspesiesrykheid en samestelling van gebrande en ongebrande Afrikaberg grasvelde wat minder gereeld gebrand word. Die minste plant spesies is aangeteken in ongebrande, onbeweide grasveld in die NR. Brande en beweiding het albei ′n effek op plantspesiesamestelling gehad wat gepaard gegaan het met ′n toename in plantspesiesrykheid. Plantgemeenskappe in grasvelde wat onlangs (<12 maande voor die steekproef geneem is) gebrand is, het slegs van die in ongebrande grasvelde verskil wanneer nie een van die twee areas bewei is nie. Op ′n soortgelyke trant het die teenwoordigheid van beeste (EN teenoor NR) slegs n effek gehad in ongebrande grasvelde. Ongebrande plantgemeenskappe in die EN wat deur beeste bewei is, was baie soos die in die NR wat deur swartwildebeeste bewei is. Dit dui daarop dat beeste die effek van inheemse wildsoorte tot ′n mate naboots. Des nieteenstaande die bogenoemde, het swaar-beweide grasvelde minder plantspesies gehad as grasvelde wat slegs matig bewei is. Ek stel voor dat brande en beweiding deel moet vorm van die bestuur van grasvelde in EN’e, want hierdie natuurlike versteuringe dra by tot ′n diverse, dinamiese grasveldekosisteem. Tog moet bestuurders versigtig wees wanneer hulle die plaaslike gemeenskap se beeste in EN’e toelaat, want swaar beweiding kan bewaringsinisiatiewe in die wiele ry.

In hoofstuk 5 het ek die klem na springkane verskuif, en die effek van jaarlikse brande, beweiding deur beeste (teenwoordigheid teenoor afwesigheid) en tydsverloop sedert laaste brand op hierdie sensitiewe insekte in Afrikaberg grasvelde ondersoek. Alhoewel springkaangemeenskappe baat gevind het by versteuringe, het hulle nie beduidend gereageer op enige van die indiwiduele versteuringe nie. Die digste sprinkaan bevolking met die hoogste spesies diversiteit is aangeteken in brandbane in die EN wat liggies deur beeste bewei is. Darenteen is die laagste bevolking en spesies diversiteit aangeteken in grasvelde in die NR wat groot hoeveelhede dooie plantmateriaal bevat wat aandui dat hierdie grasvelde nie onlangs gebrand het nie. Springkaangemeenskappe in gebrande grasvelde het slegs van ongebrande grasvelde verskil wanneer nie een van die twee bewei is nie. Die sleutelkombinasie van versteuringe wat die rykheid en samestelling van springkaangemeenskape bepaal het, was ′n hoë brandfrekwensie (soos in brandbane) en beweiding deur beeste. Wanneer een van hierdie versteuringe afwesig was, was springkaangemeenskappe tussen verskillende areas dieselfde. Alhoewel springkaangemeenskappe daarby baat gevind het wanneer brandbane elke jaar gebrand en deur beeste bewei is, kan ek nie hierdie bestuurspraktyk vir die res van die EN aanbeveel nie. Grasvelde in die res van die EN behoort eerder minder gereeld (elke 2-4 jaar) gebrand en met ′n rotasiestelsel bewei word. Sodoende sal brandbane voorsien in die behoeftes van springkane, en die res van die EN in die behoeftes van sensitiewe taksa wat onversteurde habitat benodig om te floreer.

My slotsom is dat versteuringe nodig is om die volle diversiteit van plante en springkane en die dinamika binne-in grasvelde te bewaar. Tog verdwyn daar plantspesies uit areas met ′n hoë versteuringsintensiteit of frekwensie en klein, geïsoleerde kolle natuurlike plantegroei in die EN. Daarom beveel ek aan dat natuurlike versteuringe (brande en beweiding) matig toegepas moet word in wye, aaneengeskakelde gange in die EN. Hierdie benadering tot natuurbewaring kan biodiversiteit tussen bosbouplantasies beveilig teen verdere verlies.

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Luke 12: 27-28 "Consider how the wild flowers grow. They do not labor or spin. Yet I tell you, not even Solomon in all his splendor was dressed like one of these. If that is how God clothes the grass of the field, which is here today, and tomorrow is thrown into the fire, how much more will he clothe you..."

Publication Timeline and Disclaimer

Please note that Chapters 2-5 of this dissertation were written as stand-alone papers (see below), and therefore some repetition is unavoidable.

Chapter 2

Joubert, L., Samways, M.J. & Pryke, J.S. Effect of mowing, corridor width and isolation on plant communities in a subtropical ecological network (in preparation)

Chapter 3

Joubert, L., Samways, M.J. & Pryke, J.S. Annual burning as a driver of plant communities in remnant grassland ecological network in an afforested landscape (under review)

Chapter 4

Joubert, L., Samways, M.J. & Pryke, J.S. Interactive effects of grazing and fire on Afromontane grasslands (in preparation)

Chapter 5

Joubert, L., Samways, M.J. & Pryke, J.S. Effect of burning and cattle grazing on grasshopper assemblages in an Afromontane grassland (in preparation)

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CHAPTER 1: Introduction

We are in a global biodiversity crisis, brought about by human activity (Pimm *et al.* 1995, Sala *et al.* 2000, Secretariat of the Convention on Biological Diversity 2010). Some of the areas that are most species-rich are the most severely affected (Pimm & Raven 2000, Brooks *et al.* 2002). The main drivers of anthropogenic biodiversity loss are habitat loss and habitat transformation due to agricultural expansion, overexploitation of natural resources, pollution and invasive alien species (MEA 2005, UNEP 2012). Despite integration with the Millennium Development Goals (http://www.un.org/millenniumgoals/), previous efforts to stem the current rate of biodiversity loss (e.g. the Convention on Biological Diversity 2010 target) have failed (Butchart *et al.* 2010). In response, the Aichi targets for 2020 were set, specifying that "...by 2020, at least 17 per cent of terrestrial land, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively managed, ecologically representative and well connected systems of protected areas and other conservation measures". Also the Aichi targets look to half the rate of habitat transformation, and to integrate biodiversity conservation with commercial forestry and agriculture (CBD 2010). Innovative conservation approaches are needed to reach these targets.

Landscape transformation, habitat fragmentation and biodiversity response

The expansion of commercial land uses, which is required for economic development, has negative influences on biodiversity due to habitat transformation, fragmentation and loss (Fahrig 2003, UNEP 2012). Transformation follows a process of perforation, dissection, fragmentation, shrinkage, and attrition in natural landscapes (Forman 1995). It introduces novel boundaries to the landscape, and causes remaining natural habitat patches to increase in number, decrease in size and increase in isolation (Fahrig 2003, Ewers & Didham 2006). Habitat loss, which always causes biodiversity loss (Fahrig 2003), is not independent of a change in spatial arrangement of remnant habitat patches (Didham *et al.* 2012). In fact, the issue of habitat loss is compounded with habitat fragmentation, with some taxa becoming locally extinct due to patch isolation and reduced patch size and quality, although different species might respond in very diverse ways (Tscharntke *et al.* 2002).

Transformation of the landscape matrix affects biological communities by changing (1) resource availability in the matrix, (2) microclimate and disturbance regime within remnant patches, and (3) movement of patch-dependent species between patches (Driscoll *et al.* 2013). Therefore, the effects of habitat fragmentation depend on species' attributes (e.g. trophic level and dispersal ability), and interdependency among different species within a biological community as well as interdependency among patch attributes (e.g. patch size, shape, isolation, and matrix contrast) (Saunders *et al.* 1991, Ewers & Didham 2006, Didham *et al.* 2012).

Ewers & Didham (2006) highlighted two implications of fragmentation. The first implication was that plants, as sedentary primary producers, are less responsive to habitat fragmentation than more mobile taxa at higher trophic levels. This was shown to be the case when plants were compared to butterflies in Estonian calcareous grassland (Helm *et al.* 2006, Sang *et al.* 2010). This suggests that plants might take longer to respond to the effects of fragmentation, which would cause plant diversity patterns in the current transformed landscape to still mirror historical, more contiguous distribution of natural habitat (i.e. an extinction debt). Lindborg & Eriksson (2004) found that Swedish plant communities in semi-natural grassland had an extinction debt of 50 – 100 years in their response to current configuration of habitat patches. Indeed, an extinction debt was common for transformed landscape throughout Europe (Helm *et al.* 2006, Piqueray *et al.* 2011, Cousins & Vanhoenacker 2011). Traits ascribed to a plant community that is most likely to have extinction debt were longevity and populations that are near their extinction thresholds (Hanski & Ovaskainen 2002, Piessens & Hermy 2006, Kuussaari *et al.* 2009). The second implication highlighted by Ewers & Didham (2006) was that our thinking has been shaped by Island Biogeography Theory (MacArthur & Wilson 1967). To this end our understanding of species response to habitat fragmentation is that there is a clear distinction between remnant habitat patches and the non-habitat landscape matrix. When this distinction is unclear (i.e. if the matrix edge is not perceived as a sharp, distinct boundary by the taxon of interest) the importance of matrix properties increases at the expense of patches properties (Thomas & Kunin 1999). In such a case, species richness would not necessarily respond to patch size and isolation. Nevertheless, in North American tallgrass prairie, plant species richness responded in accordance with the predictions of Island Biogeography Theory after removing those plant species that also occurred in the matrix (Cook *et al.* 2002). Thus, to overcome the effects of habitat fragmentation we need to address patch size, quality and isolation.

Conservation in transformed landscapes

Conservation bodies are looking for holistic and innovative initiatives designed to reduce or counter the effect of all major drivers of biodiversity loss (CBD 2010). Maintenance of biodiversity, ecosystem function and ecosystem resilience is possible if we connect large patches of natural habitat with wide, good quality corridors in which natural disturbances are mimicked to provide in the habitat requirements of a wide range of species within and across functional groups (Fischer *et al.* 2006, Samways 2007).

Landscape ecology is the study of the reciprocal interactions between spatial patterns and ecosystem processes within a landscape (Turner 2005). Here, a landscape is defined as a spatially-heterogeneous entity i.e. “a mosaic of patches, (which are) the components of pattern” (Urban *et al.* 1987). There are two complementary approaches within the field of landscape ecology aimed at solving problems related to habitat transformation (Turner 1989, Turner 2005). The first originated in Europe, is more anthropocentric in nature, and links closely with landscape planning i.e. how to reconcile human activities with biodiversity conservation by allocating functions to different parts of the landscape (Opdam *et al.* 2002, Jongman *et al.* 2004). The second reflects Australian and North American traditions, as it considers how biodiversity and ecosystem processes respond to changes in spatial arrangement of habitat patches. In these regions, research has focused on corridor use by different taxa (Haas 1995, Haddad *et al.* 2003, Haddad & Tewksbury 2005), and how nest predation (Chalfoun *et al.* 2002), and reproductive success (Horn *et al.* 2005) changed in fragmented landscapes. Together, these two approaches led to the formulation of landscape ecological principles, which can be applied in the real world to solve conservation problems.

A conservation approach that has been derived from these principles and has the potential to mitigate the effects of habitat fragmentation in transformed landscapes is that of ecological networks (ENs), defined as “systems of nature reserves and their interconnections that make a fragmented natural system coherent to support more biological diversity than in its non-connected form” (Jongman 2003). Typically, an EN consists of different parts (e.g. nodes, corridors, buffer zones and stepping stones) (Bischoff & Jongman 1993) with each part performing any combination of six ecological functions: habitat, conduit, filter, barrier, source and sink (Hess & Fischer 2001). Our understanding of population dynamics within ENs and how individual species behave within these systems are underpinned by metapopulation theory (Hanski 1998). Ultimately, in conservation, we strive to have as many ‘source’ and ‘habitat’ patches across the transformed landscapes as possible. The connectivity between these patches is vital to ensure that populations do not become isolated and suffer from inbreeding, and to allow the recolonisation of locally extinct populations. This becomes complex when we take what is known about population level ecology and conservation, and apply it to biodiversity in general, especially as different taxa have different ecological functions or needs from the same landscape element. Nevertheless, we need to persist in the kind of thinking that will produce solutions for populations, species as well as biological communities and, more generally, biodiversity. Ultimately, the conservation of biodiversity is more important than the conservation of single species.

ENs and statutory protected areas are two complementary conservation approaches not aimed at replacing each other, but rather complementing each other. The global distribution of statutory protected areas are skewed towards remote areas or land with low agricultural potential (Margules & Pressey 2000, Rodrigues *et al.* 2004), but ENs can be implemented in areas with high agricultural potential within the commercial production landscape due to their smaller size. ENs may be viewed as the capillary veins enabling day-to-day movement and exchange of individuals at the smaller landscape spatial scale between high conservation value patches. An example of this is how the Pan-European Ecological Network was implemented to complement and lend coherency to the existing statutory reserve network (Natura 2000) in Europe (Jongman *et al.* 2011). In addition to Western and Central Europe, ENs have been implemented on most continents, including Africa, Asia, Australia, North America and South America (Bennett & Mulongoy 2006). Nevertheless, the approach of ENs to conservation is not without its challenges. In particular, the validation of ENs with regards to their ability to connect different remnant habitat patches and to increase regional biodiversity conservation in the transformed landscape remains problematic (Boitani *et al*. 2007).

Disturbances

Disturbances are found everywhere. We cannot avoid them. They are intrinsically part of most ecosystems and influence biodiversity at all taxonomic levels (Picket *et al*. 1989, White & Jensch 2001). They can be defined as physical agents or processes causing perturbation (or stress) in an ecosystem, which is manifested in a sudden or gradual, dramatic or subtle change when measured against a reference state (Rykiel 1985, White & Jensch 2001). Disturbances are “infrequent relative to the time between disturances and they are brief in relation to the life span of species they affect” (White & Jensch 2001). They may be biotic (e.g. grazing or burrowing animals) or abiotic (e.g. fires, landslides and flooding), and natural or anthropogenic. The specific effects of disturbances depend on the disturbance regime, which is a factor of disturbance type, spatial extent, intensity, severity, frequency and predictability (Sousa 1984). By acting as drivers of the process of natural selection, they are agents of change and shape the temporal and spatial heterogeneity of many natural ecosystems (Sousa 1984, Rykiel 1985).

Global importance of grasslands

Grassland is the most widespread vegetation type in the world, as it covers 30 to 40% of global terrestrial surface (White *et al.* 2000) and occurs in North and South America, Europe, Asia, Africa and Australia. This includes a wide range of climatic envelopes (mean annual temperature: -5°C to 20°C; mean annual precipitation: 300 mm to 1 000 mm) (Whittaker 1970, Woodward & Lomas 2004). These grasslands may be divided into two types based on their photosynthetic pathway – C_4 grasslands at the warmer low latitudes, and C_3 grasslands in cooler regions farther away from the equator (Brown 1977, Woodward & Lomas 2004). The C_4 photosynthetic pathway evolved independently multiple times out of the more primitive C_3 photosynthetic pathway (Ehleringer & Monson 1993) to compensate for high photorespiration rates and carbon deficiency, such as in cases of heat, drought and low atmospheric CO_2 levels (Sage 2004). C_4 plants are better able to assimilate water and nutrients than plants with the C_3 photosynthetic pathway (Schulze *et al.* 1996). About 6-8 million years ago, there was a global expansion of C_4 grasslands that coincided with a drop in atmospheric CO_2 levels (Cerling *et al.* 1997, Kellogg 2001, Zachos *et al.* 2001). This expansion was further driven by an increase in incidences and spread of two natural disturbances, fire and grazing (Woodward *et al.* 2004, Bond *et al.* 2005). Today, C_4 plants make a significant contribution (18%) to global primary productivity (Ehleringer *et al.* 1997), dominating in most tropical, subtropical and warm temperate grasslands (Archibold 1995, Sage *et al.* 1999). That includes the summer rainfall grassland and savanna in Africa (Vogel *et al.* 1978, Schulze *et al.* 1996) and tallgrass prairie in North America where they co-occur with C_3 forbs and woody plants (Knapp *et al.* 2004).

Furthermore, the original natural drivers of C_4 grassland expansion, fire and grazing, continue to form an integral part of C_4 grasslands. Particularly in North America and South Africa, fire exclusion will cause humid C_4 grasslands to develop into closed forests (Bond *et al.* 2005, Bond 2008). Nevertheless, these fire-prone ecosystems are not anthropogenic grasslands created by forest clearing, as is the case for grasslands in Europe (Bredenkamp *et al.* 2002, Bond *et al.* 2003). Rather, C_4 grasslands in North America and southern Africa are ancient, as indicated by their high levels of endemism (Bond *et al.* 2003). They precede intensive farming activities by millennia (O'Connor & Bredenkamp 1997) and are actually busy retreating since the last glacial maximum (Dupont *et al.* 2000).

The effects of burning, mowing and grazing on diversity, with disturbances varying in frequency and intensity, and effects measured over different spatial and temporal scales, has been studied extensively in tallgrass prairie, which, as in Africa, share an evolutionary history with large grazers (Collins 1987, Collins *et al.* 1998, Collins *et al.* 2002, Collins & Smith 2006). Also, effect of domestic grazers on taxa from different trophic levels was studied in shortgrass steppe (Milchunas *et al.* 1998). In South African grasslands, fire frequency and season had a significant effect on grasses and invertebrates, but not on forbs (Uys *et al.* 2004, Uys & Hamer 2007). Unlike fire and grazing, mowing is an anthropogenic disturbance, and it interacts with other disturbances to affect plant communities in different ways. In tallgrass prairie, mowing maintained plant diversity under conditions (i.e. burning and fertilizing) that normally would have lead to species loss (Collins *et al.* 1998). However, mowing had a negative effect on plant species richness of burned grassland in South Africa. The magnitude of this negative effect increased with increasing mowing frequency (Fynn *et al*. 2004). Overall, C_4 grasslands seem to be very resilient to natural disturbances (O'Connor 1994, Parr *et al.* 2004, Uys *et al.* 2006, O'Connor *et al.* 2010, Smith *et al.* 2013), with the exception of disturbance extremities, such as heavy grazing during drought conditions, heavy grazing on annually-burned land, or when a high mowing frequency is coupled with annual burning (O'Connor 1995, O'Connor *et al.* 2004, Fynn *et al*. 2004). These disturbances caused significant changes, specifically to the composition of grassland plant communities.

Grasslands have high biodiversity value (Bond & Parr 2010), but they also have high economic value, as most anthropogenic food products are directly or indirectly derived from C_4 grasslands. Firstly, most major staple foods (e.g. maize, wheat, sorghum and rice) are derived from wild relatives in these grasslands (Brown 1999). Secondly, grasslands were converted over large spatial scales for agricultural crop production to satisfy the global demand for more food (Ellis & Ramankutty 2008, Ellis *et al.* 2010). Thirdly, grasslands (natural and pastures) provide grazing for domestic livestock (e.g. beef cattle or dairy cows) (Brown 1999). Lastly, grassland catchment areas in mountainous regions perform important ecosystem services (e.g. water provision) for urban centres (Schulze 1997, Blignaut *et al.* 2010). It is extremely important to protect these highly diverse primary grasslands from habitat transformation and to manage natural disturbances appropriately to prevent loss and/or degradation of these systems (Bond & Parr 2010).

South African conservation priority areas

South Africa contains three biodiversity hotspots that were identified based on their irreplaceability (>1500 endemic vascular plant species) and vulnerability (> 70% habitat loss) (Myers *et al.* 2000, Mittermeier *et al.* 2004, Mittermeier *et al.* 2011). They are the Cape Floristic Region biodiversity hotspot in the southern part of the Western Cape; the Succulent Karoo biodiversity hotspot along the west coast, and the Maputaland-Pondoland-Albany (MPA) biodiversity hotspot along the east coast of the country (Mittermeier *et al.* 2004, Mittermeier *et al.* 2011) (Table 1.1). Roughly coinciding with the spatial extent of these hotspots, we find a number of centres of floristic endemism (Steenkamp *et al.* 2005). The two centres of endemism outside hotspots are the Drakensberg Alpine Centre (Carbutt & Edwards 2004, Armstrong & Brand 2012) and Sneeuberg Centre of Endemism (Clark *et al.* 2009), which are located to the west of the MPA biodiversity hotspot.

Table 1.1 Summary of the status of biodiversity hotspots in South Africa.

Hotspot	**Hotspot area (km2)**	**Remnant area (km2)**	**Habitat loss (%)**	**Endemic plant species**
Cape Floristic Region	78 555	15 711	80	6 210
Succulent Karoo	102 691	29 780	71	2439
Maputaland-Pondoland-Albany	274 136	67 163	76	1 900

Data from Mittermeier *et al.* (2004) and Fonseca (2009).

Priority areas for conservation action have been identified within these hotspots. The most extensive series of studies were conducted within the Cape Floristic Region, and published in a special issue of Biological Conservation entitled ‘Conservation Planning in the Cape Floristic Region’ (Cowling 2003, Cowling *et al.* 2003, Rouget *et al.* 2003a, Rouget *et al.* 2003b). Similar studies were conducted for the Succulent Karoo (Lombard *et al.* 1999, Cowling *et al.* 1999, Cowling 1999, Desmet *et al.* 2002), but only for parts of the MPA biodiversity hotspot, which is the largest of the three hotspots in South Africa. In the MPA biodiversity hotspot, the focus was primarily on the southwestern Albany Subtropical Thicket (Rouget *et al.* 2004) and the northern Maputaland Centre of Endemism (Smith *et al.* 2006, Smith & Leader-Williams 2006, Smith *et al.* 2008). However, a study conducted within the borders of the KwaZulu-Natal Province, which constitutes the central part of this hotspot, found that the central Midlands region of the Province was a conservation priority, as it was vulnerable to further habitat transformation and insufficiently protected by statutory protected areas (Fairbanks & Benn 2000). The coastal region of the Province, which although vulnerable to further habitat loss, was nevertheless adequately protected by statutory protected areas, most notably by the World Heritage Site, iSimangaliso Wetland Park (Fairbanks & Benn 2000). However, when targets for conserving biodiversity and retaining of ecosystem services (e.g. water provision) were considered simultaneously at the national level, almost all KwaZulu-Natal was assigned high priority status (Egoh *et al.* 2011).

Habitat transformation in South Africa

Based on 1994/1995 Landsat Thematic Mapper imagery at the national level, cultivated land (12.2%), forestry plantations (1.5%) and urban areas (1.1%) collectively covered 14.8% of the country, with natural vegetation constituting almost 80% (Fairbanks *et al.* 2001). Of the different biomes, habitat transformation was worst in grassland and fynbos (Reyers *et al.* 2001, Scholes & Biggs 2005). Within the Grassland Biome, 29.2% was transformed for agriculture and 3.3% for forestry purposes (Neke & du Plessis 2004). Depending on agricultural potential, the level of transformation varied greatly (0.2% to 66%) between different areas within KwaZulu-Natal (Fairbanks & Benn 2000).

During the ten year period from 1994 to 2005, there was a slight (1.2%) increase in spatial extent of transformed land at the national level (Schoeman *et al.* 2013). However, a comparison of 1994 and 2000 land cover data for the Grassland Biome showed that habitat fragmentation, particularly in the wetter eastern parts of the biome, continued (Matsika 2007). This led to an increase in the total number of remnant grassland patches, and a decrease in size and an increase in isolation of individual patches (Matsika 2007). Also, habitat transformation in this region is likely to continue as commercial land uses shift in an easterly direction to find climatically suitable conditions for crop production (Bradley *et al.* 2012). This places great emphasis on the need for biodiversity conservation for this region.

Biodiversity response to changing land use

Biodiversity is sensitive to changes in land use (van Jaarsveld *et al.* 2005), with some land uses being more detrimental to biodiversity than others. Commercial forestry and dairy farming, for example, had a greater effect on biodiversity integrity than cattle or game ranching (O'Connor & Kuyler 2009). Fragmentation, resulting from land uses with a large, negative effect on biodiversity (e.g. commercial plantation forestry), causes clear separation of remnant habitat patches and the transformed, non-habitat matrix in the landscape. Therefore, patch characteristics should be more important than matrix characteristics for biodiversity conservation in transformed regions (Thomas & Kunin 1999).

Experimental fragmentation of Afromontane grassland resulted in fragments varying in size and degree of connectivity (van Jaarsveld *et al.* 1998). These fragments were similar in terms of plants (Bredenkamp *et al.* 1999), grasshoppers (Foord *et al.* 2002), beetles (Foord *et al.* 2003) and small mammals (Johnson *et al.* 2002) prior to fragmentation. However, three years after fragmentation, differences in patch size and isolation failed to affect any of these taxa (Kamffer 2003). This suggests that we might be dealing with a case of extinction debt, which was a common phenomenon for long-lived plant communities in European calcareous grassland (Helm *et al.* 2006, Piqueray *et al.* 2011).

Further studies in Afromontane grassland showed that the extent of commercial afforestation had a significant negative effect on grassland bird species richness (Allan *et al.* 1997). However, response of forest birds to patch size of naturally-fragmented Afromontane forest depended on matrix characteristics i.e. whether a forest patch was surrounded by indigenous Afromontane grassland or by commercial pine compartments (Wethered & Lawes 2003). As expected, patch occupancy by blue duiker (*Philantomba monticola*) and tree hyrax (*Dendrohyrax arboreus*) in Afromontane forest patches surrounded with grassland decreased with increasing patch isolation (Lawes *et al.* 2000).

In addition to the direct effects of habitat fragmentation on biodiversity, habitat fragmentation might also have a number of indirect effects on remnant patches impacting upon habitat quality. This was the case for invasion of alien species from edges into remnant grassland patches, both in South Africa and Australia (Kemper *et al.* 1999, O'Connor 2005, Cilliers *et al.* 2008). Similarly, habitat fragmentation went hand-in-hand with a change in disturbance regime, which significantly affected biological assemblages of forest and rangeland in Australia (Hobbs 2001, Ross *et al.* 2002). The phenomenon of species extinction from a few, isolated habitat patches of low quality surrounded by a matrix of intensively-managed land covers cannot be attributed to the effect of a single factor (Fischer & Lindenmayer 2007). Rather, it is the combination of different interacting drivers that causes biodiversity change (Hobbs & Huenneke 1992, Chown 2010). The indirect effects of habitat transformation on biodiversity remain poorly understood, which has important implications for conservation approaches aimed at mitigating such effects.

Integrating biodiversity conservation with commercial land uses

In line with the call to integrate biodiversity conservation with commercial development (Butchart *et al.* 2010, CBD 2010), approximately one third of commercial forestry plantation in South Africa has been permanently set aside and managed for biodiversity conservation. At the national level, that amounts to 500 000 ha of natural habitat (e.g. indigenous forest or grassland), maintained areas (e.g. firebreaks and homesteads) and special landscape features (e.g. rocky outcrops and wetlands) within the configuration of an EN of nodes and corridors aimed at offsetting the negative effect of plantation forestry on regional biodiversity (Kirkman & Pott 2002).

Over the last decade, several studies, focusing mostly on invertebrates in the Grassland Biome, have led to the development of design principles for implementing ENs in commercial production landscapes. The minimum width of grassland linkages was set at 250 m (Pryke & Samways 2001) and the importance of structural linkages to connect remnant habitat patches with natural grassland patches outside forestry plantations were demonstrated (Pryke & Samways 2003, Bullock & Samways 2005). Furthermore, it was determined that the edge zone along the borders of forestry compartments is 32 m wide (Pryke & Samways 2012) and that physical landscape features such as rockiness and, possibly, elevation might serve as a surrogates for biodiversity (Crous *et al.* 2013). However, as important as patch size and connectivity might be, it was demonstrated repeatedly that habitat quality (specifically host plant presence, as influenced by grazing intensity) is of extreme importance for the conservation of invertebrate species in grassland corridors (Pryke & Samways 2003, Bullock & Samways 2005). In some cases, management practices influencing habitat quality for certain taxa are even more important than spatial arrangement of remnant habitat patches in the landscape (Bazelet & Samways 2011). This implies that ENs, proposed as mitigation measures against biodiversity loss in fragmented production landscapes, will only be effective if we maintain high quality linkages between remnant habitat patches (Harrison & Bruna 1999).

Most ENs are confined to forestry plantations in the Grassland Biome, specifically in the Midlands of KwaZulu-Natal, a region identified as a conservation priority. Ultimately, habitat quality depends on management of two interacting natural disturbances, fire and grazing. However, there is no single disturbance regime that affects all taxa in the same way. Indeed, disturbance was shown to affect different trophic levels in many different ways in other parts of the world (Milchunas *et al.* 1998, Herbst *et al.* 2013). Understanding the response of different taxa to different disturbance regimes in remnant grassland patches among commercial forestry compartments is required to optimize biodiversity conservation of ENs in production landscapes.

Aims and objectives

The aim of this study is to determine how three different types of disturbance (fire, grazing and mowing) in grassland ecological networks among forestry plantations influence biodiversity. The study was conducted in two geographical regions in the KwaZulu-Natal Province of South Africa. The first was the topographically flat and lower-lying (<100 m.a.s.l) Zululand region north of Richards Bay adjacent to the iSimangaliso Wetland Park World Heritage Site, and the second was the rocky and hilly mid-elevation (1100 – 1500 m.a.s.l) Midlands halfway between Howick and Underberg. I chose to look at the three most important disturbances, all of which are intrinsically part of the management of grassland ecological networks among commercial forestry compartments. The three disturbance types (mowing, grazing and burning) were administered in different ways in different parts of the EN for different purposes. For example, mowing and annual burning were confined to firebreaks in Zululand and the Midlands, respectively, for fire-protection purposes. As the remainder of grassland ENs had longer (1-3 years) fire-return intervals, some of the areas had been burned during the 12 month period prior to sampling, while others had not. This created the opportunity to study time since last fire on the study taxa. Finally, domestic cattle belonging to local human communities grazed the ENs to simulate historical disturbances by indigenous ungulates, and to contribute to poverty alleviation and upliftment of local communities neighbouring forestry plantations. Effect of presence or absence of cattle grazing, as well as effect of cattle grazing intensity was determined by comparing remnant grassland in the EN with similar areas in the PA, which were not grazed by cattle.

I chose plants and grasshoppers as focal taxa for these disturbances for three main reasons. Plants and grasshoppers (1) represent two different trophic levels (primary producers and primary consumers), (2) they play a significant role in grassland ecology, (3) are relatively sensitive to changes in the environment and (4) are taxonomically well-known (Samways *et al.* 2010). Lastly, response of grasshoppers to changes in the environment is closely correlated to that of butterflies (Bazelet & Samways 2012), and may therefore also represent response of other taxonomic groups to changes in the environment.

Grassland biota have evolved with the natural disturbances, fire and grazing, over many millennia. Although the primary source of fire ignition has changed from lightning to people, and the primary grazers (indigenous game) have been largely replaced by domestic livestock over the last few centuries, I do not expect these natural disturbances *per se* to have a large, negative effect on plants or grasshoppers.

However, it is true that the current disturbance regime in firebreaks (e.g. mowing and annual burning) is probably not representative of the historical disturbance regime that has shaped the temporal dynamics and spatial distribution of grassland ecosystems. Similarly, the grazing pressure from domestic cattle in other parts of the EN probably exceeds the historical grazing pressure exerted by indigenous game in terms of intensity, frequency and duration. Rather than disappear, these disturbances are likely to escalate into the future as we are faced with the global demand for more food and more land.

Agro-forestry is a steward of biodiversity. As such, they assume responsibility to protect and conserve the biological communities on their land. In this case, it means that they are responsible for managing and adjusting the disturbances that could probably jeopardize the long-term survival of species. Knowing how different elements of biodiversity respond to the currently prevalent disturbance regimes in ENs is the first step to a management strategy for more effective conservation of biodiversity in these systems.

Breakdown of chapters

Chapter 1 provides an overview of the literature on habitat transformation, conservation priorities, and conservation approaches to stem biodiversity losses in transformed landscapes.

In Chapter 2, I consider how mowing of firebreaks, and certain design variables (particularly corridor width, number of eucalypt borders and distance from PA border) affect the capacity of a large-scale EN among forestry compartments to conserve plant communities representative of those found in an adjacent World Heritage Site, iSimangaliso Wetland Park.

In Chapter 3, I determine the effect of annual burning on firebreak plant communities when compared to longer-rotation burned grassland in the EN and PA, respectively. I consider three firebreak types: (1) plantation EN firebreaks with pine compartments on two sides, and (2) peripheral EN firebreaks separated from (3) PA firebreak by the plantation/PA fenceline. All sites were burned <12 months prior to sampling. Grazing by cattle was taken as an embedded factor for annually-burned firebreaks and longer-rotation burned grassland in the EN.

Chapter 4 tackles the issue of cattle grazing in grassland ENs. Considering only grassland with longer fire-return intervals (i.e. excluding all firebreak sites), I compare grazed sites in the EN with ungrazed sites in the PA to determine how presence of cattle grazing influence plant communities. In this chapter, I also compare sites in the EN grazed by cattle to sites in the PA grazed by black wildebeest to determine whether cattle grazing simulate the effect of native ungulates on plant communities. Lastly, I compare moderately-grazed sites in the EN with heavily-grazed sites in the EN to determine whether plant diversity is affected by grazing intensity. Seeing that grassland sites had longer fire-return intervals, some sites were burned <12 months and others >12 months prior to sampling. Time since the last fire provided the backdrop of variation in the vegetation layer, and was taken into account with analysis and interpretation of data.

The aim of Chapter 5 is to determine whether the grasshopper assemblage also responds to fire and grazing as seen by the plants in the previous chapters. I consider the individual and combined effects of fire frequency (annual vs. longer-rotation burning), time since last fire (<12 months vs. >12 months prior to sampling), and presence or absence of large grazers as well as a number of environmental variables (e.g. proportion bare ground, vegetation cover, grass height, etc.) on grasshopper species richness, species composition and density.

In my final chapter, the overall findings are discussed, particularly in regards how fire and grazing affect grassland ENs. As these grasslands are of high conservation value, we need to manage them with extreme care. To this end, I make management recommendations for how best to utilize fire and grazing to optimise biodiversity in grassland ENs.

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CHAPTER 2: Effect of mowing, corridor width and isolation on plant communities in a subtropical ecological network

Abstract

The effect of fragmentation can be mitigated by implementing ecological networks (ENs) that link good quality habitat in a transformed matrix to enable species' persistence and movement throughout production landscapes. The aim of this study was to determine how management and design of ENs, across an extensive eucalypt plantation, affect subtropical, grassland plant communities when compared to reference sites in an adjacent protected area (PA). Twenty-six sites were selected, representing firebreaks and open biotopes (< 30% shrub/tree cover) in the EN, and open biotopes in PA (reference) areas. Firebreaks were mown, while open biotopes differed in fire frequency and time since last fire. In the EN, open biotope sites differed in corridor width, number of eucalypt borders and distance to PA border. Firebreaks differed in composition and were significantly less species rich than reference sites in the PA. Plant species richness and composition of open biotopes were unaffected by fire frequency and time since last fire, but species turnover was greater in more recently-burned areas. Design variables affected open biotope plant communities in the EN, with plant species richness decreasing, and turnover increasing, in medium sized corridors farther away from the PA border. This was not the case for wide, interconnected corridors, which were similar to reference sites in the PA. Our results suggest that plant species were lost from intensively-managed firebreaks and from small, isolated patches in the EN. However, plant communities in wide, interconnected corridors had the same ecological integrity as reference sites in the PA. It is recommended that implementation of a few wide, interconnected corridors should be prioritized over many narrow corridors in these production landscapes. Also, frequent mowing should be confined to firebreaks only, as this management practice cannot be reconciled with biodiversity conservation in ENs.

Introduction

Fragmentation caused by agriculture and forestry in production landscapes is a major conservation concern. Fragmentation is a landscape spatial scale phenomenon that reduces size and connectivity of remnant patches, which, in turn, negatively affects plant communities in those patches (Saunders *et al.* 1991; Ewers & Didham 2006). In Europe, larger patches of calcareous grassland have greater plant species richness than smaller patches (Kraus *et al.* 2004; Adriaens *et al.* 2006). This was also the case for mixed-grass prairie (Collinge 2000), but not for annual grassland (Murphy & Ehrlich 1989) in North America. Connectivity affects plants in some cases (Adriaens *et al.* 2006), but not in others (Kraus *et al.* 2004).

Not only does fragmentation affect patch size and connectivity. It also influences management of remaining habitat patches, which is shown to affect plant communities in Swedish and Finnish semi-natural grassland (Luoto *et al.* 2003; Cousins & Vanhoenacker 2011), British upland hay meadows (Pacha & Petit 2008) as well as in Australian rangeland (Hobbs 2001). Indeed, management of remnant grassland in Australia is more important for plant diversity than size and connectivity of those patches (Williams *et al.* 2006). It seems as if management of remnant habitat patches might be at least as important as patch size and connectivity for the conservation of plant diversity in fragmented production landscapes.

One conservation approach to minimise the effects of fragmentation, is the implementation of ecological networks (ENs). These are defined as “systems of nature reserves and their interconnections that make a fragmented natural system coherent to support more biological diversity than in its non-connected form” (Jongman 2003). In South Africa, large-scale ENs constitute approximately one third of commercial forestry plantations (Kirkman & Pott 2002; Samways *et al.* 2010). These ENs maintain biodiversity composition and ecosystem function provided we connect large patches of natural habitat with wide, good quality corridors (Fischer *et al.* 2006; Samways 2007) where habitat quality relates to the way in which natural disturbances are managed to provide in the habitat requirements of a wide range of taxa and functional guilds (Samways *et al.* 2010).

Response of invertebrates was previously used to formulate design and management guidelines for optimizing biodiversity conservation in timber production landscapes (Pryke & Samways 2001; Bullock & Samways 2005; Bazelet & Samways 2011; Pryke & Samways 2012). However, it was shown for European calcareous grasslands that invertebrates responded differently from plants to changes in habitat patch size and connectivity (Helm *et al.* 2006; Sang *et al.* 2010) as well as to changes in disturbance regime (Kahmen *et al.* 2002;

Jacquemyn *et al.* 2011; Weiss *et al.* 2013). It is necessary to incorporate the response of plant communities to changes in patch size and isolation and to changes in management in order to fine-tune guidelines to optimize biodiversity conservation in ENs.

Consequently, this study focuses on the effect of mowing, fire frequeny, time since last fire, corridor width and isolation on grassland plant communities in ENs within a commercial forestry matrix. Specifically, I was interested in how frequent mowing affected plant communities in firebreaks when compared to open biotopes (< 30% shrub/tree cover). It is expected that intensive management of plant communities in firebreaks will negatively affect plant species richness when compared to open biotopes that were not intensively managed. If this is the case, then firebreaks do not conserve biodiversity as well as open biotopes, and only have value in their protection of timber stands from wildfire. Also, I investigate how fire frequency and time since last fire influenced plant communities of open biotopes in the EN. While it was shown that a high fire frequency may jeopardize grassland conservation efforts, the exclusion of fire for a long period of time may be equally harmful, particularly as grassland biota have adapted to relatively-frequent disturbance events in the past. Lastly, I considered whether corridor width and isolation influenced plant communities of open biotopes in the EN. In particular, I was interested in finding out if plant communities in small-isolated open biotope patches far from the PA border are poorer in species than those in wide-connected corridors close to the PA border due to the forestry compartments acting as a barrier to seed dispersal. This study also aims to contribute to future design and management of ENs in production landscapes.

Methods

The study was conducted in the Indian Ocean Coastal Belt Biome along the east coast in the lowlands (20-120 m above sea level) of KwaZulu-Natal (28°15′S; 32°22′E) (Mucina & Rutherford 2006). The region is in a subtropical climatic zone characterized by wet, warm and humid summers and mild winters without frost. Mean annual temperature is 21° C and mean annual precipitation is ~ 964 mm (Mucina *et al.* 2006). The flat coastal plains are dominated by nutrient-poor sand derived from Quaternary sediments of marine origin. There are two dominant grassland types in this region, with Maputaland Wooded Grassland occurring within a larger matrix of grasslands and thickets of Maputaland Coastal Belt (Mucina *et al.* 2006).

Study sites were in an ecological network (EN) among eucalypt (mostly *Eucalyptus grandis* varieties) forestry compartments in the St. Lucia plantations, which is part of SiyaQhubeka Forests (Ltd.). Reference sites were on the Western Shores of Lake St. Lucia in the adjacent iSimangaliso Wetland Park, a protected area (PA). Twenty-six sites were selected from north to south over 21 km and from east to west over 14 km. Three kinds of sites were selected: open biotopes in the PA (n = 5); open biotopes in the EN (n = 14) and firebreaks in the EN (n = 7) (Figure 2.1). Selection of sites was guided by availability of safe access roads, absence of dangerous large mammals (e.g. elephant (*Loxodonta africana*), buffalo (*Synercus caffer*) and hippopotamus (*Hippopotamus amphibius*)) upon arrival at site, and representation of open biotope with different disturbance regimes and different amounts of shrub/tree cover.

Open biotopes had a continuous grass or herb layer, and consisted of grassland (<10% shrub/tree cover) and open woodland (10-30% shrub/tree cover), as well as remnant, natural habitat and recovering habitat after pine compartments were clear-felled (2004-2008) (Bainbridge 2003). Remnant (n=7) and recovering areas (n=12) hosted plant communities that differed in richness and composition (Zaloumis & Bond 2011). Open biotopes were grazed by free-roaming indigenous game (e.g. blue wildebeest (*Connochaetes taurinus*), buffalo, bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*), elephant, greater kudu (*T. strepsiceros*), southern reedbuck (*Redunca arundinum*), waterbuck (*Kobus ellipsiprymnus*), white rhino (*Ceratotherium simum*) and zebra (*Equus burchellii*)). These vertebrates traversed from the PA into the EN to make use of available resources in the EN among forestry compartments.

Although grazing and burning are the two natural disturbances that shaped these grasslands (Bond *et al.* 2003; Bond 2005; Bond 2008), there was controlled burning at only three remnant, natural sites (two EN sites and one PA site) during the past 10 years. The remaining four remnant, natural sites and all recovering sites burned primarily during runaway wildfires, which occurred about once every seven years with wildfires in 1998 and 2005, prior to this study. Because only remnant natural areas were part of a burning programme, I excluded all recovering areas when investigating the effect of fire frequency and time since last fire on subtropical grassland plant communities.

Considered separately from open biotopes, intensively-managed firebreaks constitute a significant portion of the EN. Firebreaks (including powerline servitudes) were narrow (30-70 m) strips of grass alongside gravel roads. Managed for plantation protection, they were mown monthly in the warm, wet seasons from October to April to prevent accumulation of flammable plant biomass. In addition, different species of vertebrates (specifically blue wildebeest and zebra) grazed in firebreaks, which were probably perceived as grazing lawns by these mammals (Conneely 2011).

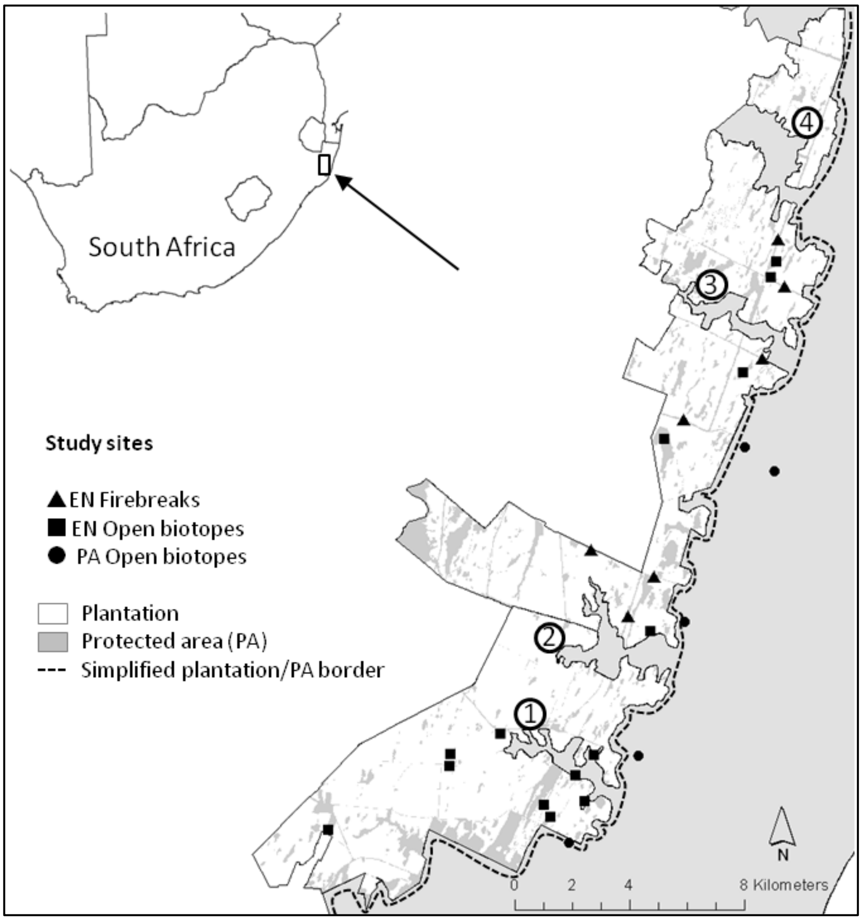

Figure 2.1 Location of study sites. There were seven firebreak sites in the ecological network (EN), 14 open biotope sites in the EN, and five reference open biotope sites on the Western Shores of Lake St. Lucia in iSimangaliso Wetland Park, a protected area (PA). Numbers 1-4 indicate the four major corridors in this EN. The area towards the west of the plantation hosted further commercial forestry plantations.

Management and design variables were categorized according to criteria in Table 2.1. Distance from PA border was the shortest distance from each site to the simplified PA border (Figure 2.1). Simplification of the PA border was necessary, because the real PA boundary line was too complex, forming corridors through the plantation, which obscured the ‘distance to mainland’ measurement. The simplified PA border was an exact replica of the real PA boundary line with the exception of four cases i.e. the four major corridors (numbered 1-4 in Figure 2.1). From here onwards, the simplied PA border will be referred to as the ‘PA border’

It was assumed that eucalypt compartments isolated open biotope patches, where isolation is defined as “the degree to which the landscape impeded movement” (Taylor *et al.* 1993).

Table 2.1 List of environmental, management and design variables for sites in the ecological network (EN) and in the adjacent protected area (PA). The environmental variable was vegetation structure. The management variables were mowing, fire frequency and time since last fire. The design variables were structural connectivity (derived from the number of borders shared with eucalypt compartments), corridor width and distance to the simplified PA border. Criteria for sites to be included into the different classes are included.

VEGETATION STRUCTURE	**Criteria**
Firebreak (n = 7)	Continuous grass/herb layer; no vertical stratification
Grassland (n = 10)	Continuous grass/herb layer; < 10% shrub/tree cover
Open woodland (n= 9)	Continuous grass/herb layer; 10-30 % shrub/tree cover

FIRE FREQUENCY	**Criteria**
Firebreak (n = 7)	Mowed once per month from October to April
2-3 yrs (n = 3)	Remnant open biotope; controlled burn every 2-3 yrs
~ 7 yrs (n= 4)	Remnant open biotope; wildfire once every 7 yrs

TIME SINCE LAST FIRE	**Criteria**
Firebreak (n = 7)	Mowed once per month from October to April
1998 (n = 3)	Remnant open biotope; last burned in 1998
Post-2005 (n= 4)	Remnant open biotope; burned post- 2005

STRUCTURAL CONNECTIVITY	**Criteria**
PA control sites (n = 5)	Open biotopes; ≤ 1 eucalypt boundaries
Firebreak (n = 7)	Firebreak; 2 eucalypt boundaries
Connected (n = 5)	Open biotopes; 2 eucalypt boundaries
Isolated (n = 9)	Open biotopes; 3-4 eucalypt boundaries

CORRIDOR WIDTH	**Criteria**
PA control sites (n = 5)	Open biotopes; sites in the PA
Narrow (n =7)	Firebreak; 0 - 75 m wide
Medium (n = 7)	Open biotopes; 75-175 m wide
Wide (n = 7)	Open biotopes; 176-1500 m wide

DISTANCE TO THE PA BORDER	**Criteria**
Firebreak (n = 7)	Firebreak
PA control sites (n = 5)	Open biotopes; sites in the PA
Near (n = 7)	Open biotopes; 0-1250 m from PA border
Far (n = 7)	Open biotopes; 1250-3200 m from PA border

Plant communities at each site were sampled in summer from January-April 2012. Different sites were >300 m apart or separated by eucalypt compartments to prevent pseudo-replication. Reference open biotope sites were in the interior of the PA, while open biotope sites in the EN were >30 m from the forestry compartment edge to avoid edge effect, previously determined using invertebrates (Samways & Moore 1991; Pryke & Samways 2012). At each open biotope site (100 m x 100 m), vegetation height and plant species were sampled at 1 m intervals along 10 randomly-orientated vegetation transects (30 m) (i.e. 300 data points per site) (Whalley & Hardy 2000). All firebreak sites were narrow and within the edge zone. Therefore, the vegetation transects of firebreak sites were positioned parallel to and at equal distances from the forestry compartment edge and gravel roads, which ran alongside firebreaks. I recorded herbaceous plant species (i.e. forbs, grasses and sedges) rooted closest to the bottom of each interval along a line transect. In addition, geophytes and woody shrub/tree species (following the definition of Scholes *et al.* (2002)) were recorded when their canopy ended less than 1 m from each interval. One herbaceous, geophytic and woody species was recorded per interval. Where a choice had to be made between specimens, the closest and then the tallest individuals were selected. By counting incidence of species at intervals, I obtained the abundance of species at each site.

I conducted three types of analyses: 1) species richness, 2) species composition and 3) species turnover based on classification of sites presented in Table 2.1. Statistical analysis of species richness data was univariate, while analyses of species composition and turnover were multivariate. After data from the ten transects at each site were pooled, SAS Enterprise Guide 5.1 software was used to calculate mean plant species richness (± standard error). As plant species richness data were normally distributed, Generalized Linear Models (GLMs) with an identity function were used to test for significant differences between different groups of sites, as classified in Table 2.1.

I used PRIMER 6.0 to determine whether management and design variables had a significant effect on species assemblage composition. Standardized species abundance data were square root transformed to reduce the effect of dominant species (PRIMER-E 2008). After constructing a Bray-Curtis resemblance matrix, comparisons of species composition were conducted using Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 unrestricted permutations of raw data (Anderson 2001).

Species turnover is ‘a measure of change in the identity, relative abundance, biomass and/or cover of individual species from one sampling unit to another along a spatial, temporal or environmental gradient’ (Anderson *et al.* 2011). I used PRIMER 6 software to determine how species turnover varied with change in management, and changes in corridor width and isolation of habitat patches (PRIMER-E, 2008). Species abundance data were transformed to presence/absence data from which a Bray-Curtis resemblance matrix was created. Using Permutational Multivariate Analysis of Dispersion (PERMDISP) (with 9999 permutations), which measures the homogeneity of multivariate dispersion, I calculated the mean distances from site to centroid (i.e. geometric centre) for each group of sites (Table 2.1) in a multi-dimensional space. Mean distances, which can be used as a measure of beta-diversity (Anderson 2006), were compared between different groups of sites with ANOVA.

Results

Corridor width as a compounding variable

Corridor width (±standard error) was not independent of other management or design variables. All narrow corridors were frequently mown, as they functioned as firebreaks. Corridor width was significantly greater in open biotopes with two eucalypt borders (407 m ±161.3) than in open biotopes bordered by ≥3 eucalypt compartments (196 m ±49.0) in the EN (GLM, Z = 22.41, P <0.001). In addition, corridor width was significantly greater near the PA border (316 m ± 127.1) than farther away (227 m ±55.5) (GLM, Z = -9.99, P <0.001).

Plant species richness

I recorded 357 plant species in this study. The 24 most abundant plant species (Table 2.2) collectively accounted for 66% of all plants recorded. The 12 most abundant grass species accounted for 83% of all grasses, and 45% of all plants recorded. Of the 12 most abundant grass species, one third (4 spp.) were indicative of light to moderate disturbance frequency and/or intensity, while the other eight species were indicative of heavy disturbance (van Oudtshoorn 2006).

As expected, mowing significantly reduced mean grass height of firebreaks when compared to open biotopes in the EN (GLM, t = -4.40, P <0.001). When compared to remnant open biotopes that were burned or grazed, mowing did not have a significant effect on plant species richness of firebreaks. Similarly, plant species richness of open biotopes was not significantly affected by fire frequency, time since last fire or vegetation structure (i.e. proportion of woody vegetation cover) (Table 2.3). However, mean plant species richness (±standard error) of open biotopes in the PA (45.4 ±5.2 spp.) was significantly greater than in narrow firebreaks (31.3 ±3.9 spp.) and open biotopes in the EN (34.1 ±2.8 spp.). Specifically, plant species richness of open biotopes in the PA was significantly greater than open biotopes in medium corridors (31.3 ±3.1 spp.), open biotopes with ≥3 eucalypt boundaries (30.9 ± 3. 7 spp.) and open biotopes far from the PA border (28.7 ±4.5 spp.) (Figure 2.2 a-c; Table 2.3). Plant species richness of open biotopes in the PA did not differ significantly from that of open biotopes in wide corridors in the EN with two eucalypt boundaries near the PA border.

Table 2.2 The 24 most abundant plant species in the study. The disturbance categories of grass species were indicated (Van Oudtshoorn 2006), but there were no such categories available for forb species.

Family	**Plant species**	**Disturbance**
Poaceae	*Acroceras macrum*	Light to moderate
Poaceae	*Brachiaria arrecta*	Light to moderate
Poaceae	*Digitaria c.f. longiflora*	Heavy
Poaceae	*Dactyloctenium geminatum*	Heavy
Poaceae	*Digitaria natalensis*	Light to moderate
Poaceae	*Eragrostis superba*	Heavy
Poaceae	*Imperata cylindrica*	Heavy
Poaceae	*Leersia hexandra*	Light to moderate
Poaceae	*Panicum maximum*	Heavy
Poaceae	*Paspalum urvillei*	Heavy
Poaceae	*Sporobolus africanus*	Heavy
Poaceae	*Stenotaphrum secundatum*	Heavy
Asteraceae	*Helichrysum krausii*	
Asteraceae	*Senecio demoides*	
Apiaceae	*Centella asiatica*	
Convolvulaceae	*Cuscuta campestris*	
Cyperaceae	*Scleria sobolifer*	
Euphorbiaceae	*Sclerocroton integerrimus*	
Fabaceae	*Crotalaria globifera*	
Fabaceae	*Desmodium incanum*	
Fabaceae	*Eriosema parvifolium*	
Fabaceae	*Tephrosia sp.4*	
Myrtaceae	*Psidium guajava*	Alien species
Smilacaceae	*Smilax anceps*	

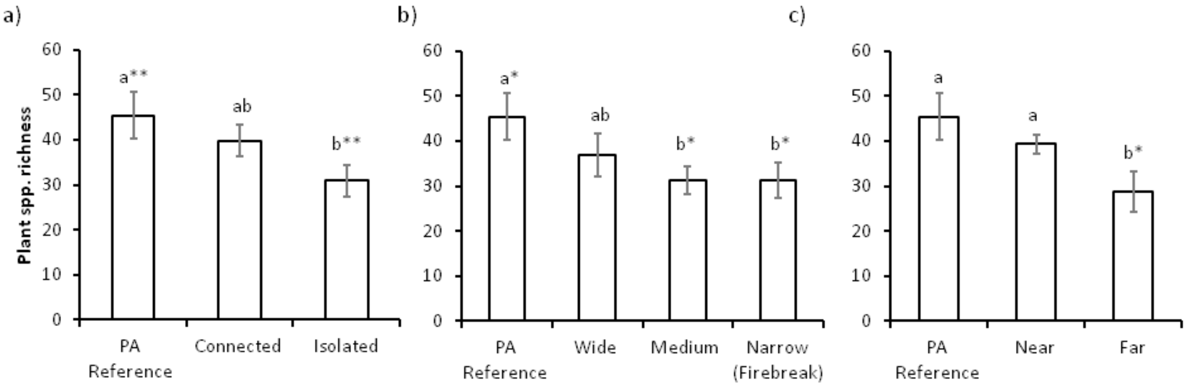

Figure 2.2 A comparison of plant species richness (using Generalized Linear Models) in open biotope in the protected area (PA), and open biotopes in the ecological network (EN) characterized by different design variables: (a) structural connectivity: connected (2 eucalypt borders) and isolated (≥3 eucalypt borders); (b) corridor width: narrow (firebreak, 0-75 m), medium (75-175 m) and wide (175-1500 m); and (c) distance to PA border: near (<1250 m) and far (1250-3000 m). Level of significance: * P <0.05, ** P <0.01, *** P <0.001.

Plant species composition and turnover

Plant communities were significantly affected by vegetation structure (i.e. percentage shrub/tree cover), as firebreaks, grasslands and open woodland were each unique in terms of species composition (Table 2.3). Species turnover was not affected by vegetation structure (Table 2.3). Fire frequency and time since last fire did not affect plant species composition, but plant species turnover of remnant open biotopes burned post-2005 was significantly greater than those last burned in 1998 (Table 2.3).

Plant species composition of firebreaks differed significantly from open biotopes in the EN and PA, burned at different frequencies and differing in time since last fire (Table 2.3). Species turnover was also significantly less in frequently-mown firebreaks than in open biotopes in the EN. Specifically, it was smaller than in open biotopes in the EN far from the PA border and those with ≥3 eucalypt borders (Table 2.3).

There were no significant differences when plant species composition of open biotopes was compared between the EN and PA (Table 2.3). Similarly, in the EN, there was no significant difference when comparing medium with wide corridors, or connected (2 eucalypt borders) with isolated (≥3 eucalypt borders) open biotopes. However, distance from the PA border (near vs. far) had a significant effect on plant communities in the EN. In addition to differences in plant species composition, species turnover of open biotopes far from the PA border was significantly greater than for those near the PA border (Table 2.3).

Table 2.3 Plant species richness (using Generalized Linear Models), plant species composition (using Permutational Multivariate Analysis of Variance (PERMANOVA)) and plant species turnover (using Permutational Multivariate Analysis of Dispersion (PERMDISP)) of biotope types in the ecological network (EN) and protected area (PA). Vegetation structure: mowed firebreaks, grassland (< 10% shrub/tree cover) and open woodland (10-30% shrub/tree cover); corridor width: narrow firebreaks (<75 m), medium (75-175 m) and wide (175-1500 m); structural connectivity: connected firebreaks (2 eucalypt borders), connected open biotopes (2 eucalypt borders) and isolated open biotopes (≥3 eucalypt borders); and distance to PA border: open biotopes near (<1250 m) and open biotopes far (1250-3000 m). Level of significance: * P <0.05, ** P <0.01, *** P <0.001.

Comparison	**Species richness**	**Species composition**	**Species turnover**
VEGETATION STRUCTURE	**Z-value**	**t-value**	**t-value**
Firebreak ↔ Grassland	-0.48	1.986***	2.135
Firebreak ↔ Open woodland	-1.71	1.888***	1.776
Grassland ↔ Open woodland	-1.42	1.356*	0.649
FIRE FREQUENCY			
Firebreak ↔ 2-3 yrs (Remnant open biotope)	-0.28	1.439**	0.948
Firebreak ↔ 7 yrs (Remnant open biotope)	-0.71	1.700**	0.506
2-3 yrs (Remnant open biotope) ↔ 7 yrs (Remnant open biotope)	-0.32	1.078	0.618
TIME SINCE LAST FIRE			
Firebreak ↔ 1998 (Remnant open biotope)	-0.46	1.645**	0.140
Firebreak ↔ post 2005 (Remnant open biotope)	-0.56	1.488**	1.903
1998 (Remnant open biotope) ↔ post 2005 (Remnant open biotope)	-0.04	1.016	2.402*
EN vs. PA			
EN Firebreak ↔ EN (Open biotope)	-0.59	2.019***	3.001*
EN (Firebreak) ↔ PA (Open biotope)	-2.38*	1.561***	0.932
EN (Open biotope) ↔ PA (Open biotope)	-2.27*	1.008	1.384
STRUCTURAL CONNECTIVITY			
Connect (Firebreak) ↔ Connect (Open biotope)	1.53	1.767**	0.626
Connect (Firebreak) ↔ Isolated (Open biotope)	0.08	1.902***	2.465*
Connect (Firebreak) ↔ PA (Open biotope)	-2.51*	1.561**	0.932
Connect (Open biotope) ↔ Isolated (Open biotope)	1.71	0.993	1.560
Connect (Open biotope) ↔ PA (Open biotope)	-0.92	0.796	0.313
Isolated (Open biotope) ↔ PA (Open biotope)	-2.77**	1.128	1.075
CORRIDOR WIDTH			

Narrow firebreak ↔ PA control (Open biotope)	-2.43*	1.561**	0.932
Narrow firebreak ↔ Medium corridor (Open biotope)	0	1.937***	1.927
Narrow firebreak ↔ Wide corridor (Open biotope)	-1.05	1.801**	1.828
Medium corridor (Open biotope) ↔ PA (Open biotope)	-2.43*	1.167	0.511
Medium corridor (Open biotope) ↔ Wide corridor (Open biotope)	-1.05	1.095	0.461
Wide corridor (Open biotope) ↔ PA (Open biotope)	1.49	0.879	0.685
DISTANCE TO PA BORDER			
Firebreak ↔ PA (Open biotope)	-2.59*	1.561**	0.932
Firebreak ↔ Far from PA border (Open biotope)	-0.52	1.700**	3.027*
Firebreak ↔ Near PA border(Open biotope)	-1.63	2.124***	0.744
Far from PA border (Open biotope) ↔ PA (Open biotope)	-3.02**	1.054	1.583
Near PA border(Open biotope) ↔ PA (Open biotope)	-1.11	1.091	0.625
Far from PA border (Open biotope) ↔ Near PA border (Open biotope)	-2.11*	1.258*	4.117***

Discussion

Open biotope types were categorized as grassland or open woodland based on a visual assessment of vegetation structure. Differences in vegetation structure coincided with differences in plant species composition, but not plant species richness or turnover. This agrees with what was found in savanna in a nearby protected area (Parr *et al.* 2012). Vegetation structure might be able to aid future classification of open biotopes for mapping purposes in our study region.

Effect of management

Plant communities in mown firebreaks were less rich in species and different in composition when compared to open biotopes in the rest of the EN and PA. Furthermore, firebreak communities differed compositionally from remnant open biotopes characterized by a more natural disturbance regime. It is possible that abiotic factors, rather than the specific treatment, are responsible for differences between different areas, as was indeed reported for a nearby reserve (Downing 1980). However, all firebreak and open biotope sites were scattered throughout a single land type (Ha45), which has similar soil types, climate and topography (ARC - Institute for Soil, Water and Climate). Therefore, differences in soil type, topography and climate were probably not responsible for differences seen between firebreaks and open biotope sites. Nevertheless, the possibility that shade from plantation trees or grazing pressure form indigenous game contributed to the changes seen in firebreak plant communities is not excluded, as game favored firebreaks over open biotopes. Furthermore, my results are consistent with those in South African grassland (Fynn *et al.* 2004); North American tallgrass prairie (Rooney & Leach 2010) and German calcareous grassland (Kahmen *et al.* 2002) where the effects of mowing on plant communities differed from the effects of burning. In addition, South African grassland that was mown twice in summer was less species-rich than sites mown only once (Fynn *et al.* 2004). I found no evidence supporting the hypothesis that species turnover was negatively correlated with disturbance frequency (Uys *et al.* 2004). As frequent mowing causes species loss and changes in the composition of plant communities, it should be avoided or at least confined to the edges of plantations.

Within remnant open biotopes, fire frequency and time since last fire did not have a significant effect on plant species richness or composition. Small sample sizes (n=3 or n=4), which was the result of availability of suitable open biotope sites, could explain lack of significant differences between these comparisons. Nevertheless, I found that species turnover was significantly greater in sites that were burned more recently, which implies that subtropical grassland sites became more homogenous when they have not been burned for a long time. Our results contrast with the relative sensitivity of plant communities to fire frequency, burning season and time since last fire in grassland in South Africa (Uys *et al.* 2004), wet (>570 MAP) savanna in South Africa (Smith *et al.* 2013), Serengeti in Tanzania (Belsky 1992) and tallgrass prairie in North America (Gibson & Hulbert 1987; Collins 1992).

Effect of design

Open biotopes in wide, interconnected corridors near the PA border were similar to reference sites in the PA. However, plant species richness of isolated, medium-sized patches far from the PA border was less than in reference open biotopes in the PA. In addition, plant species richness decreased and species turnover increased as one moved further away from the PA border into structurally isolated areas (i.e. ≥3 eucalypt boundaries) in the EN. It was not possible to separate out the individual effects of the design variables, as corridor width was co-variant with the number of eucalypt borders and distance to PA border. Furthermore, greater species turnover of more isolated patches might be due to spatial autocorrelation i.e. sites that are further apart have a tendency to be more different in plant species composition. However, these three variables were shown to be important for the conservation of grassland invertebrates in South Africa (Pryke & Samways 2001; Pryke & Samways 2003; Bullock & Samways 2005; Bazelet & Samways 2011), and for birds elsewhere (Herkert 1994;

Fuhlendorf *et al.* 2002; Lipsey & Hockey 2010). Decreases in grassland patch size had either a negative (Murphy & Ehrlich 1989) or no effect (Wilsey *et al.* 2005) on native plant species richness in North America. While smaller patches had less butterfly species and greater species turnover in calcareous grassland, isolation did not have such an effect (Kraus *et al.* 2003). Reductions in plant species richness and concomitant increases in species turnover in small patches at greater distances from the PA border points to local extinction of species followed by no/low colonization from distant potential sources, especially if the transformed landscape matrix separating patches is unsuitable habitat and acts as a barrier to movement of propagules. This explanation concords with predictions of Island Biogeography Theory (MacArthur & Wilson 1967; Brown & Kodric-Brown 1977), and with real (Piessens *et al.* 2005; Cristofoli *et al.* 2010) and expected (Lindborg & Eriksson 2004; Helm *et al.* 2006) losses of species from smaller, isolated habitat patches in transformed landscape matrices in the northern hemisphere. This study emphasizes the importance of connecting patches of natural habitat with wide corridors of good quality habitat to conserve biodiversity.

Conclusion

Lower species richness indicate that plant communities in frequently-mown firebreaks and in small, isolated patches in the EN far from the PA border have lower biodiversity value than plant communities in extensively-managed, wide, interconnected corridors. It is recommended that mowing should be confined to firebreaks, as it is not reconcilable with biodiversity conservation in the rest of the EN. Furthermore, implementation of a few wide, interconnected corridors should be prioritized over many, narrower ones.

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CHAPTER 3: Fire frequency as a driver of plant communities in remnant grassland ecological networks in an afforested landscape

Abstract

Ecological networks (ENs) are used to mitigate the negative effects of commercial timber plantations on biodiversity in southern Afromontane grasslands. Annually-burned firebreaks are fundamental to plantation forestry management, as they protect timber compartments from runaway fires. However, the effect of high impact, regular annual burning on grassland ENs has yet to be determined. Here, I first identified three firebreak types: (1) plantation firebreaks with forestry compartments on two sides (which was also a thoroughfare for domestic livestock), (2) peripheral firebreaks in the plantation bordered by a forestry compartment on one side and the protected area (PA)/plantation fenceline on the other, and (3) firebreaks in the PA adjacent the PA/plantation fenceline. I compared these firebreaks to longer-rotation burned remnant grasslands as reference sites in both the EN and PA. I estimated changes in plant species richness, composition and turnover: (1) between different firebreak types, (2) between firebreaks and longer-rotation burned grassland, and (3) between the EN and PA (longer-rotation burned sites). Comparisons among different annually-burned firebreak types showed no difference in plant species richness. However, species composition and turnover of plant communities in peripheral EN fenceline firebreaks were similar to those of PA fenceline firebreaks, but both differed from the plantation EN firebreaks. Although plant species richness was not significantly affected, plant communities of annually-burned firebreaks differed compositionally from those in the reference grasslands in the EN and PA respectively. Furthermore, plant species turnover was lower in annually-burned firebreaks than in reference EN and PA grasslands. Plant communities of longer-rotation burned grassland in the EN and PA were similar in species richness, composition and turnover. Overall, these results indicate that annual burning of firebreaks causes a shift in plant communities that coincides with a sreduction in plant species turnover, but not a significant reduction in species richness. High levels of cattle grazing appear to exacerbate these effects, as in the plantation EN firebreaks. I recommend that managers should control high intensity of cattle grazing in annually-burned areas to maintain the natural plant communities as much as possible, while at the same time protect the plantation blocks from runaway fires through necessary annual burning.

Introduction

In line with the global trend over the past 50 years (MA 2005; UN 1987; UNEP 2007), land use change, resulting in habitat transformation, has caused biodiversity loss in the Grassland Biome in South Africa (Fairbanks *et al.* 2000), the second largest biome in South Africa, occupying ~ 21% of the country. Indeed, 47% of the biome has been transformed irreversibly (Fairbanks *et al.* 2000). Three of the main contributors to habitat transformation in this biome are dryland agriculture (22.6%), communal grazing (6%) and commercial plantation forestry (3.4%) (Fairbanks *et al.* 2000). After maize, forestry is the second largest commercial land use in South Africa (DAFF 2010). Also, after urban development, forestry has the second highest impact on biodiversity integrity in the wetter eastern parts of the Grassland Biome (O'Connor & Kuyler 2009).

Forestry accounts for 1.5% of the total land surface of South Africa and for 3.3% of the Grassland Biome (Fairbanks *et al.* 2000). However, not all of the land belonging to timber companies is planted to trees. Of the 1.8 million ha of forestry plantation in South Africa (Fairbanks *et al.* 2000), one third of plantation holdings, which amounts to roughly 500 000 ha, remains permanently unplanted (Jackleman *et al.* 2006; Kirkman & Pott 2002). These unplanted areas are configured as ecological networks (ENs), which consist of interconnected patches of natural habitat (e.g. indigenous forest, wetlands, grasslands and thickets), special landscape features (e.g. hilltops) and managed areas (e.g. firebreaks and homesteads) (Samways *et al.* 2010). Together, the different landscape features of an EN offset the negative effect that alien plantation trees have on local biodiversity (Kirkman & Pott 2002; Samways 2007) by enabling persistence in, and movement of, biological species through the commercial forestry matrix at the landscape spatial scale.

After forestry compartments, firebreaks are the most extensive regularly maintained biotope type in the ENs. The primary purpose of firebreaks is to protect forestry compartments against runaway wild fires. Therefore, firebreaks are burned annually before the start of the dry winter season. Similar to road verges in other parts of the world (Eversham & Telfer 1994; Ries *et al.* 2001; Saarinen *et al.* 2005; Vermeulen 1994), firebreaks form an extensive network throughout the landscape, which enables them to contribute to biodiversity conservation in the timber production landscape. Indeed, mown firebreaks among timber compartments in the lower-lying Zululand provided early-successional habitat necessary for the survival of three grasshopper species that did not occur anywhere else in the EN (Bazelet & Samways 2011).

One of the first steps for understanding how grassland biodiversity is affected by annual burning of firebreaks is to determine how the plant community is affected, as plants are the primary producers underpinning survival of higher trophic levels in terrestrial ecosystems. Although fire can affect higher trophic levels directly, for example, through exposure to flames (Swengel 2001), studies have reported an indirect effect of fire on arthropods and birds through changes in vegetation structure (Jansen *et al.* 1999; Little *et al.* 2012). Still others have reported a direct link between the plant community and arthropods at the species level. In the KwaZulu-Natal Midlands, for example, flower-inhabiting arthropods persisted in a landscape as long as their host plants were present, irrespective of the level of disturbance to which they were subjected (Bullock & Samways 2005). A study comparing firebreaks with biennially-burned grasslands in the southern Drakensberg region found a significant difference in plant species composition, but not for species diversity (O'Connor *et al.* 2004). Another study conducted in montane grassland in the Drakensberg reported that autumn burning had a smaller effect on plant species composition than winter or spring burning (Uys *et al.* 2004). Ultimately, the plant community will determine how well firebreaks can contribute to the persistence of higher trophic levels in timber production landscapes provided that all other variables stay the same.

The overall aim of this study is to determine the plant communities in the annually-burned firebreaks in comparison to the longer-term burned areas. Specifically, I ask: 1) Do the three types of annually-burned firebreaks differ in terms of plant species richness, composition or turnover from longer-rotation burned grassland in the EN and PA respectively? I expect annually-burned firebreaks to be poorer in species than grassland with longer fire-return intervals. 2) Are all firebreaks in different parts of the landscape similar or not in terms of species richness, composition and turnover? Here, I expect cattle grazing to drive changes in plant communities causing EN firebreaks to differ from PA firebreaks. Answering these questions enables us to determine the extent to which the annually-burned firebreaks, necessary for plantation management, have conservation value.

Methods

Forty-six sites were sampled in the Midlands of KwaZulu-Natal (29°38′S; 29°58′E) in iMpendle Nature Reserve, and in three commercial forestry plantations over a maximum linear spatial scale of 17 km (Figure 3.1). Five types of sites were selected: 1) remnant longer-rotation burned grassland within ENs (natural grasslands that were not managed as firebreaks

= reference sites for comparison with annually-burned sites) (n = 14); 2) remnant longer-rotation burned grassland within the PA (= second longer-term set of reference sites for comparison with annually-burned sites) (n = 8); 3) annually-burned firebreaks within the EN and with pine compartments on both sides (plantation EN firebreaks: n = 8); 4) annually-burned firebreaks within the EN adjacent the EN/PA boundary line (peripheral EN firebreaks: n = 8), and 5) annually-burned firebreak within the PA adjacent the EN/PA boundary line (PA firebreaks: n = 8). In summary, I used the following classifications for each site: (1) EN versus PA, (2) annually-burned firebreak versus longer-rotation burned grassland (reference sites) and (3) vegetation type (see below).

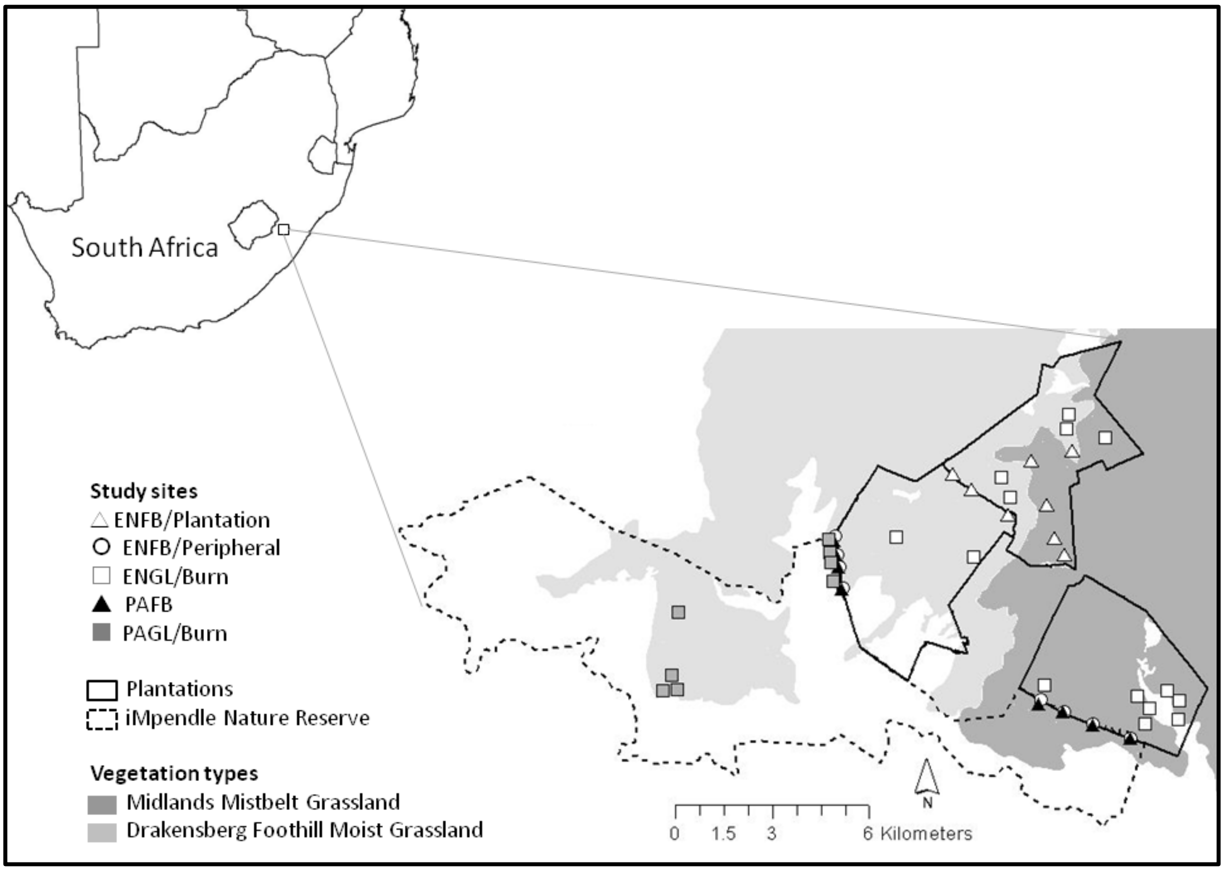

Figure 3.1 Study region in the KwaZulu-Natal Midlands of South Africa. In the ecological network (EN), study sites consisted of eight plantation firebreaks (ENFB/Plantation), eight peripheral firebreaks (ENFB/Peripheral) and 12 longer-rotation burned reference grassland sites (ENGL/Burn). In the adjacent protected area (PA), there were eight firebreaks (PAFB) and eight longer-rotation burned reference grassland sites (PAGL/Burn).

EN grasslands had been made available to local human communities for grazing by domestic cattle, whereas PA sites were protected and fenced. Thus, PA sites were grazed lightly by naturally-occurring indigenous herbivores (e.g. black wildebeest (*Connochaetes gnou*) and southern reedbuck (*Redunca arundinum*), while EN sites were grazed continually (but at various densities; Table 3.1) by free roaming cattle traversing the plantation landscape, as well as by occasional indigenous megaherbivore species. Grazing intensity in the different grassland and firebreak types was estimated from the proportion of times that cattle were encountered at any one site out of 10 site visits (high: >70%, moderate: 30-60%, low <10%) and proportion of bare ground as a result of trampling (high: >10%, low: <10%) (Table 3.1). Proportion of bare ground (i.e. % cover at 10 randomly-position 1 m^2 quadrats) was estimated at all sites during a one week period in November 2012, approximately five months after last burn for longer-rotation burned grassland and seven months after last burn for firebreaks. I took grazing intensity as an embedded factor for EN sites, although acknowledging that the impact was far greater in the plantation firebreaks than in the peripheral firebreaks or in longer-rotation burned grassland (Table 3.1).

Table 3.1 A summary of burning frequency, burning season and approximate grazing intensity at the different sites. EN = ecological network, PA = protected area, ENFB/Plantation = firebreaks in the EN with forestry compartments on two sides, ENFB/Peripheral = firebreaks in the EN with a forestry compartment on one side and the PA fenceline on the other, PAFB = firebreaks in the PA adjacent the plantation fenceline, ENGL = longer-rotation burned grassland in the EN, and PAGL = longer-rotation burned grassland in the PA.

Class	Sample size	Fire frequency	Burning season	Bare ground	Cattle occurrence
ENFB/Plantation	n = 8	Annual	Autumn	> 10%	High (>70%)
ENFB/Peripheral	n = 8	Annual	Autumn	< 10%	Low (<10%)
PAFB	n = 8	Annual	Autumn	< 10%	Low (<10%)
ENGL/Burn	n = 12	1-3 years	Winter	< 10%	Moderate (~50%)
PAGL/Burn	n = 8	1-3 years	Winter	< 10%	Low (<10%)

Firebreaks were narrow, linear strips that had been burned annually in autumn (April to May) for the past ~20 years to protect timber compartments from runaway fires in the dry winter season. All firebreaks in the EN were adjacent to plantation blocks, within the “edge zone” (<30 m from the pine compartment edge) (Pryke & Samways 2012). Firebreaks in the PA were adjacent to the plantation fenceline, but >30 m from the pine compartment edge. Annually-burned firebreaks were compared to reference grasslands sites in the EN and PA, which were burned every 1-3 years on an ad-hoc basis in winter (June to August) (Table 3.1). All firebreak and grassland sites were burned during the 12-month period prior to sampling.

These longer-rotation burned grassland sites occurred in the interior of the PA, and in wider corridors in the EN >30 m from the pine compartment edge.

The study area spanned two dominant vegetation types: Drakensberg Foothill Moist Grassland at higher elevations (880-1860 m) and Midlands Mistbelt Grassland at intermediate elevations (760-1400 m) (Mucina *et al.* 2005, 2006). These two vegetation types were included in the study design. In the EN, annually-burned firebreaks and longer-rotation burned grasslands were represented by an equal number of sites in each vegetation type. In contrast, in the PA, all longer-rotation burned remnant grassland sites were in Drakensberg Foothill Moist Grassland, because the Midlands Mistbelt Grassland section was not burned in the year preceding the study (Table 3.1).

Sites were spaced ~400 m apart. At each site, there were six randomly-orientated (30 m) vegetation transects with twenty-four vegetation quadrats (1 m^2). Vegetation quadats were positioned randomly, but within 5m from vegetation transects. The vegetation sampling method followed that of O’Connor *et al.* (2004). Unlike findings on tallgrass prairie in North America, where spatial scale of measurement determined magnitude of change caused by fire and grazing on plant communities (Collins & Smith 2006), the effect of fire frequency and burning season on plant communities in South Africa was consistent at different spatial scales (1 m^2 and 100 m^2) (Uys *et al.* 2004). In each vegetation quadrat, I determined the identity and abundance (% cover) of each plant species as well as the proportion of bare ground (% cover). Graminoid plant species (grasses and sedges) were collected and non-graminoid plant species were photographed to aid identification (Gibbs-Russell *et al.* 1990; Pooley 2003; Pooley 2005; Van Oudtshoorn 2006). After calculating the mean abundance of each plant species and the mean proportion of bare ground at each site, a data matrix was compiled with species and environmental variables in rows, and sites in columns.

Using SAS 5.1 software, I compared total species richness (with normal distribution) and bare ground (with Poisson distribution) using a Generalized Linear Model (GLM) with a log-link function, firstly, among the three different firebreak types and, secondly, among the five different site types (Table 3.1). I used Least Square Means post-hoc test to determine whether there were significant differences in total species richness and bare ground. Differences were significant when p-values were < 0.05.

To calculate the compositional changes between various types of sites, I used PRIMER 6.0 software, with data square-root transformed to reduce the effect of dominant species (PRIMER-E 2008). A resemblance matrix was created using the Bray-Curtis similarity index and data were analyzed with permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) with 9999 unrestricted permutations of raw data to determine whether annual burning and cattle grazing had a significant effect on plant species composition. These data were analyzed on the overall effects and specific effects.

For species turnover, defined as the magnitude of change in identity of plant species from one site to the next along a spatial or environmental gradient (Anderson *et al.* 2011), standardized species abundance data were transformed to presence/absence data. From this data matrix, a Bray-Curtis similarity matrix was created in PRIMER 6.0 software. Permutational multivariate analysis of dispersion (PERMDISP) with 9999 permutations was used to determine whether annual burning and cattle grazing had a significant effect on the dispersion of data. It involved measuring distance from site to centroid (defined as the geographical centre for a group of sites) in a multivariate space, and then comparing mean distances of different groups using ANOVA (Anderson 2006). I analyzed these data for differences in plant species composition and species turnover between vegetation types, between the EN and PA, between firebreaks and longer-rotation burned grasslands, and between different firebreak types.

Results

Species richness

Comparisons of plant species richness among the three different annually-burned firebreak types were not significant (Table 3.2). Comparisons among the five different types of sites were non-significant, except between plantation EN firebreaks (mean ± standard error: 61.25 ± 7.29) and longer-rotation burned reference grassland in the PA (mean ± standard error: 78.88 ± 4.98) (Table 3.2).

Table 3.2 Generalized Linear Models (with normal distribution) shows a comparison of plant species richness between firebreaks (FB) in the ecological network (EN) and those in the protected area (PA), and between the firebreaks and longer-rotation burned remnant grassland (GL). ENFB/Plantation = firebreak in the EN with pine compartments on both sides, ENFB/Peripheral = firebreak in the EN adjacent the PA, PAFB = firebreak in the PA adjacent the plantation. Results are displayed separately for Drakensberg Foothilll Moist Grassland (DBerg) and Midlands Mistbelt Grassland (MBelt). Significant (* $P<0.05$) and near significant (§ $0.05 < P < 0.01$) differences in plant species richness were indicated with a less than (<) symbol.

Vegetation type	**Comparison**	**Z**	**P-value**
DBerg	ENFB/Plantation ↔ PAFB	-0.05	0.956
DBerg	ENFB/ Plantation ↔ ENFB/Peripheral	0.30	0.763
DBerg	ENFB/Peripheral ↔ PAFB	0.25	0.805
DBerg	PAFB < PAGL	-1.91 (§)	0.056
DBerg	ENFB/Peripheral < PAGL	-1.65	0.098
DBerg	ENFB/Plantation < PAGL	-1.97 (*)	0.0494
DBerg	PAGL ↔ ENGL	0.10	0.922
DBerg	ENFB/ Plantation < ENGL	-1.92 (§)	0.055
DBerg	ENFB/Peripheral ↔ ENGL	-1.62	0.105
MBelt	ENFB/ Plantation ↔ PAFB	-1.28	0.202
MBelt	ENFB/ Plantation ↔ ENFB/ Peripheral	1.34	0.181
MBelt	ENFB/Peripheral ↔ PAFB	0.06	0.950
MBelt	ENFB/ Plantation < ENGL	-1.90 (§)	0.058
MBelt	ENFB/ Peripheral ↔ ENGL	-0.47	0.642

Species composition and turnover

Comparing Drakensberg Foothill Moist Grassland with Midlands Mistbelt Grassland

Overall plant species composition of the two grassland types (Drakensberg Foothill Moist Grassland and Midlands Mistbelt Grassland) was significantly different, but turnover of the two vegetation types was similar (Table 3.3). The exceptions were annually-burned plantation firebreaks in the EN, where plant species composition of sites in Drakensberg Foothill Moist Grassland resembled that in Midlands Mistbelt Grassland (Table 3.3), and PA firebreaks where species turnover was greater in Midlands Mistbelt Grassland (27.33 ± 0.41 mean deviation from centroid (MDC)) than in Drakensberg Foothill Moist Grassland (18.60 ± 0.98 MDC).

Comparing annually-burned firebreaks with longer-rotation burned grassland

There was a significant difference in plant species composition between annually-burned PA firebreaks and longer-rotation burned reference grassland in the PA (Figure 3.2; Table 3.3). In addition, species turnover of annually-burned PA firebreaks (18.60 ± 0.97 mean deviation from centroid (MDC)) was significantly less than that of longer-rotation burned reference grassland in the PA (26.92 ± 1.47 MDC) (Table 3.3). Seventy percent (124/177) of plant species occurring in annually-burned PA firebreaks were also found in longer-rotation burned reference grassland in the PA.

Table 3.3 A summary of comparisons of plant species composition using permutational multi-variate analysis of variance (PERMANOVA) and species turnover using permutational multi-variate analysis of dispersion (PERMDISP) between annually-burned firebreaks (FB) and longer-rotation burned reference grassland (GL) sites in the ecological network (EN) and protected area (PA) respectively. Results are displayed separately for the two vegetation types: Drakensberg Foothilll Moist Grassland (DBerg) and Midlands Mistbelt Grassland (MBelt). ENFB/Plantation = firebreak in the EN with pine compartments on both sides, ENFB/Peripheral = firebreak in the EN adjacent the PA, PAFB = firebreak in the PA adjacent the plantation.

Constant factors	**Comparison**	**PERMANOVA t-value**	**PERMANOVA P-value**	**PERMDISP t-value**	**PERMDISP P-value**
ENGLBurn	DBerg ↔ MBelt	1.429	0.004**	0.753	0.561
ENFB/ Plantation	DBerg ↔ MBelt	0.851	0.563	0.806	0.465
ENFB/ Peripheral	DBerg ↔ MBelt	1.995	0.027*	1.798	0.167
PAFB	DBerg ↔ MBelt	1.722	0.028*	8.269	0.026*
DBerg	PAGL ↔ PAFB	1.658	0.007**	3.738	0.002**
DBerg	PAGL ↔ ENFB/Plantation	1.874	0.004**	2.661	0.012*
DBerg	PAGL ↔ ENFB/Peripheral	1.805	0.005**	1.342	0.346
DBerg	PAGL ↔ ENGL	1.142	0.160	1.103	0.528
DBerg	ENGL ↔ ENFB/Plantation	1.290	0.102	0.679	0.643
DBerg	ENGL ↔ ENFB/Peripheral	1.271	0.096	1.403	0.494
DBerg	ENFB/Plantation ↔ ENFB/Peripheral	1.253	0.173	2.895	0.026*
DBerg	PAFB ↔ ENFB/Peripheral	1.072	0.376	2.394	0.087
DBerg	PAFB ↔ ENFB/Plantation	1.473	0.028*	4.433	0.027*
MBelt	ENGL ↔ ENFB/Plantation	1.607	0.015*	1.026	0.464
MBelt	ENGL ↔ ENFB/Peripheral	1.356	0.028*	4.166	0.001**
MBelt	ENFB/ Plantation ↔ ENFB/Peripheral	1.674	0.029*	9.297	0.028*
MBelt	PAFB ↔ ENFB/Peripheral	0.799	0.802	5.691	0.030*
MBelt	PAFB ↔ ENFB/ Plantation	1.577	0.026*	6.927	0.030*

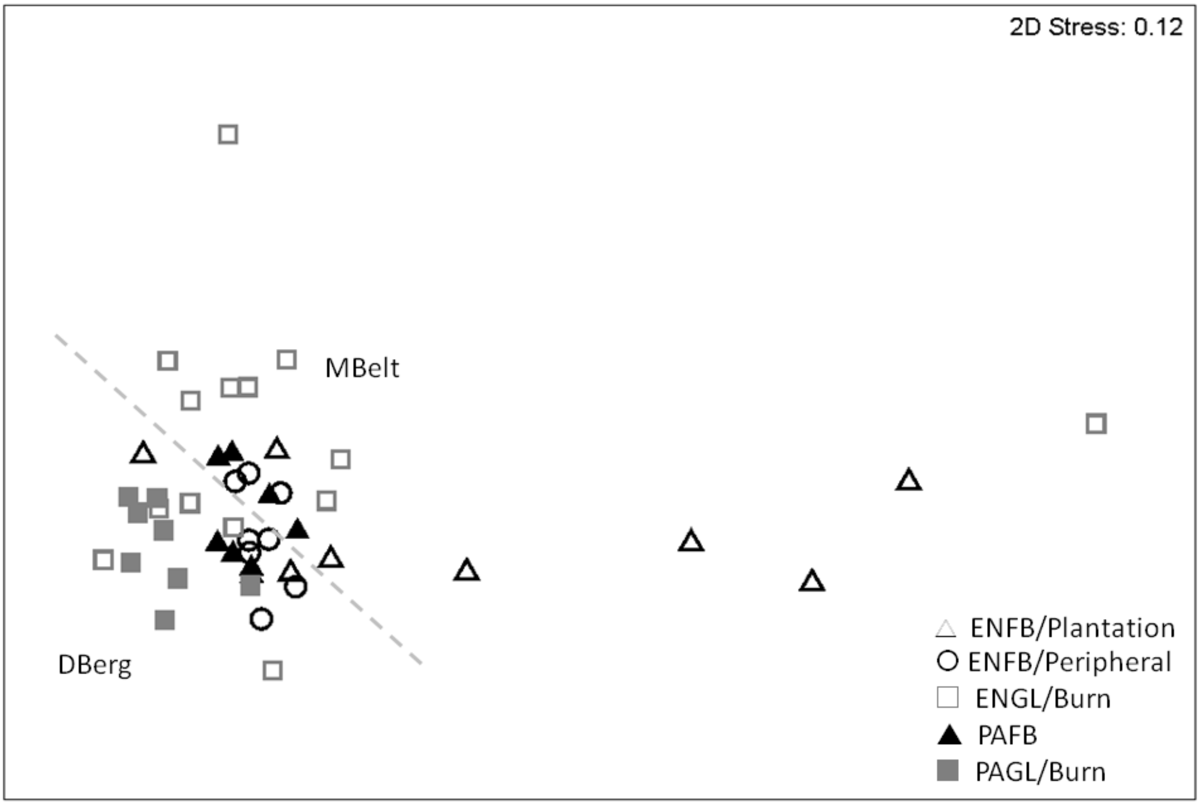

Figure 3.2 Multi Dimensional Scaling (MDS) plot based on a Bray-Curtis resemblance matrix constructed for plant species composition for different firebreak (FB) types and remnant, longer-term burned grassland (GL) in the ecological network (EN) and protected area (PA) respectively. ENFB/Plantation = firebreak in the EN with pine compartments on both sides, ENFB/Peripheral = firebreak in the EN adjacent the PA, PAFB = firebreak in the PA adjacent the plantation. The dashed line indicates the separation of the two vegetation types: MBelt = Midlands Mistbelt Grassland and DBerg = Drakensberg Foothill Moist Grassland.

In Midlands Mistbelt Grassland in the EN, there were significant differences in plant species composition when comparing any of the annually-burned firebreak types with longer-rotation burned grassland (Figure 3.2; Table 3.3). In this grassland type, species turnover was also significantly less in annually-burned peripheral firebreaks (19.53 ± 1.31 MDC) than in longer-rotation burned grassland (35.05 ± 2.50 MDC) in the EN (Table 3.3).

In contrast, in Drakensberg Foothill Moist Grassland, there were no differences in plant species composition or turnover when comparing any of the annually-burned EN firebreak types with longer-rotation burned grassland in the EN (Table 3.3).

Annually-burned PA firebreaks contained 80% of the 182 plant species that occurred in longer-rotational burned, reference grassland in the PA. Furthermore, annually-burned peripheral EN firebreaks contained 52% (155 spp.) and annually-burned plantation firebreaks contained 68% (200 spp.) of the 294 plant species documented in longer-rotational burned grassland in the EN.

Comparing different firebreak types

Comparing plant species composition and turnover of firebreaks on either side of the plantation/PA fenceline (peripheral EN firebreaks vs. PA firebreaks) showed that they supported plant communities similar in composition. The only significant difference was in species turnover, which was greater in PA firebreaks than in peripheral EN firebreaks for the one vegetation type (Table 3.3).

In Midlands Mistbelt Grassland, there were significant differences in plant species composition when comparing plantation EN firebreaks with the other two firebreak types. Also, species turnover of plantation EN firebreaks (38.93 ± 1.62 mean deviation from centroid (MDC)) was significantly greater than that of the other two firebreak types: peripheral EN firebreaks (19.53 ± 1.31 MDC) and PA firebreaks (27.33 ± 0.41 MDC) (Table 3.3).

In Drakensberg Foothill Moist Grassland, plant species composition of plantation EN firebreaks differed significantly from PA firebreaks, but not from peripheral EN firebreaks (Table 3.3). Species turnover of plantation EN firebreaks (35.65 ± 3.72 MDC) was significantly greater than that of the other two firebreak types: peripheral EN firebreaks (23.61 ± 1.85 MDC) and PA firebreaks (18.60 ± 0.97 MDC) (Table 3.3).

Bare ground

The proportion of bare ground, which could be indicative of cattle grazing pressure due to trampling, in plantation EN firebreaks (mean percentage cover ± standard error: 16.20 ± 3.4) was significantly greater than in any of the other annually-burned firebreaks or longer-rotation burned grasslands (Table 3.4).

Longer-rotation burned reference grassland sites in the EN (mean percentage cover ± standard error: 7.53 ± 1.97) had a significantly greater proportion of bare ground than longer-rotation burned grassland sites in the PA (mean percentage cover ± standard error: 5.46 ± 1.0). In turn, longer-rotation burned reference grassland sites in the PA had a significantly greater proportion of bare ground than annually-burned firebreaks in the PA (mean percentage cover ± standard error: 3.46 ± 0.8) (Table 3.4).

Table 3.4 A summary of comparisons of proportion of bare ground, using Generalized Linear Models, between the different firebreak types (FB) and longer-rotation burned grassland (GL) in the ecological nework (EN) and protected area (PA) respectively. ENFB/Plantation = firebreak in the EN with pine compartments on both sides, ENFB/Peripheral = firebreak in the EN adjacent the PA, PAFB = firebreak in the PA adjacent the plantation. Results are displayed separately for the two vegetation types: Drakensberg Foothilll Moist Grassland (DBerg) and Midlands Mistbelt Grassland (MBelt).

Vegetation type	**Comparison**	**Z**	**p-value**
DBerg	ENFB/ Plantation > ENFB/Peripheral	-4.91	< 0.0001***
DBerg	ENFB/Plantation > PAFB	5.18	< 0.0001***
DBerg	ENFB/ Peripheral = PAFB	0.76	0.448
DBerg	PAFB < PAGL	-2.51	0.012*
DBerg	ENFB/Plantation > PAGL	4.78	< 0.0001***
DBerg	ENFB/Peripheral = PAGL	-1.84	0.066
DBerg	PAGL > ENGL	-2.14	0.032*
DBerg	ENFB/ Plantation > ENGL	5.45	< 0.0001***
DBerg	ENFB/ Peripheral = ENGL	0.15	0.884
MBelt	ENFB/ Plantation > PAFB	5.18	< 0.0001***
MBelt	ENFB/Peripheral = PAFB	1.45	0.146
MBelt	ENFB/ Plantation > ENFB/ Peripheral	-4.13	< 0.0001***
MBelt	ENFB/ Plantation > ENGL	3.49	0.0005***
MBelt	ENFB/ Peripheral = ENGL	-1.59	0.112

Discussion

Effect of annual burning

Overall, I found that the grassland plant communities changed in response to annual burning. These changes were in species composition and turnover, but not in species richness. Other studies investigating the effect of different disturbance regimes on South African grasslands also found plant species composition to be more sensitive to changing fire regime than species richness (O'Connor *et al.* 2004; Uys *et al.* 2004). Therefore, it appears as if a measurement like species richness alone is not suitable for detecting shifts in plant communities induced by frequent fire rotations. Other studies in South African grassland reported either a positive (Fynn *et al.* 2004) or neutral response by plant species richness to fire frequency and burning season (O'Connor *et al.* 2004; Uys *et al.* 2004). This contrasts with species loss reported in annually-burned tallgrass prairie in North America (Collins *et al.* 1995; Veen *et al.* 2008; Collins & Calabrese 2012; Koerner & Collins 2013), and in annually-burned, grazed savanna in South African (Koerner & Collins 2013). Lightning strike density in South Africa was greatest in Afromontane grassland, such as is found in the Midlands (Manry & Knight 1986). It is possible that plant communities in these regions are pre-adapted to higher incidences of fire causing them to be less affected by annual burning than would be the case in savanna where lightning strike density and, therefore, fire incidences were lower (Manry & Knight 1986). Compared to areas with longer fire-return intervals, annual burning homogenized tallgrass prairie in North America (Collins 1992; Collins & Smith 2006) and grassland in South Africa (Uys *et al.* 2004), and changed plant species composition in savanna in South Africa (Smith *et al.* 2013).

Effect of annual burning in Midlands Mistbelt Grassland vs. Drakensberg Foothill Moist Grassland

Within Midlands Mistbelt Grassland, plant species composition of both annually-burned EN firebreak types differed significantly from longer-rotation burned grassland in the EN. This was not the case for Drakensberg Foothill Moist Grassland where no such differences were significant. This suggests that some vegetation types are more sensitive to the effects of annual burning than others. Sensitivity might be linked to climate, topography and/or soil characteristics. It was, on average, 1.2 °C cooler (mean annual temperature: 14.6°C) with ~ four times as many frost days (mean: 26 days) in the higher-elevation Drakensberg Foothill Moist Grassland (Mucina *et al.* 2006). In addition, apedal, plinthic soils in Midlands Mistbelt Grassland were derived from the shale and sandstone; whereas deep, well-drained soils in Drakensberg Foothill Moist Grassland were derived from mudstone, sandstone and dolerite (Mucina *et al.* 2006). Soil moisture and depth, and topography influenced primary productivity (Briggs & Knapp 1995), which, in turn, influenced response of grassland plant communities to fire and grazing in North America (Abrams *et al.* 1986; Harrison *et al.* 2003). It is possible that some of these environmental variables also influenced sensitivity of plant communities to the effects of annual burning.

Edge effects in firebreaks

Interestingly, neither plant species richness nor plant species composition of plant communities within peripheral EN firebreaks, which were effectively all inside the edge zone (Pryke & Samways 2012), differed from PA firebreaks > 30 m from the plantation edge. There are a few possible explanations for this phenomenon. The first one concerns the responsiveness of plant communities compared to more mobile taxa. The width of the edge zone (30m) was originally determined using grasshoppers (Samways & Moore 1991) and butterflies (Pryke & Samways 2001), and later confirmed using various other invertebrate taxa (Pryke & Samways 2012). An edge zone of similar size was found in Austrian dry grassland using grasshoppers (Bieringer & Zulka 2003). While the sharp transition from pine compartment to grassland affected behavior of butterflies (Pryke & Samways 2001) and life cycle of grasshoppers (Bieringer & Zulka 2003), perennial plant species might take longer to respond to these changes than invertebrates.

Alternatively, it is possible that plants might not respond directly to changes in vegetation structure, but rather indirectly, for example, to invasion of alien invasive plants (e.g. *Rubus* spp.) along grassland edges (Le Maitre *et al.* 2002; Richardson & van Wilgen 2004). There can be a consistently negative effect of invasive alien plant species on indigenous diversity and ecosystem function in the African context (van Wilgen *et al.* 2008). If alien invasion determines the width of edge zone for plants, it places a new priority on effective control of these species.

Lastly, similarities in plant communities at different distances from the plantation edge might be caused by the effect of annual burning through its effect on soil moisture and nutrient status (Fynn *et al.* 2003; Mills & Fey 2004; O'Connor *et al.* 2004), which is shown to contribute to edge effects of transformed landscapes on natural ecosystems elsewhere (Jagomagi *et al.* 1988; Li *et al.* 2007). If annual burning is one of the factors contributing to edge effect of timber compartments on grasslands, this management practice could effectively increase the size of the edge zone, which, in turn, could affect the size of the valuable interior zone necessary for conservation of non-generalist plant species in ENs.

Effect of annual burning and cattle grazing

Plant species richness, composition and turnover of peripheral EN firebreaks with light cattle grazing were similar to those in PA firebreaks without cattle grazing. However, these firebreak types both differed significantly from plantation EN firebreaks, which were heavily-grazed by cattle. The pattern of grazing in annually-burned firebreaks can change plant species composition (O'Connor *et al.* 2004). Indeed, heavily-grazed, annually-burned grassland differed significantly from biennially or triennially-burned grassland grazed at lower intensities in Mpumalanga (Boakye *et al.* 2013).

Also, there were significantly less plant species in heavily-grazed, annually-burned plantation firebreaks in the EN than in longer-rotation burned reference grassland in the PA. Lastly, within this firebreak type, plant species composition of the two vegetation types did not differ. Plant communities of plantation EN firebreaks in Midlands Mistbelt Grassland were similar to those in Drakensberg Foothill Moist Grassland. This indicates that grassland plant communities in plantation EN firebreaks are being simplified by annual burning and heavy grazing. Simplification of natural plant communities was also recorded for upland and lowland areas that were frequently-disturbed in tallgrass prairie (Gibson & Hulbert 1987). Here, heavy grazing in annually-burned firebreaks had a disproportionately large homogenizing, simplifying and impoverishing effect on plant communities, and from a conservation point of view, should be avoided.

Management implications

Annual burning is not ideal from a biodiversity perspective, as it changes the composition and species turnover (i.e. homogenizes) plant communities without adding species that are not already conserved in longer-rotation burned grassland. Furthermore, annual burning makes grassland plant communities more susceptible to the effects of intense grazing, which, in turn, reduces plant species richness.

However, I acknowledge that the management practice of annual burning is necessary from an economic, plantation protection point of view. Therefore, I urge managers (1) to limit the amount of annually-burned grassland in ENs to the minimum necessary for protection of the forestry plantation estates, and (2) to regulate grazing by domestic cattle for the first few months after fire to low intensities to prevent species loss from these fragile areas.

Conclusion

Annual burning of firebreaks does not seem to benefit plant diversity, as it results in homogenization and shifts in plant communities in the presence (EN) and absence (PA) of cattle grazing. Furthermore, heavy cattle grazing exacerbates the effect of annual burning on plant communities, leading to elevated levels of bare ground, species loss, and changes in species composition and turnover, as was the case for plantation EN firebreaks. However, firebreaks are a necessary component of ENs, as they protect standing timber compartments from runaway fires. Therefore, I recommend that access of domestic cattle to firebreaks should be strictly controlled, particularly during the first few months after burn, as this should aid recovery and long-term persistence of the natural plant communities.

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CHAPTER 4: Interactive effects of grazing and fire on Afromontane grasslands

Abstract

Grasslands have been shaped by fire and grazing over millennia. In South Africa, grassland ecological networks (ENs) among forestry plantations offset the negative effect that alien plantation trees have on local biodiversity. Managed for biodiversity conservation, these grasslands are burned periodically, while local human communities are allowed to graze their cattle within these ENs. The aim here is to determine how the effect of time since last fire (< 12 months vs. > 12 months) interacts with the occurrence of cattle (at different grazing intensity levels) on plant communities in Afromontane grassland. Forty four sites were selected in either a protected area (PA) or an EN. The sites in the PA were categorized as: grazed (by black wildebeest) or ungrazed, and burned or unburned. In the EN, sites were categorized as: moderately or heavily-grazed (by domestic cattle), and burned or unburned. Burned and unburned grassland in the PA differed in plant species composition, with greater species richness and turnover in burned areas. There was no effect between burned and unburned EN grasslands. A comparison of ungrazed PA vs. EN showed cattle affected plant species richness, composition and turnover of unburned grassland, but not burned grassland. A comparison of grazed, unburned PA vs. EN showed no differences, suggesting that grazing by cattle mimics that of indigenous large herbivores on grassland, provided grazing is at a moderate level. Plant species richness and composition of burned, ungrazed grassland in the PA were similar to unburned, grazed grassland in the EN, although species turnover was higher in the EN. Heavily-grazed grassland had less plant species than moderately-grazed grassland in the EN. These results indicate that burning and moderate grazing sustain plant diversity in South African grasslands, although high intensity grazing could lead to plant species loss. Fire and grazing should be incorporated into the management of grassland ENs, as they contribute to optimal biodiversity conservation in production landscapes.

Introduction

Afromontane grassland is a threatened vegetation type with high levels of diversity (Uys 2006; Bond & Parr 2010). The wetter (>650 MAP), eastern region of South Africa can support closed woodland or forest (Bond *et al.* 2003), but is maintained as grassland due to the intervention of fire and grazing (Bond 2005; Bond 2008). These consumers shape plant communities in different ways. Grazing is a biotic, selective consumer influencing the proportion of palatable and unpalatable plant species in the system (Augustine & McNaughton 1998; Bond 2005; Trollope 2011) whereas fire is an abiotic, generalist consumer often fueled by the inedible plant species (Bond & Keeley 2005).

Globally, the response of grassland plant communities to grazing is influenced by precipitation and/or productivity and its evolutionary history with large herbivores (Milchunas & Lauenroth 1993). Where grassland ecosystems developed in the presence of large herbivores, such as in southern Africa, the response of plant communities is governed by soil fertility and rainfall, with grazing having a larger effect in drier regions and fire having a larger effect on plant communities in wetter regions (Smith *et al.* 2013). Occurrence of fire in southern Africa is driven by variation in moisture and fuel load (Kerby *et al.* 2007; Archibald *et al.* 2009), while fuel load, in turn, is influenced by grazing intensity (van Langevelde *et al.* 2003; Archibald *et al.* 2005) and precipitation (Milchunas & Lauenroth 1993; Govender *et al.* 2006). Lastly, grazing intensity is greater in recently-burned grassland than in areas dominated by moribund vegetation (Archibald & Bond 2004; Fuhlendorf *et al.* 2009). Therefore, response of grassland plant communities is influenced by the interaction between grazing and fire as well as by the interaction of these two disturbances with other factors (e.g. precipitation, soil fertility and productivity).

The eastern parts of South Africa is especially well suited for the establishment of timber plantations, which now covers ~ 40 % of the KwaZulu-Natal province (DAFF 2010). However, plantations are not planted completely with timber trees. Approximately one third of each plantation, amounting to 500 000 ha at the national level (Kirkman & Pott 2002), is either natural habitat (e.g. mainly grassland and some forest), maintained areas (e.g. firebreaks or homesteads) or special landscape features (e.g. wetlands or rocky outcrops) mostly arranged in the spatial configuration of an ecological network (EN) to mitigate the negative effect of alien plantation trees on local biodiversity (Samways 2007a; Samways 2007b; Samways *et al.* 2010).

In the central Midlands of KwaZulu-Natal province, large parts of these ENs constitute natural remnant grassland, which is managed primarily for biodiversity conservation (Samways 2007b). This involves burning different parts of the EN over consecutive years so that burned and unburned grassland is available to provide habitat requirements for early as well as late-successional species (Bazelet & Samways 2011). However, large indigenous grazers are not usually present in the EN in sufficient numbers to act as a driver of diversity. To simulate the effect of large indigenous herbivores on grassland (Samways & Kreuzinger 2001), and to contribute to poverty alleviation of rural communities (DWAF 1997; Shackleton *et al.* 2007), domestic cattle from neighboring areas are allowed to graze in ENs on a periodic basis. Domestic cattle grazing in the EN affect invertebrate diversity via its effect on habitat quality and plant communities (Pryke & Samways 2003; Bullock & Samways 2005). In tallgrass prairie, grazing had a positive effect on plant diversity, especially in infrequently-burned areas (Collins & Calabrese 2012). Here, I wish to determine how grazing influences the grassland plant communities in South Africa when viewed within the context of the current fire regime in ENs.

Therefore, the overall aim of this study is to determine the effect of burning and grazing on the diversity of grassland plant communities in the ENs. To this end, I compared 1) areas burned < 12 months ago with areas burned > 12 months ago, 2) grazed with ungrazed areas, 3) burned ungrazed with unburned grazed areas, and 4) areas grazed at different intensities. As fire and grazing are the two primary natural disturbances in grassland, I expect these two disturbances to have a positive effect on plant species richness. At the same time, I expect the naturally patchy nature of grazing to have a larger effect on plant species turnover than fire, which is more evenly spread-out across the landscape. Lastly, I expect plant species to disappear from the landscape when confronted with high grazing intensity. Understanding how plant communities respond to cattle grazing and time since last fire is the first step towards honing management practices in grassland ENs to improve biodiversity conservation in timber production landscapes.

Methods

Forty-four remnant grassland sites were sampled in the KwaZulu-Natal Midlands, South Africa (29°38′S; 29°58′E). Sites were located in iMpendle Nature Reserve, a protected area (PA) and in three commercial forestry plantations, with sites spaced out over a linear maximum spatial distance of 17 km (Figure 4.1). Six types of sites were selected: 1) burned reference grassland in the PA (n = 8); 2) unburned reference grassland in the PA (n = 8); 3) burned, moderately-grazed grassland in the EN (n = 7); 4) burned, heavily-grazed grassland in the EN (n = 7); 5) unburned, moderately-grazed grassland in the EN (n = 7), and 6) unburned, heavily-grazed grassland in the EN (n = 7) (Table 4.2). Burned grassland sites in the EN and PA are the same as those used in Chapter 3.

The main difference between the EN and PA was that local people are allowed to graze their cattle in the EN, but not in the PA. Parts of the EN were grazed more heavily by cattle than others. Grazing intensity was determined based on five different measures: 1) cattle occurrence during site visits; 2) grass height of palatable grass species (mostly *Themeda triandra*); 3) bare ground cover; 4) collective aerial cover of certain forb species (unpalatable *Eriosema distinctum*, poisonous *Senecio isatideus* or *S. retrorsus*) (Pooley 2003; Pooley 2005; O'Connor *et al.* 2011) and 5) collective aerial cover of grass species which are known to be indicative of light-to-moderate or heavy grazing (van Oudtshoorn 2006) (Table 4.1). The grass species indicative of heavy grazing are *Aristida junciformis*, *Cymbopogon plurinodis*, *Elionurus muticus*, *Eragrostis curvula*, *E. plana*, and *Heteropogon contortus* (van Oudtshoorn 2006). These grass species dominated (> 50% of the grass sward) at heavily-grazed sites. Moderately-grazed sites were dominated by *Diheteropogon amplectens*, *Harplochloa falx*, *Themeda triandra*, *Trachypogon spicatus* and *Tristachya leucothrix* (van Oudtshoorn 2006). These dominant grasses typically constituted <5 % of plant species at each site. Cattle occurrence was recorded as present when > 5 cows were within a 200 m radius from the each site. Cattle occurrence was classified as low (< 40%) or high (> 40%) based on five visits to each site.

Table 4.1 Classification of grazing intensity. Sites in the ecological network (EN) were categorized into moderately-grazed and heavily-grazed sites based on cattle occurrence; composition of the grass sward (proportions of grasses indicative of light-to-moderate or heavy grazing); collective aerial cover of selected forb species; grass height of palatable grass species; and proportion of bare ground.

Grazing intensity	EN/PA	Cattle/Game	Cattle occurrence	Composition of grass sward	Forbs [§]	Grass height	Bare ground
Very light	PA	Game (excl. black wildebeest)	-	ModGraz [¢] > 50%	< 10%	> 20 cm	< 5%
Light	PA	Game (incl. black wildebeest)	-	ModGraz [¢] > 50%	< 10%	> 20 cm	< 5%
Moderate	EN	Cattle	Moderate (< 40%)	ModGraz [¢] > 50%	< 10%	> 20 cm	< 5%

Heavy	EN	Cattle	High (> 40%)	HeavGraz [¥] > 50%	> 10%	< 20 cm	> 5%

[§] Forbs: Eriosema distinctum, Senecio isatideus or S. retrorsus (Pooley 2005; O'Connor et al. 2011)
[¢] Grasses indicative of light to moderate grazing (ModGraz): *Diheteropogon amplectens*, *Harplochloa falx*, *Themeda triandra*, *Trachypogon spicatus* or *Tristachya leucothrix* (van Oudtshoorn 2006)
[¥] Grasses indicative of heavy grazing (HeavGraz): *Aristida junciformis*, *Cymbopogon plurinodis*, *Elionurus muticus*, *Eragrostis curvula*, *E. plana* or *Heteropogon contortus* (van Oudtshoorn 2006)

Grassland was burned in winter (June to August) on a rotational basis every 1-3 years. Therefore, some of the grassland sites were burned < 12 months prior to sampling (i.e. burned), while others were burned > 12 months prior to sampling (i.e. unburned). Each class was represented by an equal number of sites in each of the two vegetation types: Drakensberg Foothill Moist Grassland and Midlands Mistbelt Grassland (Mucina *et al.* 2005). Because the Midlands Mistbelt Grassland section of the PA was not burned during the last year, all burned PA grassland sites were in Drakensberg Foothill Moist Grassland (Table 4.2).

Table 4.2 Classification of sites according to grazing regime and time since last fire. Forty-four sites were classified according to four criteria: ecological network (EN) vs. protected area (PA); burned < 12 months ago (burned) or burned > 12 months ago (unburned); grazed by large herbivores (grazed) or not grazed by large herbivores (ungrazed); grazing intensity (very light, light, moderate and heavy); and Midlands Mistbelt Grassland (MBelt) or Drakensberg Foothill Moist Grassland (DBerg).

EN/PA	Burn/Unburn	Vegetation type	Grazed by large herbivores	Grazing intensity	Sample size
PA	Burn	DBerg	Ungrazed	Very light	n = 8
	Unburn	DBerg	Ungrazed	Very light	n = 4
	Unburn	MBelt	Grazed	Light	n = 4
EN	Burn	DBerg	Grazed	Heavy	n = 3
	Burn	DBerg	Grazed	Moderate	n = 3
	Burn	MBelt	Grazed	Heavy	n = 4
	Burn	MBelt	Grazed	Moderate	n = 4
	Unburn	DBerg	Grazed	Heavy	n = 3
	Unburn	DBerg	Grazed	Moderate	n = 4
	Unburn	MBelt	Grazed	Heavy	n = 4
	Unburn	MBelt	Grazed	Moderate	n = 3

The PA was dissected by a tar road, with each of the two sections fenced separately. This allowed minimal movement of indigenous game between sections. There was a small herd (~ 12 individuals) of black wildebeest (*Connochaetes gnou*) and smaller game species (e.g. bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*) and southern reedbuck (*Redunca arundinum*)) in the lower-lying Midlands Mistbelt Grassland section of the PA, but black wildebeest was absent from the higher-lying Drakensberg Foothill Moist Grassland section of the PA. The different sections of the PA were consequently classified as burned or unburned, and grazed by black wildebeest (from here onwards referred to as 'grazed') or not grazed by black wildebeest (from here onwards referred to as 'ungrazed').

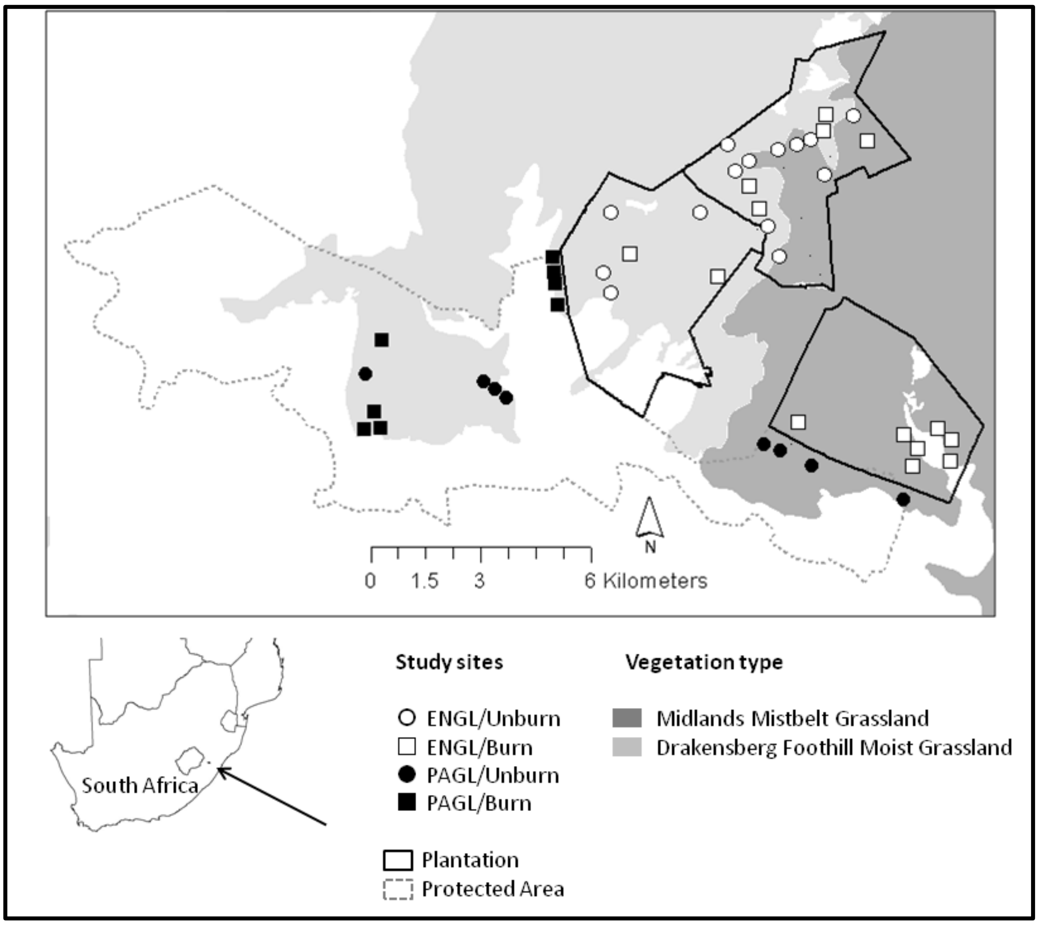

Figure 4.1 Location of sites across the landscape. Sites were in iMpendle Nature Reserve, a protected area (PA), and in an adjacent ecological network (EN) linking natural habitat of three plantations in the KwaZulu-Natal Midlands of South Africa. In the PA, there were eight grassland (GL) sites burned <12 months prior to sampling (burned) and eight sites that were burned >12 months prior to sampling (unburned). In the EN, there were seven burned, moderately-grazed sites; seven burned, heavily-grazed sites; seven unburned, moderately-grazed sites and seven unburned, heavily-grazed sites. All sites were located in either Drakensberg Foothill Moist Grassland or Midlands Mistbelt Grassland (Mucina *et al.* 2005).

Sites were positioned ~400 m apart in the interior of the PA, and > 30 m from the forestry compartment edge in the interior zone of wider (> 150 m) grassland corridors in the EN. At each site, vegetation sampling involved identifying species and quantifying the cover of each plant species in 24 randomly-spaced vegetation quadrats (1 m^2) in a 1000 $\mathbf{m^2}$ area. The vegetation sampling method was that of O'Connor *et al.* (2004). Graminoid plant species (grasses and sedges) were collected and non-graminoid plant species were photographed for identification (Gibbs-Russell *et al.* 1990; Pooley 2003; Pooley 2005; van Oudtshoorn 2006). I pooled abundances of all plant species gathered at each site, and then calculated the mean abundance of each plant species by dividing the total abundance of each plant species by twenty-four, as this was the number of vegetation quadrats per site.

I conducted comparisons of plant species richness, composition and turnover to determine how burning, the presence of large grazers, and the intensity of grazing influences grassland plant communities. To this end, I compared burned with unburned grassland, first in the presence (EN) and then in the absence of large grazers (PA). Then, I compared grazed (EN) with ungrazed (PA) grassland, first for burned and then for unburned areas to determine how time since last fire influences the effect of grazing on plant communities. Lastly, I compared moderately with heavily-grazed grassland in the EN, and then also moderately and heavily-grazed grassland with grassland in the PA, which served as the reference condition for grassland in this region. In addition, plant species composition of the two vegetation types (Midlands Mistbelt Grassland and Drakensberg Foothill Moist Grassland) were compared for each of these classes, as similarities in species composition between vegetation types is indicative of simplification of plant communities as a result of factors inherent to that class.

I used SAS 5.1 software to compare total species richness (with normal distribution) using a Generalized Linear Model (GLM) with an identity function. For each comparison, I included the remaining factors (Table 4.2), as well as vegetation type as grouping variables in the model. By alternating the grouping variables, I used Least Square Means post-hoc test to determine which comparisons yielded significant differences i.e. which disturbances had a significant effect on total species richness.

Plant species composition was compared using PRIMER 6.0 software. Plant species abundance data were square root transformed to reduce the effect of dominant plant species (PRIMER-E 2008). After constructing a Bray-Curtis resemblance matrix, I used permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) with 9999 unrestricted permutations of raw data to determine which variables affected species composition.

Species turnover (i.e. the extent of change within a class) was calculated for the EN and PA, burned and unburned grassland, and moderately and heavily-grazed grassland. Species turnover is the "extent of change in the identity, relative abundance, biomass and/or cover of individual species from one sampling unit to another along a spatial, temporal or environmental gradient" (Vellend 2001; Anderson *et al.* 2011). Using PRIMER 6.0 software, standardized species abundance data were transformed to presence/absence data from which a Bray-Curtis similarity matrix was created. I used permutational multivariate analysis of dispersion (PERMDISP) with 9999 permutations to determine which factors affected the dispersion of data, which is a measure of species turnover within a group of sites. It involved measuring distance from site to centroid (defined as the geographical centre for a group of sites) in a multivariate space, and then comparing mean distances of different groups using ANOVA (Anderson 2006) to determine which variables had an effect on the species turnover of plant communities.

Results

Vegetation type

Comparisons of plant species richness between the two vegetation types were only significant for unburned grassland in the PA and moderately-grazed grassland in the EN. Plant species richness of unburned Midlands Mistbelt Grassland (mean ± standard error: 71.50 ± 3.80 spp.) was significantly greater than in unburned Drakensberg Foothill Moist Grassland (48.0 ± 1.68 spp.) in the PA (Table 4.3), while plant species richness of moderately-grazed Drakensberg Foothill Moist Grassland (88.13 ± 3.82 spp.) was significantly greater than in moderately-grazed Midlands Mistbelt Grassland (79.89 ± 3.62 spp.) in the EN (Table 4.4).

Generally, plant communities of the two vegetation types differed significantly in terms of species composition, but not species turnover (Table 4.3). The exceptions were similarities in plant species composition between the two vegetation types in heavily-grazed grassland in the EN (Table 4.4), and significantly greater turnover in unburned Midlands

Mistbelt Grassland (28.49 ± 2.15 mean deviation from centroid (MDC)) than in unburned Drakensberg Foothill Moist Grassland (20.12 ± 0.96 MDC) in the PA (Table 4.3).

Ecological network vs. protected area: effect of large grazer presence

Overall, plant species richness, composition and turnover of grasslands in the EN were similar to that of the PA (Table 4.3). The exception was unburned Drakensberg Foothill Moist Grassland in the EN, which differed compositionally from the same vegetation type in the PA. Also for this vegetation type, plant species richness and turnover were significantly greater in the grazed EN (mean species richness ± standard error: 81.83 ± 4.92; species turnover ± standard error: 32.91 ± 1.59 mean deviation from centroid (MDC)) than in the ungrazed PA (species richness: 48.00 ± 1.68; species turnover: 20.12 ± 0.96 MDC) (Figure 4.2a-c; Table 4.3).

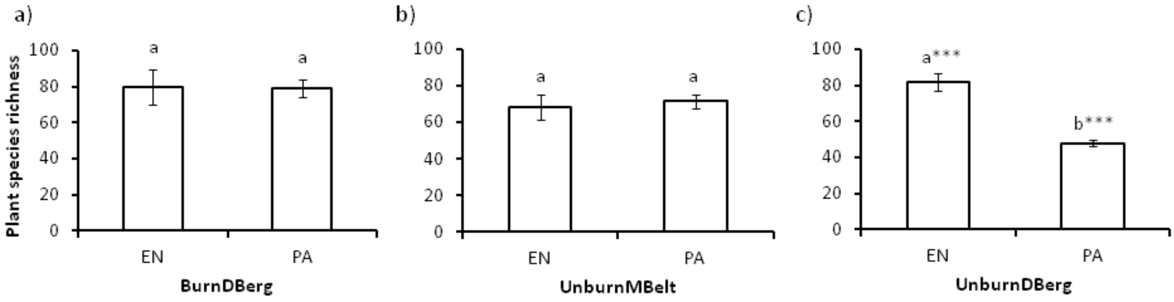

Figure 4.2 Mean plant species richness (± standard error) in grassland in the ecological network (EN) and protected area (PA) respectively. Burn = burned <12 months prior to sampling; Unburn = burned >12 months prior to sampling; DBerg = Drakensberg Foothill Moist Grassland and MBelt = Midlands Mistbelt Grassland. Different letters (a and b) indicate significant differences. Levels of significance * P < 0.05, ** P < 0.01 and *** P < 0.001.

Table 4.3 Total plant species richness (using Generalized Linear Models, GLM), plant species composition (using permutational multivariate analysis of variance, PERMANOVA) and plant species turnover (using permutational multivariate analysis of dispersion, PERMDISP) in grassland in the ecological network (EN) and protected area (PA) respectively. Burn = burned <12 months prior to sampling; Unburn = burned >12 months prior to sampling; DBerg = Drakensberg Foothilll Moist Grassland and MBelt = Midlands Mistbelt Grassland.

Constant factors	**Comparison**	**Richness Z-value**	**Richness p-value**	**Composition t-value**	**Composition p-value**	**Turnover t-value**	**Turnover p-value**

None	DBerg ↔ MBelt	0.00	0.998	2.27***	0.0001	2.25	0.053
PAUnburn	DBerg ↔ MBelt	-6.53***	<0.0001	2.01*	0.026	3.56*	0.029
ENUnburn	DBerg ↔ MBelt	1.67	0.094	1.38*	0.038	1.13	0.478
ENBurn	DBerg ↔ MBelt	-0.17	0.865	1.43**	0.004	0.75	0.557
None	EN ↔ PA	1.59	0.112	1.81***	0.0001	2.24	0.052
BurnDBerg	EN ↔ PA	0.08	0. 936	1.14	0.166	1.10	0.529
UnburnDBerg	EN ↔ PA	5.30***	< 0.0001	1.69**	0.004	6.01**	0.005
UnburnMBelt	EN ↔ PA	-0.35	0.723	1.38	0.080	1.88	0.180

Grazing intensity

Species richness of reference grassland in the PA (mean ± standard error: 69.31 ± 4.17 spp.) was similar to heavily-grazed grassland in the EN (71.75 ± 5.56 spp.), but significantly less than moderately-grazed grassland in the EN (82.57 ± 3.22 spp.) (Table 4.4). For burned plant communities, there were no significant differences in plant species richness between reference grassland in the PA, heavily-grazed grassland in the EN and moderately-grazed grassland in the EN (Figure 4.3a). In contrast, in unburned plant communities, moderately-grazed grassland in the EN (85.14 ± 3.94 spp.) had significantly greater plant species richness than heavily-grazed grassland in the EN (62.33 ± 5.56 spp.) and reference grassland in the PA (59.75 ± 13.69 spp.) (Figure 4.3d).

In unburned grassland, ~ 35% of plant species (103 spp.) occurred at all sites, irrespective of grazing intensity or whether sites were in the EN or PA. Unburned plant communities in the PA shared 37 species with moderately-grazed grassland, but only seven with heavily-grazed grassland in the EN. Moderately-grazed grassland shared 23 species with heavily-grazed grassland. Species that occurred in moderately-grazed grassland, but not in heavily-grazed areas, represented 29 plant families. Sixty-one percent of these lost species were perennial herbs (i.e. species with corms, rhizomes, bulbs or other underground storage organs). Also, 75% of lost species were singletons, and all of them were small in size (i.e. < 1% cover).

For Drakensberg Foothill Moist Grassland, plant species richness in burned reference grassland in the PA (mean ± standard error: 78.88 ± 4.98 spp.) was not significantly different from that of moderately-grazed, burned grassland in the EN (89.00 ± 9.87 spp.) or heavily-grazed, burned grassland in the EN (65.50 ± 17.50 spp.). However, plant species richness was significantly greater in moderately-grazed, burned than in heavily-grazed, burned grassland in the EN (Table 4.4; Figure 4.3b-c).

Unburned Drakensberg Foothill Moist Grassland in the EN when moderately-grazed had the most plant species (88.25 ± 8.62 spp.), followed by heavily-grazed grassland in the EN (69.0 ± 2.83 spp.) and ungrazed reference grassland in the PA (48.0 ± 3.37 spp.). All differences were highly significant for this vegetation type (Table 4.4; Figure 4.3e). For unburned Midlands Mistbelt Grassland, moderately-grazed grassland in the EN had the most plant species (81.0 ± 13.0 spp.), followed by grazed reference grassland in the PA (71.50 ± 7.59 spp.) and, lastly, heavily-grazed grassland in the EN (59.0 ± 16.19 spp.). For this vegetation type, the difference in plant species richness was only significant when comparing moderately with heavily-grazed grassland in the EN (Table 4.4; Figure 4.3f).

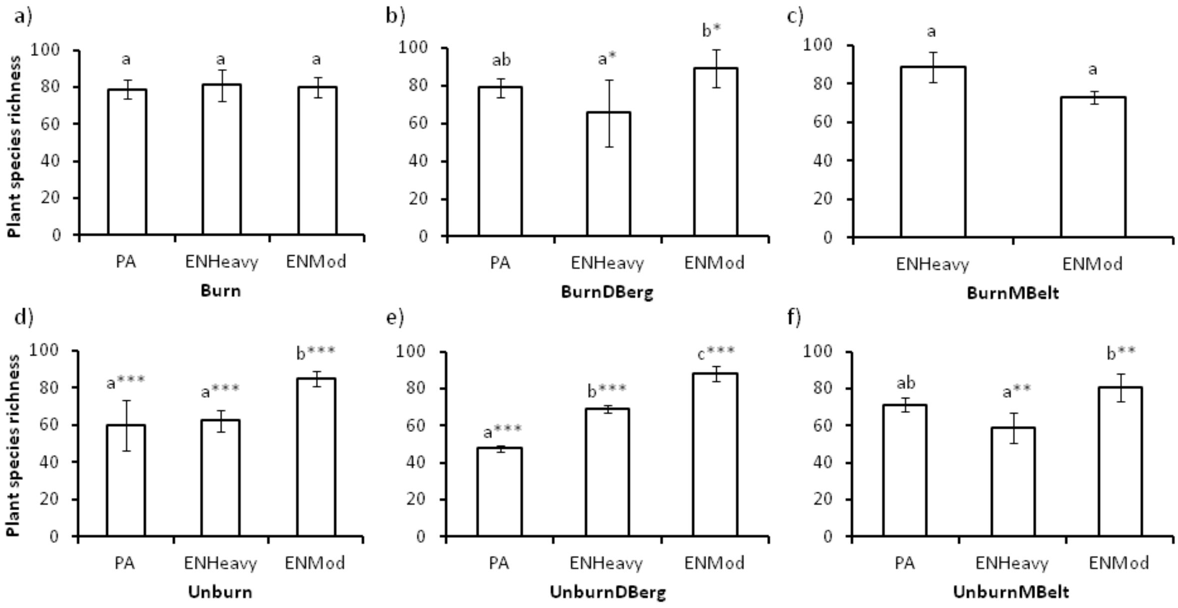

Figure 4.3 Mean plant species richness (± standard error) in reference sites in the protected area (PA), and moderately (Mod) and heavily-grazed (Heavy) grassland in the ecological network (EN). Burn = burned <12 months prior to sampling; Unburn = burned >12 months prior to sampling; DBerg = Drakensberg Foothill Moist Grassland and MBelt = Midlands Mistbelt Grassland. Different letters (a, b and c) indicate significant differences. Levels of significance are indicated as follow * P < 0.05; ** P < 0.01 and *** P < 0.001.

Plant species composition of grassland in the EN was not affected by grazing intensity. However, species composition of reference grassland in the PA differed significantly from moderately-grazed and heavily-grazed grassland in the EN (Table 4.4). This was the case for unburned Midlands Mistbelt Grassland and unburned Drakensberg Foothill Moist Grassland, but not for burned Drakensberg Foothill Moist Grassland. The exception was heavily-grazed, unburned Drakensberg Foothill Moist Grassland in the EN, which did not differ significantly from unburned reference grassland of the same vegetation type in the PA (Table 4).

Species turnover of reference grasslands in the PA (32.64 ± 1.29 mean deviation from centroid (MDC)) was similar to moderately-grazed grassland (34.34 ± 2.01 MDC), but significantly less than heavily-grazed grassland in the EN (40.99 ± 2.41 MDC). Furthermore, species turnover of burned reference grassland in the PA; heavily-grazed, burned grassland; and moderately-grazed, burned grassland in the EN were not significantly different (Table 4.4). For unburned grassland, species turnover of unburned, grazed reference grassland in the PA (28.49 ± 2.15 MDC) was less than that of heavily-grazed, unburned grassland (37.29 ± 2.60 MDC) for Midlands Mistbelt Grassland. In addition, species turnover of unburned, ungrazed reference grassland in the PA (20.12 ± 0.96 MDC) was less than that of moderately-grazed, unburned grassland (29.37 ± 1.12 MDC) for Drakensberg Foothill Moist Grassland (Table 4.4). In the Midlands Mistbelt Grassland section of the EN, species turnover of heavily-grazed, unburned grassland (37.29 ± 2.60 MDC) was significantly greater than that of moderately-grazed, unburned grassland (21.72 ± 2.52 MDC) (Table 4.4).

Table 4.4 Plant species richness (using Generalized Linear Models, GLM), plant species composition (using permutational multi-variate analysis of variance, PERMANOVA) and plant species turnover (using permutational multi-variate analysis of dispersion, PERMDISP) of grassland sites in the ecological network (EN) and protected area (PA) respectively. Heav = heavy grazing intensity; Mod = moderate grazing intensity; Burn = burned <12 months prior to sampling; Unburn = burned >12 months prior to sampling; DBerg = Drakensberg Foothilll Moist Grassland and MBelt = Midlands Mistbelt Grassland.

Constant factors	Comparison	Richness Z-value	Richness p-value	Composition t-value	Composition p-value	Turnover t-value	Turnover p-value
ENMod	DBerg ↔ MBelt	2.25*	0.025	1.549**	0.002	1.08	0.420
ENHeav	DBerg ↔ MBelt	-0.60	0.551	1.204	0.121	0.47	0.830
None	ENHeavy ↔ ENMod	-1.85	0.065	1.16	0.141	2.14	0.072
MBelt	ENMod ↔ ENHeav	-0.32	0.7491	1.20	0.119	1.40	0.296
BurnMBelt	ENMod ↔ ENHeav	1.50	0.133	0.97	0.607	1.41	0.398
UnburnMBelt	ENMod ↔ ENHeav	-2.64**	0.008	1.34	0.135	4.17*	0.030

DBerg	ENMod ↔ ENHeav	-2.49*	0.013	0.94	0.510	2.33	0.115
BurnDBerg	ENMod ↔ ENHeav	-2.22*	0.027	0.88	0.802	3.73	0.305
UnburnDBerg	ENMod ↔ ENHeav	-4.08***	< 00001	0.86	0.734	1.50	0.800
None	PA ↔ ENHeav	0.43	0.664	1.84***	0.0001	3.27**	0.005
BurnDBerg	PA ↔ ENHeav	-1.45	0.147	1.14	0.240	2.79	0.131
UnburnDBerg	PA ↔ ENHeav	4.83***	< 0.0001	1.47	0.065	8.15	0.068
UnburnMBelt	PA ↔ ENHeav	-1.61	0.107	1.60*	0.027	2.61	0.056
None	PA ↔ ENMod	2.45*	0.014	1.59**	0.001	0.73	0.526
BurnDBerg	PA ↔ ENMod	1.40	0.163	1.09	0.243	1.59	0.362
UnburnDBerg	PA ↔ ENMod	9.98***	< 0.0001	1.75*	0.029	6.26*	0.030
UnburnMBelt	PA ↔ ENMod	1.15	0.250	1.34*	0.027	2.05	0.228

Burned vs. unburned grassland

There were significant differences in plant species richness and composition between burned and unburned grassland, with greater species richness recorded in burned (mean ± standard error: 79.90 ± 3.32 spp.) than in unburned grassland (68.95 ± 3.67 spp.) (Table 4.5). In the ungrazed Drakensberg Foothill Moist Grassland section of the PA, there were significant differences in plant species richness, composition and turnover when comparing burned with unburned grassland. Here, plant species richness and turnover were greater in burned (mean species richness ± standard error: 78.88 ± 4.98; species turnover ± standard error: 26.22 ± 1.47 mean deviation from centroid (MDC)) than in unburned grassland (species richness: 48.00 ± 1.68 spp.; species turnover: 20.12 ± 0.96 MDC) (Table 4.5; Figure 4.4a-c). In the EN, plant species composition of burned and unburned grassland differed significantly for Midlands Mistbelt Grassland (Table 4.3). No other comparisons were significant.

Plant species richness and composition of unburned, grazed grassland in the EN were similar to burned, ungrazed grassland in the PA, but species turnover was significantly greater in grazed grassland in the EN (32.91 ± 1.59 MDC) than in burned grassland in the PA (26.22 ± 1.47 MDC) (Table 4.5).

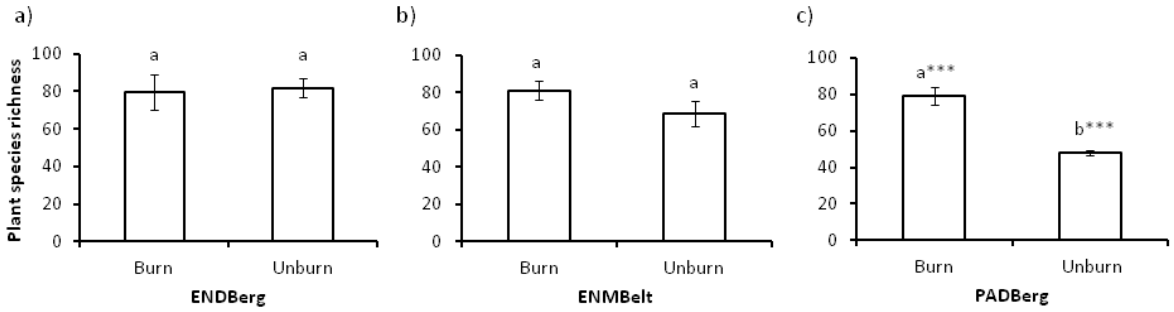

Figure 4.4 Mean plant species richness (± standard error) in sites burned < 12 months prior to sampling (Burn) and sites burned > 12 months prior to sampling (Unburn) in the ecological network (EN) and protected area (PA) respectively. Sites were either in Drakensberg Foothill Moist Grassland (DBerg) or Midlands Mistbelt Grassland (MBelt) (Mucina *et al.* 2005). Different letters (a and b) indicate significant differences. Levels of significance * P < 0.05, ** P < 0.01 and *** P < 0.001.

Table 4.5 Total plant species richness (using Generalized Linear Models, GLM), plant species composition (using permutational multi-variate analysis of variance, PERMANOVA) and plant species turnover (using permutational multi-variate analysis of dispersion, PERMDISP). I compared grassland burned <12 months ago (Burn) with grassland burned >12 months ago (Unburn). EN = ecological network; PA = protected area; DBerg = Drakensberg Foothilll Moist Grassland and MBelt = Midlands Mistbelt Grassland

Constant factors	Comparison	Richness Z-value	Richness p-value	Composition t-value	Composition p-value	Turnover t-value	Turnover p-value
None	Burn ↔ Unburn	2.25*	0.024	1.44**	0.004	0.85	0.465
PADBerg	Burn ↔ Unburn	4.02***	< 0.0001	1.80**	0.007	3.06*	0.013
ENDBerg	Burn ↔ Unburn	-0.24	0.810	0.94	0.530	0.33	0.818
ENMBelt	Burn ↔ Unburn	1.63	0.104	1.31*	0.039	0.54	0.666
DBerg	PABurn ↔ ENGrazed	0.42	0.678	1.27	0.0546	2.74*	0.036

Discussion

Disturbance caused by grazing and/or burning affected plant species richness, composition and turnover of plant communities in these grasslands, but plant communities responded to these disturbances in different ways. Overall, plant species turnover was more affected by grazing than by burning. Unburned, ungrazed grassland in the PA were the most homogeneous and had fewest species. When considered separately, burning and grazing both increased plant species richness and turnover, and changed species composition. Burned and unburned EN grasslands did not differ when both were grazed by cattle. Similarly, grazed (EN) and ungrazed (PA) grasslands did not differ when both were burned <12 months prior to sampling. It was only in unburned areas that presence of cattle grazing affected plant communities. Here, presence of cattle grazing in the EN resulted in higher species richness and turnover, and a change in plant species composition when compared to ungrazed reference grassland in the PA. An increase in grazing intensity in the EN from moderate to high resulted in higher turnover, lower species richness, but no change in species composition.

Burned vs. unburned grassland

In the case of burning in the absence of large grazers in the PA, plant species richness, composition and turnover of burned grassland (i.e. areas that were burned <12 months ago) differed from that of unburned grassland. Specifically, plant species richness and turnover was significantly greater in burned sites than in unburned ones. Greater species richness in burned, ungrazed grassland might be explained by removal of plant biomass (Grace 1999) and by fire-stimulated emergence of non-graminoid plant species (Hilliard & Burtt 1987). An experiment investigating the effect of burning on plant communities found that species richness declined as biomass accumulated, and that disturbances were necessary to maximize grass species richness in South African mesic grassland (Fynn *et al.* 2004). The opposite was true for lowlands of North American tallgrass prairie where plant species richness peaked ~ 6 years after last fire (Gibson & Hulbert 1987) and for biennially-burned South African grassland where plant species richness was greater in ungrazed, unburned areas than in burned, grazed areas (O'Connor *et al.* 2011). It appears that older (> 2 yrs), unburned grasslands in South Africa are naturally less species-rich and more homogeneous than younger, recently-burned grasslands, possibly because of competitive exclusion by dominant grass species.

In the presence of cattle in the EN, there were no differences in plant species richness or turnover between burned and unburned areas for either of the vegetation types. Plant species composition was also similar between burned and unburned sites for the one vegetation type. This implies that the presence of cattle in the EN affected temporal dynamics of grassland by delaying the change in plant communities i.e. by not allowing certain plants to dominate these systems.

In the EN, there was a significant difference in plant species composition when comparing steep, burned slopes with flatter, unburned areas in Midlands Mistbelt Grassland.

Differences in topographic position was shown to influence plant species composition in temperate Australian grassland (McIntyre & Lavorel 1994), and plant species richness in tallgrass prairie (Gibson & Hulbert 1987; Collins & Calabrese 2012) as well as in South African savanna (Shackleton 2000). Differences in plant species richness and composition were due to differences between well-drained soils in higher lying areas and poorly-drained soils in lower-lying areas in Argentine grassland (Cingolani *et al.* 2003). The effect of topographic position can confound the effect of burning and grazing treatments on plant communities.

In this study, I did not find the expected difference in plant species composition when comparing higher elevation, mountainous Drakensberg Foothill Moist Grassland with lower elevation, hilly Midlands Mistbelt Grassland in heavily-grazed grassland in the EN. In tallgrass prairie, differences in plant assemblages between upland and lowland sites diminished when burned frequently (Gibson & Hulbert 1987). These findings indicate that different toposcapes support plant communities that differ in richness and/or composition, but that high grazing intensity can simplify grassland plant communities to the point where such differences are no longer visible.

Ecological network vs. protected area: the presence of a large grazer

Cattle grazing in the EN did not significantly affect burned grassland plant communities. Here, species richness, composition and turnover of ungrazed reference sites in the PA were similar to those of grazed (without considering grazing intensity) grassland in the EN. These results contrast with findings in tallgrass prairie, where grazed, burned areas had higher plant diversity than ungrazed, burned areas (Collins 1987). Furthermore, different grazing regimes did not affect plant species richness of recently-burned grassland in South African savanna (Koerner & Collins 2013). However, these results support others in South African grassland (Little *et al.* 2012) where burning, and not grazing, was the primary driver of diversity in grassland during the first year after fire.

Plant species turnover of unburned, grazed (without considering grazing intensity) grassland in the EN was greater than in burned, ungrazed grassland in the PA. Plant communities in grazed grassland also differed from burned grassland in tallgrass prairie (Spasojevic *et al.* 2010). Because burning and grazing influences the plant communities in different ways, they cannot substitute each other in maintaining dynamic grassland ecosystems.

When I compared unburned, grazed grassland in the EN (without considering grazing intensity) with unburned, ungrazed grassland in the PA, I found significant differences in species richness, composition and turnover. Species richness and turnover were greater in grazed grassland in the EN. There was also a positive relationship between species richness and turnover in the Serengeti grazed by indigenous nomadic ungulates (McNaughton 1983) and in tallgrass prairie (Collins 1992; Collins *et al*. 1998). Furthermore, these findings agree with results from tallgrass prairie in North America and savanna in South Africa, which both had more plant species (Hickman *et al.* 2004; Veen *et al.* 2008; Burns *et al.* 2009; Koerner & Collins 2013) and greater heterogeneity (Koerner & Collins 2013) in unburned, grazed than in unburned, ungrazed areas. Grazing also increased plant diversity in annually-burned tallgrass prairie (Collins *et al.* 1998). Two other studies in tallgrass prairie that pooled plant data from burned and unburned grassland found that bison grazing reduced (Collins & Smith 2006) and increased (Hartnett *et al.* 1996) spatial heterogeneity, respectively.

Unburned plant communities in the EN grazed by cattle were similar to unburned plant communities in the PA (grazed by black wildebeest) in terms of plant species richness, composition and turnover. In the southern Drakensberg region, differences in grazing regime caused compositional changes to plant communities without affecting plant species richness (O'Connor 2005). In tallgrass prairie, plant communities grazed by bison were 85% similar to those grazed by domestic cattle after 10 years of grazing (Towne *et al*. 2005). Although intact ungulate communities, ranging in size and feeding guild, is most desirable for driving diversity patterns in African grasslands (du Toit & Cumming 1999), cattle grazing simulated the effect of indigenous game on arthropod communities (Rivers-Moore & Samways 1996; Samways & Kreuzinger 2001). Here, I have shown that this might also be the case for plants. This implies that large grazers, irrespective of whether they are indigenous ungulate species or domestic cattle, influence plant communities in a similar manner, by creating, reinforcing or maintaining patchiness in the landscape. Greater species richness and heterogeneity of grazed sites were the result of microsites created by indigenous bison in North America (Hartnett *et al.* 1996). A later study found that grazing influenced species turnover of plant communities directly by reducing dominant grass cover and not indirectly by changing availability and variability of resources (Veen *et al.* 2008). Here, breaking up of the dense vegetation layer by large herbivores most likely contributed to changes seen in plant species richness and composition. Samways and Kreuzinger (2001) found the same for grasshoppers in South African savanna.

Effect of grazing intensity on plant communities

After separating EN grassland into those areas that were moderately and heavily-grazed, respectively, I found that grazing intensity generally did not affect burned plant communities. For burned grassland, plant species composition and turnover were similar between ungrazed reference grassland in the PA, moderately-grazed grassland in the EN, and heavily-grazed grassland in the EN. Plant species richness of burned reference grassland in the PA was intermediate to, but not significantly different from, that found in moderately-grazed, burned grassland or heavily-grazed, burned grassland in the EN. However, plant species richness of heavily-grazed, burned grassland was significantly less than in moderately-grazed, burned grassland in the EN.

Plant species richness in unburned Drakensberg Foothill Moist Grassland had a unimodal response to increasing grazing intensity i.e. it increased from ungrazed grassland in the PA to moderately-grazed grassland in the EN, and decreased from moderately-grazed grassland to heavily-grazed grassland in the EN. This response of species richness to grazing intensity can be explained by competitive exclusion of sub-dominant species in an environment where certain resources (e.g. light) are limited by the dominant plant species. These results contrast with those on the effect of disturbance intensity on plant species richness, which found that an increase in grazing intensity correlated with an increase in plant species richness in tallgrass prairie (Collins 1987; Hickman *et al.* 2004), mesic grassland in KwaZulu-Natal (Martindale 2007), as well as savanna in South Africa (Koerner & Collins 2013). High intensity grazing either had a positive or no effect on plant species richness in South African grassland, depending on topographic position (O'Connor *et al.* 2011). Differences in topographic position and soil nutrient status (Proulx & Mazumder 1998), sample size or spatial scale of investigation (Gross *et al.* 2000) might partly explain differences between this study and others.

Also for unburned areas, heavily-grazed grassland in the EN had significantly more plant species than ungrazed reference areas in the PA, but there was no difference in plant species richness when comparing heavily-grazed grassland in the EN with grazed reference areas in the PA. This contrasts with studies in the Eastern Cape (Rutherford & Powrie 2011) and Lowveld of South Africa (Shackleton 2000) where plant species richness in heavily-grazed communal grassland was higher than in an adjacent PA grazed by large indigenous grazers, primarily due to replacement with annual herb species.

As a whole, plant species composition of unburned grassland in the EN grazed by cattle (but without considering grazing intensity) was similar to unburned reference Midlands Mistbelt Grassland in the PA grazed by black wildebeest. However, after considering grazing intensity, species composition of grazed grassland in the PA differed significantly from that of heavily-grazed as well as moderately-grazed grassland in the EN. Grazing by black wildebeest was not a uniform disturbance, but was patchily dispersed throughout unburned grassland in the PA. Plant communities in the PA that were subjected to this patchy grazing pattern of black wildebeest were only represented by EN grasslands when plant data from heavily-grazed as well as moderately-grazed EN grasslands were pooled. It appears that high intensity grazing, when confined to small areas, can contribute to the overall conservation value of grassland ENs relative to the PA.

Management recommendation and conclusions

Burning and grazing are necessary for maintaining species-rich, temporally and spatially dynamic grassland ecosystems. In the absence of these disturbances (in the PA), plant species retreat underground where they stay until burning and/or grazing provides the necessary stimuli (e.g. flush of nutrients or light availability due to breaking up of the dominant grass layer) for them to reappear. A decline in species richness in unburned, ungrazed grassland is not indicative of local extinction. If it was, plant species richness, composition and turnover would not have recovered in response to burning. Although less rich in plant species, undisturbed grassland in the landscape should be valued and reserved for the conservation of species at higher trophic levels that are either intolerant to disturbance or dependent on a dense grass layer for reproduction (e.g. grassland birds).

However, the problem is, quite often, not the absence of disturbance, but rather too much disturbance. When comparing grassland in the EN (with cattle grazing) with grassland in the PA (with black wildebeest grazing), plant communities were similar. This indicates that cattle served as a substitute for indigenous game in driving diversity patterns in grassland plant communities. When comparing grassland in the EN (with cattle grazing) with grassland in the PA (without large mammal grazing), I found significant differences in unburned grassland. However, these differences were not permanent, as the EN and PA became similar when both areas were burned. It is recommended that cattle grazing at moderate intensities should be allowed in grassland ENs, as it contributes to temporal dynamics of grassland by causing changes to plant communities that can be reversed by burning.

In contrast, when I compared grassland grazed at different intensities in the EN, there were consistently and significantly less plant species in heavily-grazed grassland than in moderately-grazed grassland. This response in plant species richness to heavy grazing was observed in burned and unburned Drakensberg Foothill Moist Grassland, which indicates that changes could not, as in earlier cases, be erased or undone by burning and are, therefore, relatively permanent. This has important consequences for long-term conservation of grassland plant diversity in production landscapes. Therefore, I recommend that heavy grazing by domestic cattle should be prevented or, at least, confined to specific areas, as the alternative would jeopardize short and long-term biodiversity conservation potential of ENs in a commercially afforested landscape matrix.

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CHAPTER 5: Effect of burning and cattle grazing on grasshopper assemblages in an Afromontane grassland

Abstract

Grasshoppers constitute a significant proportion of invertebrate diversity in grasslands, with assemblage structure influenced by fire, grazing and weather. Little is known about how different disturbances influence grasshopper diversity in Afromontane grassland, and how these disturbances should be managed to maximize biodiversity conservation in remnant grassland patches and corridors (i.e. in ecological networks (ENs)) among commercial forestry compartments. Here I aim to determine how these remnant grasslands within a production landscape should be managed for grasshopper diversity. Sites were in an EN (n=34) with control sites in an adjacent protected area (PA; n=23). They represented the dominant disturbance regimes: annual vs. longer-rotation burning; <12 months vs. >12 months prior to last fire; and grazed by large mammals vs. ungrazed. The EN was grazed by domestic cattle, while the PA was either ungrazed or grazed by the indigenous black wildebeest (*Connochaetes gnou*). I also measured 14 environmental variables at each site. Generally, grasshopper assemblages did not respond to the effect of individual disturbance factors, but rather to the combination of different disturbances. Grasshopper species richness and abundance was highest in annually-burned and grazed firebreaks in the EN. Increasing time since last fire negatively affected grasshopper species richness and abundance, but only in the absence of large grazers (PA). Grasshopper species composition was significantly affected by fire frequency and large mammal grazing, but not by time since last fire. However, perennial forb species richness and moribund vegetation cover, which were indicative of time since last fire, significantly affected grasshopper species composition, suggesting that grasshoppers respond to changes in the plant community. Despite annual burning with cattle grazing being most beneficial for grasshopper diversity, this disturbance regime will most likely not benefit other taxa (e.g. grassland birds and beetles) that are sensitive to disturbance. Therefore, I recommend a less intense disturbance regime of extensive, rotational cattle grazing and longer (2-4 year) fire-return interval for grassland in the EN to provide for the needs of other species outside firebreaks.

Introduction

Grasshoppers (Caelifera: Acrididae and Tetrigidae) are intricately linked with grassland ecology, and affected by the three primary drivers of grassland ecosystem dynamics: weather, fire and grazing (Todd *et al.* 2002, Jonas & Joern 2007). As primary consumers, grasshoppers play a major role in nutrient cycling (Sinclair 1975, Gandar 1982, Detling 1988). Their distribution and, specifically, their occupancy of a site are intricately linked to the availability of oviposition sites, vegetation height and biomass and vegetation composition (i.e. preferred food plants) (Clarke 1948). These factors are all influenced by the management regime (Clarke 1948, Gardiner 2009). Different grasshopper species have very specific requirements for oviposition sites, with the most obvious difference between hygrophilous grasshoppers, which lay their eggs in the vegetation layer near the soil surface, and mesophilous grasshoppers, which lay their eggs in the top soil layer (Waloff 1950, Brown 1983). Grazing or burning may cause direct mortality of hygrophilous grasshopper eggs, but not of mesophilous grasshopper eggs (Waloff 1950). Microclimate in particular, is of great importance for grasshopper egg development and, later, nymph and adult activity, and is mostly influenced by a variation in vegetation height and abundance (Mulkern 1969, van Wingerden *et al.* 1991). Grasshoppers have an overall preference for short (100-200 mm), early-successional grassland (Gardiner *et al.* 2002, Fartmann *et al.* 2012). Yet, they use tall vegetation patches to escape from predators (Fowler *et al.* 1991, Bock *et al.* 1992) and, possibly from heat (Gardiner & Hassall 2009). Therefore, heterogeneity in vegetation structure is important for grasshoppers to perform all functions necessary to complete their life cycle.

Grasshoppers selectively feed on certain plant species, based on physical traits (e.g. moisture content, toughness and leaf texture) and chemical properties (Mulkern 1969, Bernays & Chapman 1970a, Bernays & Chapman 1970b, Bernays & Chapman 1977, Gardiner *et al.* 2002). Of the three herbivory grasshopper guilds (forb-feeders, grass-feeders and mixed-feeders), grass feeding grasshoppers are the most abundant in frequently burned grasslands (Jonas & Joern 2007) with abundance of forb and mixed-feeders increasing with increasing time since last fire (Evans 1988a, Evans 1988b). Grass feeding grasshopper species actively reject forbs, and carefully select preferred grass species from the vegetation layer (Bernays & Chapman 1970a). Indeed, there is a hierarchy of preferences for different grass species, with the tender leaves of *Agrostis hiemalis* preferred over the tougher leaves of *Sporobolus heterolepis* (Landa & Rabinowitz 1983) although changes in plant nutrient content might affect grasshopper host plant preferences (Jonas & Joern 2008, Joern *et al.*

2012). The exact properties affecting palatability for grasshoppers are not known, and differ from properties affecting palatability for livestock. For example, grasses (e.g. *Lolium perenne*) in improved pastures deemed ideal for livestock production are completely avoided by grasshoppers (Gardiner *et al.* 2002). Similarly, grasshoppers avoided *Brachiaria nigropedata* and *B. serrata* that were palatable to livestock, but ate *Eragrostis pallens* that were impalatable to livestock (Gandar 1982).

Grasshopper assemblages are indirectly influenced by burning and grazing via their effects on the plant community, particularly plant species richness and composition, tissue quality, total biomass and structural heterogeneity of vegetation (Joern & Laws 2013). However, the importance of different aspects of the plant community varies, with vegetation structure reported as more important for grasshopper assemblages in South African savanna and North American tallgrass prairie (Gandar 1982, Collins 2000), and plant species composition being more important in European calcareous grassland (Schaffers *et al.* 2008).

Grasshopper communities respond to plant successional trajectories (Chambers & Samways 1998, Fartmann *et al.* 2012), which might be the effect of fire and/or grazing. When considering specific disturbance regimes, time since last fire and bison grazing were important determinants of grasshopper species composition in North American tallgrass prairie (Jonas & Joern 2007). Bison grazing also had a positive effect on grasshopper species richness and abundance, which were positively correlated with an increase in structural heterogeneity of vegetation and plant species richness, and negatively correlated with an increase in vegetation height and biomass (Joern 2004, Joern 2005). Fire frequency however, did not have a consistent effect on grasshopper assemblages. In North American tallgrass prairie, grasshopper communities in annually-burned areas differed from those in areas with longer fire-return intervals in some cases (Collins 2000), but not in others (Joern 2005). Grasshopper species richness was higher in annually-burned grassland in South Africa (Chambers & Samways 1998).

Afromontane grassland is an ancient African vegetation type with high degrees of endemism (Bond & Parr 2010). Large portions of this vegetation type have been transformed into commercial forestry plantations of alien trees (mostly, *Pinus* spp., *Eucalyptus* spp. and *Acacia mearnsii*), which are detrimental to biodiversity (O'Connor & Kuyler 2009). Large-scale ecological networks (ENs) of mostly natural habitat (including Afromontane grassland) have been implemented among forestry compartments to mitigate the negative effect of this land use on biodiversity (Samways *et al.* 2010). These ENs cover approximately one third of each plantation, which amounts to 500 000 ha at the national level (Kirkman & Pott 2002). Grasshoppers are an important component of biodiversity in grassland ENs (Bazelet & Samways 2011a). However, apart from management guidelines to mimic natural disturbances (Samways 2007), and to maintain a mosaic of different successional stages (Bazelet & Samways 2011b), we know little about how these grasslands should be managed if we want to maintain the natural grasshopper assemblages.

The aim of this study is to further understand how these sensitive, selective grazers respond to different management regimes in fire dominated, grazed Afromontane grassland. I aim to determine how grasshopper assemblages respond to fire and grazing – individually, and through their combined effect. I hypothesize that fire frequency (annual burning vs. longer-rotation burning), time since last fire (< 12 months ago vs. > 12 months ago), and grazing by large mammals will affect grasshopper assemblages, with grasshoppers benefitting from some level of disturbance (Sheil & Burslem 2013, Fox 2013). Understanding the combined and interactive effects of fire and grazing on grasshopper assemblages will determine to what extent different management regimes will promote grasshopper diversity. This study will then shed light on resilience of grasshopper assemblages to fire, and will suggest which management practices can be used to conserve grasshopper diversity effectively within an African context.

Methods

The study was conducted in the wetter (~ 900 MAP), eastern parts of the Grassland Biome in the KwaZulu-Natal Midlands (29°40′ S; 29°55′ E), South Africa. The area has a temperate climate, characterized by a mean annual temperature of 15°C and mean annual precipitation is ~900 mm. Precipitation took the form of summer thunderstorms, winter cold fronts and mist. Frost was common in winter (Mucina *et al.* 2006). Altitude varies between 1168 m and 1573 m above sea level. The topography is hilly to mountainous, with river gorges of forest occurring within a larger grassland matrix (Mucina *et al.* 2006). This study was in the two most dominant grassland types in this region: Drakensberg Foothill Moist Grassland and Midlands Mistbelt Grassland (Mucina & Rutherford 2006). Whenever possible, sites were distributed equally between these two grassland types (Table 5.1).

Sites occurred in an ecological network (EN) of remnant natural habitat among commercial forestry compartments. Reference sites were in the adjacent iMpendle Nature

Reserve, a protected area (PA). There were 57 remnant grassland sites spaced out from north to south over 10 km and from east to west over 16 km (Figure 5.1). Sites were classified according to fire frequency, time since last fire and presence or absence of large (>100 kg) mammalian grazers (predominately domestic cattle or black wildebeest (*Connochaetes gnou*) (Table 5.1). Sites represented all fire and grazing regimes in the landscape. Some of the sites were burned during the 12 month period prior to sampling (burned), while others were burned >12 months prior to sampling (unburned). Annually-burned firebreaks were burned in autumn (April to May), while grasslands with longer (2-3 years) fire-return intervals were burned in winter (June to August). The main difference in management between the EN and PA was that domestic cattle belonging to local human communities were allowed to graze in the EN (grazed), but not in the PA. A small (~ 12 individuals) herd of black wildebeest grazed in the Midlands Mistbelt Grassland section, but not in the Drakensberg Foothill Moist Grassland section of the PA. The different sections of the PA were consequently classified as grazed (by black wildebeest) or ungrazed.

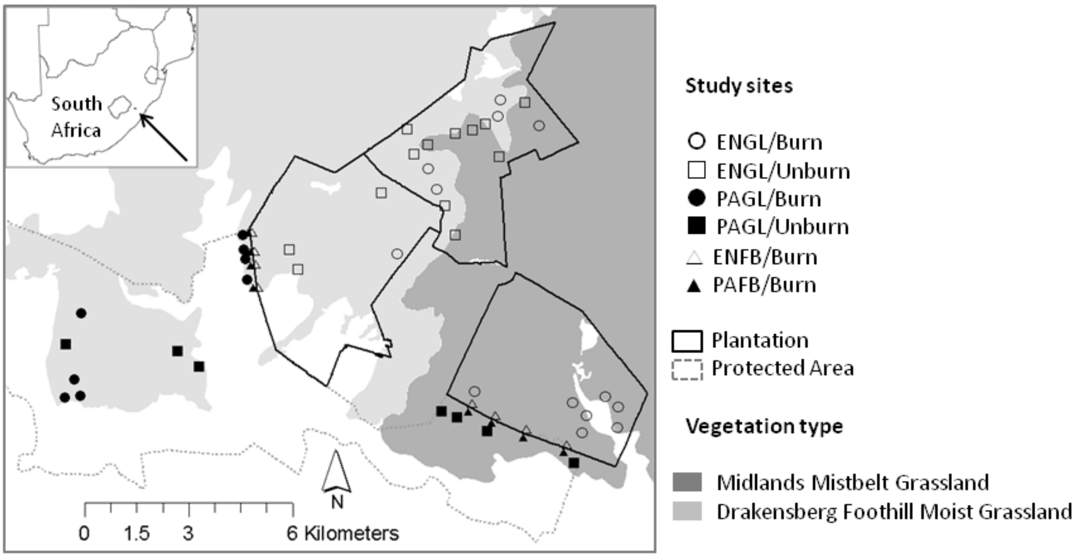

Figure 5.1 Study sites were in the KwaZulu-Natal Midlands in a grassland ecological network (EN) among forestry plantations. Reference sites were in the adjacent protected area (PA), iMpendle Nature Reserve. Burn = burned <12 months prior to sampling; Unburn = burned >12 months prior to sampling; FB = annually-burned firebreak; GL = grassland with longer fire-return intervals.

Table 5.1 Classification variables recorded for each site. EN = ecological network; PA = protected area; burned = burned <12 months prior to sampling; unburned = burned >12 months prior to sampling; grazed = grazed by large herbivores (domestic cattle in the EN and black wildebeest in the PA); ungrazed = not grazed by large herbivores; DBerg = Drakensberg Foothill Moist Grassland and MBelt = Midlands Mistbelt Grassland.

Class	EN/ PA	Vegetation type	Grazed by large herbivores	Burn/Unburn	Fire frequency and season	Sample size
1	PA	DBerg	Ungrazed	Burn	Annual, autumn	n = 4
2	PA	DBerg	Ungrazed	Burn	Longer-rotation, winter	n = 8
3	PA	DBerg	Ungrazed	Unburn	Longer-rotation, winter	n = 3
4	PA	MBelt	Grazed	Burn	Annual, autumn	n = 4
5	PA	MBelt	Grazed	Unburn	Longer-rotation, winter	n = 4
6	EN	DBerg	Grazed	Burn	Annual, autumn	n = 4
7	EN	DBerg	Grazed	Burn	Longer-rotation, winter	n = 5
8	EN	DBerg	Grazed	Unburn	Longer-rotation, winter	n = 6
9	EN	MBelt	Grazed	Burn	Annual, autumn	n = 4
10	EN	MBelt	Grazed	Burn	Longer-rotation, winter	n = 8
11	EN	MBelt	Grazed	Unburn	Longer-rotation, winter	n = 7

Sites (~1 000 m^2) were spaced 400 m apart to prevent pseudo-replication. Except for annually-burned firebreaks on either side of the plantation/PA fenceline, sites were in the interior of the PA and > 30 m from forestry compartment edges in the EN (Pryke & Samways 2012). At each site, grasshoppers were sampled three times: late-spring (November 2012), mid-summer (January 2013) and early-autumn (March 2013). I followed the standard procedure of sweep netting to sample grasshoppers, as it was a quick, inexpensive, frequently-used method of sampling grasshoppers at moderate to high densities in short grass (Gardiner *et al.* 2005). This entailed sweeping the net (diameter: 400 mm; mesh size: 2 mm) back and forth in a 180° arch with each step along four parallel transects (100 m) spaced 5 m apart (400 sweeps/survey; total: 1200 sweeps/site). Nets were emptied into a plastic bag after ~ 25 sweeps to prevent agile specimens from escaping. Grasshopper samples were frozen, sorted and identified to the lowest possible taxonomic level by Dr C. Bazelet (Dirsh 1965, Johnsen 1984, Johnsen 1991, Eades *et al.* 2009). In addition, I recorded altitude and aspect for each site, as well as certain environmental variables in 24 randomly-positioned vegetation quadrats (1 m^2) and along six randomly-positioned transects (30 m) to account for vegetation structure at each site (Table 5.2). Plant species were identified and grouped into growth forms (Gibbs-Russell *et al.* 1990, Pooley 2003, Pooley 2005, Van Oudtshoorn 2006).

Table 5.2 Continuous environmental variables recorded at each site.

Environmental variable	**Transect/ quadrat**	**No of measurements/sites**
Altitude (m.a.s.l)	Site	1
Rock cover (%)	Quadrats	24
Bare ground (%)	Quadrats	24
Vegetation cover (%)	Quadrats	24
Moribund vegetation cover (%)	Quadrats	24
Shrub/tree cover (%)	Quadrats	24
Perennial forb cover (%)	Quadrats	24
Annual forb cover (%)	Quadrats	24
Grass cover (%)	Quadrats	24
Total plant species richness	Quadrats	24
Perennial forb species richness	Quadrats	24
Annual forb species richness	Quadrats	24
Grass species richness	Quadrats	24
Vegetation height (cm)	Transect	180

Grasshopper data from the three surveys (late-spring, middle-summer and early-autumn) were pooled, and entered into a data matrix with species in rows and sites in columns (Ludwig & Reynolds 1988). Disturbance classes (Table 5.1) and environmental variables (Table 5.2) were entered beneath species data for each site (Ludwig & Reynolds 1988). To determine which disturbances significantly affected grasshopper species richness and abundance, I conducted comparisons of disturbance classes using Generalized Linear Models (GLM) (with Least-Square Means post-hoc test) in SAS Enterprise Guide 5.1 software (Stokes *et al.* 2000, Zuur *et al.* 2010). An identity-link function was selected for normally-distributed grasshopper species richness data and a log-link function was selected for grasshopper abundance data with a Poisson distribution. Vegetation type (Drakensberg Foothill Moist Grassland or Midlands Mistbelt Grassland) was added as grouping variables.

Effects of disturbance classes and environmental variables on grasshopper species composition were determined using CANOCO for Windows 4.5 software (Ter Braak & Smilauer 2002). I conducted a Canonical Correspondence Analyses (CCA), which is a constrained, direct, unimodal gradient analysis that determines which disturbance classes and environmental variables best explained variation in the species dataset. As the focus was on inter-sample distance, I selected the Hill's formula to scale scores on the ordination axes (Leps & Smilauer 2003). Species data were square-root transformed to reduce importance of abundant species. With automatic forward selection (9999 unrestricted permutations), Monte Carlo Tests were employed to identify variables with a significant effect on grasshopper species composition (Ter Braak & Smilauer 2002). I constructed a CCA graph of samples and only used significant variables in CanoDraw for Windows.

In addition, I created a Bray-Curtis similarity matrix from standardized, square-root transformed grasshopper species data in PRIMER 6.0 software (PRIMER-E 2008). To determine how grasshopper species composition responded to each disturbance type individually as well as to different combinations of fire frequency, time since last fire and grazing by large mammals, I conducted comparisons of different disturbance classes using Permutational Multi-variate Analysis of Variance (PERMANOVA) with 9999 unrestricted permutations of raw data (Anderson 2001).

Results

Grasshopper species richness and abundance

A total of 2 223 grasshopper individuals from 46 species were collected, which represented four families (Acrididae, Pyrgomorphidae, Tetrigidae and Tettigoniidae) and fourteen subfamilies. The three most common species (*Orthochtha dasycnemis nana* (relative abundance: 26.5%), *Tetrigid* sp.1 (19.1%) and *Coryphosima stenoptera stenoptera* (18.7%)) together constituted ~ 64% of all grasshoppers. Relative abundances of all other grasshopper species were < 5%.

Fire frequency, time since last fire, and presence (EN) or absence (PA) of domestic cattle influenced grasshopper species richness and abundance in Drakensberg Foothill Moist Grassland, but not in Midlands Mistbelt Grassland (Table 5.3). In Midlands Mistbelt Grassland, grasshopper species richness in unburned, grazed grassland in the PA was significantly less than in any of the other sites (Figure 5.2c-d; Table 5.3). In Drakensberg Foothill Moist Grassland, grasshopper species richness and abundance of annually-burned, grazed firebreaks in the EN were significantly greater than in any of the other sites (Figure 5.2a-b; Table 5.3). In addition, grasshopper species richness and abundance of unburned, ungrazed grassland in the PA was significantly less than that of burned, ungrazed grassland in the PA (Figure 5.2a-b; Table 5.3). When comparing different vegetation types with each other, grasshopper species richness and abundance was significantly greater in Drakensberg Foothill Moist Grassland than in Midlands Mistbelt Grassland for annually-burned, grazed firebreaks in the EN and for unburned grassland in the PA (Table 5.3).

Table 5.3 Comparisons of grasshopper species richness, grasshopper abundance (using Generalized Linear Models) and grasshopper species composition (using permutational multi-variate analysis of variance). EN = ecological network; PA = protected area; FB = annually-burned firebreaks; GL = grassland with longer fire-return intervals; burned = burned <12 months prior to sampling; unburn = burned >12 months prior to sampling; graz = grazed by large mammals (domestic cattle or black wildebeest); ungraz = not grazed by large mammals. Levels of significance: *P<0.05, **P<0.01 and ***P<0.001.

Constant factors	**Comparison**	**Grasshopper abundance Z-value**	**Grasshoper richness Z-value**	**Grasshopper composition t-value**
EFFECT OF VEGETATION TYPE				
PAGLUnburn	DBerg ↔ MBelt	4.61***	2.65**	1.40
PAFBBurn	DBerg ↔ MBelt	0.02	0.27	0.69
ENGLUnburn	DBerg ↔ MBelt	-1.21	-0.90	1.10
ENGLBurn	DBerg ↔ MBelt	-0.88	-1.00	1.21
ENFBBurn	DBerg ↔ MBelt	3.94***	2.11*	0.92
EFFECT OF ANNUAL BURNING				
PABurnDBerg	FB ↔ GL	-1.15	-1.14	1.27
ENBurnDBerg	FB ↔ GL	3.95***	3.48***	1.27*
ENBurnMBelt	FB ↔ GL	-1.09	0.08	0.96
EFFECT OF CATTLE GRAZING				
GLUnburnDBerg	EN ↔ PA	0.37	0.20	1.11
GLUnburnMBelt	EN ↔ PA	1.74	2.86**	0.96
GLBurnDBerg	EN ↔ PA	-1.35	-1.37	1.29
FBBurnDBerg	EN ↔ PA	3.66***	3.18**	1.13
FBBurnMBelt	EN ↔ PA	-0.21	1.01	1.02
EFFECT OF TIME SINCE LAST FIRE				
PAGLDBerg	Burn ↔ Unburn	2.18*	2.08*	1.23
ENGLDBerg	Burn ↔ Unburn	0.73	0.80	0.80
ENGLMBelt	Burn ↔ Unburn	0.29	0.77	0.998
EFFECT OF TIME SINCE LAST FIRE + GRAZING				
DBerg: PAGLUnburnUngrazed ↔ ENGLBurnGrazed		0.97	0.86	1.01
EFFECT OF ANNUAL BURNING + GRAZING				
DBerg: PAGLBurnUngrazed ↔ ENFBBurnGrazed		3.07**	2.54**	1.93**

EFFECT OF ANNUAL BURNING + TIME SINCE LAST FIRE (ALL UNGRAZED)			
DBerg: PAGLUnburnUngrazed ↔ PAFBBurnUngrazed	1.01	0.93	1.23
EFFECT OF ANNUAL BURNING + TIME SINCE LAST FIRE (ALL GRAZED)			
MBelt: PAGLUnburnGrazed ↔ PAFBBurnGrazed	1.03	2.16*	1.61*
MBelt: ENGLUnburnGrazed ↔ ENFBBurnGrazed	-0.82	0.72	1.18
DBerg: ENGLUnburnGrazed ↔ ENFBBurnGrazed	4.79***	4.37***	1.45*
EFFECT OF ANNUAL BURNING + TIME SINCE LAST FIRE + GRAZING			
DBerg: PAGLUnburnUngrazed ↔ ENFBBurnGrazed	4.40***	3.88***	1.98*

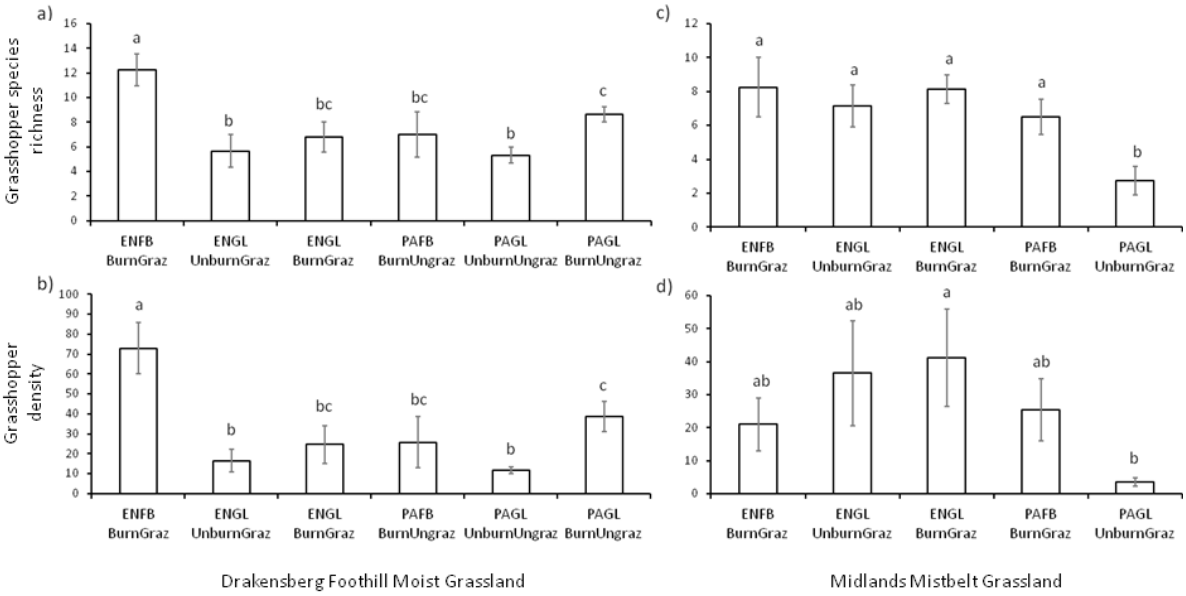

Figure 5.2 Mean grasshopper species richness and abundance (±standard error) in the ecological network (EN) and protected area (PA). Results are displayed separately for Drakensberg Foothill Moist Grassland (a and b) and Midlands Mistbelt Grassland (c and d). FB = annually-burned firebreaks; GL = grassland with longer fire-return intervals; burn = burned <12 months prior to sampling; unburn = burned >12 months prior to sampling; graz = grazed by large mammals (domestic cattle or black wildebeest); ungraz = not grazed by large mammals.

Overall explanation of grasshopper species composition

Grasshopper species composition was significantly influenced by vegetation type, two disturbance types (fire frequency and grazing by large mammals) and three plant community variables (moribund vegetation cover, perennial forb species richness, and shrub cover)

(Figure 5.3; Table 5.4). The first two primary ordination axes (annual burning and large mammal grazing) collectively explained 27.4% of the variation in the dataset.

Table 5.4 Summary of forward selection results (Monte-Carlo tests) in a Canonical Correspondence Analysis of the effect of disturbances and environmental variables on grasshopper species composition. EN = ecological network; PA = protected area; burned = burned <12 months prior to sampling; unburned = burned >12 months prior to sampling; grazed = grazed by large herbivores (domestic cattle in the EN and black wildebeest in the PA); ungrazed = not grazed by large herbivores; DBerg = Drakensberg Foothill Moist Grassland; MBelt = Midlands Mistbelt Grassland

Variables	**F-value**	**P-value**
Categorical data		
Annual vs. longer-rotation burning	1.46*	0.02
Burned vs. Unburned	0.75	0.807
EN vs. PA	1.23	0.202
Grazed vs. Ungrazed	2.06***	<0.001
Vegetation type: DBerg vs. MBelt	1.49*	0.022
Continuous data		
Altitude	0.54	0.944
Bare ground (%)	0.7	0.865
Rock cover (%)	1.17	0.244
Vegetation height (cm)	1.19	0.207
Vegetation cover (%)	1.44	0.077
Grass cover (%)	0.64	0.906
Annual forb cover (%)	1.83	0.098
Perennial forb cover (%)	1.04	0.415
Moribund vegetation cover (%)	3.42*	0.012
Total plant species richness	1.12	0.293
Grass species richness	1.02	0.434
Annual forb species richness	0.68	0.864
Perennial forb species richness	1.41*	0.045
Shrub/tree cover (%)	2.3**	0.003

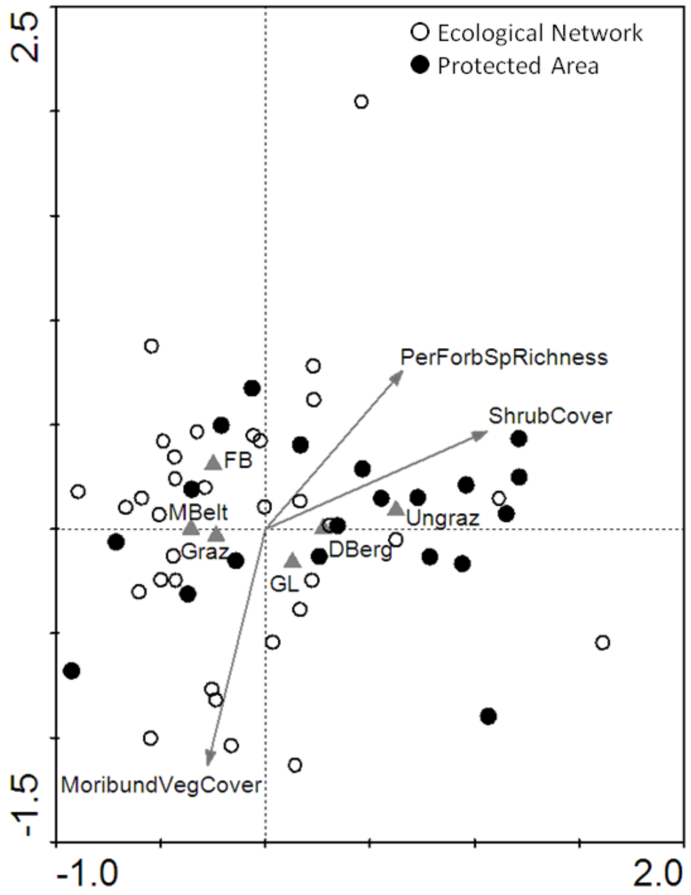

Figure 5.3 Canonical Correspondence Analysis of sites (excluding outliers) and the variables that significantly contributed to an explanation of variation in the grasshopper species dataset. The two primary ordination axes collectively explained 27.4% of variation in species data. FB = annually-burned firebreaks; GL = grassland with longer fire-return intervls; graz = grazed by large mammals (domestic cattle or black wildebeest); ungraz = not grazed by large mammals; DBerg = Drakensberg Foothill Moist Grassland; MBelt = Midlands Mistbelt Grassland.

Effects of variables on grasshopper species composition

When each disturbance variable was considered individually, they did not have significant effects on grasshopper species composition. This was the case for both vegetation types in the EN and PA (Table 5.3). The exception was Drakensberg Foothill Moist Grassland in the EN where grasshopper composition of annually-burned, grazed firebreaks differed significantly from longer-rotation burned, grazed grassland (Table 5.3).

It appears that changes to grasshopper species composition was the result of the effect of a few disturbances acting in combination rather than the result of individual disturbances. Furthermore, different combinations of disturbances were more effective drivers of grasshopper assemblages than others. For example, the combined effect of grazing by large mammals and recent burning failed to cause any significant changes to grasshopper species composition in Drakensberg Foothill Moist Grassland (Table 5.3). However, the combined effect of grazing by large mammals and annual burning had a significant effect on the composition of grasshopper communities in the same vegetation type (Table 5.3). A comparison of annually-burned firebreaks with unburned grassland was necessary to determine the combined effect of annual burning and time since last fire on grasshopper assemblages. In the PA without large grazers, this combination did not have a significant effect i.e. grasshopper species composition of annually-burned, ungrazed firebreaks was similar to that of unburned, ungrazed grassland (Table 5.3). However, when confining the analysis to those areas *with* domestic cattle or black wildebeest, grasshopper species composition of annually-burned firebreaks differed from that of unburned grassland. The exception was Midlands Mistbelt Grassland in the EN, which failed to respond in this manner (Table 5.3). Lastly, the combined effect of fire frequency, time since last fire and grazing by large mammals on grasshopper species composition was significant, as annually-burned, grazed firebreaks in the EN was significantly different from unburned, ungrazed grassland in the PA (Table 5.3).

Comparing effects of different disturbances on grasshopper species composition

When I compared burned, ungrazed grassland in the PA with unburned, grazed grassland in the EN, I found that the effect of grazing by domestic cattle on grasshopper assemblages differed from the effect of burning (Abundance: GLM, Z=-2.24, P<0.05; Species richness: GLM, Z=-2.35, P<0.05; Species composition: PERMANOVA, t=1.72, P<0.01). In contrast, when I compared a burned, ungrazed firebreak in the PA with burned, grazed grassland in the EN, I found that the effect of annual burning was similar to the effect of grazing by domestic cattle (Abundance: GLM, Z=-0.09, P>0.05; Species richness: GLM, Z=-0.13, P>0.05; Species composition: PERMANOVA, t=1.04, P>0.05).

Discussion

Grasshopper assemblages in South African grasslands were remarkably resilient to changes in disturbance regime, with significant responses mostly documented at extremes on the disturbance continuum, for example, in annually-burned, grazed firebreaks in the EN, and in grassland with high moribund vegetation loads, indicative of an area that has not been burned for many years. Non-responsiveness of grasshopper assemblages partly indicates that they have co-adapted with large native mammals in frequently-burned ecosystems (Samways & Kreuzinger 2001). Similar scenarios were documented for tallgrass prairie, where grasshopper assemblages fluctuated within certain limits due to site-specific assemblage dynamics determined by, among others, weather conditions and topography (Evans 1988a, Jonas & Joern 2007).

Grasshopper species abundance, richness and composition

Overall, the total amount of grasshopper species recorded in this study (46 spp.) was comparable to that of another study in Afromontane grassland (48 spp.) (Crous *et al.* 2013). Grasshopper species composition was significantly affected by six variables: vegetation type, fire frequency, presence of large mammalian grazers, perennial forb species richness, moribund vegetation cover, and shrub cover. None of these variables had a significant individual effect on grasshopper species composition. However, grasshoppers responded to a combination of certain disturbances, most notably annual burning with large mammal grazing. Our findings support a recent observation that grassland arthropods generally respond to “fire-grazing interactions rather than the effect of either factor alone” (Joern & Laws 2013).

Effect of annual burning and large mammal grazing

Large mammal grazing (grazed vs. ungrazed) had a significant effect on grasshopper assemblages in annually-burned firebreaks, but not in burned or unburned grasslands with longer fire-return intervals. Conversely, grasshopper assemblages in firebreaks differed significantly from unburned grassland (annual vs. longer fire-return intervals) when both were grazed by large mammals, but not in the absence of large mammalian grazers.

The positive effect of large mammalian grazers on grasshopper assemblages is well established in literature, particularly for North American prairies (Quin & Walgenbach 1990, Milchunas *et al.* 1998, Joern 2004, Jonas & Joern 2007). However, studies investigating the effect of fire frequency on grasshoppers yielded inconsistent results. Annual burning had a significant effect on overall grasshopper species composition in some cases (Evans 1988b, Chambers & Samways 1998, Collins 2000), but other studies reported no such effects (Joern 2004, Uys & Hamer 2007, Jonas & Joern 2007). Different responses might be explained by differences in spatial scale of measurement or by the covariation between fire frequency and time since last fire, with most frequently-burned sites also most recently burned (Swengel, 2001). Alternatively, it might be explained by site-specific conditions that limited response of grasshopper communities to this disturbance (Evans 1988a). Here, in this study, changes in grasshopper assemblages were most pronounced when annual burning was combined with large mammal grazing.

The effect of annual burning with large mammal grazing was an increase in grasshopper species richness and abundance. In fact, grasshopper species richness and abundance in annually-burned, grazed firebreaks in the EN was significantly greater than in any of the other areas. Annual burning had a positive effect on grasshopper species richness and abundance in Afromontane grassland (Chambers & Samways 1998, Little *et al.* 2012), but it was equally likely to have a negative (Evans 1988b) or no effect in tallgrass prairie (Joern 2005, Jonas & Joern 2007). The importance of large mammal grazing for maintaining grasshopper diversity is seen in both regions (Samways & Kreuzinger 2001, Joern 2004, Joern 2005). However, few studies have looked at the interaction between annual burning and large mammal grazing on grasshopper species richness and abundance.

Following on from this, I found that grasshopper species richness and abundance was greater in the annually-burned, grazed firebreak on the EN side of the plantation/PA fenceline than in the annually-burned, ungrazed firebreak on the PA side. These differences might be due to movement of grasshoppers from one side of the fenceline to the other to make optimal use of variation in vegetation height and biomass (Joern 1982). Short, grazed firebreaks in the EN might offer warmth and suitable oviposition sites (van Wingerden *et al.* 1991, Gardiner *et al.* 2002), while tall, ungrazed firebreaks in the PA might present an opportunity to escape from avian predators and/or the heat (Bock *et al.* 1992, Gardiner & Hassall 2009). Grasshopper assemblages did not respond to patches of short and tall grass, created by indigenous ungulate grazers, in the Swiss Alps (Spalinger *et al.* 2012), but they did respond to patchiness in North Amerian tallgrass prairie (Engle *et al.* 2008).

Effect of time since last fire

Grasshopper species composition was not significantly affected by time since last fire (<12 months vs. >12 months). However, it was significantly affected by perennial forb species richness and moribund vegetation cover, which is indicative of time since last fire. Grasshopper species composition responded to time since last fire in South African grassland (Bazelet & Samways 2011c, Little *et al.* 2012) as well as tallgrass prairie (Jonas & Joern 2007). Here, I showed that grasshoppers' response was to a change in plant communities rather than time since last fire *per se*.

I found grasshopper species richness and abundance were significantly greater in burned than in unburned grassland within an ungrazed part of the PA. Increases in grasshopper abundance during the first year after fire is a common occurrence elsewhere (Nagel 1973, Hansen 1986, Swengel 2001). However, time since last fire did not have an effect on grasshopper communities in the EN where domestic cattle were present, which is consistent with findings in tall grass prairie (Engle *et al.* 2008). These results imply that the negative effect of increasing time since last fire on grasshopper species richness and abundance was nullified by the effect of large mammalian grazers, possibly by stimulating primary productivity (Frank & McNaughton 1993, Siemann 1998) and/or by reducing the accumulation rate of moribund plant biomass (O'Neill *et al.* 2003, Joern 2005). Indeed, extensive grazing was recommended as an optimal management strategy for steppe grassland in Central Europe, as grazers created an ideal habitat for grasshoppers with warm oviposition sites on bare ground, little litter accumulation, ample food, and shelter from predators (Fartmann *et al.* 2012).

Effect of plant communities and altitude

The two vegetation types, Drakensberg Foothill Moist Grassland and Midlands Mistbelt Grassland, occurred at different altitudes (Mucina *et al.* 2006), and harbored different plant communities (Chapter 3 and 4) and grasshopper assemblages. Although altitude did not affect grasshopper species composition in this study, grasshopper assemblages at higher altitudes in Drakensberg Foothill Moist Grassland were more likely to respond to changes in the disturbance regime than grasshopper assemblages at the lower altitudinal Midlands Mistbelt Grassland. Altitude was previously shown to affect plant and grasshopper assemblages (Crous *et al.* 2013) as well as dung beetles (Davis *et al.* 1999) in Afromontane grassland. Here, I propose that grasshoppers at higher altitudes were more likely to respond to changes in the disturbance regime due to greater fluctuations in microclimate (Crous *et al.* 2013). Alternatively, different grasshopper assemblages in the two vegetation types might be due to an interaction between altitude and plant community, as was the case for the beetles of this region (Foord *et al.* 2003).

Conclusion

This study contributes to a growing body of literature on the effect of disturbances on grassland arthropods. I have shown that grasshopper assemblages overall were resilient to most individual disturbance types. However, the combination of annual burning with large mammal grazing, which is a common management practice in firebreaks in the EN, drove changes in grasshopper species composition, and resulted in the greatest number of grasshopper individuals and species recorded in this study. Despite high grasshopper diversity in firebreaks in the EN, I do not recommend that this management practice of annual burning with cattle grazing should be employed throughout the EN, as other fire-intolerant taxa (e.g. grassland-breeding birds and some Coleoptera and Hemiptera species, as in Little *et al*. 2012) might not respond as favorably to this disturbance regime as grasshoppers.

It was previously recommended that grassland in ENs should be managed as a mosaic of different successional stages, with recently-disturbed patches interspersed among relatively undisturbed patches and vice versa (Bazelet & Samways 2011b). I agree with this, as this management approach will provide in the habitat requirements of biological assemblages with diverse needs. Therefore, I recommend that the rest of the EN should have longer (2-4 years) fire-return intervals with extensive and/or rotational cattle grazing to complement early-successional annually-burned, grazed firebreaks. In this way, firebreaks will represent heavily-disturbed habitat conducive for the survival of most grasshopper species, while the rest of the EN will provide in the needs of taxa with a lower tolerance for these intense disturbances.

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CHAPTER 6: Synthesis and General Conclusions

The detrimental effects of habitat transformation on local biodiversity may be mitigated by implementing large-scale ecological networks (ENs) of natural land within the commercial landscape. This has been done by the South African forestry industry where approximately one third of each plantation, amounting to 500 000 ha at the national level, was set aside for biodiversity conservation (Samways 2007, Samways *et al*. 2010). While management is crucial for the successful conservation of biodiversity (Bazelet & Samways 2011), little is known about how different disturbances should be managed to optimize biodiversity conservation in these ENs (Chapter 1). This study addressed this knowledge gap by considering the effects of three most common disturbance types in ENs (mowing, burning and grazing) on plant (primary producer) and grasshopper (small, sensitive herbivore group) diversity. Chapter 2 considered how *design and disturbances* influenced plant diversity in a subtropical grassland EN in the lower-lying northern Zululand region (Chapter 2), while the other three data chapters considered the effect of only *disturbances* on plant (Chapters 3 and 4) and grasshopper assemblages (Chapter 5) in an Afromontane grassland EN in the Midlands of KwaZulu-Natal.

Overall, frequently-mown firebreaks and small, isolated patches of subtropical grassland surrounded by a forestry plantation matrix supported fewer plant species than wide, interconnected corridors near the protected area (PA) border, which, in turn, were similar to reference sites in the PA. In Afromontane grassland, plants and grasshoppers benefited from some form of disturbance, as species richness for both taxonomic groups was lowest in unburned, ungrazed grassland. However, intense forms of disturbance (e.g. heavy cattle grazing) were detrimental to plant species richness.

Design

- In subtropical grassland, the combined effect of size and isolation is illustrated, with plant species lost from small, isolated patches (bordered by eucalypt compartments on >2 sides) in the EN that were far from the PA border. Plant communities in wide, interconnected corridors near the PA border were similar to reference sites in the PA. Design of ENs should prioritize implementation of wide, interconnected corridors, as such corridors have been shown to influence conservation of invertebrate as well as plant communities (Chapter 2, Pryke & Samways 2001).

- In Afromontane grassland, the plant community was not as sensitive as the invertebrate community to distance from forestry plantation edge *per se* (Chapter 3, Pryke & Samways 2012). This might be due to extinction debt and/or the role that disturbances (e.g. annual burning or invasive alien species) play in determining the size of the edge zone. If this is the case, proportion edge and core zone in a remnant patch might be altered by adapting the disturbance regime, which could have far-reaching consequences for biodiversity conservation in ENs.

Management in subtropical grassland

- Frequent mowing of narrow firebreaks (i.e. mowing monthly for six months during the growing season of each year) negatively affected plant species richness and changed plant species composition (Chapter 2). These findings are consistent with Fynn *et al.* (2004). Therefore, this management practice should be confined to demarcated areas, such as firebreaks and forestry compartment edges.
- Different types of disturbances shaped plant communities in different ways (Fynn *et al.* 2005), with plant species composition of frequently-mown firebreaks differing from grasslands that were periodically burned and grazed (Chapter 2).
- Outside of firebreaks, plant species turnover of more recently burned areas was greater (Chapter 2), which indicates that composition of plant communities in subtropical grassland simplify as they become older, probably through competition. Burning is necessary to maintain diverse, dynamic subtropical grassland in ENs.

Annual burning in Afromontane grassland

- Annual burning of firebreaks caused a shift in the composition of plant communities that went hand-in-hand with a non-significant decrease in plant species richness when compared to reference grassland in the EN and PA, respectively (Chapter 3). However, grasshopper species richness and abundance was greatest in grazed firebreaks in the EN (Chapter 5). Therefore, I recommend that the practice of annual burning of firebreaks should be included with the patch mosaic burning program, suggested for South African grassland (Uys *et al.* 2004, O'Connor *et al.* 2004). However, the practice of annual burning should be limited to firebreaks and not be implemented in the rest of the EN, as it could jeopardize long-term survival of species that are intolerant to intense or frequent disturbances.

- Plant communities in annually-burned EN firebreaks with light cattle grazing were identical to those in the PA with only annual burning. However, heavy cattle grazing in annually-burned EN firebreaks caused plant species loss and should be avoided.
- Grasshopper communities were not significantly influenced by annual burning, cattle grazing or time since last fire when these disturbances were considered individually (Chapter 5). However, when annual burning and cattle grazing were considered together, this resulted in significant changes in grasshopper composition, with the highest species richness and abundance within the ENs, which had annually-burned firebreaks and were lightly grazed by cattle. Specifically, grasshopper species richness and abundance in lightly-grazed EN firebreaks was greater than in annually-burned, ungrazed firebreaks on the opposite side of the plantation/PA fenceline. A previous study has shown that grasshoppers preferred warm, short grass (Gardiner *et al.* 2002). Here, grasshoppers probably moved from the warmer, grazed EN firebreaks through the fenceline to the taller, ungrazed grass of PA firebreaks to escape predators and/or heat. This highlights the importance of maintaining grassland patches of different height throughout the EN.

Time since last fire and grazing in Afromontane grassland

- Plant species richness as well as grasshopper species richness and abundance were lowest in undisturbed (unburned and ungrazed) grassland in the PA (Chapter 4 and 5), which indicates that both taxa benefit from some level of disturbance. Still, undisturbed areas are valuable, because they provide habitat for disturbance-sensitive taxa (Little *et al.* 2012).
- For plants, lower species richness in undisturbed grassland was attributed to competitive exclusion of light-sensitive species. Burning and grazing reduced the suppressive effect of accumulated plant biomass and stimulated the emergence of, particularly, non-graminoid plant species. This resulted in a change in plant species composition, which was marked by an increase in plant species richness and turnover (Chapter 4). It appears that disturbances are necessary for maintaining maximum plant

species richness in South African grassland (Fynn *et al.* 2004). Therefore, burning and grazing should continue to form part of grassland management in ENs.

- Grasshopper species composition was significantly influenced by moribund vegetation cover and perennial plant species richness, which were both correlated with time since last fire (Chapters 4 and 5). However, it was only in the absence of large mammalian grazers in the PA that grasshopper species composition in burned grassland was affected, and that species richness and abundance was greater than in unburned grassland. Time since last fire (burned vs. unburned grassland) in the grazed EN had no effect on grasshopper assemblages.
- Domestic cattle grazing accurately represented the effect of grazing by a large indigenous ungulate species (*Connochaetes gnou*), with unburned plant communities on either side of the plantation/PA fenceline similar in species richness, composition and turnover. However, heavy cattle grazing caused loss of plant species and a reduction in the resilience of grassland ENs. Furthermore, this intense disturbance eroded the uniqueness of the two vegetation types (Midlands Mistbelt Grassland and Drakensberg Foothill Moist Grassland), causing them to become more similar in composition (Chapter 4). Conservation of regional plant diversity depends on the spatial extent of these intense disturbances, and places a premium on effective control of cattle grazing in grassland ENs.

The combined effects of different disturbances

- Burning (burned vs. unburned) only affected plant communities in the absence of large grazers (PA), and presence of large grazers (EN vs. PA) only affected plant communities in unburned grassland (Chapter 4). In the EN, recently-burned, grazed grassland and unburned, grazed grassland hosted similar plant communities. Nevertheless, the effect of burning and grazing on plant communities are not identical, with grazing having a greater effect on plant species turnover. Therefore, burning and grazing should not replace one another in grassland management.
- There was a similar situation to this in the case of grasshoppers, where burned and unburned grassland supported different assemblages in the ungrazed PA, but similar assemblages in the grazed EN (Chapter 5). This suggests that the effect of burning was nullified by the effect of cattle grazing, which emphasizes the importance of a rotational grazing system in ENs so that there are always grazed and ungrazed sections

available to provide in the habitat requirements of taxa with different habitat requirements.

- Although they have similar effects on grasshopper assemblages, the combination of cattle grazing and annual burning resulted in significant changes in grasshopper species composition, and increases in grasshopper species richness and abundance (Chapter 5). This suggests that the additive/synergistic effect of these two disturbances can drive changes in grasshopper communities in Afromontane grassland.
- In addition to this, grasshopper communities in annually-burned firebreaks differed significantly from recently-burned, as well as unburned Drakensberg Foothill Moist Grassland, but only when sites were grazed by cattle. In the ungrazed PA, these areas supported similar grasshopper communities, irrespective of fire frequency or time since last fire (Chapter 5). This suggests that cattle (or other large grazers) are the drivers of change in grasshopper assemblages in Afromontane grassland.

Vegetation mapping

- In subtropical grassland in the lower-lying areas of KwaZulu-Natal, a change in vegetation structure (i.e. percentage shrub/tree cover) coincided with a change in plant species composition without affecting plant species richness or turnover (Chapter 2). This is useful to know when mapping vegetation in new areas.
- In Afromontane grassland in the Midlands, the national vegetation map for South Africa, Lesotho and Swaziland identified Midlands Mistbelt Grassland and Drakensberg Foothill Moist Grassland as two separate vegetation types (Mucina & Rutherford 2006). Generally, these two vegetation types were similar in terms of plant species richness and turnover, but differed in composition (Chapters 3 and 4).

Diversity measurements

- Plant species composition is more reliable than species richness when measuring the effect of burning or mowing on plant communities (Chapters 2 and 3). However, plant species richness was better than species composition in measuring the effect of disturbance intensity (e.g. heavy grazing) or the effect of patch size and isolation (Chapters 2 and 4).

Generalizations

- It would not be wise to extrapolate the findings here to other regions without ground-truthing them. However, even in this one study, we found that plant communities in Midlands Mistbelt Grassland were more sensitive to the effects of annual burning and cattle grazing than Drakensberg Foothill Moist Grassland (Chapters 3 and 4), while grasshopper assemblages in Drakensberg Foothill Moist Grassland were more likely to respond significantly to different disturbance regimes (Chapter 5). Response might be linked to abiotic variables (e.g. soil, or temperature fluctuations), which influenced plants and grasshoppers via their effect on primary productivity and biomass accumulation. If it can be determined which abiotic variables affected the responsiveness of these communities to different disturbances (Joern & Laws 2013), it might be possible to adjust management practices to lessen the effect of, for example, predicted fluctuations in rainfall or temperature. Such a highly advanced management system might be necessary in the face of global climate change.
- Although Afromontane grassland and tallgrass prairie are both fire-driven ecosystems, their response to fire differs (Koerner & Collins 2013). For example, annual burning had no effect on Afromontane grassland (Chapter 3), but it has a negative effect on tallgrass prairie. Also, plant species richness was greatest during the first two years after fire in Afromontane grassland, but it peaked only after 6 years in tallgrass prairie. However, large mammal grazing positively affected plant and grasshopper diversity in both Afromontane grassland and tallgrass prairie.

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Appendix A

Location of sampling sites at SiyaQhubeka Forests (Ltd.) and iSimangaliso Wetland Park, KwaZulu-Natal, South Africa. EucSides = Number of sides shared with eucalypt compartments; DistPA = Distance from simplified PA border (m); CorWidth = Corridor width

Site	South	East	EN/ PA	FB/ OpenBiotope	Remnant/ Recovering	EucSides	DistPA	CorWidth
1	32.3976791	-28.1649818	EN	Firebreak	Firebreak	2	568	53
2	32.4010527	-28.1794127	EN	Firebreak	Firebreak	2	774	40
3	32.3525673	-28.2859818	EN	Firebreak	Firebreak	2	1634	38
4	32.3945483	-28.2025992	EN	Firebreak	Firebreak	2	144	47
5	32.3378073	-28.2657645	EN	Firebreak	Firebreak	2	3146	38
6	32.3610158	-28.2732000	EN	Firebreak	Firebreak	2	747	19
7	32.3680042	-28.2233508	EN	Firebreak	Firebreak	2	2117	80
8	32.3606718	-28.2901118	EN	Open biotope	Restore	2	962	1023
9	32.2923258	-28.3364892	EN	Open biotope	Restore	4	2342	102
10	32.2924159	-28.3325894	EN	Open biotope	Restore	4	2725	151
11	32.3095462	-28.3252400	EN	Open biotope	Restore	3	3759	78
12	32.3433218	-28.3300791	EN	Open biotope	Restore	3	634	464
13	32.3615000	-28.2297868	EN	Open biotope	Remnant	4	2539	432
14	32.3290800	-28.3504250	EN	Open biotope	Remnant	3	403	137
15	32.3371973	-28.3369509	EN	Open biotope	Restore	2	1380	432
16	32.3268225	-28.3468717	EN	Open biotope	Restore	2	711	228
17	32.3882242	-28.2074133	EN	Open biotope	Remnant	3	1131	105
18	32.3959569	-28.1769815	EN	Open biotope	Remnant	2	1180	151
19	32.3973361	-28.1718506	EN	Open biotope	Remnant	2	1502	201
20	32.3409450	-28.3449650	EN	Open biotope	Restore	3	737	103
21	32.2503908	-28.3587483	EN	Open biotope	Remnant	3	1905	196
22	32.3592417	-28.3296217	PA	Open biotope	Restore	1	0	0
23	32.4015618	-28.2378064	PA	Open biotope	Remnant	0	0	0
24	32.3365118	-28.3582355	PA	Open biotope	Restore	1	0	0
25	32.3903155	-28.2306409	PA	Open biotope	Restore	1	0	0
26	32.3726091	-28.2865682	PA	Open biotope	Restore	1	0	0

Appendix B

Location of sampling sites in Good Hope, Mount Shannon and iMpendle Nature Reserve in the KwaZulu-Natal Midlands, South Africa.

	South	**East**	**EN/ PA**	**Firebreak/ Grassland**	**National Vegetation Map**
1	29.677600	29.904140	EN	FB/Peripheral	Drakensberg Foothill Moist Grassland
2	29.681000	29.904870	EN	FB/Peripheral	Drakensberg Foothill Moist Grassland
3	29.672360	29.903040	EN	FB/Peripheral	Drakensberg Foothill Moist Grassland
4	29.686890	29.906210	EN	FB/Peripheral	Drakensberg Foothill Moist Grassland
5	29.725310	30.000360	EN	FB/Peripheral	Midlands Mistbelt Grassland
6	29.721890	29.988290	EN	FB/Peripheral	Midlands Mistbelt Grassland
7	29.718620	29.978690	EN	FB/Peripheral	Midlands Mistbelt Grassland
8	29.715660	29.971340	EN	FB/Peripheral	Midlands Mistbelt Grassland
9	29.645890	29.978350	EN	FB/Plantation	Drakensberg Foothill Moist Grassland
10	29.664510	29.958440	EN	FB/Plantation	Drakensberg Foothill Moist Grassland
11	29.653940	29.940280	EN	FB/Plantation	Drakensberg Foothill Moist Grassland
12	29.657850	29.946620	EN	FB/Plantation	Drakensberg Foothill Moist Grassland
13	29.649320	29.965140	EN	FB/Plantation	Midlands Mistbelt Grassland
14	29.661460	29.970660	EN	FB/Plantation	Midlands Mistbelt Grassland
15	29.670480	29.973850	EN	FB/Plantation	Midlands Mistbelt Grassland
16	29.674960	29.976940	EN	FB/Plantation	Midlands Mistbelt Grassland
17	29.640040	29.975780	EN	Grassland	Drakensberg Foothill Moist Grassland
18	29.672000	29.922540	EN	Grassland	Drakensberg Foothill Moist Grassland
19	29.676730	29.947590	EN	Grassland	Drakensberg Foothill Moist Grassland
20	29.650760	29.951530	EN	Grassland	Drakensberg Foothill Moist Grassland
21	29.661990	29.916900	EN	Grassland	Drakensberg Foothill Moist Grassland
22	29.676800	29.915360	EN	Grassland	Drakensberg Foothill Moist Grassland
23	29.635780	29.976360	EN	Grassland	Drakensberg Foothill Moist Grassland
24	29.659580	29.958600	EN	Grassland	Drakensberg Foothill Moist Grassland
25	29.654340	29.955640	EN	Grassland	Drakensberg Foothill Moist Grassland
26	29.663840	29.961190	EN	Grassland	Drakensberg Foothill Moist Grassland
27	29.644210	29.948950	EN	Grassland	Drakensberg Foothill Moist Grassland
28	29.681790	29.918000	EN	Grassland	Drakensberg Foothill Moist Grassland
29	29.661060	29.942030	EN	Grassland	Drakensberg Foothill Moist Grassland
30	29.716730	30.005980	EN	Grassland	Midlands Mistbelt Grassland
31	29.641930	29.988310	EN	Grassland	Midlands Mistbelt Grassland
32	29.721280	30.004950	EN	Grassland	Midlands Mistbelt Grassland
33	29.719530	30.015380	EN	Grassland	Midlands Mistbelt Grassland
34	29.636010	29.983990	EN	Grassland	Midlands Mistbelt Grassland
35	29.643700	29.968690	EN	Grassland	Midlands Mistbelt Grassland
36	29.642150	29.972260	EN	Grassland	Midlands Mistbelt Grassland
37	29.650530	29.976780	EN	Grassland	Midlands Mistbelt Grassland

38	29.713510	30.001920	EN	Grassland	Midlands Mistbelt Grassland
39	29.711700	30.011400	EN	Grassland	Midlands Mistbelt Grassland
40	29.714220	30.015550	EN	Grassland	Midlands Mistbelt Grassland
41	29.711600	29.972230	EN	Grassland	Midlands Mistbelt Grassland
42	29.644970	29.963400	EN	Grassland	Midlands Mistbelt Grassland
43	29.648080	29.955360	EN	Grassland	Midlands Mistbelt Grassland
44	29.671260	29.964840	EN	Grassland	Midlands Mistbelt Grassland
45	29.677580	29.903920	PA	FB/PA	Drakensberg Foothill Moist Grassland
46	29.681100	29.904710	PA	FB/PA	Drakensberg Foothill Moist Grassland
47	29.673570	29.902940	PA	FB/PA	Drakensberg Foothill Moist Grassland
48	29.687070	29.905830	PA	FB/PA	Drakensberg Foothill Moist Grassland
49	29.725380	30.000420	PA	FB/PA	Midlands Mistbelt Grassland
50	29.721980	29.988270	PA	FB/PA	Midlands Mistbelt Grassland
51	29.718650	29.978330	PA	FB/PA	Midlands Mistbelt Grassland
52	29.716920	29.970740	PA	FB/PA	Midlands Mistbelt Grassland
53	29.673410	29.901120	PA	Grassland	Drakensberg Foothill Moist Grassland
54	29.677180	29.901770	PA	Grassland	Drakensberg Foothill Moist Grassland
55	29.717540	29.849880	PA	Grassland	Drakensberg Foothill Moist Grassland
56	29.716930	29.854460	PA	Grassland	Drakensberg Foothill Moist Grassland
57	29.712860	29.852600	PA	Grassland	Drakensberg Foothill Moist Grassland
58	29.684970	29.902940	PA	Grassland	Drakensberg Foothill Moist Grassland
59	29.679820	29.902190	PA	Grassland	Drakensberg Foothill Moist Grassland
60	29.695540	29.853860	PA	Grassland	Drakensberg Foothill Moist Grassland
61	29.703740	29.849540	PA	Grassland	Drakensberg Foothill Moist Grassland
62	29.704380	29.883180	PA	Grassland	Drakensberg Foothill Moist Grassland
63	29.706340	29.886340	PA	Grassland	Drakensberg Foothill Moist Grassland
64	29.708210	29.889810	PA	Grassland	Drakensberg Foothill Moist Grassland
65	29.729080	30.002950	PA	Grassland	Midlands Mistbelt Grassland
66	29.721700	29.976610	PA	Grassland	Midlands Mistbelt Grassland
67	29.718550	29.967430	PA	Grassland	Midlands Mistbelt Grassland
68	29.717050	29.962910	PA	Grassland	Midlands Mistbelt Grassland

Appendix C

List of plant species recorded in subterranean grassland in the lower-elevation Zululand.

Group	Scientific name
Non-graminoid forbs	*Adenium gummifloa*
Non-graminoid forbs	*Ageratum conyzoides*
Non-graminoid forbs	*Ageratum conyzoides*
Non-graminoid forbs	*Aristaceae gangetica*
Non-graminoid forbs	*Aristea gerardii*
Non-graminoid forbs	*Asparagus fulcatus* *
Non-graminoid forbs	*Asparagus setiformus*
Non-graminoid forbs	*Astripomoea malvaceae*
Non-graminoid forbs	*Centella asiatica*
Non-graminoid forbs	*Cheilanthes viridus*
Non-graminoid forbs	*Cissampelos torulosa*
Non-graminoid forbs	*Commelina (c.f.) africana*
Non-graminoid forbs	*Commelina ecklonianа*
Non-graminoid forbs	*Commelina erecta*
Non-graminoid forbs	*Conyza bonariensis*
Non-graminoid forbs	*Conyza canadiensis*
Non-graminoid forbs	*Conyza* sp.1
Non-graminoid forbs	*Croteleria globifera*
Non-graminoid forbs	*Cucumis hirsutus*
Non-graminoid forbs	*Cucumis* sp.1
Non-graminoid forbs	*Cucumis* sp.2
Non-graminoid forbs	*Cucumis* sp.3
Non-graminoid forbs	*Cucumis* sp.4
Non-graminoid forbs	*Cuscuta campestris*
Non-graminoid forbs	*Cyclosorus interuptus*
Non-graminoid forbs	*Desmodium dregeanum*
Non-graminoid forbs	*Desmodium incanum*
Non-graminoid forbs	*Desmodium* sp.2
Non-graminoid forbs	*Dioscoria silvaticus*
Non-graminoid forbs	*Dioscurea (c.f.) sylvatica*
Non-graminoid forbs	*Drimiopsis* sp.1
Non-graminoid forbs	*Eriosema cordatum*
Non-graminoid forbs	*Eriosema parvifolium*
Non-graminoid forbs	*Eriosema saligna*
Non-graminoid forbs	*Eriosema* sp.1
Non-graminoid forbs	*Eriosema* sp.2
Non-graminoid forbs	*Gerbera (c.f.) ambigua*
Non-graminoid forbs	*Gladiolus crassifolius*
Non-graminoid forbs	*Gomphocarpus physocarpus*
Non-graminoid forbs	*Helichrysum (c.f.) longifolium*
Non-graminoid forbs	*Helichrysum longifolium*
Non-graminoid forbs	*Helichrysum* sp.1
Non-graminoid forbs	*Hybiscus (c.f.) surratensis*
Non-graminoid forbs	*Hypoestes aristata*
Non-graminoid forbs	*Hypoxis (c.f.) angastifolia*
Non-graminoid forbs	*Hypoxis (c.f.) hemerocallidea*

Non-graminoid forbs	*Hypoxis angustifolia*
Non-graminoid forbs	*Indigofera heydiantha*
Non-graminoid forbs	*Indigofera sanguinea*
Non-graminoid forbs	*Indigofera* sp.1
Non-graminoid forbs	*Indigofera* sp.2
Non-graminoid forbs	*Indigofera* sp.3
Non-graminoid forbs	*Indigofera* sp.4
Non-graminoid forbs	*Indigofera* sp.5
Non-graminoid forbs	*Indigofera* sp.6
Non-graminoid forbs	*Ipomoea mauritiana*
Non-graminoid forbs	*Ipomoea* sp.1
Non-graminoid forbs	*Landolphia kurkii*
Non-graminoid forbs	*Lediboria* sp.1
Non-graminoid forbs	*Lobelia erinus*
Non-graminoid forbs	*Manulea parviflora*
Non-graminoid forbs	*Meremia tridentata*
Non-graminoid forbs	*Microsorum scolopendria*
Non-graminoid forbs	*Nettle* sp.1
Non-graminoid forbs	*Nettle* sp.2
Non-graminoid forbs	*Oxalis corniculata*
Non-graminoid forbs	*Pasiflora* sp.1
Non-graminoid forbs	*Pentadon pentandris*
Non-graminoid forbs	*Pentrandus* sp.1
Non-graminoid forbs	*Polygala* sp.1
Non-graminoid forbs	*Pteridium aquilinum*
Non-graminoid forbs	*Rhoicissus digitata*
Non-graminoid forbs	*Rhyncosia* sp.1
Non-graminoid forbs	*Richardia* sp.1
Non-graminoid forbs	*Sarcostemma viminale*
Non-graminoid forbs	*Secamone filiformus*
Non-graminoid forbs	*Secemone alpinii*
Non-graminoid forbs	*Senecio demoides*
Non-graminoid forbs	*Senecio polyanthenoides*
Non-graminoid forbs	*Smilax anceps*
Non-graminoid forbs	*Solanum (c.f.) panderiforma*
Non-graminoid forbs	*Stenoclaena tenuifolia*
Non-graminoid forbs	*Synaptolepsis kurkii*
Non-graminoid forbs	*Tephrosia liniaris*
Non-graminoid forbs	*Tephrosia* sp.1
Non-graminoid forbs	*Tephrosia* sp.2
Non-graminoid forbs	*Tephrosia* sp.3
Non-graminoid forbs	*Tephrosia* sp.4
Non-graminoid forbs	*Tephrosia* sp.5
Non-graminoid forbs	*Thesium asterius*
Non-graminoid forbs	*Thesium* sp.1
Non-graminoid forbs	*Thunbergia atriplisifolia*
Non-graminoid forbs	*Trachyandra* sp.1
Non-graminoid forbs	*Triumfetta rhomboidea*
Non-graminoid forbs	*Vernonia centeroides*
Non-graminoid forbs	*Vigna (c.f.) vexillata*
Non-graminoid forbs	*Vigna* sp.1
Non-graminoid forbs	*Vigna* sp.2
Non-graminoid forbs	*Vigna* sp.3
Non-graminoid forbs	*Zornia capensis*
Graminoid	*Acroceras macrum*
Graminoid	*Allopteropsis semialata*
Graminoid	*Andropogon (c.f.) huillensis*

Graminoid	*Aristida junciformis subsp. babicilas*
Graminoid	*Aristida junciformis subsp. junciformis*
Graminoid	*Aristida junciformis* subsp.1
Graminoid	*Brachiaria erecta*
Graminoid	*Brachiaria humidicola*
Graminoid	*Brachiaria serrata*
Graminoid	*Chloris virgata*
Graminoid	*Cynodon dactylon*
Graminoid	*Dactyloctenium australe*
Graminoid	*Dactyloctenium geminatum*
Graminoid	*Digitaria (c.f.) eriantha*
Graminoid	*Digitaria diversinervis*
Graminoid	*Digitaria diversinervis albomarginata*
Graminoid	*Digitaria diversinovis*
Graminoid	*Digitaria longiflora*
Graminoid	*Digitaria natalensis*
Graminoid	*Digitaria scalerum*
Graminoid	*Digitaria* sp.1
Graminoid	*Diheteropogon filifolius*
Graminoid	*Eragrostis (c.f.) curvula*
Graminoid	*Eragrostis capensis*
Graminoid	*Eragrostis ciliaris*
Graminoid	*Eragrostis curvula*
Graminoid	*Eragrostis inamoena*
Graminoid	*Eragrostis lappula*
Graminoid	*Eragrostis plana*
Graminoid	*Eragrostis racemosa*
Graminoid	*Eragrostis* sp.1
Graminoid	*Eragrostis superba*
Graminoid	*Erharthia calycina*
Graminoid	*Hemarthria altissima*
Graminoid	*Imperata cylindrica*
Graminoid	*Ischaemum fasciculatum*
Graminoid	*Leersia hexandra*
Graminoid	*Melinis repens*
Graminoid	*Oplismenis italis*
Graminoid	*Oplismenus* sp.1
Graminoid	*Oplisminus hurtellis*
Graminoid	*Panicum dregeanum*
Graminoid	*Panicum hyminochilium*
Graminoid	*Panicum maximum*
Graminoid	*Panicum* sp.1
Graminoid	*Panicum subalbidum*
Graminoid	*Paspalum scrobiculatum*
Graminoid	*Paspalum urvillei*
Graminoid	*Pennisetum clandestinum*
Graminoid	*Perotis patens*
Graminoid	*Phragmites australis*
Graminoid	*Sacciolepsis curvata*
Graminoid	*Setaria megaphylla*
Graminoid	*Setaria sphacelata*
Graminoid	*Sorghastrum stipoides*
Graminoid	*Sporobolus africanus*
Graminoid	*Sporobolus pyramidalis*
Graminoid	*Sporobolus* sp.1
Graminoid	*Sporobolus subtilus*
Graminoid	*Stenotaphrum secundatum*

Graminoid	*Themeda triandra*
Graminoid	*Tristachya leucothrix*
Graminoid	*Uroletrum agropyroides*
Graminoid	*Restio zuluensis*
Graminoid	*Balbustylus contexta*
Graminoid	*Calinga alba*
Graminoid	*Cyperus (c.f.) solidus*
Graminoid	*Cyperus natalensis*
Graminoid	*Cyperus obtusifolius*
Graminoid	*Cyperus sphaeropermus*
Graminoid	*Fuirina (c.f.) pubescens*
Graminoid	*Fuirina pachyrrhiza*
Graminoid	*Fuirina pubescens*
Graminoid	*Fymbrostylis camplanata*
Graminoid	*Juncus krausii*
Graminoid	*Mariscus dubicus*
Graminoid	*Mariscus* sp.1
Graminoid	*Meriscus (c.f.) sumatrensis*
Graminoid	*Meriscus distans*
Graminoid	*Persicaria attenuata*
Graminoid	*Pycreus polystachyos*
Graminoid	*Pycrius* sp.1
Graminoid	*Rhyncosia corambosa* *
Graminoid	*Ricosporia brownii* *
Graminoid	*Schoenoplectus erectus*
Graminoid	*Scleria scobolifera*
Graminoid	*Trachyandra saltii*
Invasive alien species	*Catharanthus roseus*
Invasive alien species	*Cirsium vulgare*
Invasive alien species	*Eucalyptus* sp.1
Invasive alien species	*Lantana rugosa*
Invasive alien species	*Pinus* sp.1
Invasive alien species	*Psidium guajava*
Invasive alien species	*Rivonia humilis*
Invasive alien species	*Rubus* sp.1
Invasive alien species	*Solanum linnaeanum*
Invasive alien species	*Solanum mauritianum*
Shrub/tree	*Acacia burkeii*
Shrub/tree	*Acacia kosiensis*
Shrub/tree	*Acacia krausiana*
Shrub/tree	*Acacia robusta*
Shrub/tree	*Albizia adianthifolia*
Shrub/tree	*Annona senegalensis*
Shrub/tree	*Antidesma venosum*
Shrub/tree	*Apodytes dimidiata*
Shrub/tree	*Brachylaena discolor*
Shrub/tree	*Bridelia cathartica*
Shrub/tree	*Bridelia micrantha*
Shrub/tree	*Canthium inerme*
Shrub/tree	*Carissa macrocarpa*
Shrub/tree	*Catunaregam spinosa*
Shrub/tree	*Chaemocrista mimosoides*
Shrub/tree	*Chaetacme aristata*
Shrub/tree	*Chamaecrista camosa*
Shrub/tree	*Chrysamthemoides monilifera*
Shrub/tree	*Clerodendrum glabrum*
Shrub/tree	*Dichrostachys cinerea*

Shrub/tree	*Diospyros lycioides*
Shrub/tree	*Diospyros natalensis*
Shrub/tree	*Diospyrus dicrophylla*
Shrub/tree	*Diospyrus villosa*
Shrub/tree	*Elephantaryza elephantina*
Shrub/tree	*Euclea natalensis*
Shrub/tree	*Eugenia albanensis*
Shrub/tree	*Eugenia capensis* *
Shrub/tree	*Eugenia capensis capensis*
Shrub/tree	*Eugenia capensis subsp Mossambicensis*
Shrub/tree	*Ficus sur*
Shrub/tree	*Ficus trichopoda*
Shrub/tree	*Garcinia livingstonia*
Shrub/tree	*Haleria lucida*
Shrub/tree	*Helichrysum krausii*
Shrub/tree	*Hymenocardia* sp.1
Shrub/tree	*Hymenocardia ulmoides*
Shrub/tree	*Krausia floribunda*
Shrub/tree	*Landolphia kurkii*
Shrub/tree	*Ludwigii octovalvis*
Shrub/tree	*Macaranga capensis*
Shrub/tree	*Mananthotaxis caffra*
Shrub/tree	*Ochna natalitia*
Shrub/tree	*Oldenlandia* sp.1
Shrub/tree	*Parninari capensis incohata*
Shrub/tree	*Peddiea africana*
Shrub/tree	*Pervetta* sp.1
Shrub/tree	*Phoenix reclinata*
Shrub/tree	*Psydrax obovatum*
Shrub/tree	*Rhus (c.f.) chirendensis*
Shrub/tree	*Rhus nebulosa*
Shrub/tree	*Rothmania globosa*
Shrub/tree	*Rubiaceae*, Unknown sp.1
Shrub/tree	*Salacia krausii*
Shrub/tree	*Sapium intergerrinum*
Shrub/tree	*Sclerocarya birrea*
Shrub/tree	*Sclerocroton integerrimum*
Shrub/tree	*Scutia myrtina*
Shrub/tree	*Sida cordifolia*
Shrub/tree	*Strelitzia nicolai*
Shrub/tree	*Strychnos gerardii*
Shrub/tree	*Strychnos spinosa*
Shrub/tree	*Syzigium (c.f.) jambos*
Shrub/tree	*Syzigium cordata*
Shrub/tree	*Trema orientalis*
Shrub/tree	*Tricalysia (c.f.) lanceolata*
Shrub/tree	*Tricalysia sonderiana*
Shrub/tree	*Triomfeta (c.f.) pilosa*
Shrub/tree	*Trychelia emetica*
Shrub/tree	*Uvaria caffra*
Shrub/tree	*Vepris lanceolata*
Shrub/tree	*Wahltheria indica*
Shrub/tree	*Zanthozylum capensis*

Appendix D

List of plant species recorded in Afromontane grassland in the KwaZulu-Natal Midlands.

Family	**Scientific Name**
Acanthaceae - Acanthus family	*Barleria obtusa*
Acanthaceae - Acanthus family	*Crabbea hirsuta*
Acanthaceae - Acanthus family	*Crabbea* sp.1
Acanthaceae - Acanthus family	*Crabbea* sp.2
Acanthaceae - Acanthus family	*Dyschoriste* sp.1
Adiantaceae - Terrestrial ferns	*Cheilanthes quadripinnata*
Adiantaceae - Terrestrial ferns	*Pellaea calomelanos*
Aizoaceae - Brakbos family	*Psammotropha mucronata*
Alliaceae - Onion family	*Agapanthus c.f. campanulatus*
Alliaceae - Onion family	*Tulbaghia c.f. natalensis*
Anacardiaceae - Mango/Cashew family	*Rhus c.f. pyroides*
Anacardiaceae - Mango/Cashew family	*Rhus discolor*
Anacardiaceae - Mango/Cashew family	*Rhus* sp.1
Apiaceae - Carrot family	*Alepidea c.f. amatymbica*
Apiaceae - Carrot family	*Alepidea natalensis*
Apiaceae - Carrot family	*Alepidea* sp.1
Apiaceae - Carrot family	*Pimpinella c.f. caffra*
Asclepiadaceae - Milkweed/Butterflyweed family	*Asclepias albens*
Asclepiadaceae - Milkweed/Butterflyweed family	*Asclepias macropus*
Asclepiadaceae - Milkweed/Butterflyweed family	*Pachycarpus c.f. natalensis*
Asclepiadaceae - Milkweed/Butterflyweed family	*Pachycarpus dealbatus*
Asclepiadaceae - Milkweed/Butterflyweed family	*Periglossum angustifolium*
Asclepiadaceae - Milkweed/Butterflyweed family	*Schizoglossum bidens subsp. Pachyglossum*
Asclepiadaceae - Milkweed/Butterflyweed family	*Sisyranthus c.f. fanniniae*
Asclepiadaceae - Milkweed/Butterflyweed family	*Xysmalobium c.f. involucratum*
Asparagaceae - Asparagus family	*Asparagus* sp.1
Asphodelaceae	*Aloe* sp.1
Asphodelaceae	*Kniphofia buchananii*
Asphodelaceae	*Kniphofia c.f. brachystachya*
Asphodelaceae	*Kniphofia laxiflora*
Asphodelaceae	*Kniphofia* sp.1
Asteraceae - Daisy family	*Aster bakerianus*
Asteraceae - Daisy family	*Aster* sp.1
Asteraceae - Daisy family	*Dimorphotheca* sp.1
Asteraceae - Daisy family	*Felicia* sp.1
Asteraceae - Daisy family	*Osteospermum* sp.1
Asteraceae - Daisy family	*Athrixia c.f. phylicoides*
Asteraceae - Daisy family	*Berkheya rhapontica*
Asteraceae - Daisy family	*Berkheya setifera*

Asteraceae - Daisy family	*Berkheya* sp.1
Asteraceae - Daisy family	*Berkheya* sp.2
Asteraceae - Daisy family	*Berkheya* sp.3
Asteraceae - Daisy family	*Berkheya* sp.4
Asteraceae - Daisy family	*Conyza* sp.1
Asteraceae - Daisy family	*Dicoma anomala*
Asteraceae - Daisy family	*Euryops c.f. laxus*
Asteraceae - Daisy family	*Gazania krebsiana*
Asteraceae - Daisy family	*Gerbera* sp.1
Asteraceae - Daisy family	*Gerbera* sp.2
Asteraceae - Daisy family	*Helichrysum appendiculatum*
Asteraceae - Daisy family	*Helichrysum aureonitens*
Asteraceae - Daisy family	*Helichrysum c.f. allioides*
Asteraceae - Daisy family	*Helichrysum c.f. auriceps*
Asteraceae - Daisy family	*Helichrysum c.f. cephaloideum*
Asteraceae - Daisy family	*Helichrysum c.f. krookii*
Asteraceae - Daisy family	*Helichrysum c.f. nudifolium*
Asteraceae - Daisy family	*Helichrysum c.f. pallidum*
Asteraceae - Daisy family	*Helichrysum c.f. spiralepis*
Asteraceae - Daisy family	*Helichrysum herbaceum*
Asteraceae - Daisy family	*Helichrysum nudifolium*
Asteraceae - Daisy family	*Helichrysum pilosellum*
Asteraceae - Daisy family	*Helichrysum* sp.1
Asteraceae - Daisy family	*Helichrysum* sp.2
Asteraceae - Daisy family	*Helichrysum* sp.3
Asteraceae - Daisy family	*Helichrysum* sp.4
Asteraceae - Daisy family	*Helichrysum* sp.5
Asteraceae - Daisy family	*Helichrysum* sp.6
Asteraceae - Daisy family	*Helichrysum* sp.7
Asteraceae - Daisy family	*Helichrysum* sp.8
Asteraceae - Daisy family	*Helichrysum* sp.9
Asteraceae - Daisy family	*Helichrysum umbraculigerum*
Asteraceae - Daisy family	*Hypochaeris c.f. radicata*
Asteraceae - Daisy family	*Macowania* sp.1
Asteraceae - Daisy family	*Nidorella c.f. anomala*
Asteraceae - Daisy family	*Nidorella* sp.1
Asteraceae - Daisy family	*Schistostephium crataegifolium*
Asteraceae - Daisy family	*Senecio c.f. ulopterus*
Asteraceae - Daisy family	*Senecio isatideus*
Asteraceae - Daisy family	*Senecio oxyriifolius*
Asteraceae - Daisy family	*Senecio scitus*
Asteraceae - Daisy family	*Senecio* sp.1
Asteraceae - Daisy family	*Senecio* sp.2
Asteraceae - Daisy family	*Senecio* sp.3
Asteraceae - Daisy family	*Senecio* sp.4
Asteraceae - Daisy family	*Senecio subrubriflorus*
Asteraceae - Daisy family	*Vernonia c.f. hirsuta*
Asteraceae - Daisy family	*Vernonia c.f. thodei*

Asteraceae - Daisy family	*Vernonia c.f. tigna*
Asteraceae - Daisy family	*Vernonia natalensis*
Campanulaceae - Bell flower/Canterbury Bell family	*Craterocapsa tarsodes*
Campanulaceae - Bell flower/Canterbury Bell family	*Wahlenbergia krebsii*
Caryophyllaceae - Carnation family	*Dianthus* sp.1
Caryophyllaceae - Carnation family	*Silene c.f. burchellii*
Commelinaceae - Commelina family	*Commelina africana*
Commelinaceae - Commelina family	*Cyanotis speciosa*
Crassulaceae - Crassula family	*Crassula alba*
Crassulaceae - Crassula family	*Crassula c.f. brachypetala*
Crassulaceae - Crassula family	*Crassula pellucida*
Crassulaceae - Crassula family	*Crassula* sp.1
Cucurbitaceae - Cucumber/Pumpkin family	*Cucumis* sp.1
Cucurbitaceae - Cucumber/Pumpkin family	*Cucumis zeyheri*
Cyperaceae - Sedge family	*Bulbostylis* sp.1
Cyperaceae - Sedge family	*Kyllinga alba*
Dennstaedtiaceae	*Pteridium aquilinum*
Dipsacaceae - Scabiosa family	*Scabiosa columbaria*
Eriospermaceae	*Eriospermum cooperi*
Euphorbiaceae - Euphorbia/Rubber family	*Acalypha peduncularis*
Euphorbiaceae - Euphorbia/Rubber family	*Acalypha punctata*
Euphorbiaceae - Euphorbia/Rubber family	*Acalypha schinzii*
Euphorbiaceae - Euphorbia/Rubber family	*Acalypha* sp.1
Euphorbiaceae - Euphorbia/Rubber family	*Clutia* sp.1
Euphorbiaceae - Euphorbia/Rubber family	*Clutia* sp.2
Euphorbiaceae - Euphorbia/Rubber family	*Euphorbia c.f. striata*
Fabaceae - Pea/Legume family	*Argyrolobium c.f. stipulaceum*
Fabaceae - Pea/Legume family	*Argyrolobium* sp.1
Fabaceae - Pea/Legume family	*Argyrolobium* sp.2
Fabaceae - Pea/Legume family	*Argyrolobium tuberosum*
Fabaceae - Pea/Legume family	*Aspalathus* sp.1
Fabaceae - Pea/Legume family	*Chamaecrista* sp.1
Fabaceae - Pea/Legume family	*Eriosema distinctum*
Fabaceae - Pea/Legume family	*Eriosema kraussianum*
Fabaceae - Pea/Legume family	*Eriosema salignum*
Fabaceae - Pea/Legume family	*Eriosema* sp.1
Fabaceae - Pea/Legume family	*Indigofera c.f. foliosa*
Fabaceae - Pea/Legume family	*Indigofera c.f. hilaris*
Fabaceae - Pea/Legume family	*Indigofera c.f. sanguinea?*
Fabaceae - Pea/Legume family	*Indigofera* sp.1
Fabaceae - Pea/Legume family	*Indigofera* sp.2
Fabaceae - Pea/Legume family	*Indigofera* sp.3
Fabaceae - Pea/Legume family	*Indigofera* sp.4
Fabaceae - Pea/Legume family	*Indigofera tristis*
Fabaceae - Pea/Legume family	*Indigofera woodii*
Fabaceae - Pea/Legume family	*Lotononis c.f. foliosa*
Fabaceae - Pea/Legume family	*Lotononis c.f. pulchella*
Fabaceae - Pea/Legume family	*Lotononis corymbosa*

Fabaceae - Pea/Legume family	*Rhyncosia totta*
Fabaceae - Pea/Legume family	*Tephrosia c.f. marginella*
Fabaceae - Pea/Legume family	*Tephrosia* sp.1
Fabaceae - Pea/Legume family	*Tephrosia* sp.2
Fabaceae - Pea/Legume family	*Tephrosia* sp.3
Fabaceae - Pea/Legume family	*Vigna vexillata*
Fabaceae - Pea/Legume family	*Zornia capensis*
Gentianaceae - Gentian family	*Sebaea c.f. sedoides*
Geraniaceae - Geranium family	*Geranium c.f. multisectum*
Geraniaceae - Geranium family	*Geranium schlecteri*
Geraniaceae - Geranium family	*Geranium* sp.1
Geraniaceae - Geranium family	*Pelargonium c.f. alchemilloides*
Geraniaceae - Geranium family	*Pelargonium luridum*
Geraniaceae - Geranium family	*Pelargonium schlechteri*
Hyacinthacea	*Eucomis autumnalis*
Hyacinthacea	*Ledebouria c.f. ovatifolia*
Hyacinthacea	*Ledebouria c.f. sandersonii*
Hyacinthacea	*Ledebouria ovatifolia*
Hyacinthacea	*Ledebouria* sp.1
Hyacinthacea	*Ledebouria* sp.2
Hyacinthacea	*Ledebouria* sp.3
Hyacinthacea	*Scilla c.f. natalensis*
Hyacinthacea	*Scilla nervosa*
Hyacinthacea	*Scilla* sp.1
Hypericaceae - Hypericum family	*Hypericum c.f. aethiopicum*
Hypericaceae - Hypericum family	*Hypericum c.f. lalandi*
Hypericaceae - Hypericum family	*Hypericum* sp.1
Hypoxidaceae - Star-flower family	*Hypoxis acuminata*
Hypoxidaceae - Star-flower family	*Hypoxis c.f. argentea*
Hypoxidaceae - Star-flower family	*Hypoxis c.f. augustifolia*
Hypoxidaceae - Star-flower family	*Hypoxis c.f. rigidula*
Hypoxidaceae - Star-flower family	*Hypoxis costata*
Hypoxidaceae - Star-flower family	*Hypoxis parvula var. albiflora*
Hypoxidaceae - Star-flower family	*Hypoxis* sp.1
Hypoxidaceae - Star-flower family	*Hypoxis* sp.2
Hypoxidaceae - Star-flower family	*Hypoxis* sp.3
Invasive Alien Species	*Acacia mearnsii*
Invasive Alien Species	*Agrimonia procera*
Invasive Alien Species	*Bidens pilosa*
Invasive Alien Species	*Cirsium vulgare*
Iridaceae - Iris family	*Aristea angolensis*
Iridaceae - Iris family	*Aristea* sp.2
Iridaceae - Iris family	*Aristea* sp1
Iridaceae - Iris family	*Aristea woodii*
Iridaceae - Iris family	*Dierama c.f. latifolium*
Iridaceae - Iris family	*Dierama* sp.1
Iridaceae - Iris family	*Gladiolus ecklonii*
Iridaceae - Iris family	*Gladiolus* sp.1

Iridaceae - Iris family	*Watsonia c.f. lepida*
Iridaceae - Iris family	*Watsonia pillansii*
Iridaceae - Iris family	*Watsonia* sp.1
Lamiaceae - Sage/Mint family	*Ajuga ophrydis*
Lamiaceae - Sage/Mint family	*Ajuga* sp.1
Lamiaceae - Sage/Mint family	*Becium obovatum*
Lamiaceae - Sage/Mint family	*Hemizygia c.f. teucriifolia*
Lamiaceae - Sage/Mint family	*Leonotis intermedia*
Lamiaceae - Sage/Mint family	*Rabdosiella c.f. calycina*
Lamiaceae - Sage/Mint family	*Stachys aethiopica*
Lamiaceae - Sage/Mint family	*Stachys c.f. natalensis*
Linaceae - Flax family	*Linum thunbergii*
Lobeliaceae - Lobelia family	*Cyphia c.f. longifolia*
Lobeliaceae - Lobelia family	*Cyphia elata*
Lobeliaceae - Lobelia family	*Lobelia c.f. vanreenensis*
Lobeliaceae - Lobelia family	*Lobelia flaccida*
Lobeliaceae - Lobelia family	*Monopsis decipiens*
Malvaceae - Hibiscus family	*Hibiscus aethiopicus*
Malvaceae - Hibiscus family	*Hibiscus* sp.1
Myricaceae - Waxberry Family	*Myrica c.f. brevifolia*
Onagraceae - Evening Primrose family	*Epilobium c.f. capense*
Ophioglossaceae - Snake/Adder's Tongue Ferns	*Mohria c.f. vestita*
Ophioglossaceae - Snake/Adder's Tongue Ferns	*Ophioglossum vulgatum*
Orchidaceae - Orchid family	*Eulophia clavicornis*
Orchidaceae - Orchid family	*Habenaria chlorotica*
Orchidaceae - Orchid family	*Habenaria dives*
Orchidaceae - Orchid family	*Habenaria dregeana*
Orchidaceae - Orchid family	*Habenaria sp.1*
Orchidaceae - Orchid family	*Satyrium cristatum*
Orchidaceae - Orchid family	*Satyrium longicauda*
Oxalidaceae - Sorrel family	*Oxalis obliquifolia*
Oxalidaceae - Sorrel family	*Oxalis semiloba*
Oxalidaceae - Sorrel family	*Oxalis smithiana*
Plantaginaceae - Plaintain/Plantago family	*Plantago lanceolata*
Plantaginaceae - Plaintain/Plantago family	*Plantago major*
Poaceae - Grass family	*Alloteropsis semialata*
Poaceae - Grass family	*Aristida junciformis*
Poaceae - Grass family	*Bromus catharticus*
Poaceae - Grass family	*Cymbopogon excavatus*
Poaceae - Grass family	*Cymbopogon plurinodis*
Poaceae - Grass family	*Digitaria longiflora*
Poaceae - Grass family	*Diheteropogon amplectens*
Poaceae - Grass family	*Elionurus muticus*
Poaceae - Grass family	*Eragrostis capensis*
Poaceae - Grass family	*Eragrostis chloromelas*
Poaceae - Grass family	*Eragrostis curvula*
Poaceae - Grass family	*Eragrostis plana*
Poaceae - Grass family	*Eragrostis racemosa*

Poaceae - Grass family	*Harpochloa falx*
Poaceae - Grass family	*Hemarthria altissima*
Poaceae - Grass family	*Heteropogon contortus*
Poaceae - Grass family	*Hyparrhenia hirta*
Poaceae - Grass family	*Hyparrhenia* sp.1
Poaceae - Grass family	*Lolium perenne*
Poaceae - Grass family	*Lolium perenne*
Poaceae - Grass family	*Loudetia simplex*
Poaceae - Grass family	*Melinis repens*
Poaceae - Grass family	*Microchloa caffra*
Poaceae - Grass family	*Monocymbium ceresiiforme*
Poaceae - Grass family	*Paspalum c.f. scrobiculatum*
Poaceae - Grass family	*Paspalum dilatatum*
Poaceae - Grass family	*Pennisetum clandestinum*
Poaceae - Grass family	*Sporobolus africanus*
Poaceae - Grass family	*Themeda triandra*
Poaceae - Grass family	*Trachypogon spicatus*
Poaceae - Grass family	*Tristachya leucothrix*
Polygalaceae - Milkwort family	*Polygala c.f. gracilenta*
Polygalaceae - Milkwort family	*Polygala c.f. refracta*
Polygalaceae - Milkwort family	*Polygala confusa*
Polygalaceae - Milkwort family	*Polygala hottentotta*
Polygalaceae - Milkwort family	*Polygala* sp.1
Proteaceae - Protea family	*Protea c.f. simplex*
Ranunculaceae - Buttercup family	*Anemone fanninii*
Ranunculaceae - Buttercup family	*Ranunculus meyeri*
Rosaceae - Rose family	*Alchemilla sp*
Rosaceae - Rose family	*Leucosidea sericea*
Rosaceae - Rose family	*Rubus ludwigii*
Rosaceae - Rose family	*Rubus rigidus*
Rubiaceae - Gardenia/Coffee family	*Anthospermum c.f streyi*
Rubiaceae - Gardenia/Coffee family	*Anthospermum herbaceum*
Rubiaceae - Gardenia/Coffee family	*Conostomium natalense*
Rubiaceae - Gardenia/Coffee family	*Pentanisia augustifolia*
Rubiaceae - Gardenia/Coffee family	*Pentanisia prunelloides*
Rubiaceae - Gardenia/Coffee family	*Pygmaeothamnus chamaedendrum*
Santalaceae - Sandalwood family	*Thesium c.f. pallidum*
Schizaeaceae - Cockscomb Fern family	*Schizaea pectinata*
Scrophulariaceae - Snapdragon family	*Alectra sessiliflora*
Scrophulariaceae - Snapdragon family	*Buchnera simplex*
Scrophulariaceae - Snapdragon family	*Buchnera* sp.1
Scrophulariaceae - Snapdragon family	*Diclis reptans*
Scrophulariaceae - Snapdragon family	*Diclis rotundifolia*
Scrophulariaceae - Snapdragon family	*Graderia scabbra*
Scrophulariaceae - Snapdragon family	*Hebenstretia c.f. dura*
Scrophulariaceae - Snapdragon family	*Jamesbrittenia breviflora*
Scrophulariaceae - Snapdragon family	*Nemesia c.f. caerulea*
Scrophulariaceae - Snapdragon family	*Sopubia cana*

Scrophulariaceae - Snapdragon family	*Striga asiatica*
Scrophulariaceae - Snapdragon family	*Striga bilabiata*
Scrophulariaceae - Snapdragon family	*Zaluzianskya elongata*
Scrophulariaceae - Snapdragon family	*Zaluzianskya natalensis*
Sterculiaceae - Cocoa/Sterculia family	*Hermannia woodii*
Thymelaeaceae - Fibre-bark/Gonna family	*Gnidia c.f. kraussiana*
Thymelaeaceae - Fibre-bark/Gonna family	*Passerina montana*
Thymelaeaceae - Fibre-bark/Gonna family	*Struthiola* sp.1
Tiliaceae - Jute/Linden family	*Sparrmannia ricinocarpa*
Verbenaceae - Verbena/Teak family	*Verbena bonariensis*

Appendix E

List of grasshopper species recorded in the KwaZulu-Natal Midlands

Family	**Species**
Acrididae	*Acanthoxia natalensis*
Acrididae	*Acorypha ferrifer*
Acrididae	*Acrida* sp.1
Acrididae	*Aiolopus thalassinus*
Acrididae	*Anablepia pilosa*
Acrididae	*Anthermus granosus*
Acrididae	*Calliptamicus* or *Calliptamulus*
Acrididae	*Catantops ochthephilus*
Acrididae	*Coryphosima stenoptera stenoptera*
Acrididae	*Cyrtacanthacris aeruginosa*
Acrididae	*Dnopherula callosa*
Acrididae	*Eyprepocnemis calceata*
Acrididae	*Faureia milanjica*
Acrididae	*Gastrimargus determinatus vitripennis*
Acrididae	*Gastrimargus drakensbergensis*
Acrididae	*Gastrimargus verticalis verticalis*
Acrididae	*Gastrimargus wahlbergii*
Acrididae	*Gomphocerinae* sp.1
Acrididae	*Gymnobothrus lineaalba*
Acrididae	*Gymnobothrus temporalis temporalis*
Acrididae	*Heteracris* sp.1
Acrididae	*Heteracris* sp.2
Acrididae	*Heteropternis* sp.1
Acrididae	*Machaeridia conspersa*
Acrididae	*Orthochtha dasycnemis nana*
Acrididae	*Orthochtha* sp1
Acrididae	*Orthochtha* sp2
Acrididae	*Oxya glabra*
Acrididae	*Oxya hyla*
Acrididae	*Phaeocatantops sulphureus*
Acrididae	*Pnorisa squalus squalus*
Acrididae	*Pseudoarcyptera bechuana*
Acrididae	*Pseudoarcyptera cephalica*
Acrididae	*Scintharista rosacea*
Acrididae	*Spathosternum nigrotaeniatum*
Acrididae	*Vitticatantops maculatus*
Pyrgomorphidae	*Dictyophorus spumans*
Pyrgomorphidae	*Maura rubroornata*
Pyrgomorphidae	*Ochrophlebia cafra ligneola*

Pyrgomorphidae	*Phymateus leprosus*
Pyrgomorphidae	*Phymateus morbillosus*
Tetrigidae	Tetrigid sp.1
Tetrigidae	Tetrigid sp.2
Tetrigidae	Tetrigid sp.3
Tetrigidae	Tetrigid sp.4
Tettigoniidae	*Conocephalus* sp.1