Biodiversity value of grassland ecological networks in afforested areas, KwaZulu-Natal, South Africa

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Declaration

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Abstract

The current biodiversity crisis requires creative initiatives for mitigating further biodiversity loss. The use of ecological networks (ENs) is such an initiative. The South African forestry industry recognizes that there is loss of biodiversity at the smaller patch scale, while attempting to mitigate this loss at the landscape scale by implementing large-scale ENs.

The aim of this study was to determine how representative grassland biodiversity in ENs are of similar habitat in a nature reserves (NR). The study was conducted in the northeast of the KwaZulu-Natal Province, adjacent iSimangaliso Wetland Park, which is a natural World Heritage site. A systematic approach compared a wide range of taxa, namely plants, decomposition macrofungi, vertebrates (birds and large mammals) and faunal manifestations (e.g. molehills, dung and ant nests) between the EN and nature reserve, while controlling for differences in disturbance regime. Species richness was compared using Mann-Whitney U tests, while differences in species composition were determined using Correspondence Analyses, Multi-Dimensional Scaling and Analyses of Similarity.

Grassland ENs had significantly less plant species. In addition, there were differences in plant and fungi species composition. Differences were probably caused by (1) degree of isolation i.e. proximity to source habitat patches in the surrounding matrix, and (2) habitat quality. Habitat quality was determined by local disturbance regimes (e.g. grazing and fire) and plantation-induced drought for plants, and size and amount of coarse woody debris for fungi. In addition, significant differences in abundances of mole hills (NR>EN) and small mammal burrows (EN>NR) might have had an effect on succession and regeneration of plant communities.

There were differences in plant species composition between grassland EN and that at the adjacent nature reserve. However, differences between EN and NR were small when compared to differences between habitat types at the landscape spatial scale. It is concluded that grassland ENs among forestry plantations contribute to biodiversity conservation in the commercially-productive landscape. This approach to land use planning should be explored for other commercial land uses.

Opsomming

Die huidige biodiversiteitskrisis vereis kreatiewe strategieë om ‘n verdere verlies in biodiversiteit te bekamp. Ekologiese Netwerke (EN’e) is een voorbeeld van sulke kreatiewe strategieë. Die Suid Afrikaanse bosbou-industrie erken die verlies in biodiversiteit wat kenmerkend in plantasies gevind word. Implementering van grootskaalse EN’e kan egter die verlies aan biodiversiteit, wat in plantasies ondervind word, temper.

Die doel van hierdie studie was om vas te stel hoe goed biodiversiteit in grasveld EN’e soortgelyke habitat in ‘n nabygeleë natuurreservaat verteenwoordig. Die studie was uitgevoer in die noordooste van KwaZulu-Natal, langs iSimangaliso Wetland Park wat ‘n wêrelderfenisgebied is. Ons het ‘n stelselmatige benadering gevolg waartydens ‘n wye verskeidenheid taksa, naamlik plante, makro-fungi, vertebrate (groot soogdiere en voëls) en tekens van diere-aktiwiteit (bv. miersneste, dieremis en molshope), in die EN vergelyk is met die van ‘n natuurreservaat terwyl ons vir verskillende versteuringe gekontrolleer het. Spesiesrykheid is vergelyk met Mann-Whitney U toetse terwyl verskille in spesiessamestelling vasgestel is met Correspondence Analyses, Multi-Dimensional Scaling en Analyses of Similarity.

Daar was ‘n statisties beduidende verskil in die hoeveelheid spesies tussen grasveld EN’e en die natuurreservaat. Grasveld EN’e het minder plant spesies gehad. Boonop was daar verskille in die samestelling van plant en fungi gemeenskappe. Verskille was waarskynlik veroorsaak deur (1) isolasie of die hoeveelheid nabygeleë habitatbronne in die omliggende omgewing, en (2) habitat kwaliteit. Habitat kwaliteit word bepaal deur versteuringe (bv. brand en beweiding) en die uitdrogingseffek van plantasies vir plante, en die hoeveelheid en grootte van growwe houtagtige puin vir fungi. Daar was ook beduidende verskille in die hoeveelheid molshope (NR>EN) en klein soogdier gate (EN>NR), wat moontlik ‘n effek kon hê op suksessie en herstel van plantgemeenskappe.

Daar was verskille in plantspesiessamestelling tussen grasveld EN’e en die van die langsliggende natuurreservaat. Hierdie verskille was egter klein wanneer dit vergelyk word met die verskille tussen verskillende soorte habitatte in die landskap. Daarom kom ons tot die gevolgtrekking dat grasveld EN’e tussen bosbouplantasies bydra tot die bewaring van biodiversiteit in kommersiële landskappe. Hierdie benadering tot grondgebruik behoort verder verken te word vir ander kommersiële bosbou en boerderypraktyke.

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Table of Contents

List of figures

List of tables

List of abbreviations

ANOSIM	Analysis of Similarity
BP	**B**urned, **p**ristine grassland with wetland elements
CA	Correspondence Analysis
CBD	Convention on Biological Diversity
CFR	Cape Floristic Region
ECDB	The Environmental Conservation Database (1997)
EN	Ecological Network
EV	Environmental variable
FSC	Forestry Stewardship Council
GIS	Geographic Information System
Grn vc	Green/live vegetation cover
HD	100% vegetation cover, high density
IAS	Invasive alien species
LD	100% vegetation cover, low density
LL. & Morib	Leaf litter & moribund vegetation cover
LSDI	Lubombo Spatial Development Initiative
MD	100% vegetation cover, medium density
MDS	Multi-Dimensional Scaling
NR	Nature Reserve
PEEN	Pan-European Ecological Network
PGL	**P**ristine, burned **g**rass**l**and without wetland elements
RGL	**R**ehabilitated **g**rass**l**and (plantations cleared in 2005)
SAFCOL	South African Forestry Company (Ltd)
SQF	SiyaQhubeka Forests (Ltd)
SU	Sampling unit
TFCA	Transfrontier Conservation Area
TSES	Territorial Systems of Ecological Stability
UNESCO	United Nations Educational, Scientific and Cultural Organization
Vheight	Vegetation height
YR	**Y**ounger, **r**ehabilitated grassland (plantations cleared in 2006)

Introduction

The global biodiversity crisis

“Changes in biodiversity due to human activities were more rapid in the past 50 years than at any time in human history… The most important direct drivers of biodiversity loss are habitat change (including land use change), climate change, invasive alien species, overexploitation, and pollution” (Millennium Ecosystem Assessment 2005).

Land use change (i.e. conversion of natural ecosystems to commercially-productive landscapes) cause habitat loss (i.e. total amount of habitat in landscape) and fragmentation of natural ecosystems. Habitat fragmentation is defined as “changes in habitat configuration that result from the breaking apart of habitat, independent of habitat loss” (Fahrig 2003). While habitat loss has a large, negative effect on biodiversity, the effect of habitat fragmentation on biodiversity is usually weaker and not always negative (Fahrig 2003). Commercial activity (e.g. agriculture, urbanization, construction of infrastructure or forestry) in the landscape is necessary for economic growth of a country, but generally results in natural habitat loss. This negatively affects biodiversity at local, national and global spatial scales.

Parties of the Convention on Biological Diversity committed themselves to “achieve by 2010 a significant reduction in the current rate of biodiversity loss at the global, regional, and national spatial scale as a contribution to poverty alleviation and to the benefit of all life on Earth” (Secretariat of the Convention on Biological Diversity 2006). Some developed countries aim to halt biodiversity loss. However, in most developing countries, where most of the Earth’s biodiversity is located (Rosendal 2000), poverty alleviation has higher priority status than biodiversity conservation. Comparatively low priority status of biodiversity conservation, coupled with insufficient financial, human and technical resources to take action against biodiversity loss, has jeopardized effective conservation action (Secretariat of the Convention on Biological Diversity 2006).

Global conservation action

Ecological Networks (ENs) have been proposed as a mitigation measure against further biodiversity loss in commercially-productive landscapes by counteracting habitat fragmentation (Crooks & Sanjayan 2006). ENs are defined as “systems of nature reserves and their interconnections that make a fragmented natural system coherent, so as to support more biological diversity than in its non connected form" (Jongman 2004). An alternative definition is "a coherent system of natural and/or semi-natural landscape elements that is configured and managed with the objective of maintaining or restoring ecological functions as a means to conserve biodiversity while also providing appropriate opportunities for the sustainable use of natural resources" (Bennett & Wit 2001).

These two definitions reflect how development, implementation and management of ENs can either reflect a purely biodiversity conservation approach or can adopt a more integrative, multifunctional approach to conservation. For example, western countries (i.e. West Europe, North America and Australia) place strong emphasis on biodiversity conservation and connectivity. However, approaches towards EN development in Asia, South America, and Central and Eastern Europe emphasize sustainable resource use and community development strongly, even though biodiversity conservation still remains a priority (Bennett & Mulongoy 2006).

ENs can have any of the following objectives: (1) conservation of species, (2) conservation of habitat, (3) conservation of ecological and evolutionary processes, (4) facilitate sustainable use of natural resources, (5) facilitate sustainable development (including community development), and (6) conservation of cultural heritage (including indigenous cultures) (Bennett & Wit 2001). While the first three objectives focus on biodiversity conservation, the last three explore the multifunctional role that ENs might perform in some countries (Bennett & Wit 2001).

There has been proactive conservation action worldwide at local, national and international scales in an attempt to conserve biodiversity. The ~ 200 ENs, which are at different stages of implementation, are evidence of this fact. These ENs represents most major geographical regions, namely Africa, Asia, Australia, Central and Eastern Europe, North and South America, Russia and Western Europe (Bennett & Mulongoy 2006). Probably the most well-known is the Pan-European Ecological Network (PEEN), which is "a physical network of core areas and other appropriate measures, linked by corridors and supported by buffer zones, thus, facilitating the dispersal and migration of species" (Council of Europe 1996). The PEEN is one of the main projects of the Pan-European Biological and Landscape Diversity Strategy and is aimed at conserving and managing biodiversity at all hierarchical levels (i.e.

ecosystems, landscapes, habitats and species) within and across 52 countries throughout Eurasia (Bennett & Mulongoy 2006; Bonnin *et al.* 2007).

A similar approach is followed in North America. Four megalinkages were identified in an attempt to restore connectivity in the landscape. Each of these megalinkages runs either from north to south, or from east to west, and comprises clusters of ENs (i.e. nature reserves, buffer zones and corridors). For example, the “Spine of the Continent” Wildlands Project runs from north to south and incorporates six ENs, namely the Yellowstone-to-Yukon Conservation Initiative, the Great Divide Wildlands Network, the Southern Rockies Wildlands Network, the New Mexico Link Wildlands Network, the Sky Islands Wildlands Network, the Sierra Madre Occidental Biological Corridor and the Grand Canyon Wildlands Network (Terborgh & Soule 1999). While some of these ENs have been implemented, others are still in the planning phase.

Territorial Systems of Ecological Stability (TSES) are implemented at the local, regional and national spatial scale in the Czech Republic, which are then linked to the PEEN. TSES are multifunctional, and incorporate both natural and semi-natural, modified landscapes. However, their aim is still the conservation of biodiversity in the landscape, by facilitating migration, contact and spread of organisms (Bucek *et al.* 2007; Mackovcìn 2000). This multifunctional approach to ENs is also found in Estonia, where traditional farming practices and recreation are allowed in some areas (e.g. buffer zones around core areas) (Jongman 1995; Sepp & Kaasik 2002).

Important conservation areas in South Africa

Conservation assessments occur over different geographical scales. Conservation-worthy areas (from here onwards referred to as “priority areas”) are first identified at a global scale (Rodrigues and Brooks 2007), then at a regional spatial scale (Margules and Pressey 2000; Knight *et al*. 2006), followed, in turn, by smaller spatial scales (Knight *et al*. 2006). The aim of identifying priority areas is to schedule conservation action i.e. deciding which areas should be protected first (Pressey and Taffs 2001).

There are three important biodiversity areas in South Africa, namely the Succulent Karoo region along the west coast, the Cape Floristic Region (CFR) in the southwest, and the Maputaland-Pondoland-Albany region along the east coast. These three areas were identified using three different approaches: biodiversity hotspots (Mittermeier *et al*. 2005; Myers *et al.* 2000), priority ecoregions (Olson & Dinerstein 1998) and the national spatial biodiversity assessment (Driver *et al.*2005).

Assigning biodiversity hotspot status to an area depends on concentration of endemic species (≥ 1500 endemic plant species) and degree of habitat transformation (≥ 70% of original vegetation type lost) (Myers *et al.* 2000). There were 6 210 endemic plant species in the CFR, 2 439 in the Succulent Karoo biodiversity hotspot and 1 900 in the Maputaland-Pondoland-Albany biodiversity hotspot (Mittermeier *et al*. 2005). In addition, 80% (62 844 km^2) of natural habitat in the CFR, 71% (2567 km^2) of natural habitat in the Succulent Karoo biodiversity hotspot and 76% (206 973 km^2) of natural habitat in the Maputaland-Pondoland-Albany biodiversity hotspots have been transformed (Conservation International. Therefore, these three areas were classified as biodiversity hotspots (Downloaded from http://www.conservation.org/explore/priority_areas/hotspots/hotspots_revisited/key_findings/Pages/remaining_habitat.aspx on 30 September 2010).

The priority ecoregion approach mapped areas of global importance for biodiversity conservation. Priority ecoregions were identified based on species richness and endemism (Table 1), taxonomic uniqueness, unusual ecological/evolutionary phenomena and global rarity of that biome (Olson & Dinerstein 1998). This approach identified the three biodiversity hotspots as priority ecoregions.

Conservation status of priority ecoregions were based on total habitat loss, degree of habitat fragmentation, future threats to biodiversity and representation in formally-protected areas (Olson and Dinerstein 1998). Conservation status of these three priority ecoregions was categorized as critically endangered (Olson and Dinerstein 1998).

Table 1 Species richness and percentage endemism of different taxa for the three priority conservation regions in South Africa. (Data sources were as follow: Cape Floristic Region (Conservation International. Downloaded from http://www.biodiversityhotspots.org/xp/hotspots/cape_floristic/Pages/biodiversity.aspx on 30 September 2010), Succulent Karoo (Driver *et al*. 2003) and Maputaland-Pondoland-Albany (Conservation International Southern African Hotspots Programme and South African National Biodiversity Institute 2010)).

Cape Floristic Region

	Species richness	**Endemic species**	**Endemism (%)**
Plants	9000	6210	69
Mammals	91	4	4.4
Birds	323	6	1.9
Reptiles	100	22	22
Amphibians	46	16	34.8
Freshwater fish	34	14	41.

Succulent Karoo

	Species richness	**Endemic species**	**Endemism (%)**
Plants	6356	2535	40
Mammals	68	6	9
Birds	431	1	<1
Reptiles	121	24	20
Amphibians	17	5	29
Bees and termites	177	68	38
Scorpions	70	18	26

Maputaland-Pondoland-Albany

	Species richness	**Endemic species**	**Endemism (%)**
Plants	8100	1900	23.5
Mammals	194	4	0
Birds	541	0	14.4
Reptiles	209	30	15.3
Amphibians	72	11	27
Freshwater fish	73	20	4

The national spatial biodiversity assessment for South Africa identified nine broad priority areas that require conservation action at a national level (Driver *et al*. 2005). Priority areas were selected based on biodiversity features, degree of representation of biodiversity features in protected areas, and current and future threats. Biodiversity features were accounted for by considering species of special concern (threatened species and species endemic to South Africa), ecological processes operating at the national spatial scale (e.g. areas of C-sequestration and altitudinal and climatic gradients represented by mountain ranges), and degree of irreversible biodiversity loss as a result of specific land uses (e.g. plantations, cultivated areas, urban development, mines and quarries) in different ecosystems (Driver *et al*. 2005). Using this approach, the Succulent Karoo, Cape Floristic Region, Albany thicket and wildcoast, and Maputaland-Pondoland were, once again, included as areas requiring conservation action at national level (Driver *et al*. 2005).

Threats to biodiversity in South Africa

Biodiversity loss in South Africa is increasing and ecosystem health is declining as human pressure on ecysystems is increasing (Department of Environmental Affairs and Tourism 2006). Approximately 13% of plant species, ~ 10% of birds, ~10% of frogs and ~ 20% of mammals are threatened with extinction (Critically Endangered, Endangered and Vulnerable) (Department of Environmental Affairs and Tourism 2006).

In addition to 2 577 threatened plant species (~13 %), a further 11% of plants (2 232 species) are of conservation concern (Extinct, Extinct in the Wild, Near Threatened, Data Deficient, Critically Rare, Rare and Declining) (Raimondo and von Staden 2009). Of the threatened plant species, 67% (1726 species) are located in the Fynbos Biome (Raimondo and von Staden 2009), 10% (269 species) are in the Succulent Karoo Biome (Raimondo and von Staden 2009) and 20% (535 species) are in the Maputaland-Pondoland-Albany biodiversity hotspot (Conservation International Southern African Hotspots Programme and South African National Biodiversity Institute 2010).

In decending order of importance, the three primary threats to plant species in South Africa are habitat loss (e.g. crop cultivation, and urban and coastal development), habitat degradation (e.g. overgrazing and changes in natural fire regime) and invasive alien species (Raimondo and von Staden 2009).

Important conservation areas in KwaZulu-Natal

Assigning priority status depends on vulnerability and irreplaceability of that specific area. Areas with highest priority status are those with high vulnerability and high irreplaceability (Pressey and Taffs 2001). Vulnerability is based on the probability of habitat transformation (e.g. threat of future habitat transformation), while irreplaceability is defined as "the likelihood that a given site will be needed to ensure achievement of a set of regional conservation targets" (Ferrier *et al*. 2000).

The concept of irreplaceability is underpinned by the principle of complementarity, which entails selection of 'new' reserve areas that complement existing nature reserves (i.e. selection criteria that prevent duplication of existing formally-protected areas) (Justus & Sarkar 2002). Therefore, the aim of priority areas is to complement formally-protected areas in reaching representation goals across the landscape (Fairbanks & Benn 2000).

In the past, however, formally-protected areas were established in an ad hoc manner on land with low agricultural potential or were aimed at conserving only a few charismatic species (Pressey 1994). Representation of regional biodiversity was, therefore, invariably biased. Fertile landscapes, suitable for agriculture and forestry, were under-represented, while landscapes unsuitable for commercial activity were over-represented (Pressey 1994). Future conservation action should not reinforce this existing bias (Government of South Africa 2010). Rather, a combination of existing formally-protected areas and 'new' priority areas should conserve biodiversity patterns, as well as processes that drive long-term persistence of these patterns (Fairbanks & Benn 2000; Pressey 1994; Knight *et al*. 2007).

Regional-scale spatial planning in KwaZulu-Natal Province

The approach of selecting priority areas are framed by the hierarchical approach to biodiversity (i.e. genes, species, populations, communities and landscapes, as in Noss (1990)). Based on different levels in the biodiversity hierarchy (i.e. species and landscapes), two different approaches of identifying priority conservation areas can be seen within the administrative boundaries of KwaZulu-Natal province, South Africa.

The first conservation assessment evaluated how well existing protected areas in KwaZulu-Natal represent distributions of 37 endemic insect species, representing five orders (Coleoptera, Diptera, Lepidoptera, Mecoptera and Odonata) (Armstrong 2002). The aim of this conservation assessment was to assign conservation value to landscape units, as this would guide decision-making regarding authorization of proposed land use changes (e.g. livestock grazing to forestry) (Armstrong 2002).

The second conservation assessment for the KwaZulu-Natal province followed a biophysical approach, where the whole province was first divided into landscape units based on their physical environment (i.e. topographic position and climate). These landscape units were then grouped into ecoregions based on vegetation type (i.e. biological environment) and soil nutrient status (as derived from geological data) (Fairbanks & Benn 2000).

Interestingly, both conservation assessments identified the high-lying areas in the northwest and the central midlands of KwaZulu-Natal as priority areas worthy of conservation. Also, both approaches found the northeastern coastal zones and adjacent inland areas, and the high-lying Drakensberg regions adequately protected (Armstrong 2002; Fairbanks & Benn 2000).

A conservation assessment for the Maputaland Centre of Endemism (spanning the northeastern parts of KwaZulu-Natal (South Africa), eastern parts of Swaziland and southern parts of Mozambique) was conducted as part of the Lubombo Transfrontier Conservation Area (TFCA) (Smith *et al.* 2008). This conservation assessment identified priority conservation areas within the Maputaland Centre of Endemism based on 111 conservation features (i.e. species distribution, landcover types and ecological processes), future risk of agricultural transformation and current levels of protection. The conservation features were 44 natural landcover types, 14 ecological processes and 53 species. Of these species, 20 were plant species, 13 were invertebrate species and 20 were vertebrate species. Vertebrate species were further divided into 11 species with wide distribution ranges and nine species that were restricted to a specific land cover. The ecological processes were selected in such a manner that they could be represented spatially. They were (1) sufficiently large patch size to maintain natural fire regimes, (2) sufficiently large patch size to maintain natural grazing regimes and (3) linkages to maintain connectivity throughout the landscape (Smith *et al.* 2008).

The Metapopulation trio of large patch size, good habitat quality and reduced patch isolation (Samways 2007b) is addressed in this conservation assessment, as large areas are needed to optimize management of natural disturbance regimes and linkages will reduce patch isolation. These linkages include habitat that has been transformed to some degree by agricultural practices (Smith *et al.* 2008). However, none of these linkages have been implemented in the proposed conservation landscape. Thus, no data are available on whether proposed structural linkages will connect landscapes functionally, and whether these linkages contribute to biodiversity conservation.

In addition to 44 natural landcover types, there were four anthropogenic landcover types (towns, subsistence agriculture, commercial agriculture and plantations). If these four anthropogenic landcover types exceeded a predefined limit, they were excluded from conservation portfolios (Smith & Leader-Williams 2006). The reason for excluding these land uses was to avoid conflict between contrasting land uses (e.g. commercial agricultural vs. conservation) (Smith *et al.* 2008) and because these anthropogenic landcover types seldom support high levels of indigenous biodiversity.

Reconciling anthropogenic land uses with biodiversity conservation

The landscape can be roughly divided into two categories, natural vegetation and transformed habitat. Generally, natural vegetation is transformed for commercial purposes (e.g. agriculture or forestry) and results in biodiversity loss. As the aim of conservation action is to reduce the current rate of biodiversity loss, innovative ways of reconciling commercial activities with conservation have to be found. ENs of natural vegetation, managed for biodiversity conservation purposes and located within the commercially-productive landscape, is one such an approach.

Regional conservation assessments (Armstrong 2002; Smith *et al.* 2008) identify priority conservation areas at the regional spatial scale and can be seen as arteries allowing regional movement of fauna (e.g. migration routes). Landscape ENs can be seen as capillary blood vessels that facilitate movement of animals over smaller spatial scales e.g. from nature reserves to other core areas in the landscape. Core areas might be either formally-protected nature reserves or large tracts of high quality natural habitat in a transformed matrix. Core habitat areas provide in all resource required by target species to complete their life cycle and, therefore, sustain source populations of these species.

Commercial forestry plantations in the Grassland Biome

Grasslands are globally widespread, and often cover large areas (Zedler 2007). In South Africa, the Grassland Biome covers ~ 16.5 % of the country, although only 1.6% is formally conserved (Neke & du Plessis 2004). The Grassland Biome is generally at high elevations in areas with high rainfall and fertile soils (MacDonald 1989). These grassland areas are extensively utilized by humans (Hannah *et al.* 1994), partially due to grasslands' suitability for farming and forestry purposes (O'Connor 2005). With the exception of livestock and game ranching, all farming and forestry activities have a severe impact on the function and composition (i.e. habitat and species) of South African moist grassland (O'Connor & Kuyler 2009). The magnitude of the effect of these land uses on ecosystem function and composition depend on the extent of habitat transformation (O'Connor & Kuyler 2009).

Established to fulfill the timber demands of South Africa (Witt 2002), commercial plantations currently cover 1.257 million hectares or 1.1% of the total land area (Department of Water Affairs and Forestry 2009). These plantations occur mostly in the Grassland Biome. Commercial forestry has fragmented the natural landscape, causing isolation of remnant grassland patches, which impedes movement and jeopardizes local survival of sensitive species. In addition to the effect of fragmentation on suitable habitat, commercial plantations affect species composition of birds (Allan *et al.* 1997), plants (Proenca *et al.* 2010) and ground-living invertebrates (Bonham *et al.* 2002; Ratsirarson *et al.* 2002; Samways *et al.* 1996), and also impact on catchment hydrology (Scott & Lesch 1997; Vertessy 2001; Huang *et al.* 2003), soil carbon cycles (Davis & Condron 2002; Zinn *et al.* 2002) and soil bulk density, which, in turn, influences soil erosion (Tewari 2001).

Despite the detrimental effect of commercial forestry on natural grassland ecosystems, indigenous forest is not a feasible alternative to supply the timber demand of South Africa, as it is the smallest biome in South Africa, covering ~ 0.3 % of the total surface area (Fairbanks *et al.* 2000). In addition, extraction of timber resources from indigenous forest would pose a serious operational challenge, as the Indigenous Forest Biome is extensively fragmented with most forest fragments < 1 km^2 in size (Low & Rebelo 1996). Rather than considering indigenous forest as an alternative source of timber, alternative ways of reconciling commercial forestry practices with conservation had to be found. Grassland ENs situated among commercial forestry plantations, and managed for biodiversity conservation were such an alternative, and were the focus of this study.

For the purpose of this study, ENs are interconnections of corridors, nodes and spatial landscape features (e.g. rocky outcrops, wetlands and hills) among forestry plantations (Samways *et al.* 2010). Approximately a third of land belonging to forestry companies remains permanently unplanted and constitutes the EN (Samways 2007a). It includes wetland, grassland and indigenous forest, as well as firebreaks, access roads and power lines (Samways *et al.* 2010). ENs are implemented in addition to formally-protected nature reserves (Samways 2007a) and are not meant to replace them.

The primary objective of ENs among forestry plantations in South Africa is biodiversity conservation (C. Burchmore, pers. comm.), while it is acknowledged that successful conservation is not possible without the support of local communities (Knight *et al.* 2006). In Russia, support of local communities in affairs concerning public goods was strongly influenced by their socio-economic background, which, in turn, influenced local communities' trust in strangers' fairness and their fear of being exploited (Gachter *et al.* 2004). For this reason, socio-economic history of local communities needs to be taken into account when development, implementation and management (including goals) of ENs are considered.

The landscape spatial scale of these ENs coupled with land typically belonging to a single landowner (i.e. forestry company), means that planning and implementation of ENs are simpler than in cases where multiple administrative boundaries and multiple landowners need to be considered (e.g. Pan-European Ecological Network).

Previous research on Ecological Networks (ENs) among commercial forestry plantations

Depending on the geographic area in question, implementation of ENs among forestry plantations was completed between six and 20 years ago. This presented the unique opportunity to test various aspects of these landscape features that could not be tested before implementation was completed. All these studies were conducted in the Midlands of KwaZulu-Natal, one of the priority regions identified in provincial conservation assessments (Armstrong 2002; Fairbanks & Benn 2000).

Spatial parameters

Occurrence, movement patterns and behavior of butterflies and birds provided insight into these species' responses to certain landscape design parameters for ENs in a South African context. For butterflies, a wide (~ 250 m) corridor not only functioned as a conduit for movement between desirable habitat patches, but also as habitat per se (Pryke & Samways 2001). As a result of reproductive, basking, resting and territorial behavior in wide corridors, butterfly densities was higher than in narrow corridors. In addition, there were more plant species in wide corridors than in narrow corridors, which meant that some specialist butterfly species could be accommodated (Pryke & Samways 2003).

A study on birds in ENs among forestry plantations found that grassland specialist birds were also not affected by design variables (e.g. corridor width, distance to nearest nature reserve, proportion edge habitat or physical connectivity provided by corridors), but rather by specific habitat types associated with narrow and wide corridors, respectively (Lipsey and Hockey 2010). Amount of open habitat within a 100 ha area and time since last fire affected grassland specialist birds (Lipsey and Hockey 2010).

Generally, these results agreed with findings from another study that investigated ecological associations between flowers and arthropods in ENs among forestry plantations (Bullock and Samways 2005). In this study, arthropod-plant associations were not significantly affected by distance to nearest nature reserve, number of plantation borders or corridor width. Rather, arthropod-plant associations were most strongly influenced by host plant occurrence. Host plant occurrence, in turn, was negatively affected by high levels of disturbance (i.e. grazing and trampling). Thus, cattle grazing was identified as the main threat for arthropod-plant associations (Bullock & Samways 2005).

Habitat quality

Habitat quality is intricately linked to the retention and persistence of spatial patterns in biodiversity, which, in turn, is the result of ecological and evolutionary processes. Some processes that influence persistence of biodiversity in the Succulent Karoo were (1) maintenance of interspecific interactions (e.g. faunal dispersal and pollination, plant-herbivore interactions and predator-prey interactions), (2) maintenance of regional faunal movement (e.g. migration, refugia against extreme climatic conditions and breeding ground for birds), (3) maintenance of disturbance regimes (e.g. fire, grazing and small mammal soil disturbances) and (4) resilience to climate change (e.g. elevational and rainfall gradients) (Cowling *et al*. 1999).

Similar factors probably influenced butterfly communities in the Grassland Biome. For example, high quality grassland habitat was essential for biodiversity conservation in ENs among forestry plantations, with wide, undisturbed grassland corridors having similar butterfly species richness and abundance than adjacent nature reserves (Pryke & Samways 2003). There were three factors relating to habitat quality that affected butterfly assemblages. In decreasing order of importance, they were (1) nectar plants, (2) cattle disturbance and grass height, and (3) percentage alien plant cover. These three factors had a larger effect on butterflies than any of the design variables (e.g. corridor width or distance to nearest nature reserve) (Pryke & Samways 2003). At this point, it is not known how well ENs will ensure long-term persistence of these and other species in the landscape.

Edge effect

Habitat quality is not only affected by intensive cattle grazing, but also by proximity to pine trees. The negative effect of pine plantations on grasshopper species richness and diversity reached ~ 30 m beyond the tree border (Samways & Moore 1991), while butterflies were affected up to ~ 20 m (Pryke & Samways 2001). While grasshoppers were influenced through the effect of pines on plant diversity, vegetation cover and vegetation structure (Samways & Moore 1991), butterflies were influenced behaviorally, as butterflies turned away from the plantation edge (Pryke & Samways 2003).

Cattle grazing

It is clear that high-intensity cattle grazing can jeopardize biodiversity conservation in landscape ENs. In the southern Drakensberg, grazing pressure on communual areas was higher than on commercial areas (O'Connor 2005). These different grazing regimes had an effect on plant species composition, but not on plant species richness of indigenous grassland in the southern Drakensberg grasslands (O'Connor 2005). In the Succulent Karoo, invertebrate species richness was greater on commercial farms with moderate grazing intensity, but invertebrate abundance was higher on communual land with high grazing intensity (Seymour and Dean 1999). Although there were no differences in plant species richness between communual land and commercial farms, there were differences in plant species composition (Todd and Hoffman 1999). There were more plants tolerant of heavy grazing (e.g. annuals and geophytes) on communual land and more large palatable shrubs and leaf succulents on commercial farms (Todd and Hoffman 1999). Another study investigated the effect of different shrub densities, which is linked to heavy grazing, on arthropods in semi-arid savanna in the Southern Kalahari. Increased shrub cover was found to be linked to an increase in abundance of ants, scorpions and dung beetles, but a decline in abundance of grasshoppers and solifuges (Blaum *et al*. 2009).

Although arid regions are more sensitive to impacts of domestic livestock than areas with wetter climates or areas that evolved with large mammals (Mack and Thompson 1982), grazing also had an effect on biota of the Grassland Biome. Commercial sheep farms in highland grassland of the Mpumalanga province affected diet of redwing francolin (*Francolinus levaillantii*) (Jansen *et al*. 2001). Areas that were heavily grazed and frequently burned had lower grass height, lower vegetation cover, and lower abundance and diversity of redwing francolin food plants. These changes in food plant availability were reflected in redwing francolin diet, as fewer francolin food plants and more invertebrates were ingested in heavily-grazed and frequently-burned areas (Jansen *et al*. 2001).

These results are similar to studies conducted elsewhere. In Germany, extensively grazed pastures had higher insect species richness than intensively grazed pastures. Differences in insect species richness were explained by differences in vegetation height (Kruess and Tscharntke 2002). In Britain, it was shown that grazing affects arthropod species richness and abundance through its effect on vegetation structure (Morris 2000).

Although the importance of an “insulating blanket” of vegetation for some invertebrates (e.g. grasshoppers in Samways 1990) is not denied, South African grasslands and associated invertebrates are adapted to grazing by indigenous herbivores. It was found that grazing and trampling by indigenous game is accurately represented by the effect that cattle have on grasshopper communities (Samways & Kreuzinger 2001). Grasshopper species richness was not negatively affected by cattle grazing per se. Rather, it was the intensity of defoliation and trampling that resulted in depauperate invertebrate communities (Gebeyehu & Samways 2002).

Burning

Correct management of burning and grazing regimes are two of the most important management objectives in grassland ENs among forestry plantations. Both burning and grazing affect vegetation structure. Grasshoppers generally prefer tall grass with high percentage cover (Samways & Moore 1991), as it provides protection against predators (Joern 1982) and microclimatic stability (Samways 1990). In contrast, grassland specialist bird species prefer regularly-burned grassland in wide, open grassland areas (Lipsey & Hockey 2010).

Fire is a natural disturbance in South African grasslands, originally caused by lightning strikes. In South Africa, density of lightning strikes increases with elevation up to 1 500 m above sea level, and decreases thereafter (Bhikha 2007). Lightning strike density ranges between 6 and 12 strikes/year/km^2 in the lowlands of KwaZulu-Natal, but is substantially higher in the midlands (25-50 strikes/year/km^2) (Bhikha 2007).

However, it is only a small percentage of lightning strikes that ignites vegetation nowadays, as most savannas and grasslands in Africa are shaped and maintained by anthropogenic fires (Trollope 2003). Indeed, anthropogenic fires (e.g. prescribed burning, and fires ignited by refugees and poachers) were responsible for 90% of the total area burned in Kruger National Park from 1985 to 1992. Only 10% of the total burned area was ignited by lightning (Trollope 2003).

In Africa, fire can be used to manage relative proportions of palatable and unpalatable grass species, to control invasion of woody species, to conserve fire-dependent plant communities and to reduce fire hazard around forestry plantations (Bond and van Wilgen 1996). *Why* we burn greatly influenced *how* we burn. For example, intensity of fires aimed at controlling bush encroachment will be high, while fire intensity in grassland ENs will be low, as fire hazard of commercial plantations needed to be considered. Fire management in grassland ENs follow a ‘forage management’ approach, as burning was recommended when abundance of unpalatable, climax grass species that were typical of underutilized grassland (i.e. increaser 1) increased above a certain threshold (F. de Wet, pers. comm.).

Commercial forestry plantations adjacent iSimangaliso Wetland Park

iSimangaliso Wetland Park, in northeastern KwaZulu-Natal, was proclaimed in 1895 specifically for the conservation of large game species (Thompson 2002). It is the oldest and one of the largest formally protected areas in South Africa (Department of Environmental Affairs and Tourism 2004). Declared as a RAMSAR site in 1986 and a UNESCO World Heritage Site in 1999, iSimangaliso Wetland Park contributes significantly to biodiversity conservation in the region (United Nations Environment Programme & World Conservation Monitoring Centre 2008). "The natural systems of the iSimangaliso Wetland Park are unique within southern Africa… for hydrological and ecological processes of Lake St. Lucia with its fluctuating salinity and adapted biota "(United Nations Environment Programme & World Conservation Monitoring Centre 2008). However, forestry was identified as one of three land uses that negatively affected hydrology of Lake St. Lucia (Weston *et al.* 1995) and associated biota.

The area surrounding Lake St. Lucia originally belonged to the State, and was managed by the Department of Forestry during the 1950s. During this time, commercial plantations were established on the Western and Eastern Shores of Lake St. Lucia (Bainbridge 2003; Thompson 2002). In 1990, government authorities agreed that plantations should be cleared over the next 20 years, and that the area should be managed as a statutory conservation reserve (Kruger *et al.* 1997). Consequently, ~ 5 600 ha of plantations on the Eastern Shores were cleared. This did not immediately apply to plantations on the Western Shores (Bainbridge 2003).

In 2001, effect of plantations on iSimangaliso Wetland Park was investigated by the Lubombo Spatial Development Initiative (LSDI), as plantations could affect tourism potential of iSimangaliso Wetland Park and the surrounding area. It was found that plantations close to Lake St. Lucia, in the eastern extremity of the Western shores, had a negative effect on hydrology of the lake. However, plantations in the western extremity of the Western Shores did not have any significant effect. Therefore, the landscape was divided into two zones: the Natural Zone (~ 9 000 ha) in the east, adjacent Lake St. Lucia, and the Commercial Afforestation Zone in the west (~ 15 000 ha) (Bainbridge 2003).

Criteria for inclusion into the Natural Zone were (1) important natural communities (e.g. swamp forest), (2) water source areas (e.g. catchment areas) and (3) wetlands (i.e.

hydromorphic soils). Thus, the curvilinear, delineation boundary (also known as the "Ecotrack") separates hydromorphic wetland soils of the Natural Zone from dryland soils of the Commercial Afforestation Zone (Bainbridge 2003).

In 2004, the new plantation holder (SiyaQhubeka Forests (Ltd.)) and iSimangaliso Wetland Park signed the Buffer Zone Incorporation Agreement. This agreement entails a commitment to conservation from all interested parties, and resulted in clearing of plantations in the Natural Zone. After plantations were cleared, the Natural Zone was consolidated with iSimangaliso Wetland Park and rehabilitated back to near-natural wetland and grassland habitat (Bainbridge 2003).

In addition to the Natural Zone, there are 2 170 ha (~ 14 % of the Commercial Afforestation Zone) of unplanted land interspersed among commercial plantations (Karumbidza 2006). While some of these unplanted areas are remnant vegetation that has never been planted (e.g. seasonal wetland, grassland, shrubland or forest), other unplanted areas have been cleared of plantations and are also currently undergoing rehabilitation.

The Ecotrack represents the ownership boundary between SiyaQhubeka Forests (SQF) and iSimangaliso Wetland Park, but the boundary fence does not run along the Ecotrack. It runs around the Commercial Afforestation Zone. Thus, the Natural Zone and other unplanted areas among commercial plantations (e.g. nodes, corridors and stepping stones) are fenced in with iSimangaliso Wetland Park. These unplanted areas are in the spatial configuration of an EN.

This EN, however, has not been assessed according to its primary objective (biodiversity conservation) after implementation. Addressing this knowledge gap will increase conservation efficiency at the landscape and regional spatial scale, for commercial forestry as well as for other commercial land uses. Therefore, the aim of this study was to determine how representative biodiversity found in grassland ENs was of that found in the nature reserve.

Aims and objectives

The overall aim of this study is to determine the biodiversity value of grassland ENs (i.e. unplanted grassland habitat that is managed for biodiversity conservation purposes.) in comparison with an adjacent nature reserve. In other words, does the EN provide suitable habitat for species beyond the borders of the nature reserve?

Representatives of biodiversity will be selected from among faunal manifestations (e.g. dung, tracks, ant nests and molehills) and a wide range of taxa, representing plants, decomposition macrofungi and vertebrates (large mammals and birds). Species richness and composition of this representative sample of biodiversity will then be used to compare grassland habitats in the EN with that in the adjacent nature reserve, while controlling for differences in disturbance regime.

The specific objectives of this study:

- To provide a measure of the extent to which ENs are capable of supporting biodiversity in comparison to an adjacent nature reserve.
- To infer reasons for differences in representatives of biodiversity from peer-reviewed, observational and experimental studies that has been done in grassland and shrubland ecosystems throughout the world.
- To provide guidelines for better management of grassland ENs.

Methods

Study area

In 2001, SiyaQhubeka Forests (Pty) Ltd (SQF) came into existence when Safcol (South African Forestry Company (Pty) Ltd) sold 75% of its shares in the KwaZulu-Natal commercial forests to the SiyaQhubeka Consortium as part of a privatisation process (Breed *et al.* 2005). SiyaQhubeka Consortium is a partnership between Mondi South Africa Ltd (61.8%) and I.L. Holdings (13.2%), a black empowerment partner (SiyaQhubeka. Downloaded from http://www.siyaqhubeka.co.za on 18 October 2010).

SQF is divided into three estates: Port Dunford, Kwambonambi, and the St. Lucia plantations (formerly Dukuduku and Nyalazi) (SGS Qualifor 2007) (E 32°25'; S 28°5') (Figure 1). The St. Lucia plantations (from here onwards referred to as “SQF”) constitute approximately 56% (15 073 ha) of SQF’s total land area, and are fenced in with iSimangaliso Wetland Park (formerly known as Greater St. Lucia Wetland Park) (SGS Qualifor 2007).

iSimangaliso Wetland Park covers ~ 150 000 ha of terrestrial land along the east coast of South Africa in northern KwaZulu-Natal, and is approximately 160 km from Durban. In 1999, it was declared a World Heritage Site under natural criteria vii, ix and x (United Nations Environment Programme & World Conservation Monitoring Centre 2008), which include (1) areas of natural beauty, (2) on-going ecological and biological processes (such as adaptation of flora and fauna to fluctuating salinity in Lake St. Lucia), and (3) its importance for in-situ conservation of biodiversity in natural habitats (World Heritage. Downloaded from http://whc.unesco.org/en/criteria/ on 25 October 2010).

Figure 1 The study area was in the KwaZulu-Natal Province, on the east coast of South Africa. The St. Lucia plantations are displayed in grey (EN study sites:●).

Climate and topography

iSimangaliso Wetland Park and SQF lie within a tropical to sub-tropical climatic zone, with warm, wet summers and mild, dry winters. Rainfall varies considerably from the coast (~ 1200 mm) towards the western, inland areas (~ 800 mm). The mean annual temperature is ~ 21°C (SGS Qualifor 2007; United Nations Environment Programme & World Conservation Monitoring Centre 2008).

The study area is on the southern border of the Mozambique coastal plain, and is characterised by a gentle undulating, flat, sandy landscape that lies between 5 m and 60 m above mean sea level (SGS Qualifor 2007). The topography, together with the high annual precipitation, gives rise to a poorly-drained landscape, where high watertables have caused wetlands to develop within a matrix of higher-lying areas. These wetlands and drainage lines are characterised by clay and hydromorphic soils, with deep sandy soils prevailing and serving as an aquifer within the larger context (Van Wyk 2003).

The whole SQF lies within a single land type (Ha45), which means that the climate, topography and soil type is similar everywhere on the property (Figure 2).

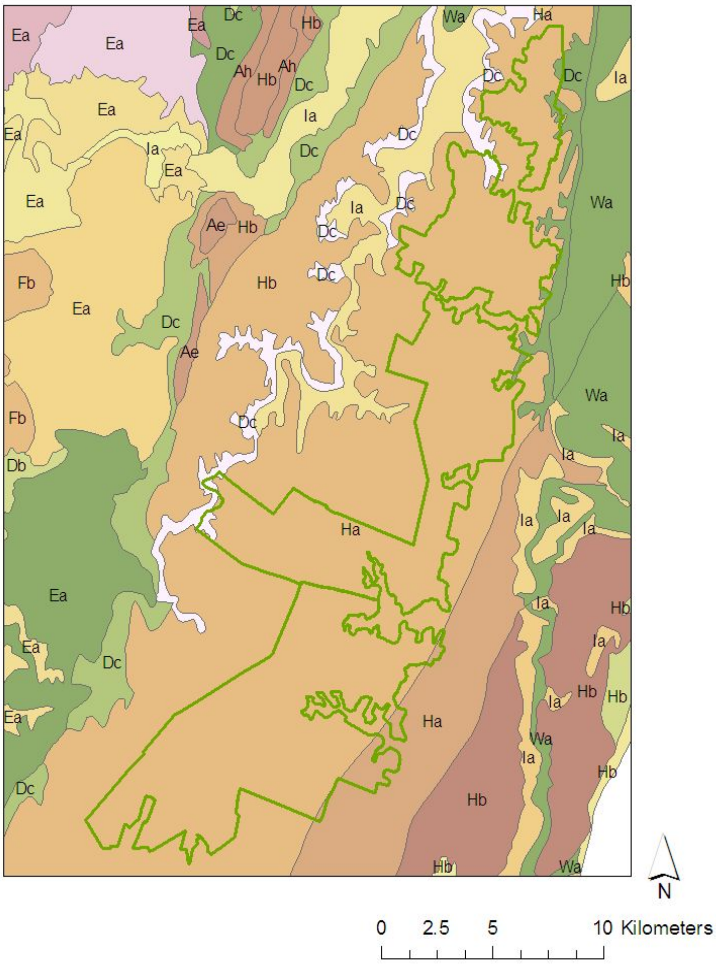

Figure 2 The whole of SiyaQhubeka Forest falls within one land type (Ha), which means that the climate, topography and soil type are similar everywhere on the property. Land type data obtained from the Agricultural Research Council - Institute for Soil, Climate and Water.

Vegetation

The study area was at the southern extreme of the Maputuland Centre of Endemism (van Wyk & van Wyk 1997). According to the National Vegetation Map of South Africa, Lesotho and Swaziland, three dominant vegetation types at SQF are (1) Maputaland Coastal Belt, (2) Maputuland Wooded Grassland, and (3) Northern Coastal Forest (**Error! Reference ource not found.**) (Mucina *et al.* 2005; SGS Qualifor 2007). Local vegetation patterns are mainly controlled by disturbances (e.g. fire and grazing) and water availability (van Aarde *et al.* 2008).

Forestry companies use a different vegetation classification system (The Environmental Conservation Database 1997). A GIS layer of Environmental Conservation Database (ECDB) vegetation classes for all non-commercial areas at SQF was completed in 2001. The system is more detailed than the Vegetation Map of SA, Lesotho and Swaziland (Mucina *et al*. 2005), but it only covers forestry land, not nature reserves.

According to the Vegetation Map of SA, Lesotho and Swaziland (Mucina *et al*. 2005), this study took place in Maputaland Coastal Belt and Maputaland Wooded Grassland. According to the ECDB vegetation classification system (The Environmental Conservation Database 1997), it focuses on undifferentiated wetland areas and closed grassland (Table 2). An undifferentiated wetland area is an area that is not characterised by *Phragmites* reed, *Papyrus* reed, standing water or an artificial dam (The Environmental Conservation Database 1997). Closed grassland has 75-100% grass cover, but less than 10% shrub and tree cover (The Environmental Conservation Database 1997).

Table 2 The Environmental Conservation Database (ECDB) classification system is used by forestry companies to communicate vegetation type at conservation areas in the Ecological Network (EN) (The Environmental Conservation Database 1997). The ECDB GIS layer was completed in 2001, and is shown on all the GIS maps of EN sites.

Natural vegetation categories	**Abbreviation**
Indigenous Forest Undifferentiated	Na
Closed Woodland	Pb
Open Woodland	Pc
Sparse Woodland	Pd
Thicket Undifferentiated	Ka
Bushland Undifferentiated	Ua
Closed Shrubland	Sb
Open Shrubland	Sc
Sparse Shrubland	Sd
Shrubland Proteoid Fynbos	Se
Shrubland Ericaceous Fynbos	Sf
Shrubland Restoid Fynbos	Sg
Shrubland Grassy Fynbos	Sh
Shrubland Fynbos Undifferentiated	Si
Closed Grassland	Gb
Open Grassland	Gc
Wetland categories	**Abbreviation**
Wetland Area Undifferentiated	Wa
Wetland Water	Wb
Wetland Vegetation - Phragmites	Wc
Wetland Vegetation - Papyrus	Wd
Man -Made Dam	We
Transitional area categories	**Abbreviation**
Transitional Area Undifferentiated	Ta
Transitional Plantation Area	Tb
Transitional Weed Area	Tc
Maintained area categories	**Abbreviation**
Maintained Area Undifferentiated	Ma
Maintained Recreational Area	Mb
Maintained Homestead Area	Mc
Bare land categories	**Abbreviation**

Bare Land Undifferentiated	Ba
Bare Land Quarry	Bb
Bare Land Rocky Outcrop	Bc
Bare Land Eroded Area	Bd

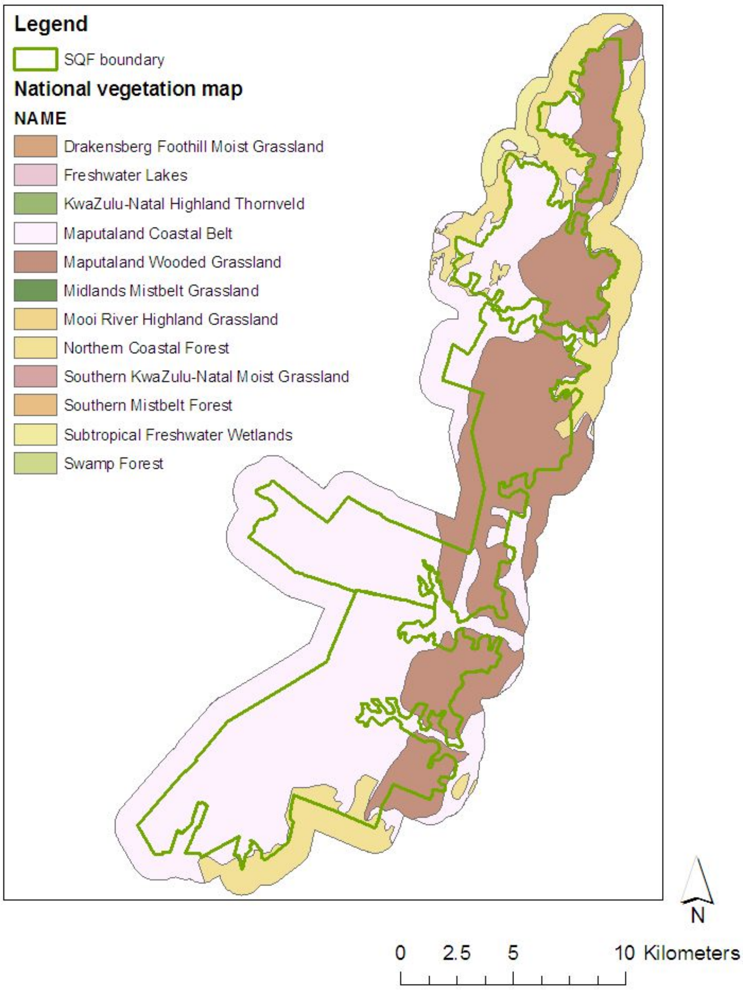

Figure 3 The vegetation type is the same for the majority of SiyaQhubeka Forest (SQF). The two major vegetation types in SQF are Maputaland Coastal Belt (white) and Maputaland Wooded Grassland (purple). Northern coastal forest (lightbrown) is just outside the boundary of SQF. Vegetation data obtained from Mucina *et al*. 2005.

Fauna

iSimangaliso Wetland Park has a wide variety of amphibians (49 species) (Combrink & Kyle 2009a), birds (432 species) (Combrink & Kyle 2009b), mammals (120 species) (Combrink & Kyle 2009c) and reptiles (114 species) (Combrink & Kyle 2009d) (Table 3). According to the iSimangaliso Wetland Park – Threatened Species Program, the Western Shores section of iSimangaliso Wetland Park where the study was conducted is home to 76% of all amphibian species (37 species) (Combrink & Kyle 2009a), 58% of all bird species species (252 species) (Combrink & Kyle 2009b), 47% of all mammal species (56 species) (Combrink & Kyle 2009c) and 46% of all reptile species (52 species) (Combrink & Kyle 2009d). Threatened species of all taxa are listed in Table 4.

Table 3 Total species richness and number of threatened species in iSimangaliso Wetland Park as a whole and for the Western Shores section of iSimangaliso Wetland Park where the study was conducted.

	iSimangaliso Wetland Park Total spp richness	**Western Shores Total spp richness**	**iSimangaliso Wetland Park Nr of threatened spp**	**Western Shores Nr of threatened spp**
Amphibians	49	37 (76%)	4	3 (75%)
Birds	432	252 (58%)	62	32 (51%)
Mammals	120	56 (47%)	43	11 (25%)
Reptiles	114	52 (46%)	18	6 (33%)

A survey of birds, reptiles, mammals (excluding bats) and amphibians at Dukuduku Forestry Estate (SiyaQhubeka Forests) yielded 68 bird species (including two threatened species, namely Rudd’s Apalis and Southern Banded Snake-Eagle), seven amphibian species (including one threatened species, namely Whistling Rain Frog), six reptile species and nine mammal species (including four threatened species, namely Samango’s Monkey, Hottentot Golden Mole, Greater Dwarf Shrew and Forest Shrew (Harvey 2010).

A similar survey at Nyalazi Forestry Estate (SiyaQhubeka Forests) yielded 34 bird species (including two threatened bird species, namely Swamp Nightjar and Black-bellied Bustard), six amphibian species (including two threatened species, namely Whistling Rain Frog and Spotted Shovel-nosed Frog), nine reptile species and 10 mammal species (including two threatened species, namely Reddish-grey Mush Shrew and Least Dwarf Shrew) (Harvey 2010). See Table 4 for scientific names of threatened species.

Table 4 Red Data Listed reptile, mammal and amphibian species occurring on the Western Shores of iSimangaliso Wetland Park.

Common name	**Scientific name**
Amphibians	
Whistling Rain Frog	*Breviceps sopranus*
Spotted Shovel-nosed Frog	*Hemisus guttatus*
Striped Caco	*Cacosternum striatum*
Mammals	
Hottentot Golden Mole	*Amblysomus hottentotus iris*
African Marsh Rat	*Dasymys i. incomtus*
Tonga Red Squirrel	*Paraxerus palliates tongensis*
Samango Monkey	*Cercopithecus albogularis erythrarchus*
Greater Dwarf Shrew	*Suncus lixus gratulus*
Butterfly Bat	*Glauconycteris v. variegata*
Hairy Slit-faced Bat	*Nycteris hispida villosa*
Serval	*Leptailurus s. serval*
Black Rhinoceros	*Diceros bicornis minor*
Honey Badger	*Mellivora c. capensis*
Tsessebe	*Damaliscus l. lunatus*

Reptiles	
Mashona Hinged Terrapin	*Pelusios rhodesianus*
Yellow Bellied Hinged Terrapin	*Pelusios c. castanoides*
Setaro’s Dwarf Chameleon	*Bradypodion setaroi*
Southern African Python	*Python natalensis*
Gaboon Adder	*Bitis gabonica*
Nile Crocodile	*Crocodylus niloticus*

Birds	
African Pygmy-Goose	*Nettapus auritus*
Southern Ground Hornbill	*Bucorvus leadbeateri*
Mangrove Kingfisher	*Halcyon senegaloides*
Black Coucal	*Centropus grillii*
African Grass-Owl	*Tyto capensis*
Swamp Nightjar	*Caprimulgus natalensis*
Denham’s Bustard	*Neotis denhami*
Black-bellied Korhaan	*Lissotis melanogaster*
African Finfoot	*Podica senegalensis*
Collared Pranticole	*Glareola pratincola*
Caspian Tern	*Sterna caspia*
White-backed Vulture	*Gyps africanus*
Cape Vulture	*Gyps coprotheres*
Southern Banded Snake-Eagle	*Circaetus fasciolatus*
African Marsh Harrier	*Circus ranivorus*
Secretarybird	*Sagittarius serpentarius*
African Crowned Eagle	*Stephanoaetus coronatus*
Martial Eagle	*Polemaetus bellicosus*
Pink-backed Pelican	*Pelecanus rufescens*
Great White Pelican	*Pelecanus onocrotalus*
Lesser Flamingo	*Phoenicopterus minor*
Greater Flamingo	*Phoenicopterus ruber*
Yellow-billed Stork	*Mycteria ibis*
Woolly-necked Stork	*Ciconia episcopus*
Saddle-billed Stork	*Ephippiorhynchus senegalensis*
African Broadbill	*Smithornis capensis*
Woodwards’ Batis	*Batis fratrum*

Birds (continued)	
Rudd’s Apalis	*Apalis ruddi*
Red-billed Oxpecker	*Buphagus erythrorhynchus*
Neergaard’s Sunbird	*Cinnyris neergaardi*
Pink-throated Twinspot	*Hypargos margaritatus*
Rosy-throated Longclaw	*Macronyx ameliae*

Description of the study sites

On average, one third of plantation holdings remain unplanted with trees (i.e. exotic *Acacia*, *Pinus* and *Eucalyptus* spp.). These unplanted, non-commercial areas are in the spatial configuration of an Ecological Network (EN) with nodes, corridors and special landscape features (e.g. hilltops and wetlands) (Samways *et al.* 2010). Since plantation trees impact on local biodiversity, the aim of the EN is to mitigate against biodiversity loss experienced at the local spatial scale by implementing ENs at the landscape spatial scale (Samways *et al.* 2010).

Four spatially separated, replicated, matched pairs of sites were selected (to overcome pseudoreplication), with one of the pair within the nature reserve, and the other in the adjacent EN. Of the EN sites, two were near-natural, remnant (from here onwards referred to as “natural”), and two had been cleared of plantations and rehabilitated since 2005 and 2006, respectively. All EN sites were paired with sites in the reserve i.e. two natural sites in the EN were compared with two in the reserve, and similarly, two rehabilitated sites in the EN were compared with two rehabilitated sites in the nature reserve (Table 5). These pairs were designated BP, PGL, RGL and YR and are summarized in Table 5.

The four EN sites were spread throughout the EN (Figure 4). According to the Vegetation Map of SA, Lesotho and Swaziland (2005), vegetation type was Maputaland Wooded Grassland at three pairs of sites, and Maputaland Coastal Grassland at the fourth (PGL) (Figure 4). ECDB classifications were available for two natural EN sites. The natural Maputaland Wooded Grassland site was classified as undifferentiated wetland, and the other natural Maputaland Coastal Belt site was classified as closed grassland (Table 5).

According to the Vegetation Map of South Africa, Lesotho and Swaziland (Mucina *et al.* 2005), two of the four NR sites matched the EN sites with respect to vegetation type. The mismatch of the other two sites (BP and PGL) may have been due to mapping inaccuracies (Thompson *et al*. 2001) or sequential fluctuation in the woody cover as a result of certain management practices (e.g. burning). Nevertheless, pairs of sites were deemed similar by local grassland ecologist, Rick van Wyk, and, therefore, fit for comparison.

Table 5 Pairing Nature Reserve (NR) vs. Ecological Network (EN), the four pairs of study sites according to vegetation type. The pair of sites is first classified according to the Vegetation Map of South Africa, Lesotho and Swaziland (2005) and then the EN sites are classified according to the GIS ECDB layer (2001). Letters printed in bold indicate origin of abbreviation used for each pair of sites. See Table 2 for descriptions of other Environmental Conservation Database (ECDB) abbreviations. The overall vegetation characteristics of the surrounding matrix are also given (⇕ represent site pairs).

Pairs of sites	**NR BP vs. EN BP**	**NR PGL vs. EN PGL**	**NR RGL vs. EN RGL**	**NR YR vs. EN YR**
Site description:	**B**urned, near-**p**ristine grassland with wetland elements	Burned, near-**p**ristine **g**rass**l**and without wetland elements	**R**ehabilitated **g**rass**l**and, cleared in 2005	**Y**ounger, **r**ehabilitated grassland, cleared in 2006
NR sites:	Maputaland Coastal Belt	Maputaland Wooded Grassland	Maputaland Wooded Grassland	Maputaland Wooded Grassland
	⇕	⇕	⇕	⇕
EN sites:	Maputaland Wooded Grassland	Maputaland Coastal Belt	Maputaland Wooded Grassland	Maputaland Wooded Grassland
ECDB vegetation classes (2001)	Undifferentiated Wetland	Closed grassland	Ecotrack Unclassified	Ecotrack Unclassified
Surrounding matrix	Transitional weed areas	Mowed firebreaks & staff housing	Swamp forest Coastal lowland forest Secondary grassland & bushland	Dry forest & thicket

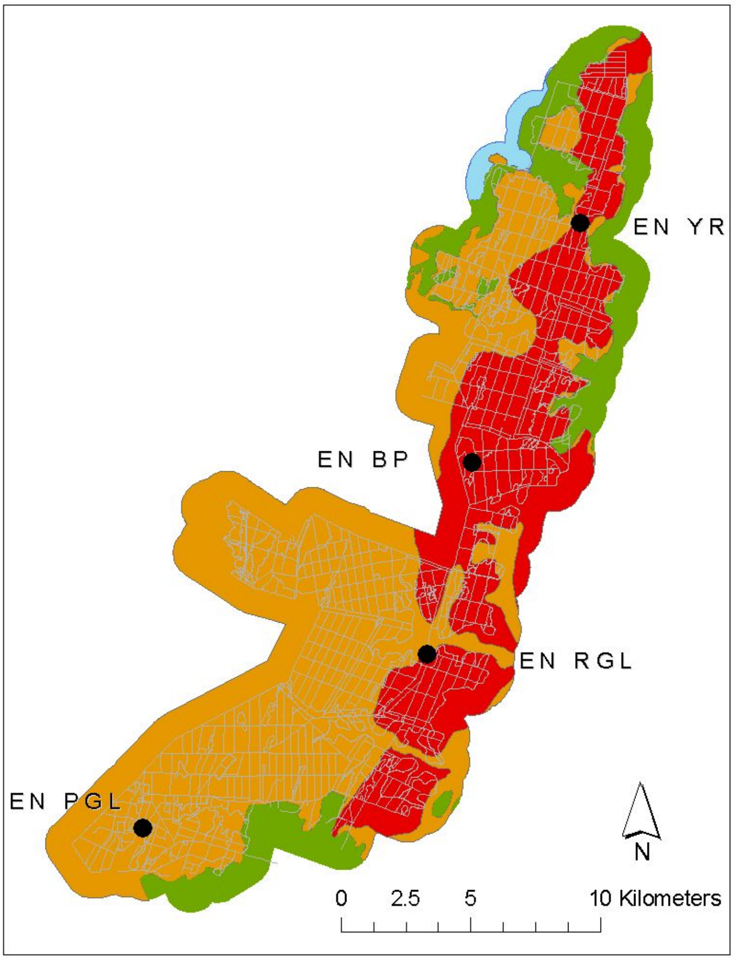

Figure 4 The national vegetation map for SiyaQhubeka (SQF) - St. Lucia plantations. The four EN study sites (solid circles) at SQF are spread out throughout the whole plantation. YR, BP and RGL are located in Maputaland Wooded Grassland (red). Only PGL lies in Maputaland Coastal Belt (yellow). No sites were in Northern Coastal Forest (green) or Subtropical Freshwater Wetlands (blue) (Lines: Roads). See Table 5 for a description of pairs of sites. Vegetation data obtained from Mucina *et al*. 2005.

Table 6 Each EN site was in wide (>200 m) conservation corridors, with a minimum size of 8 ha.

	BP	**PGL**	**RGL**	**YR**
Length (m)	1 900 m	600 m	1700 m	500 m
Width (m)	340 m	230 m	400 m	500 m
Size (ha)	44.8 ha	14.4 ha	~68 ha	~25 ha

EN sites were in wide (>200 m) conservation corridors of good quality, near-natural grassland bordered by commercial eucalypt plantations. Each was within > 8 ha contiguous grassland (Table 6).

Control sites in the NR matched EN sites in terms of aspect, gradient, soil type, habitat type and disturbance history. Disturbance history comprised five categories: (1) approximate time since last fire, (2) grazing intensity, (3) rehabilitation, (4) invasive alien species, and (5) proximity to water sources. Disturbances at each of these pairs of sites are summarized in Table 7.

Table 7 Control sites (NR) were matched to EN sites in each disturbance category. The abbreviations for the grazing intensity are high (H) and moderate (M). Other environmental variables were recorded as yes (Y), no (N) and seasonal (S). A description of each pair of sites is in Table 5. (EN: Ecological Network, NR: Nature Reserve and IAS: invasive alien species)

Pairs of sites	**BP**		**PGL**		**RGL**		**YR**	
Disturbances	**EN**	**NR**	**EN**	**NR**	**EN**	**NR**	**EN**	**NR**
Time since last fire	<6 mnths	<6 mnths	<6 mnths	<6 mnths	~ 3 yrs	~ 3 yrs	~ 2 yrs	~ 2 yrs
Grazing intensity	H	H	H	H	M	M	M	M
Rehabilitation	N	N	N	N	Y	Y	Y	Y
IAS: Guava	N	N	N	N	Y	Y	N	N
IAS: Bugweed	N	N	N	N	N	N	N	N
IAS: Triffid weed	N	N	N	N	N	N	N	N
IAS: Lantana	N	N	N	N	N	N	N	N
Near water source	S	Y	N	Y	Y	S	S	S

Based on availability of large-sized grassland sites in the EN and in the nature reserve, pairs of sites were divided into two categories: burned <6 months ago, and burned ≥ 2 years ago. Grazing intensity was estimated based on a combination of the mean number of animals recorded during four visits to the site, the vegetation structure (vegetation height and density) and the proximity of this site to other areas where animals can graze, assuming large mammals moved through ENs. The invasive alien species recorded were bugweed (*Solanum mauritianum*), triffid weed (*Chromolaena odorata*), lantana (*Lantana camara*) and guava

(*Psidium guajava*). The invasive alien plant species were assigned "present" when more than five plants were encountered on the vegetation transects or if they made up > 10% of the vegetation cover at a site (Table 7). The water sources refer specifically to those where animals could drink water, which included streams and artificial water points. The NR sites matched the EN sites for all disturbances except proximity to water sources (Table 7). This was mostly due to the construction of an artificial water point near the "natural" NR sites, which influenced the control sites for the two natural EN sites (PGL and BP).

1st pair of sites: EN PGL vs. NR PGL

The natural grassland site without wetland elements (EN PGL) was relatively isolated from other good quality grassland sites. The closest, large-sized (7 ha) grassland site was 1.2 km away. In total, there were only 23.4 ha of good quality grassland areas within a 2.5 km radius of EN PGL (Figure 5). This causes a concentration of animals at the available sites and, thus, high grazing pressure (Table 7).

The control site (NR PGL) had a strong woody component in the grass cover, with scattered trees, which sometimes occurred in small (< 40 m^2) clumps. The NR PGL site was located ~ 50 km north of the EN site, and is buffered from commercial plantations by 4 km of Northern Coastal Forest, Maputaland Coastal Belt and Maputaland Wooded Grassland. There were twenty one trial pine plantations, ranging in size between 11 ha and 26 ha, north of the NR PGL site, but these were cleared before 1992 and have since been rehabilitated (i.e. invasive species control and burning). Opposite the road from the NR PGL site was a pine compartment, but it was felled in 2000 and rehabilitated (i.e. burnt). The rehabilitated plantation areas, indigenous tree clumps and gravel road that ran through the site were avoided during sampling.

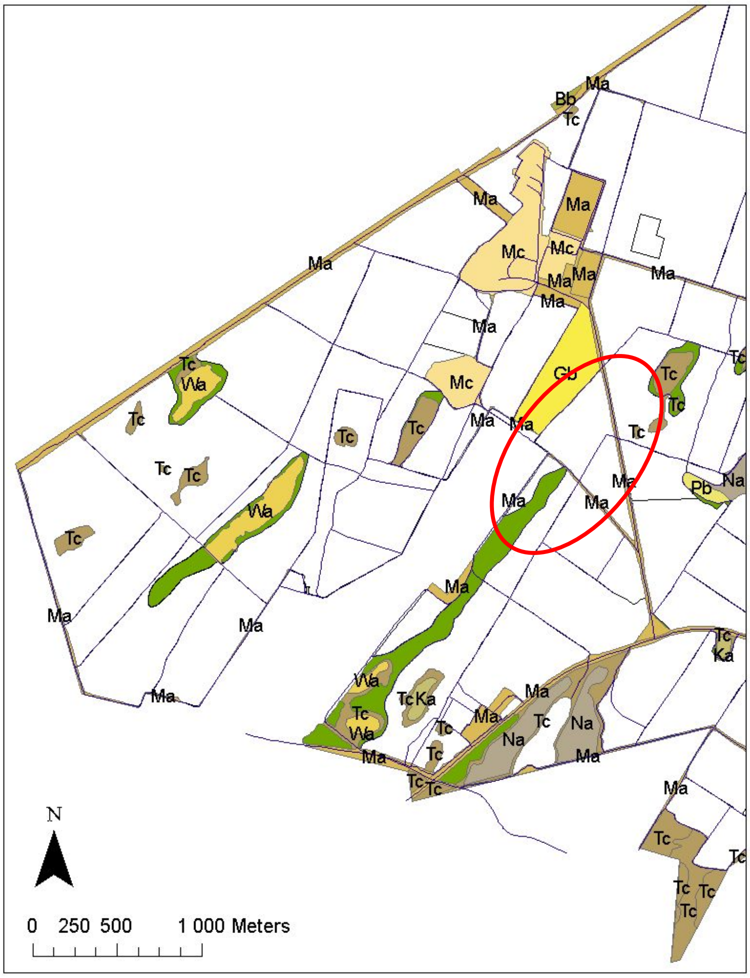

Figure 5 The natural, closed grassland site (EN PGL) is indicated with a red circle. White areas indicate forestry compartments, lines are roads and all colored areas non-commercial areas. All colors except green indicate different Environmental Conservation Database (ECDB) vegetation classes. Green indicates non-commercial areas that do not have ECDB classifications and are currently being rehabilitated. Refer to Table 2 for a description of abbreviations used in the ECDB classification system (The Environmental Conservation Database 1997) and Table 5 for a description of pairs of sites.

2nd pair of sites: EN BP vs. NR BP

The natural, undifferentiated wetland site (EN BP) is the largest natural area within a radius of 2.5 km, and the largest, natural grassland area in the SQF – St. Lucia plantations. It lies against the SQF border, which is demarcated by a gravel road and a 2 m high game fence. The natural, core area of undifferentiated wetland (Wa) is surrounded by a transitional weedy area (Tc), which was previously planted under eucalypt trees, but cleared in 2006 (Figure 6). Sampling was confined to the natural, core area. Herds of zebra (*Equus burchelli*) and blue wildebeest (*Connochaetes taurinus*) occur in this area on a semi-permanent basis. As a result, the grazing pressure is high (Table 7).

The control site (NR BP) is 22 km northeast from the EN site (EN BP), directly adjacent NR PGL, which was the control site for the previous pair of sites (PGL). Thus, 4 km of natural vegetation buffers NR BP from the effect of commercial plantations. The site was partially surrounded with Maputaland Wooded Grassland and Northern Coastal Forest.

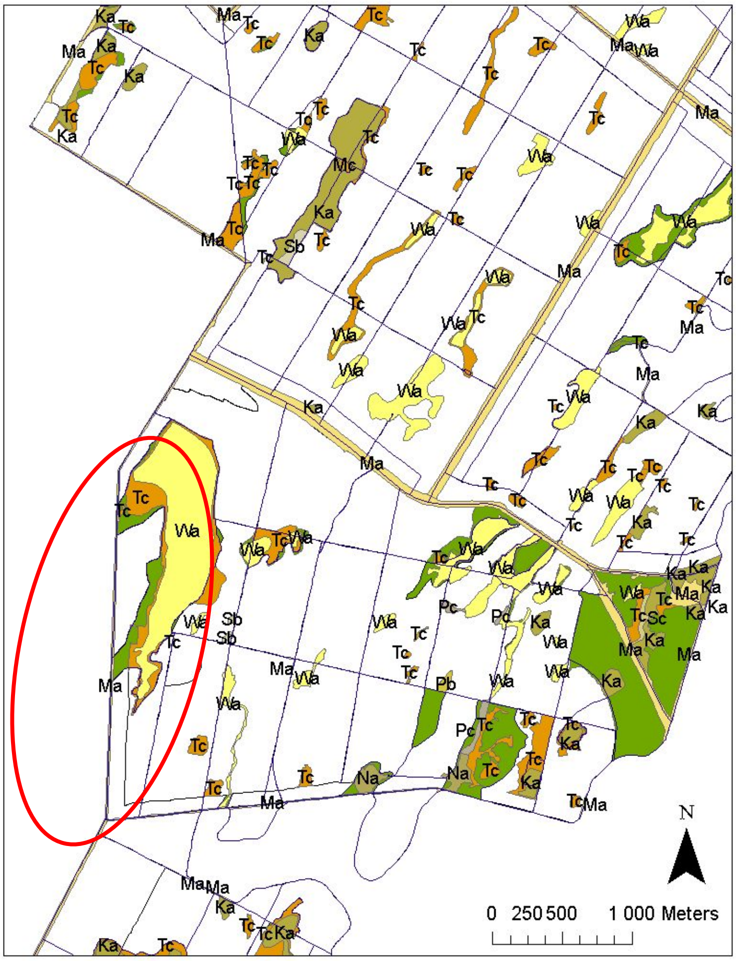

Figure 6 The second natural EN site (EN BP) is indicated with a red circle. It is the largest natural patch in the area, although many smaller patches are in close proximity. White areas indicate forestry compartments, lines are roads and all colored areas non-commercial areas. All colors except green indicate different Environmental Conservation Database (ECDB) vegetation classes. Green indicates non-commercial areas that do not have ECDB classifications and are currently being rehabilitated. Refer to Table 2 for a description of abbreviations used in the ECDB classification system and Table 5 for a description of pairs of sites.

3^{rd} pair of sites: EN RGL vs. NR RGL

According to the Vegetation Map, the older, rehabilitated site (EN RGL) lies on the verge of the Maputaland Wooded Grassland, and Maputaland Coastal Belt (Figure 4). Since it is not possible to map the actual boundary between two vegetation types with absolute accuracy (Thompson *et al.* 2001), it is not possible to say with confidence in which vegetation type the site actually falls. In addition, an ECDB classification is not available for this and other Ecotrack areas, because only conservation areas belonging to SQF have been mapped (Figure 7). The Ecotrack belongs to iSimangaliso Wetland Park and not to SQF. The basic vegetation description for the Ecotrack obtained from iSimangaliso Wetland Park dates back to 2004 just before the pine trees were felled. GIS layers did not keep track with the high rate at which former plantation areas were cleared for conservation purposes (Figure 7). Therefore, the EN RGL site is still mapped as “plantation”.

The last cycle of pine trees at this site (EN RGL) was harvested in 2005. After the logs were stacked, SQF had an extensive runaway fire (September 2005) that burned this and many other areas. As a result, almost none of the logs could be marketed with the majority being rejected and scattered in the field.

Sampling was confined to an area planted under pines pre-2005, currently scattered with burned timber logs and undergoing rehabilitation (i.e. burns and invasive alien species control). Other vegetation types (e.g. coastal forest, secondary grassland and bushland) were avoided (Figure 7). White rhino (*Ceratotherium simum*), hippopotamus (*Hippopotamus amphibius*), buffalo (*Syncerus caffer*), zebra and kudu (*Tragelaphus strepsiceros*) pass through the area on a regular basis. However, animals were free to move and graze throughout the Ecotrack, which caused grazing pressure not to be concentrated at this one site (Table 7).

The control site (NR RGL) was ~ 2 km from the EN RGL site. Although inside iSimangaliso Wetland Park, the site was within close proximity (~ 150 m) of commercial plantations. Timber logs at this site were not scattered, but stacked in piles. Similar to EN RGL, a stream fringed with indigenous forest ran through the site. Forest vegetation was not sampled, as it was not part of the matched pair comparison.

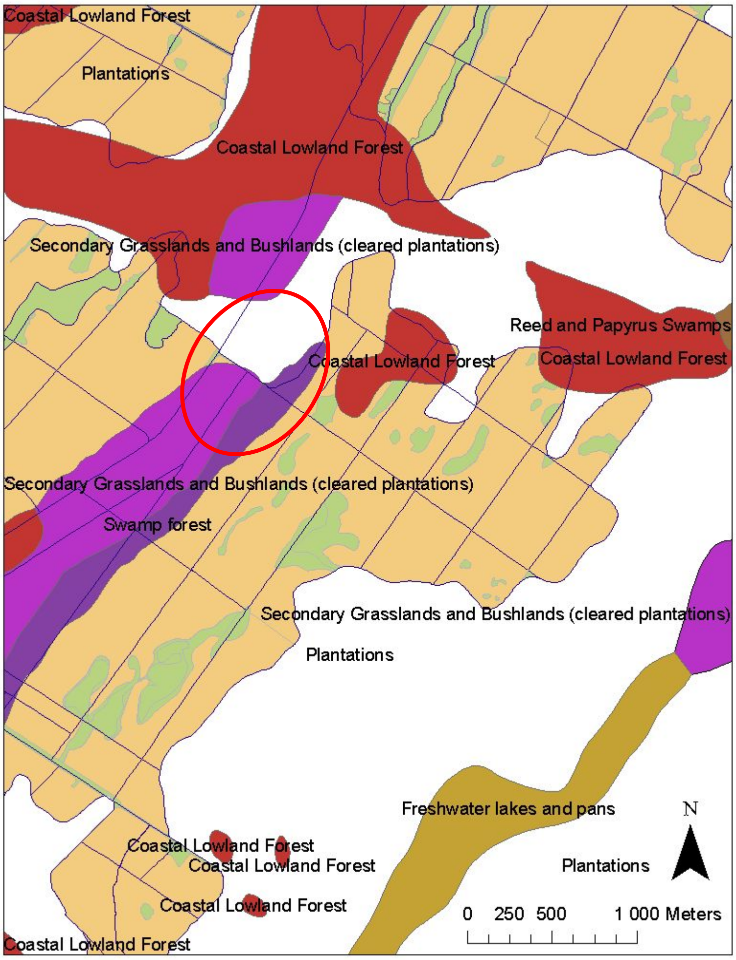

Figure 7 The older, rehabilitated site (EN RGL) is indicated with a red circle. White areas indicate areas that were historically plantations, but that are currently being rehabilitated. Roads (lines), forestry compartments (light brown) and non-commercial areas (green) among the plantations show the context of EN RGL. iSimangaliso Wetland Park provided basic vegetation description (2004) for the Ecotrack, in which this EN site is located. Refer to Table 5 for a description of pairs of sites.

4th pair of sites: EN YR vs. NR YR

The younger, rehabilitated site (EN YR) is in a Maputaland Coastal Belt section of the Ecotrack, very close to Northern Coastal Forest (Figure 8). No ECDB classification is available for the site, as it is located in the Ecotrack (Figure 8). The basic vegetation description for the area, obtained from iSimangaliso Wetland Park (Figure 8), is outdated, as the area is still mapped as "plantation" even though it was cleared of pine trees in 2006, and rehabilitated (i.e. biennial burns and controlling young pine and eucalypt trees) ever since. Sampling was restricted to the rehabilitated grassland on the western side of the gravel road

(Figure 8). Dry forest and thicket vegetation west of the rehabilitated grassland area were avoided, as they were not part of the comparison.

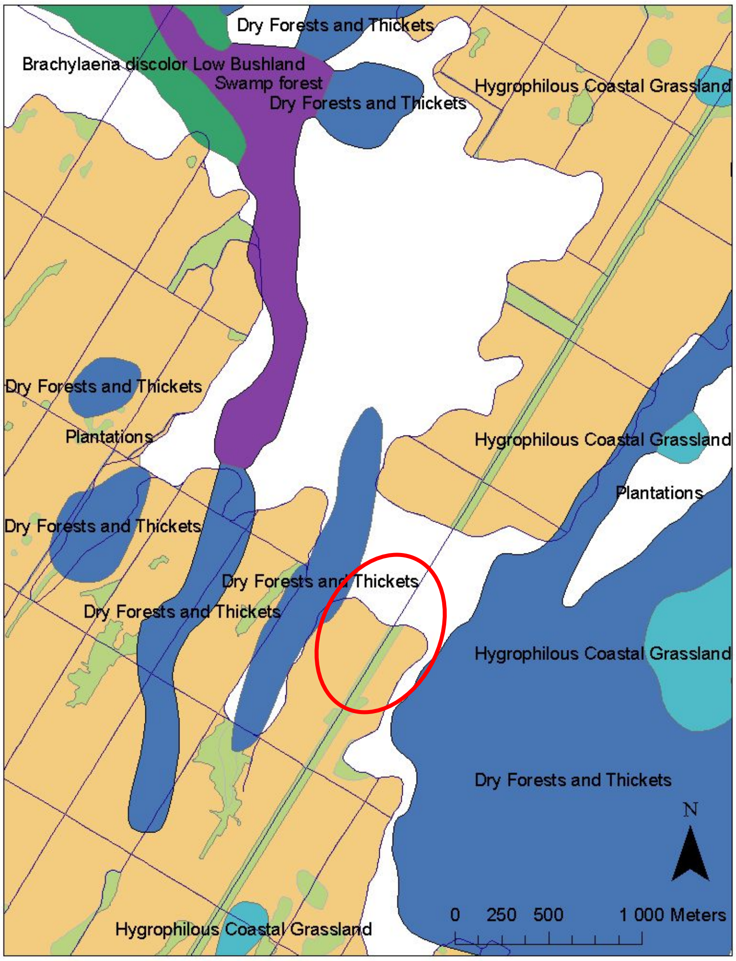

Figure 8 The younger, rehabilitated site (EN YR) is indicated with a red circle. White areas indicate areas that were historically plantations, but that are currently being rehabilitated. Roads (lines), forestry compartments (light brown) and non-commercial areas (green) among the plantations show the context of EN YR. iSimangaliso Wetland Park provided basic vegetation description (2004) for the Ecotrack in which this EN site was located. Refer to Table 5 for a description of pairs of sites.

The younger, rehabilitated site (EN YR) was approximately 2 km from a large-sized (13 ha) undifferentiated wetland area (Figure 8). However, in this current situation, where reliable information on the vegetation type of the Ecotrack is lacking, it is indeed possible that this site forms a continuum with other similar vegetation types. Southern reedbuck (*Redunca arundinum*) frequently visits the area.

The control site (NR YR) was ~ 13 km from the EN YR site, and was buffered from the effect of the plantations by a 600 m wide strip of Maputaland Wooded Grassland. Similar to EN YR, the area was within close proximity (~ 100 m) of indigenous forest. Sampling was confined to the grassland areas around a small (50 m x 50 m) pan depression. The area is frequently visited by blue wildebeest, southern reedbuck, warthog (*Phacochoerus aethiopicus*) and zebra.

This rehabilitated grassland site was part of plantations that were cleared on the Western Shores of iSimangaliso Wetland Park. Thus, grazing pressure by large mammals was not concentrated at any rehabilitated NR site.

Sampling procedure

Sampling was undertaken during October and November 2008. All sites had ten independent sampling units. These sampling units (SUs) were randomly positioned within a site, but spaced at least 50 m apart and at least 50 m from the plantation to avoid the edge effect of the eucalypt plantation matrix (Figure 9).

In each SU, environmental variables (see below), as well as a measure of biodiversity (see below), were measured within a 900 m^2 (30 m x 30 m) area.

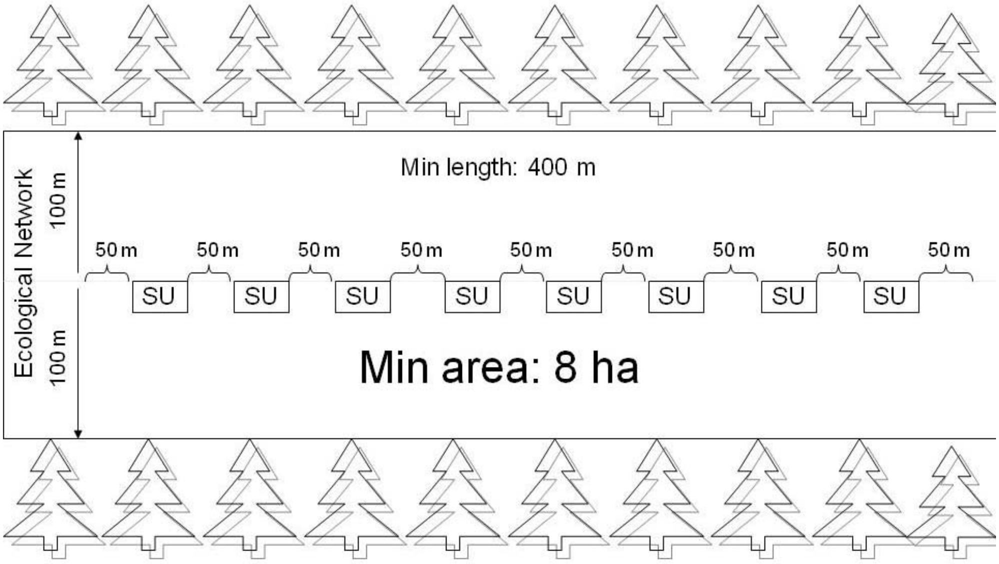

Figure 9 The minimum size of each site was 8 ha. This equals an approximate width of 200 m and a length of 400 m. All sites selected for the purpose of this study were larger than 8 ha (see Table 6).

Biodiversity sampling

A range of taxa (plants, fungi, birds and mammals) and faunal manifestations (e.g. tracks, dung and molehills), that are easy to sample and identify, were selected to represent a broad range of biodiversity. In addition, sampling procedure was designed in such a way that non-expert field rangers would be able, in the future, to sample biodiversity at these sites and elsewhere as part of a monitoring program evaluating conservation success of ENs.

Biodiversity sampling at each SU involved (1) four 4 m^2 (2 m x 2 m) randomly-positioned vegetation quadrats, and (2) an active search for fungi and manifestations (see below) within the 900 m^2 area (Figure 10). Visual sampling accounted for the presence and abundance of more mobile animals (birds and mammals).

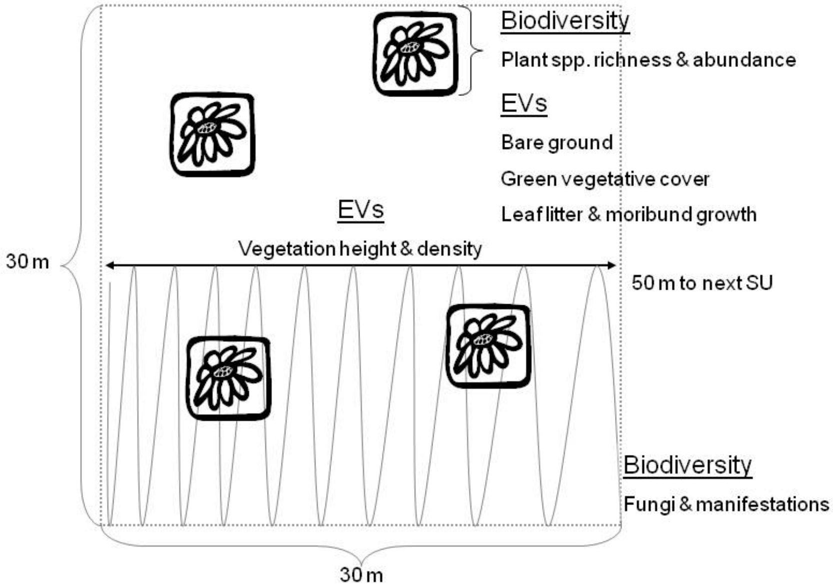

Figure 10 Each sampling unit involved the measurement of environmental variables (EVs) and biodiversity. Biodiversity measurement involved an estimate of plant species richness and abundance (vegetation quadrats), an estimate of the fungi species richness and abundance (active search), and the number of different manifestations (active search). The EVs measured were vegetation height and density (transect), and the percentage bare ground, green vegetative cover, and leaf litter and moribund growth, all of which were estimated in the vegetation quadrats.

Vegetation sampling in the vegetation quadrats accounted for plant species richness and abundance. Percentage cover of each species was estimated, and rounded to the nearest

5%. Where plant species cover was between 1% and 5%, cover was rounded to either 1% or 5%.

If a grass species was not flowering during the sampling period and it had a cover > 1%, it was identified using a grass key based on vegetative traits (Van Wyk 1984). If a geophyte, herb, shrub or sedge species was not flowering during the sampling period and it had a cover of > 1%, it was identified to lowest taxonomic level (Pooley 2005). All plant species that could not be identified, were given morphospecies names and identified later by a local grassland consultant (Rick van Wyk) familiar with plants of the area.

If a geophytes, herbs, shrub, sedge or grass species had a cover of < 1%; it was classified into its relevant growth form category. Cover of the growth form category was then estimated and rounded to the nearest 5%. Where growth category cover was between 1% and 5%, cover was rounded to either 1% or 5%.

Active searches recorded all decomposition macro fungi (from here onwards referred to as ‘fungi’) and manifestations (signs of animal activity e.g. dung, tracks, molehills, ant nests, spider webs) (Table 8) within a 900 m^2 (30 m x 30 m) area. All fungi and all quantifiable manifestations were recorded for 10 minutes (i.e. sampling effort = 5 minutes x 2 people). In the case of animal tracks and dung, it is very difficult for the inexperienced tracker to state the number of animals that moved through the area. Therefore, each type of animal was simply recorded as present or absent (incidence data) when its dung and/or tracks were encountered. The same principle was applied to the small mammal tunnels that were visible in the dense grass.

Animals (i.e. birds and large mammals) occupied much larger areas than the other taxa. Therefore, all birds were documented for 15 minutes per SU (i.e. 1.5 hours per site, at all times of day) within 100 m from the centre of the SU (Figure 11). Large mammals were documented for 1 hour per SU (i.e. 10 hours per site, at all times of day) up to 200 m from the centre of the SU (Figure 11).

Data from surveys at different SUs were summed for each site (Figure 12). The four pairs of sites (BP, PGL, RGL and YR) served as replicates at the spatial scale of the EN and nature reserve, respectively. Based on total number of animal individuals and species at each EN and NR site, mean animal abundance and species richness were calculated for EN and NR.

Table 8 List of manifestations recorded for this study. For data analysis, all manifestations of a single species (e.g. kudu dung and tracks) were pooled as 'present'.

Manifestation types
Ant lion nest
Ant nest (Altar pipe)
Ant nest (Concrete)
Ant nest (Crack)
Ant nest (Granular pile)
Ant nest (Pellet)
Ant nest (Stick)
Blouwildebeest digging
Blouwildebeest dung
Blouwildebeest track
Buffalo track
Bushbuck track
Bushpig track
Common Duiker tracks
Dung beetle burrow
Dung beetle on dung ball
Earthworm casts
Elephant dung
Grazing lawn
Hippo dung
Hippo track
Kudu dung
Kudu track
Mole hill
Nyala track
Otter dung (crab exoskeleton)
Porcupine quills
Praying mantid nest
Red Duiker track
Sandy burrows / Small mammal hole
Sleep / resting spot
Small mammal grass tunnels
Southern Reedbuck dung
Southern Reedbuck track
Spider burrow (Stick)
Spider nest
Spider nest (Grass sack)
Spider tunnel
Spider web
Steenbok track
Termite activity (Plant material/Saw dust)
Termite mound
Warthog burrow
Warthog digging (food)
Warthog dung
Warthog skull
Warthog track
Wasp mud nest ball
Wasp nest
Wasp sandy hole
Waterbuck track
White rhino midden
Zebra dung
Zebra spoor

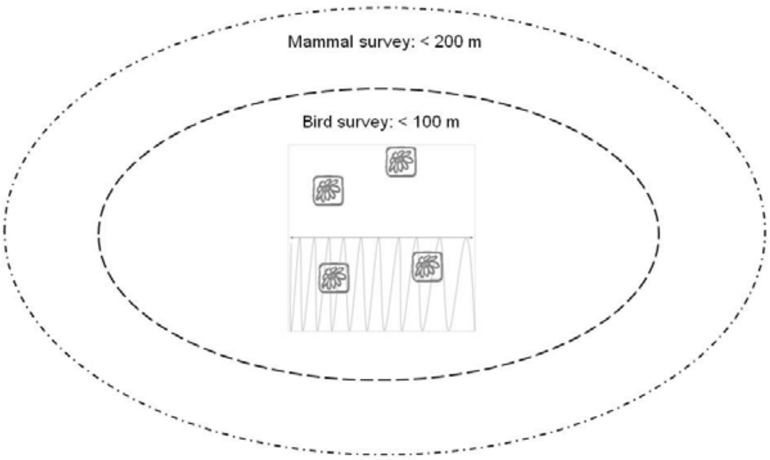

Figure 11 Birds and mammals were each surveyed at different scales. Birds were surveyed within 100 m of the centre of the sampling unit, and mammals up to 200 m.

1

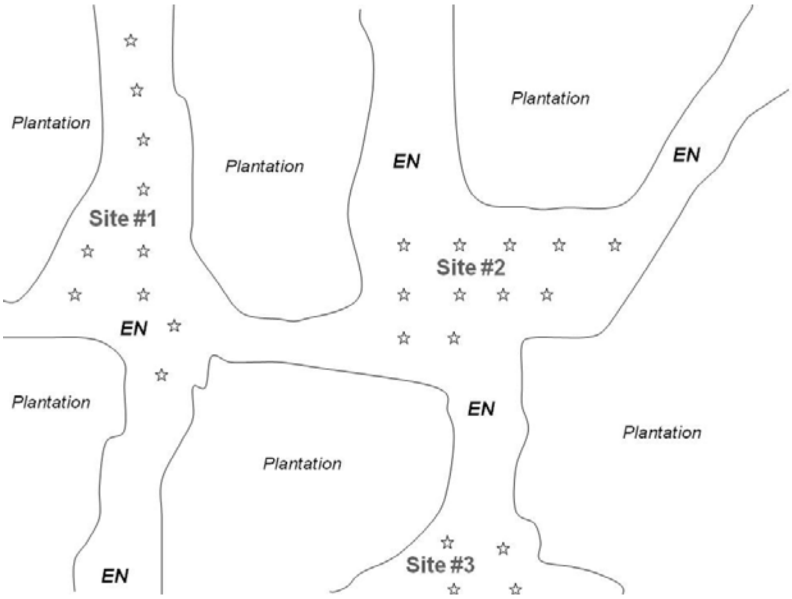

Figure 12 For all taxa, except mammals and birds, data were obtained from 10 sampling units (SUs) (☆) at each site. However, mammals and birds utilize very large areas and are often not seen at the SU spatial scale. Therefore, data from different SUs within a site were pooled. The four pairs of sites (BP, PGL, RGL and YR) then served as four replicates at the Ecological Network and Nature Reserve spatial scale, respectively. See Table 5 for a description of pairs of sites.

2

Butterflies were sampled for 15 minutes per SU within 30 m from the centre of the SU. The use of butterflies in the study was not successful. Upon arrival at SiyaQhubeka Forests on 29 September 2008, the butterflies had not hatched. By the end of October, when enough species have hatched to warrant their inclusion in the study, the wind blew strongly. Thus, once again, very few butterflies were seen. All butterfly data were consequently excluded from analyses.

Environmental variables

Environmental variables (EVs) were (1) % bare ground, (2) % vegetation cover, (3) wind velocity, (4) % cloud cover, (5) maximum vegetation height, and (6) vegetation density.

Percentage cloud cover and wind velocity were recorded upon arrival at the site, and were adapted as the weather conditions changed. Wind strength was recorded according to the Beaufort Wind Scale, adjusted for commercial eucalypt plantations at SQF (Table 9).

Table 9 Wind speed was recorded as an environmental variable according to the Beaufort Wind Scale. Common signs for recognition were adjusted to fit Eucalypt plantations.

Abbreviation	Wind speed (m/s)	Common signs for recognition
0	0-1	Smoke rises vertically
1	1-2	Smoke drifts slowly
2	2-3	Leaves just move
3	4-5	Leaves move constantly
4	6-8	Small branches move
5	9-11	Small trees sway
6	12-14	Large branches move
7	15-17	Large trees sway
8	18-20	Small branches break
9	21-24	Large branches break
10	25-26	Small trees uprooted

In the vegetation quadrats, (1) % bare ground and (2) % vegetation cover, which are mutually exclusive, were recorded. Vegetation cover was divided into live/green vegetation cover, and leaflitter and moribund vegetative growth. Thus, the amount of bare ground, the green vegetation cover, and the leaflitter and moribund vegetative growth = 100% in the vegetation quadrat (Figure 10).

Vegetation height and density, as well as the dominant growth form and dominant grass species, were documented at 1 m intervals along each 30 m transect, which ran through the centre of each SU (Figure 10). Maximum height of vegetation was measured with a measuring stick, and rounded to the closest 5 cm. Vegetation density was classified into one of five classes (0 = bare ground, 1 < 100% vegetation cover, 2 = 100% vegetation cover, low density, 3 = 100% vegetation cover, medium density, and 4 = 100% vegetation cover, high density).

Data analyses

All biodiversity and environmental data were recorded in a data matrix, with the species in rows and the SUs in columns (Ludwig & Reynolds 1988). There were three types of biodiversity data: cover data for vegetation, count data for birds, mammals, fungi and manifestations and incidence (presence/absence) data for mammal tracks and grass tunnels. The mean percentage cover of each plant species recorded in the four vegetation quadrats was calculated for each SU.

All EVs were recorded directly below the species in the data matrix (Ludwig & Reynolds 1988). The EV section of the data matrix had three kinds of data; (1) actual measurements for vegetation height, green vegetation, bare ground, and leaf litter and moribund vegetative growth; (2) ordinal data for vegetation density and (3) categorical data for dominant growth form and dominant grass species.

A simple mean was calculated for all EVs with actual measurements. The mode (the value that occurred most times) of the density classes was calculated for each SU. The EVs with categorical data were slightly more complex. It is theoretically possible to treat dominant growth form and dominant grass species the same as vegetation density. However, this could cause a reduction in the resolution of data, since only the one dominant growth form or grass species will be displayed.

To retain information regarding sub-dominant growth forms and grass species, all categorical data were transformed into nominal (presence/absence) data. Thus, each dominant growth form class (grass, sedge, tree, shrub, geophyte or herb) and dominant grass species was recorded in a separate row. The mode was then calculated in each row for each SU, where a zero or a one signified presence or absence.

Species richness and environmental data were not normally distributed. Therefore, a non-parametric, Mann-Whitney U test was performed to test for differences between EN and NR; first as a whole, and then specifically for each pair of sites. Using Statistica 9 software, the tests were run for the species richness of fungi, animals (birds and mammals) and plants, and for all EVs with an actual measurement.

Animal data were replicated at the landscape level i.e. at the spatial scale of the EN and NR. Therefore, animal data from all SUs within a site were pooled. Number of animal individuals at each SU was summed to account for total animal abundance at each EN and NR site. Based on total animal abundance at each EN and NR site, mean animal abundance was calculated for EN and NR, respectively. Similarly, total number of animal species for each EN and NR site was calculated, followed by the mean number of animal species for EN and NR, respectively.

The question of differences in species composition lends itself to descriptive methods of data analysis. CANOCO 4.5 was used to draw a Correspondence Analysis (CA) graph of the species data at each pair of sites. The rare species were downweighed and there was equal emphasis on inter-sample and inter-species distance. EVs were included as supplementary variables to interpret patterns extracted from variation in the dataset. EVs with ordinal data (vegetation density) and incidence data (dominant grass species and growth forms) were displayed as nominal variables.

Non-metric multi-dimensional scaling (MDS) is an alternative ordination method for Correspondence Analyses. Based on the Bray-Curtis similarity index, MDS generates a graph that plots SUs in a multi-dimensional space. Analysis of similarity (ANOSIM) quantifies the magnitude of differences in species composition *between* sites as opposed to differences among SUs *within* a site (Clarke & Warwick 2001). The result of ANOSIM is an R statistic that can take on any value between -1 and 1. However, it mostly falls within the range between zero and 1. R=0 indicates that similarity between and within sites are on average the same, while R approaches 1 when SUs within a site are more similar to each other than SUs between sites (Clarke & Warwick 2001). An R value of -1 is unlikely to occur as it indicates a higher similarity between sites than within a site. In Primer v.5.0 software, MDS (based on

Bray-Curtis similarity indexes) can be combined with ANOSIM to indicate differences in species composition, and to quantify the magnitude of such differences.

Both methods (CA and MDS) make few assumptions about the data, but MDS is more flexible than CA (Clarke & Warwick 2001).

Results

Environmental variables

Bare ground

Overall, the percentage bare ground in the EN was significantly higher than in the NR ($Z = 1.894$, $p=0.058$) (Table 10). The difference was significant for two natural pairs of sites (BP: $Z = 3.061$, $p<0.01$ and PGL: $Z = 2.91$, $p<0.01$) (Figure 13; Table 10).

Live/green vegetative growth

Amount of green/live vegetation in the NR was significantly greater than that in the EN ($Z = -2.535$, $p=0.01$) (Table 10). The difference was significant for the two natural pairs of sites (BP: $Z = -2.759$, $p<0.01$ and PGL: $Z = -2.910$, $p<0.01$) (Figure 13; Table 10).

Moribund vegetative growth and leaf litter

Amount of moribund vegetative growth and leaf litter in the EN was not significantly more than in the NR ($Z = 1.2846$, $p=0.199$) (Table 10). However, the difference was significant for one pair of sites: PGL ($Z = 3.250$, $p<0.01$) (Figure 13; Table 10).

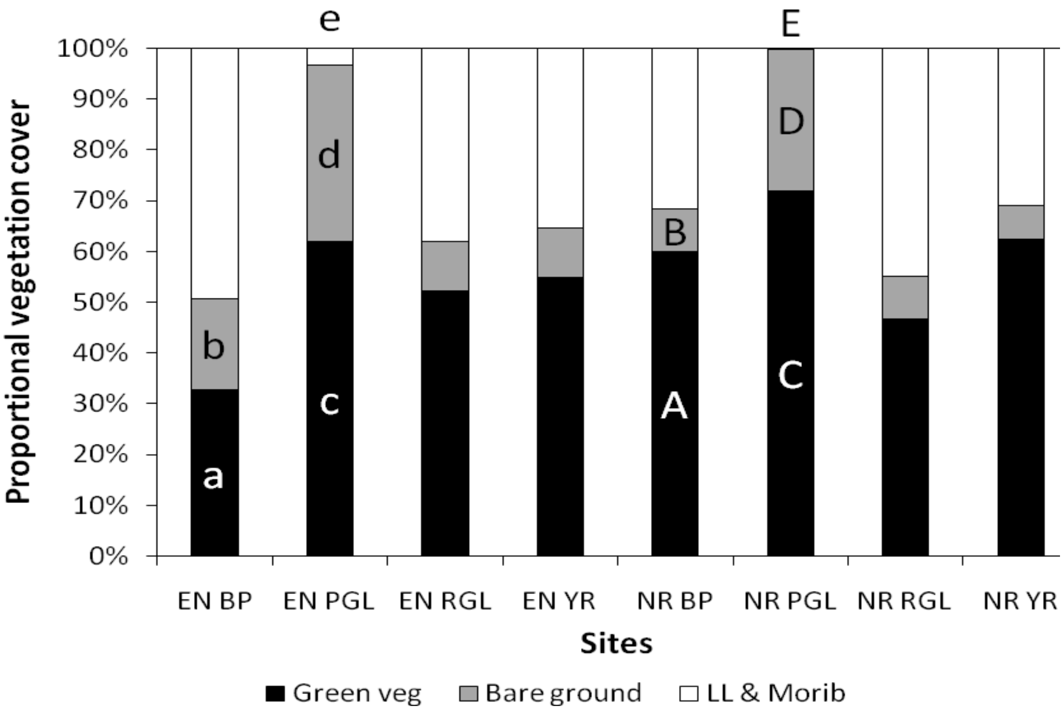

Figure 13 Proportional vegetation cover types (Green veg: Green/live vegetation cover and LL&Morib: Leaf litter and moribund vegetative cover) and bare ground in the vegetation quadrats of the Ecological Network (EN) sites (left) were compared to Nature Reserve (NR) sites (right). I tested for differences between EN and NR using a Mann-Whitney U test. Different letters on the column bar indicated significant differences at $p<0.01$ level (BP: a-A and b-B, and PGL: c-C, d-D and e-E). The two natural EN sites differed substantially from NR sites. See Table 2 for a description of pairs of sites.

<u>Vegetation height and density</u>

Overall, vegetation height in the EN was significantly higher than in the NR ($Z = 2.045$, $p<0.05$), and also significant for PGL ($Z = 3.741$, $p<0.01$) and YR ($Z =3.666$, $p<0.01$) (Table 10). However, it was significantly lower in the EN for BP ($Z = -2.532$, $p=0.01$) (Figure 14; Table 10).

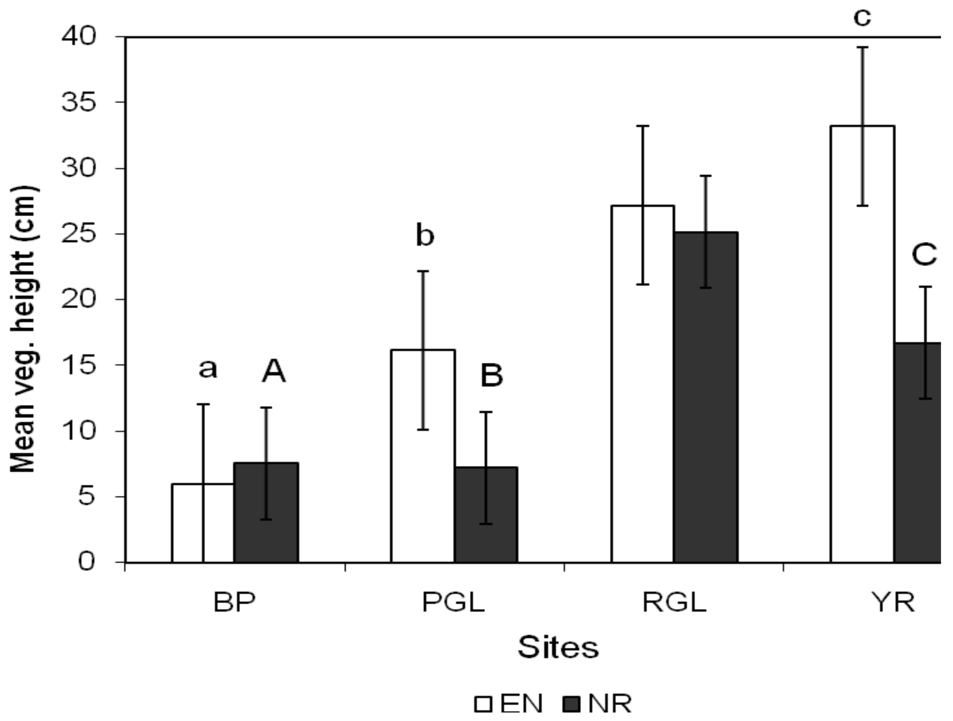

Figure 14 Mean vegetation height (± std error) at each of the Ecological Network (EN) sites (open bars) was compared to Nature Reserve (NR) sites (solid bars) using a Mann-Whitney U test. Different letters indicated significant differences in vegetation height ($p<0.01$). Vegetation height was significantly higher in the EN than in the NR for two sites: PGL (b-B) and YR (c-C), and lower at one site: BP (a-A). See Table 2 for a description of pairs of sites.

Vegetation density in the EN equals that of the NR for two pairs of sites: PGL and YR. Vegetation density at the other two pairs of sites (BP and RGL) was lower in the EN (density class = 1) than in the NR (density class = 2) (Table 11). Density classes 1 and 2 were both characterised by a low-density vegetation cover. However, density class 1 has < 100% vegetation cover, while 2 had 100% vegetation cover. Thus, although the vegetation density was low for both sites, there was more bare ground in the EN.

Table 10 Means for each environmental variable (EV) measured in the quadrats were displayed for each pair of sites (BP, PGL, RGL and YR) (EN vs. NR). Results were graphically displayed in Figure 13. See Table 14 for an explanation of abbreviations for EVs and Table 2 for a description of pairs of sites.

Paired sites	**Overall**			**BP**			**PGL**			**RGL**			**YR**		
EVs	**EN**	**NR**	**p**	**EN**	**NR**	**p**	**EN**	**NR**	**p**	**EN**	**NR**	**p**	**EN**	**NR**	**p**
Bare	18.19	12.69	0.058	17.88	8.13	0.002	35.50	28.13	0.004	9.75	7.88	0.940	9.63	6.63	0.427
Grn vc	50.49	59.39	0.011	32.55	59.20	0.005	63.03	72.25	0.004	52.50	43.63	0.140	53.88	62.50	0.070
LL & Moribund	31.38	26.16	0.199	49.00	31.28	0.082	3.28	0.13	0.001	38.38	42.13	0.450	34.88	31.13	0.427
Vheight	20.63	14.14	0.041	5.98	7.53	0.011	16.15	7.19	0.0002	27.18	25.15	0.57	33.19	16.69	0.0002

Table 11 A summary of the density classes at each site where 0 = bare ground, 1 = < 100% vegetation cover, 2 = 100% vegetation cover, low vegetation density, 3 = 100% vegetation cover, medium vegetation density and 4 = 100% vegetation cover, high vegetation density. One natural pair of sites (PGL) and one rehabilitated pair of sites (YR) have the same approximate vegetation density.

	EN BP	**NR BP**	**EN PGL**	**NR PGL**	**EN RGL**	**NR RGL**	**EN YR**	**NR YR**
Density classes	1	2	1	1	1	2	2	2

Species richness

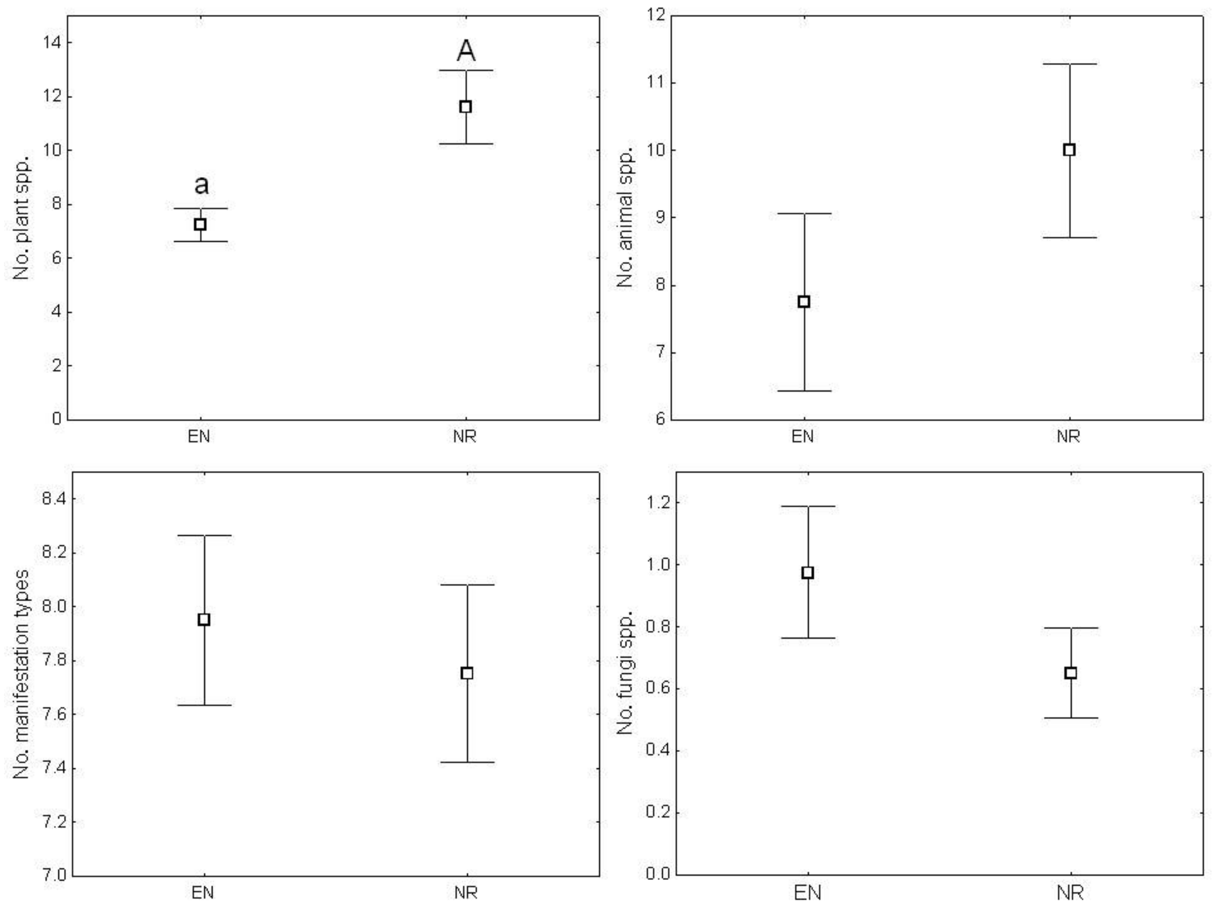

Figure 15 Mean number of species (± std error) of each taxonomic group. I tested for differences in species richness between the Ecological Network (EN) and the Nature Reserve (NR) using a Mann-Whitney U test. Letters indicated significant differences. There were significantly less plant species (a-A) in the EN than in the NR (p<0.01).

Plants

Significantly more plant species were recorded in the NR than in the EN (Z = -2.406, p=0.016) (Figure 15). This was the case for all pairs of sites, but the difference was significant only for three of the four pairs of sites: BP (Z = -2.154, p<0.05), PGL (Z = -3.742, p<0.01) and YR (Z = -2.116, p<0.05) (Figure 16).

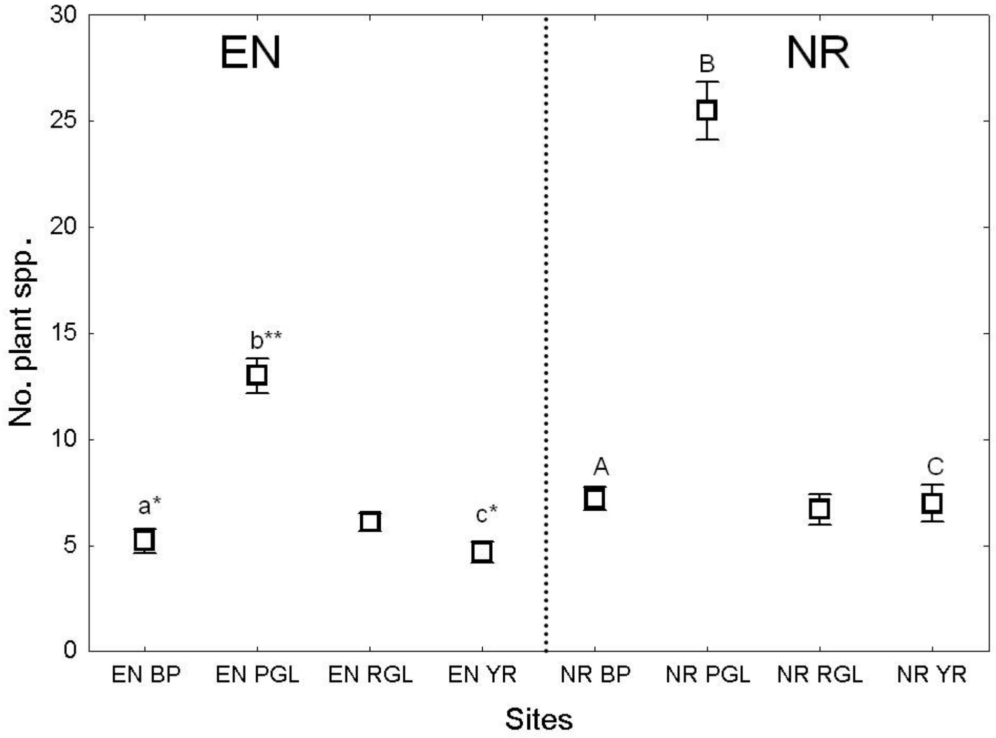

Figure 16 Mean plant species richness (± std error) at each of the Ecological Network (EN) sites (left) was compared to Nature Reserve (NR) sites (right) using a Mann-Whitney U test. Letters indicated significant differences for BP (a-A), PGL (b-B) and YR (c-C) (** p<0.01; * p<0.05). See Table 2 for a description of pairs of sites.

Manifestations

Generally, there was no difference between the number of different manifestations found in NR and the EN (Z = 0.24, p=0.810) (Figure 15) for any of the pairs of sites (Figure 17).

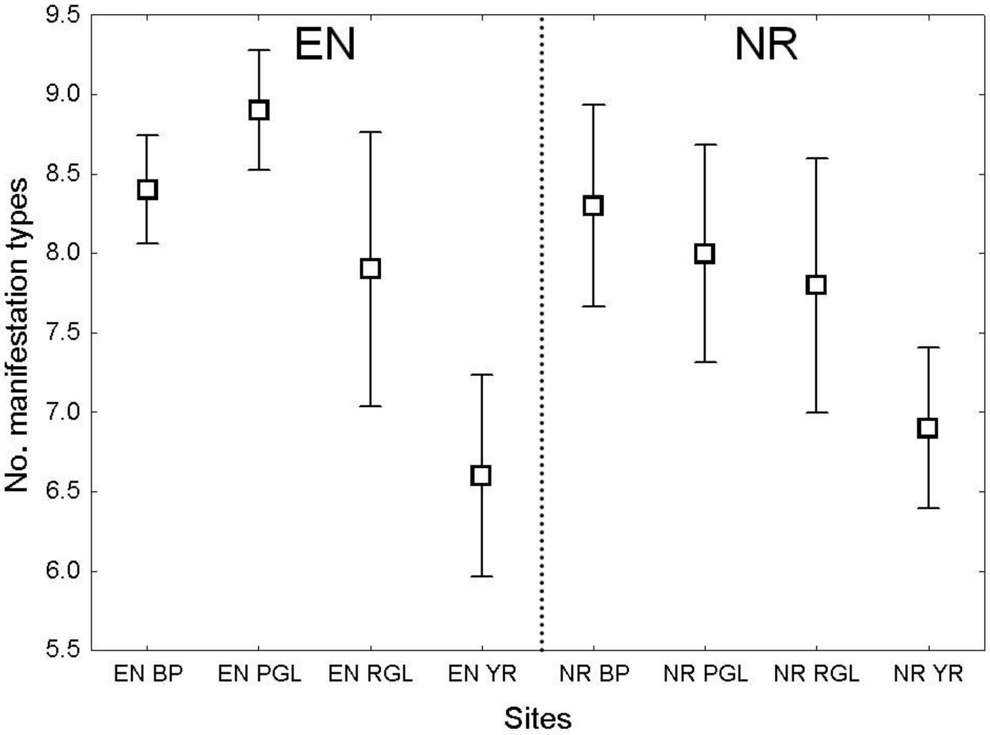

Figure 17 Manifestation types (± std error) at each of the Ecological Network (EN) sites (left) were compared to Nature Reserve (NR) sites (right) using a Mann-Whitney U test. There were no significant differences between pairs of sites. See Table 2 for a description of pairs of sites.

When abundance of specific manifestations was compared between EN and NR, significant differences were found.

Molehills

Overall, there was significantly more molehills in NR (21.6) than in the EN (8.8) ($Z = -3.099$, $p=0.001$). This was the case for all pairs of sites, but the difference was significant only for two of the four pairs of sites: BP ($Z = -2.003$, $p<0.05$) and YR ($Z = -2.532$, $p<0.05$).

Small mammal burrow entrances

Overall, there was significantly more small mammal burrow entrances in EN (5.8) than in NR (3.2) ($Z = 1.949$, $p=0.05$). This was the case for all pairs of sites, but the difference was significant only for one pair of sites: PGL ($Z = 2.419$, $p<0.05$).

Spider webs and ant nests

There was no significant difference in the number of spider webs/burrows/nests or ant nests between EN and NR, overall or for any specific pair of sites.

Fungi

There was no difference between the number of fungi species observed in the NR and the EN (Z = 0.702, p=0.48) (Figure 15). No pair of sites showed any significant difference between NR and EN (Figure 18).

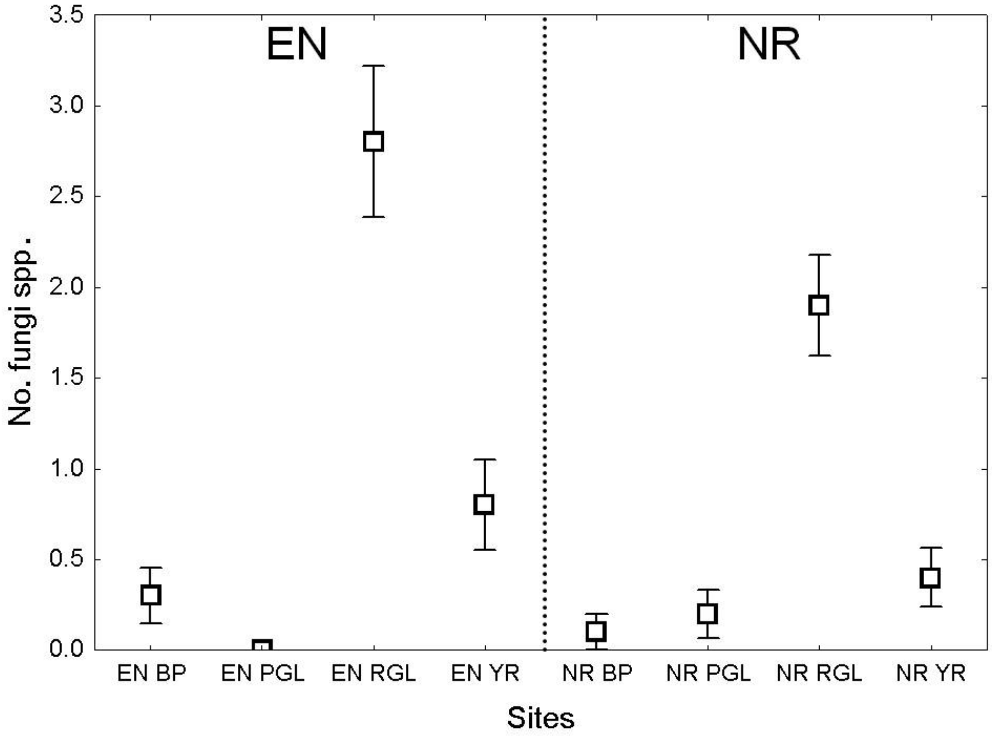

Figure 18 Mean fungi species richness (± std error) at each of the Ecological Network (EN) sites (left) was compared to Nature Reserve (NR) sites (right) using a Mann-Whitney U test. There were no significant differences between pairs of sites. See Table 2 for a description of pairs of sites.

Vertebrates

More bird and large mammal species were seen in NR (10) than in EN (8). In addition, animal abundance was higher in NR (72) than in EN (41). Neither of these differences was significant. (Vertebrate species richness: Z = -0,866, p=0.386 (Figure 15) and vertebrate abundance: Z = -0.433, p=0.665 (Figure 19)).

The majority of recorded animals were birds. Of the 49 recorded animal species, 38 species were birds. Of all individuals, 63% and 67% in EN and NR, respectively, were birds.

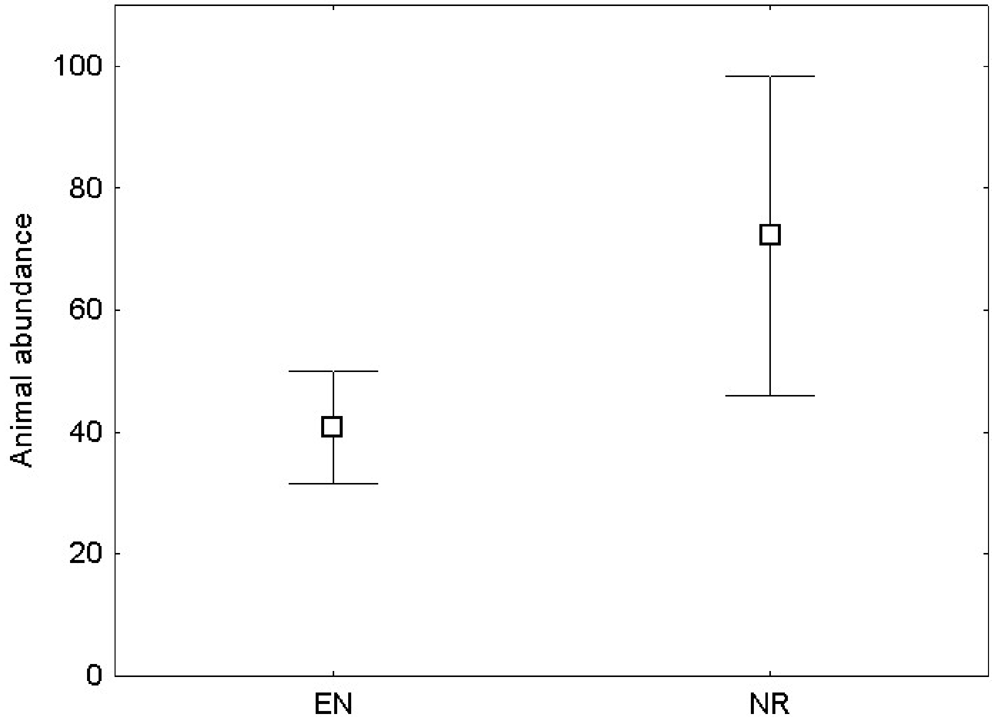

Figure 19 Mean animal (bird and large mammal) abundance (± standard error) in the Ecological Network (EN) was compared to Nature Reserve (NR) using a Mann-Whitney U test. Although the mean of EN (41) and NR (72) differed, the difference was not statistically significant.

Species composition

Plants

Overall, the variation in plant species composition within pairs of sites (e.g., EN BP vs. NR BP) was smaller than differences between habitats at a landscape level (Figure 20). Both CA (Figure 20, Table 12) and ANOSIM (Table 13) confirmed this. On average, ANOSIM yielded smaller R-values for the pair-wise comparisons between EN and NR than between pairs of sites (Table 13). The two primary ordination axes of CA explained 21.9% of the variation in plant species composition for four pairs of sites: BP, PGL, RGL and YR. Except for one EN site (EN PGL) and one NR site (NR RGL), all EN SUs plotted below the first primary ordination axis, and all NR SUs left of the second primary ordination axis. Furthermore, all SUs from all pairs of sites (except RGL) plotted left of the second primary ordination axis (Figure 20).

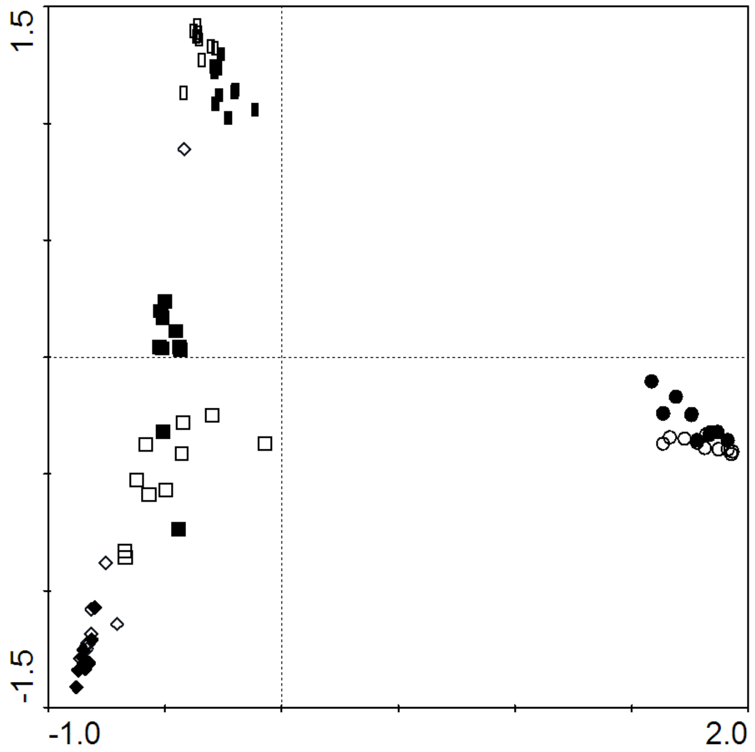

Figure 20 Correspondence Analysis of plant species composition for four pairs of sites (RGL, PGL, BP and YR). Pairs of sites grouped together. Thus, the difference in species composition between habitats (i.e. between different symbols) was larger than the difference between Ecological Network (EN) (open symbol) and Nature Reserve (NR) (solid symbol). Different symbols indicated different pairs of sites: ○ EN RGL, ● NR RGL, ☐ EN YR, ■ NR YR, ▯ EN PGL, è NR PGL, ◊ EN BP and ♦ NR BP. See Table 2 for a description of pairs of sites.

Table 12 A summary of the eigenvalues and cumulative variation explained by the two primary ordination axes of the Correspondence Analysis for plant species composition at all pairs of sites.

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.902	0.956	0.965	0.904	
Cumulative percentage variance					
of species data:	11.3	21.9	31.5	38.9	
of species-environment relationship:	14.5	29.8	44.0	53.5	
Sum of all eigenvalues					8.252
Sum of all canonical eigenvalues					5.223

Table 13 On average, ANOSIM yielded lower R-values for comparisons within pairs of sites (Ecological Network (EN) vs. Nature Reserve (NR)) than between different pairs of sites. Thus, natural variation at the landscape level (beta or gamma diversity) was larger than the difference between EN and NR. See Table 2 for a description of pairs of sites.

	Pairwise comparisons	**R statistic**	**p-value**
Comparisons between EN & NR	EN BP vs. NR BP	0.544	0.001
	EN PGL vs. NR PGL	0.999	0.001
	EN RGL vs. NR RGL	0.322	0.006
	EN YR vs. NR YR	0.559	0.001
Comparisons between pairs of sites	BP vs. PGL	0.880	0.001
	BP vs. RGL	0.899	0.001
	BP vs. YR	0.773	0.001
	PGL vs. RGL	0.997	0.001
	PGL vs. YR	0.984	0.001
	RGL vs. YR	0.727	0.001

When including EVs as supplementary variables in the CA, the cumulative variation of the species-EV relationship explained by the two primary ordination axes was 29.8% (Table 12). Bare ground cover (i.e. density class 0: 0% vegetation cover) characterized one natural pair of sites (PGL), while patterns in plant species composition at one rehabilitated pair of sites (RGL) was explained by high maximum vegetation height, medium-to-high vegetation density and scattered timber logs (Figure 21). Leaf litter and moribund vegetative growth influenced plant species composition strongly, but did not associate with any specific pair of sites (Figure 21).

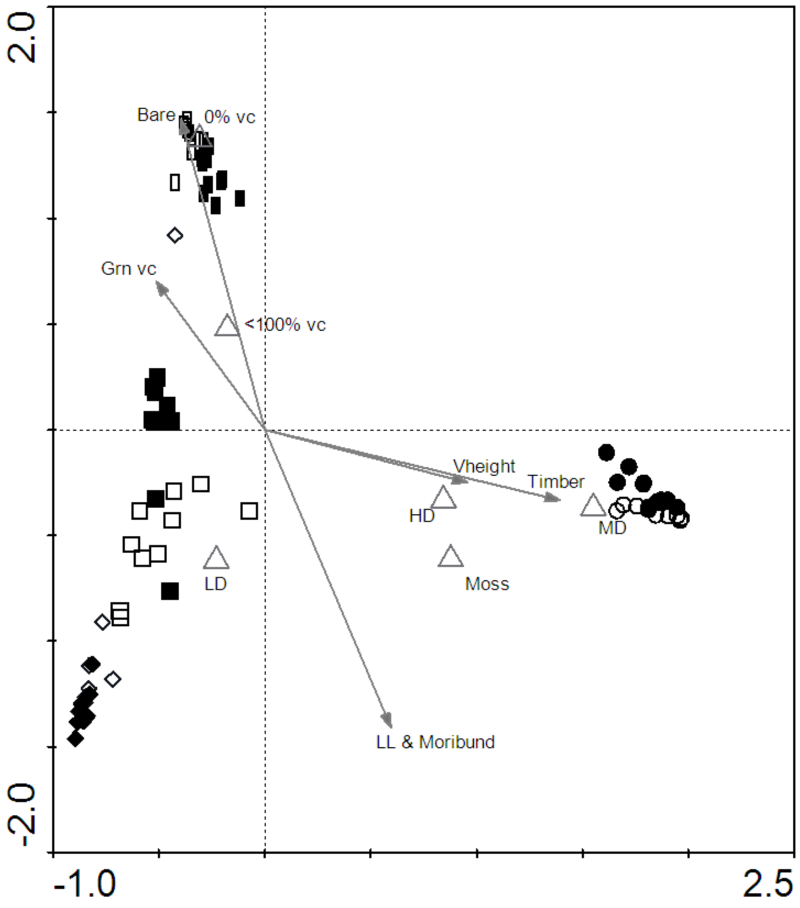

Figure 21 Environmental variables (EV) explained some of the patterns in the plant species composition observed at different pairs of sites. Bare ground (Bare) and density class 1 (0% vc: 0% vegetation cover) characterized one natural pair of sites (PGL), while one rehabilitated pair of sites (RGL) was characterized by timber, high maximum vegetation height (Vheight), and a medium-to-high vegetation density (MD and HD). Leaf litter and moribund vegetative cover (LL & Moribund) influenced species composition strongly, but did not associate with one specific pair of sites. Different symbols indicated different pairs of sites: ○ EN RGL, ● NR RGL, ☐ EN YR, ■ NR YR, ▯ EN PGL, Î NR PGL, ◇ EN BP and ◆ NR BP. See Table 2 for a description of pairs of sites and Table 14 for an explanation of EV abbreviations.

Table 14 Descriptions of abbreviations of environmental variables (EVs), included on Correspondence Analysis (CA) graphs to explain patterns observed in species composition.

Abbreviation	**Environmental variable**
Bare	Bare ground
Grn vc	Green/live vegetation cover
LL & Moribund	Leaf litter and moribund vegetation cover
Vheight	Maximum vegetation height
Density classes	
0% vc	0% vegetation cover
<100% vc	<100% vegetation cover
LD	100% vegetation cover, low vegetation density
MD	100% vegetation cover, medium vegetation density
HD	100% vegetation cover, high vegetation density

Different suites of dominant species characterized different pairs of sites. Ten dominant plant species made up most of the vegetative cover in natural pairs of sites (BP and PGL), compared to only five dominant species in rehabilitated pairs (YR and RGL). Of the eighteen dominant plant species documented, six species (*Digitaria* sp. 1, *Helichrysum krausii*, *Panicum natalensis*, *Trystachya leucothrix*, *Eragrostis racemosa* and *Salacia kraussii*) associated strongly with one natural pair of sites (PGL) and four (*Acroceras macrum*, *Centella asiatica*, *Cyperus sphaerospermum* and one unidentified herbaceous creeper) with the other natural pair of sites (BP). Four dominant species (*Chloris gayana*, *Cyperus natalensis*, *Ischaemum* sp. 1 and *Stenotaphrum secundatum*[1]) associated strongly with one rehabilitated pair of sites (YR) and one dominant species (*P. deustum*) with the other rehabilitated pair of sites (RGL). Three dominant species (*P. maximum*, *Dactyloctenium geminatum* and *Melinis repens*) occurred in both, natural and rehabilitated, pairs of sites (Figure 22).

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[1] *S. secundatum* was the only alien dominant grass species documented in this study. It is originally from North America, West Indies and Australia, but now occurs in most tropical parts of the world. It is a good stabiliser of soil, and relies mainly in vegetative regeneration (van Oudtshoorn 1992).

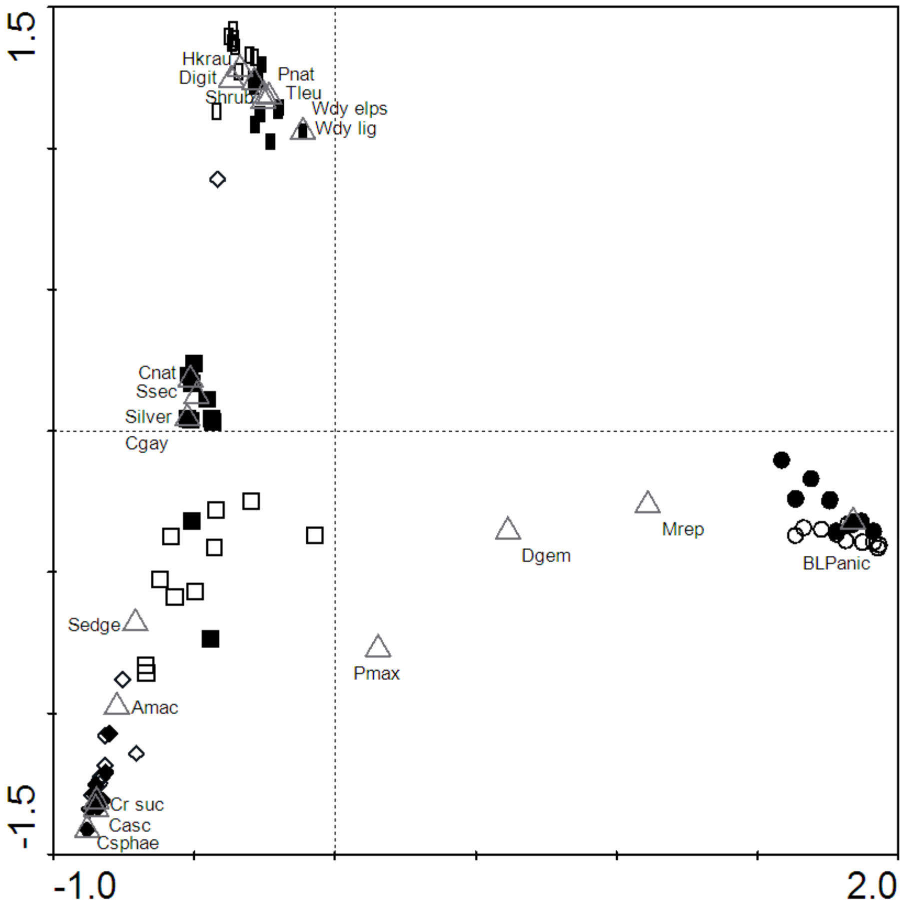

Figure 22 Different suites of dominant species characterized different pairs of sites. Only three grass species (Pmax: *Panicum maximum*, Dgem: *Dactyloctenium geminatum* and Mrep: *Melinis repens*) did not associate exclusively with one pair of sites. See Table 15 for scientific names of other dominant species' abbreviations. Different symbols indicated different pairs of sites: ○ EN RGL, ● NR RGL, ☐ EN YR, ■ NR YR, ▯ EN PGL, Î NR PGL, ◊ EN BP and ♦ NR BP. See Table 2 for a description of pairs of sites.

Table 15 Scientific names for the dominant species' abbreviations used in Correspondence Analysis graphs.

Abbreviation	**Growth form**	**Species name**
Amac	Grass	*Acroceras macrum*
Dgem	Grass	*Dactyloctenium geminatum*
BLPanic	Grass	*Panicum deustum*
Casc	Herb	*Centella asiatica*
Cgay	Grass	*Chloris gayana*
Cr suc	Herb	Unidentified herb sp.
Cnat	Sedge	*Cyperus natalensis*
Csphae	Sedge	*Cyperus sphaerospermum*
Digit	Grass	*Digitaria sp. 1*
Grass #3	Grass	*Imperata cylindrica*
Hkrau	Shrub	*Helichrysum krausii*
Mrep	Grass	*Melinis repens*
Pmax	Grass	*Panicum maximum*
Pnat	Grass	*Panicum natalensis*
Silver	Grass	Ischaemum sp. 1
Ssec	Grass	*Stenotaphrum secundatum*
Tleu	Grass	*Trystachya leucothrix*
Weli	Shrub	Salacia kraussii
Wdy ligule	Grass	Eragrostis racemosa

1st pair of sites: EN PGL vs. NR PGL

At one natural pair of sites (PGL), difference in species composition between EN and NR was large (ANOSIM, R = 0.999, p<0.01), i.e. similar to the level of variation observed at landscape level between habitat types (Table 13). CA for this pair of sites, with two primary ordination axes explaining 45.7% of the variation in the species composition (Table 16), confirms that species composition in EN and NR is different, as all NR SUs group to the left of the second ordination axis, while the EN SUs group to the right (Figure 23). Only eight out of the 111 plant species observed at this pair of sites (EN: 44 spp. and NR: 67 spp.) occurred in both, NR and EN. These species were *C. obtusifolius*, *Eriosema* sp., *H. athrixiifolium*, *H. kraussii*, *Pentanissia pruniloides*, *Salacia kraussii*, *Tephrosia* sp. 2 and *Zornia capensis*.

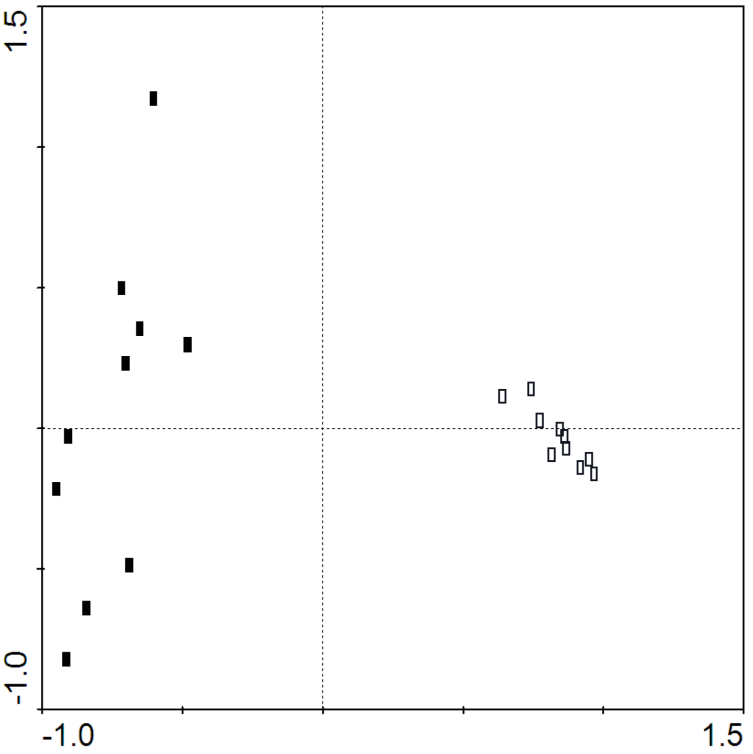

Figure 23 Correspondence Analysis graph of plant species composition at one natural pair of sites: PGL. Ecological Network (EN) (▯) and Nature Reserve (NR) (Î) sampling units separated completely i.e. species composition in EN differed from NR. See Table 2 for a description of pairs of sites.

Table 16 A summary of the eigenvalues and the cumulative variation explained by the two primary ordination axes of the Correspondence Analysis drawn for plant species composition at one natural pair of sites: PGL.

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.996	0.870	0.817	0.647	
Cumulative percentage variance					
of species data:	36.3	45.7	52.4	58.4	
of species-environment relationship:	47.8	57.2	63.1	66.4	
Sum of all eigenvalues					1.760
Sum of all canonical eigenvalues					1.327

EVs greatly contributed to an explanation of patterns observed in plant species composition for one natural pair of sites: PGL. When EVs were added, cumulative variation, explained by the two primary ordination axes, equated 57.2% of species–EV relationship (Table 16). On average, EN SUs had higher maximum vegetation height, more bare ground (i.e. density class 0: 0% vegetation cover) and more moribund vegetative growth than NR SUs, which, in turn, had more green vegetation cover (Figure 24).

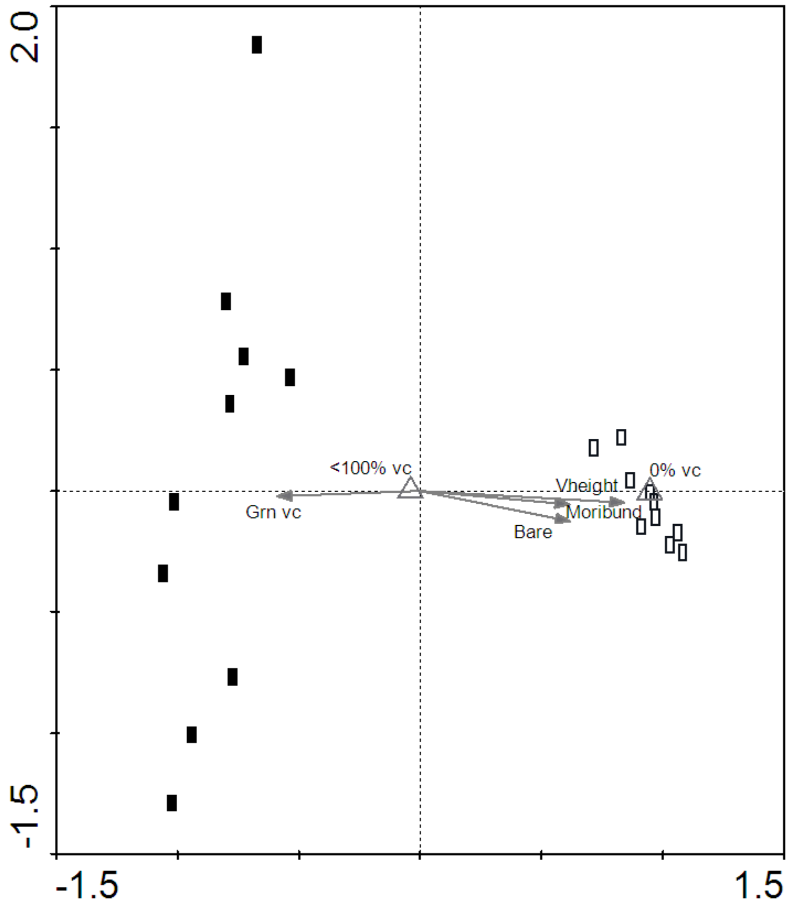

Figure 24 Correspondence Analysis with supplementary environmental variables (EVs) explained species pattern at one natural pair of sites (PGL). Ecological Network (EN) sampling units (SUs) (▯) have higher maximum vegetation height and more bare ground (i.e. density class 1: 0% vegetation cover). For same aged vegetation, Nature Reserve (NR) SUs (Î) have more green vegetation cover than EN SUs, which, in turn, have more moribund growth. See Table 2 for a description of pairs of sites and Table 14 for an explanation of EV abbreviations.

There were two dominant species at the EN site (*H. krausii* and *Digitaria* sp. 1) and four at NR, of which three were grasses (*P. natalensis*, *Trystachya leucothrix* and *Eragrostis racemosa*) and one a shrub, *Salacia kraussii* (Figure 25). While *Digitaria* sp. 1 at EN PGL was a tall bunch grass, two of three dominant grass species at NR PGL (*P. natalensis* and *T. leucothrix*) were lawn grasses. Although lawn grasses are shorter, they provide greater ground cover than bunch grasses.

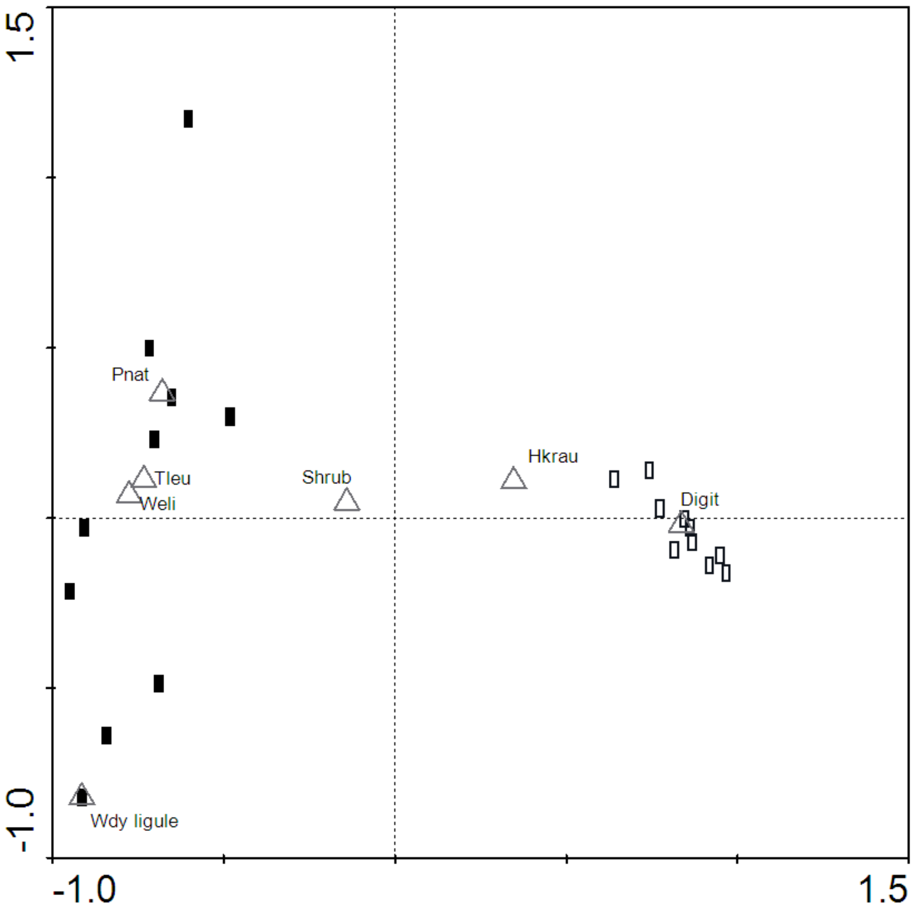

Figure 25 There were two dominant species at EN PGL sites (▯), but four at NR PGL (Î). Both sites have one woody shrub species, which explained the proximity of the “shrub” growth form to the centroid. (EN: Ecological Network, NR: Nature Reserve). See Table 15 for scientific names of dominant species’ abbreviations and Table 2 for a description of pairs of sites.

2nd pair of sites: EN BP vs. NR BP

At the other natural pair of sites (BP), separation of EN and NR SUs based on their plant species composition was not as distinct (ANOSIM, R = 0.544, p<0.01) as for the previous pair of sites (Table 13). The two primary ordination axes of the CA explained 45.0% of the variation observed in the plant species composition (Table 17). After exclusion of an outlier SU (EN BP 8), most NR SUs (eight out of 10) grouped to the left of the second ordination axis, while most EN SUs (eight out of nine) grouped to the right (Figure 26).

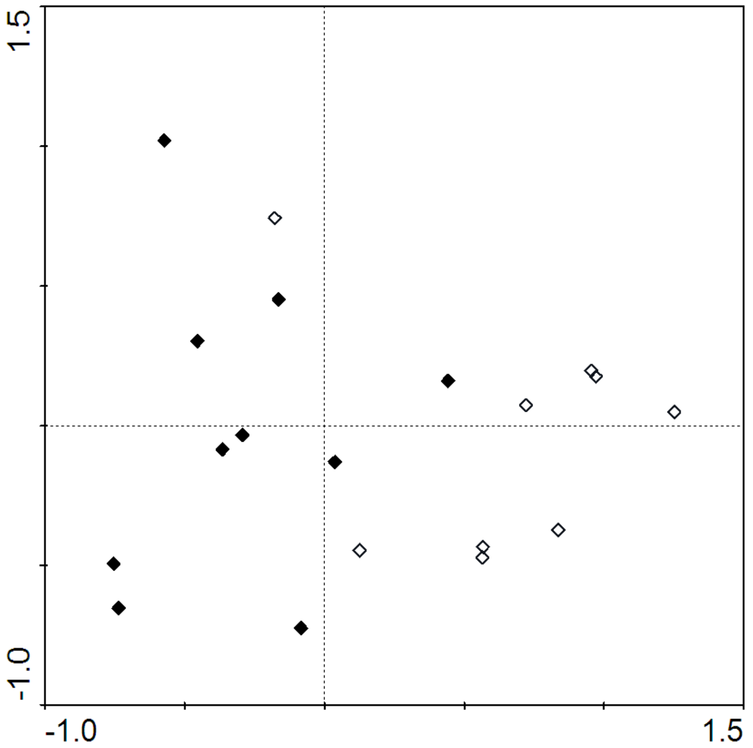

Figure 26 Based on Correspondence Analysis of plant species composition at the second, natural pair of sites (BP), separation of Ecological Network (EN) (◊) and Nature Reserve (NR) (♦) sampling units (SUs) was vague. However, most NR SUs grouped the left of the second ordination axis, while most EN SUs grouped to the right.

Table 17 A summary of the eigenvalues and the cumulative variation of the ordination axes of the Correspondence Analysis drawn for plant species at the second natural pair of sites: BP (after the exclusion of outlier sampling unit BP EN 8).

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.921	0.935	0.980	0.870	
Cumulative percentage variance					
of species data:	28.3	45.0	57.8	69.1	
of species-environment relationship:	28.9	46.5	61.2	71.5	
Sum of all eigenvalues					1.457
Sum of all canonical eigenvalues					1.212

Upon the inclusion of EVs, cumulative variation of the species-EV relationship explained by the two primary ordination axes was 46.5%, which is only 1.5% greater than when only species data were considered (Table 17). Nevertheless, EN SUs had more bare ground and moribund growth than NR SUs, which, in turn, had more green vegetative cover and higher maximum vegetation height. One EN SU grouped with NR SUs. Moss associated strongly with this EN SU (Figure 27).

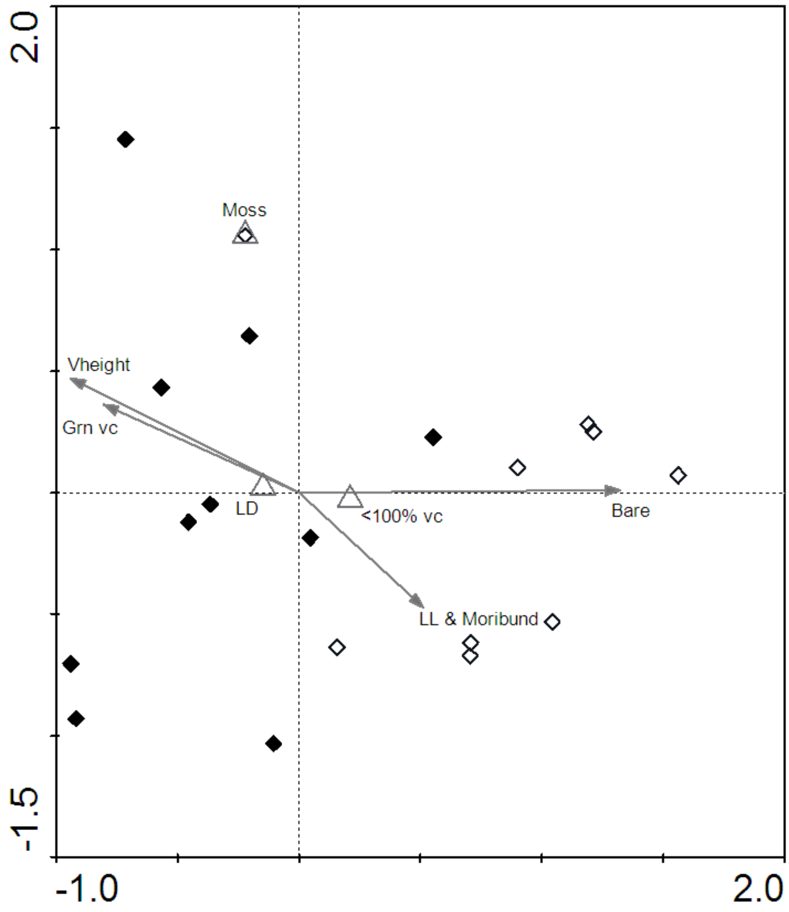

Figure 27 Environmental variables (EVs) at the second natural site (BP) explained some of the plant species composition patterns observed on the Correspondence Analysis graph. Ecological Network (EN) sampling units (SUs) (◊) have more bare ground and more moribund vegetative growth than Nature Reserve (NR) SUs (♦), which, in turn, have more green vegetative growth and a higher maximum vegetation height. See Table 2 for a description of pairs of sites and Table 14 for an explanation of EV abbreviations.

C. asiatica and an unidentified herbaceous creeper dominated at NR SUs. At least one NR SU associated with dominant sedge cover. *P. maximum* did not discriminate between EN and NR SUs, as it occurred in both. *A. macrum* and *Digitaria* sp. 1 dominated EN SUs (Figure 28).

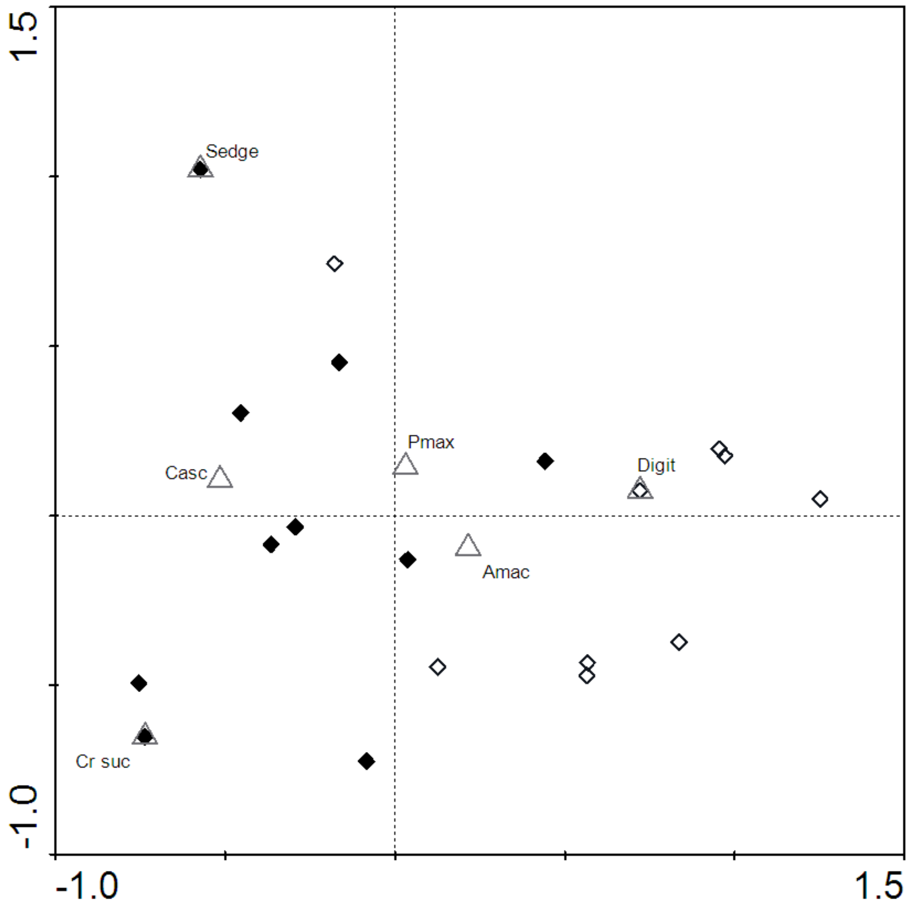

Figure 28 At the second, natural pair of sites (BP), dominant species were *Digitaria* sp. 1 (Digit) and *Acroceras macrum* (Amac) in Ecological Network (EN) sampling units (SUs), and *Centella asiatica* (Casc) and a herbaceous creeper (Cr suc) in Nature Reserve (NR) SUs. Sedges associated largely with NR SUs. *Panicum maximum* (Pmax) dominated in both, EN and NR SUs. See Table 2 for a description of pairs of sites.

3rd pair of sites: EN RGL vs. NR RGL

At the older, rehabilitated pair of sites, plant species composition in EN and NR differed less than for any of the other pairs of sites (ANOSIM, R = 0.322, p<0.06; Table 13). Based on the two primary ordination axes of the CA, which explained 44.3% of the variation observed in plant species composition (Table 18), EN SUs and NR SUs grouped separately. Most EN SUs (eight out of 10) plotted to the left of the second ordination axis, while most NR SUs (nine out of 10) plotted to the right (Figure 29).

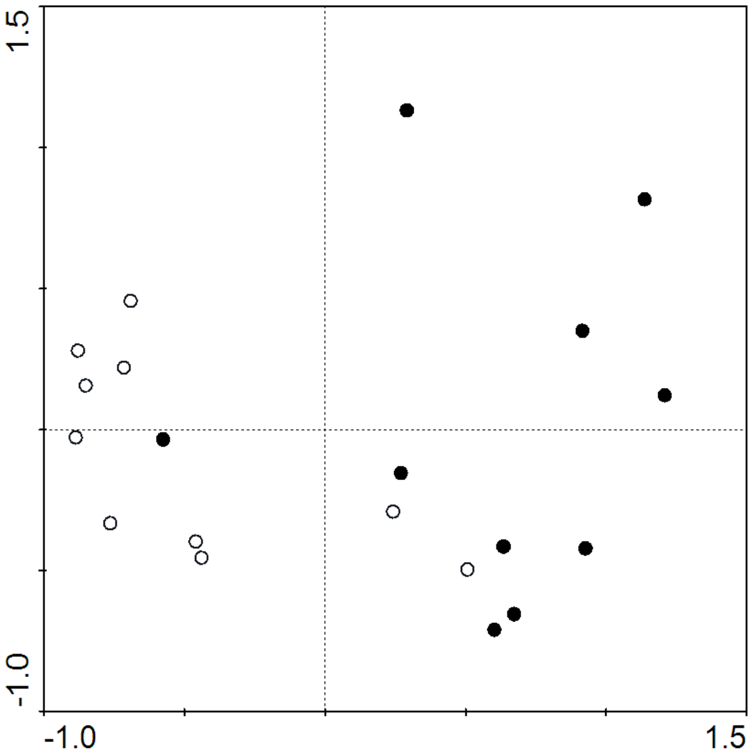

Figure 29 Based on plant species composition at the second rehabilitated pair of sites (RGL), Ecological Network (EN) (○) and Nature Reserve (NR) (●) sampling units (SUs) separated. Most EN SUs grouped to the left of the second primary ordination axis, while most NR SUs grouped to the right.

Table 18 A summary of the eigenvalues and the cumulative variation explained by the two primary ordination axes of the Correspondence Analysis for plant species at the second rehabilitated pair of sites: RGL.

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.927	0.969	0.852	0.895	
Cumulative percentage variance					
of species data:	30.7	44.3	56.5	68.1	
of species-environment relationship:	33.8	50.3	61.7	73.6	
Sum of all eigenvalues					1.681
Sum of all canonical eigenvalues					1.309

When EVs were included in the CA, the variation in species-EV relationship explained by the two primary ordination axes was 50.3% (Table 18). EN SUs had more old timber logs, bare ground (i.e. density class 1: < 100% vegetation cover) and green vegetation cover than NR. On average, vegetation density was higher in EN, but vegetation height and moribund vegetative growth were higher in NR SUs. Moss was found in NR, but not in EN (Figure 30).

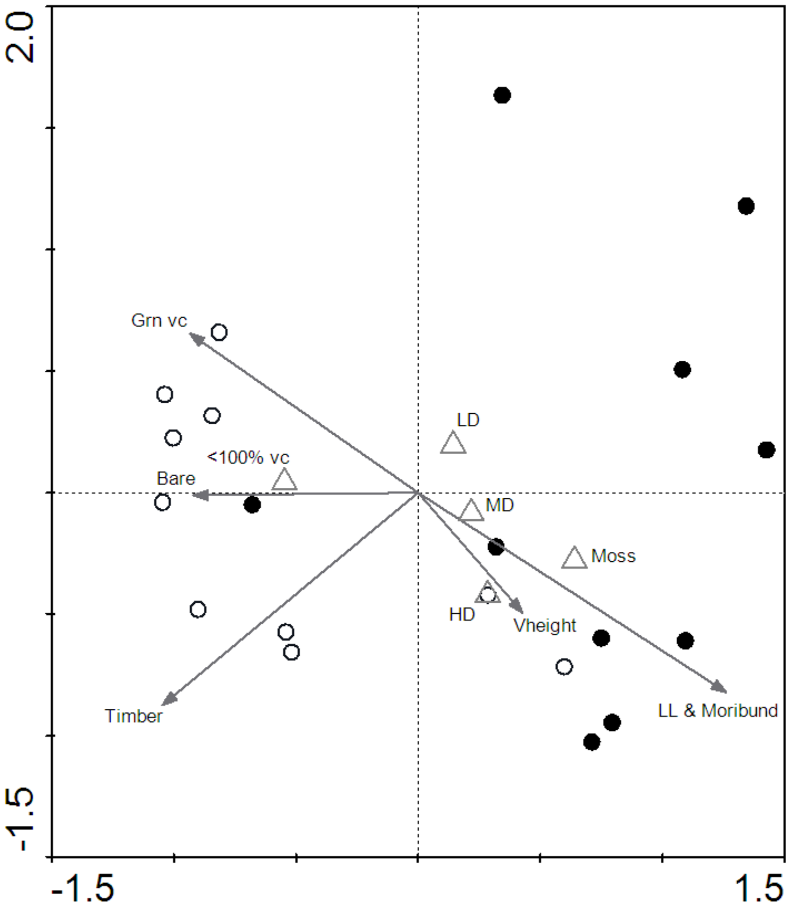

Figure 30 At the first, rehabilitated pair of sites (RGL), Ecological Network (EN) sampling units (SUs) (○) have more timber, more bare ground and more green vegetation cover than Nature Reserve (NR) SUs (●). Maximum vegetation height was higher and there was more moribund growth in NR SUs. See Table 2 for a description of pairs of sites and Table 14 for an explanation of environmental variable abbreviations.

An equal number of dominant species was found in EN and NR. *D. geminatum* and *P. deustum* associated with NR, while *P. maximum* and *M. repens* associated with EN (Figure 31).

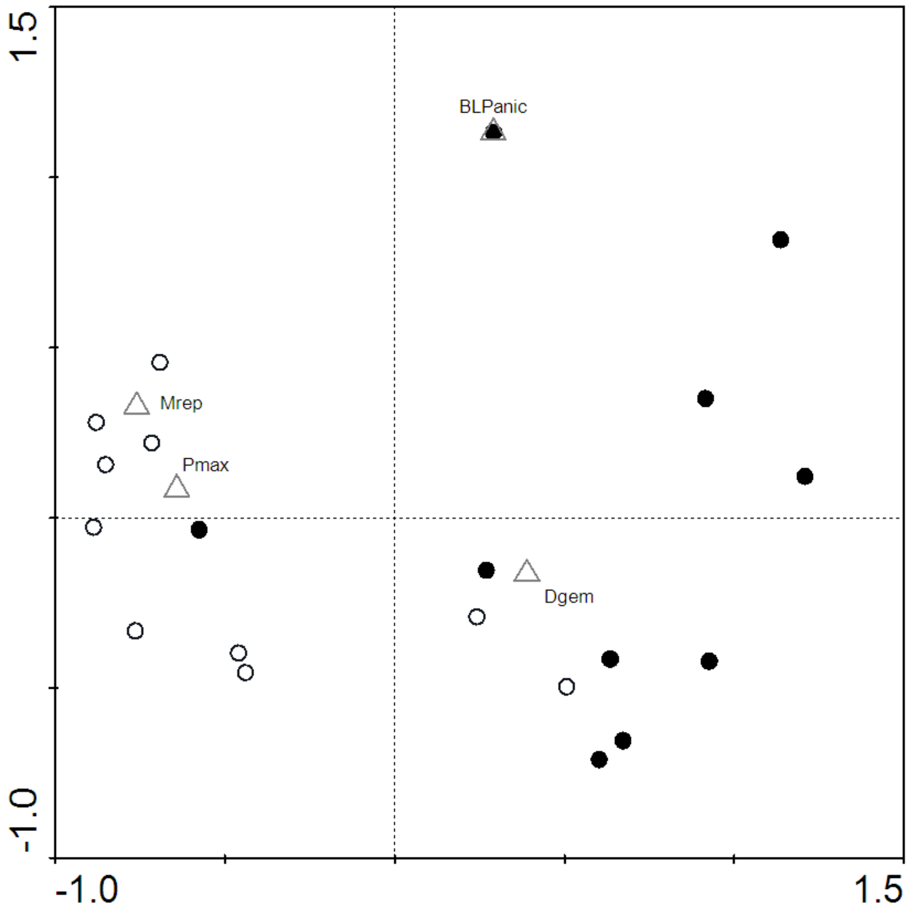

Figure 31 Two grass species (*Melinis repens* and *Panicum maximum*) dominated at EN RGL (○), while two other grass species (*D. geminatum* and *P. deustum*) dominated at NR RGL (●). See Table 15 for scientific names of dominant species' abbreviations and Table 2 for a description of pairs of sites.

4th pair of sites: EN YR vs. NR YR

At the other rehabilitated site (YR), plant species composition of EN and NR SUs were different (ANOSIM, R = 0.559, $p<0.01$; Table 13). According to the two primary ordination axes of CA that explained 43.1% of the variation observed in species composition (Table 19), there was a distinct separation of EN and NR SUs (Figure 32). Most EN SUs grouped in the bottom left quadrant, while NR SUs plotted in the other three.

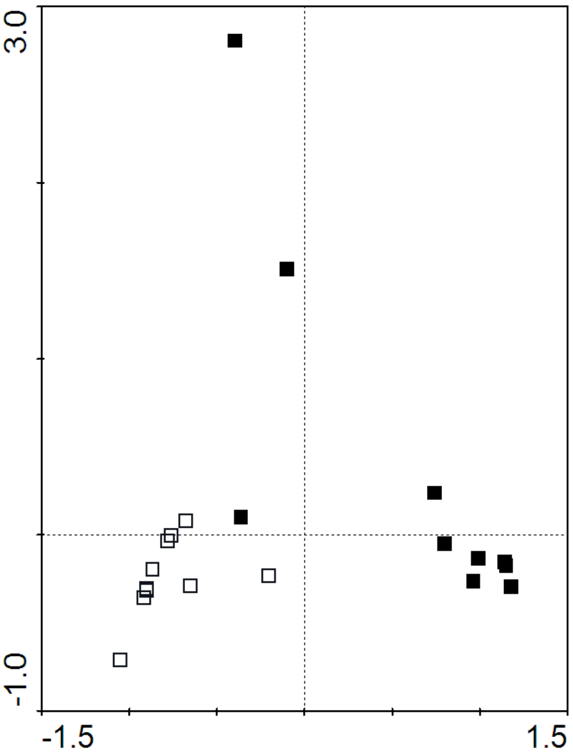

Figure 32 Based on the plant species composition at one rehabilitated pair of sites (YR), Ecological Network (☐) and Nature Reserve (■) sampling units separated on the Corresponcence Analysis graph. See Table 2 for a description of pairs of sites.

Table 19 A summary of the eigenvalues and cumulative variation explained by the two primary ordination axes of the Correspondence Analysis for plant species at the other rehabilitated pair of sites: YR.

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.987	0.819	0.978	0.936	
Cumulative percentage variance					
of species data:	26.2	43.1	57.9	68.2	
of species-environment relationship:	30.1	43.4	60.2	70.8	
Sum of all eigenvalues					2.760
Sum of all canonical eigenvalues					2.341

The two primary ordination axes of CA explained 43.4% of the species-EV relationship. Compared to 43.1% of variation in species data explained, EVs did not greatly contribute to interpretation of patterns observed in the species composition data. However, vegetation height and density were higher at EN (MD: medium density and HD: high density) than at NR, which had higher green vegetation cover. Bare ground (i.e. density classes 1: <

100% vegetation cover and LD: low density) and timber did not associate strongly with either EN or NR (Figure 33).

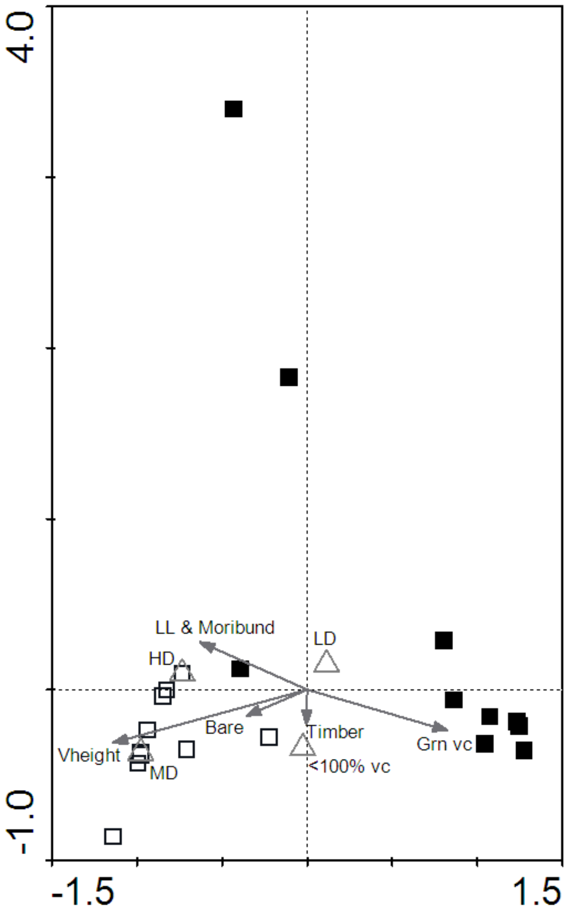

Figure 33 At the one rehabilitated pair of sites (YR), maximum vegetation height and density were higher in Ecological Network sampling units (SUs) (□), while green vegetation cover was more in Nature Reserve SUs (■).See Table 2 for a description of pairs of sites and Table 14 for an explanation of environmental variable abbreviations.

Sedges (*C. natalensis*) and four other grass species (*C. gayana*, *M. repens*, *S. secundatum* and *Ischaemum* sp. 1) dominated at NR, while *D. geminatum* and *P. maximum* dominated at EN (Figure 34). *S. secundatum* was the only dominant alien grass species documented in this study.

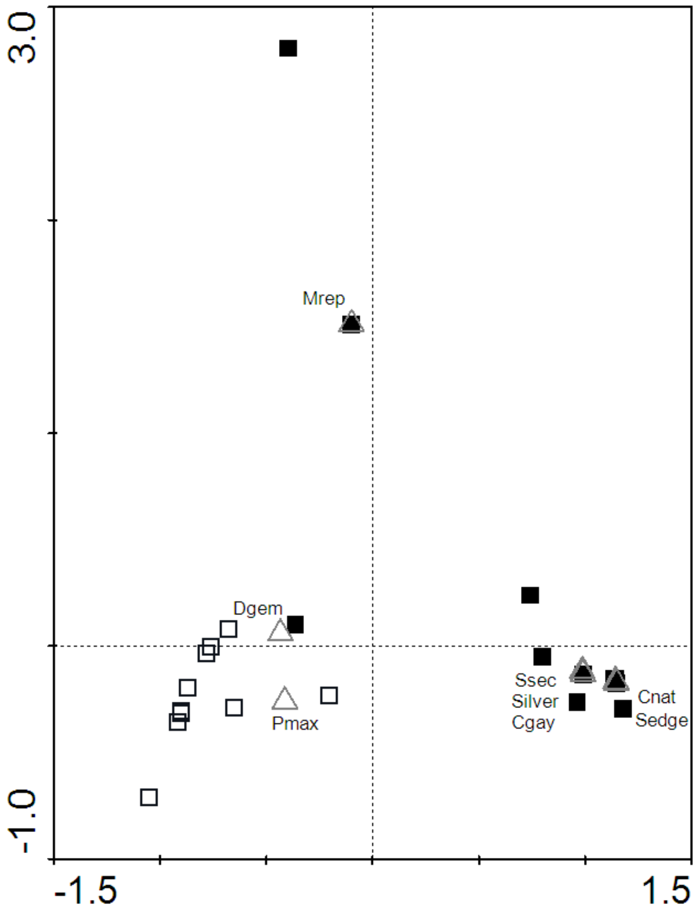

Figure 34 At the younger, rehabilitated pair of sites (YR), sedges (*Cyperus natalensis*), and four grass species (Mrep: *Melinis repens*, Silver: Ischaemum sp. 1, Ssec: *Stenotaphrum secundata*, Cgay: *Chloris gayana*) dominated at Nature Reserve sampling units (SUs) (■) compared to only two grass species (Pmax: *Panicum maximum*, Dgem: *Dactyloctenium geminatum*) at Ecological Network SUs (☐). See Table 2 for a description of pairs of sites.

Manifestations

On average, the difference between pairs of sites (EN vs. NR) was smaller than the difference between sites (Table 20). However, manifestations at the younger, rehabilitated pair of sites (YR) was very similar to the older, rehabilitated pair of sites (RGL) (ANOSIM, R=0.397, p<0.01) and one natural pair of sites (BP) (ANOSIM, R=0.399, p<0.01), respectively (Table 20). These are all sites with vegetation density 2 or higher i.e. 100% vegetation cover (Table 11).

Table 20 On average, ANOSIM yielded lower R-values for comparisons of manifestations between pairs of sites (Ecological Network (EN) vs. Nature Reserve (NR)) than between different sites (i.e. habitats).

	Pairwise comparisons	**R statistic**	**p-value**
Comparisons between EN & NR	EN BP vs. NR BP	0.324	0.005
	EN PGL vs. NR PGL	0.225	0.021
	EN RGL vs. NR RGL	0.17	0.02
	EN YR vs. NR YR	0.197	0.013
Comparisons between sites	BP vs. PGL	0.885	0.001
	BP vs. RGL	0.852	0.001
	BP vs. YR	0.399	0.001
	PGL vs. RGL	0.988	0.001
	PGL vs. YR	0.812	0.001
	RGL vs. YR	0.397	0.001

When manifestation types from all pairs of sites were combined in CA, variation explained by the two primary ordination axes was 33.5% (Table 21). In the CA, only natural pairs of sites (BP and PGL) grouped together (Figure 35). The one natural pair of sites (PGL) grouped left of the second primary ordination axis, with EN SUs above the first primary ordination axis and NR SUs below (Figure 35). The other natural pair of sites (BP) grouped below the first primary ordination axis, mostly in the bottom-right quadrant (Figure 35). SUs from rehabilitated pairs of sites were scattered vertically.

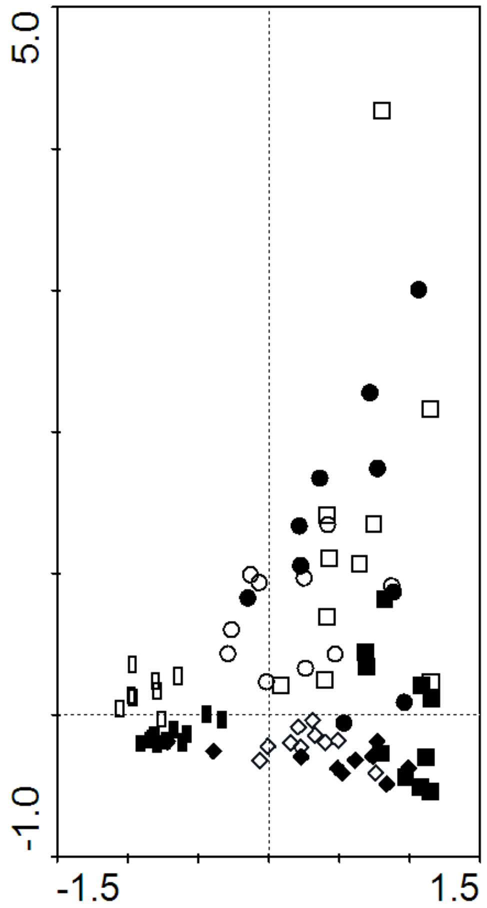

Figure 35 In Correspondence Analysis of manifestation, only sampling units (SUs) from two natural pair of sites, PGL and BP, grouped together. SUs from rehabilitated pairs of sites, YR and RGL, were scattered. Different symbols indicated different pairs of sites: ○ EN RGL, ● NR RGL, □ EN YR, ■ NR YR, ▯ EN PGL, Î NR PGL, ◊ EN BP and ♦ NR BP. See Table 2 for a description of pairs of sites.

Table 21 A summary of the eigenvalues and the cumulative variation of the ordination axes of the Correspondence Analysis drawn for manifestations at all sites.

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.949	0.849	0.704	0.759	
Cumulative percentage variance					
of species data:	22.3	33.5	41.7	48.6	
of species-environment relation:	37.1	51.9	59.4	66.8	
Sum of all eigenvalues					2.415
Sum of all canonical eigenvalues					1.312

Upon inclusion of EVs, cumulative variation of the manifestations-EV relationship explained by the two primary ordination axes rose to 51.9% (Table 21). Vegetation density classes explained variation in manifestation data. Vegetation density classes 0-2 summarized three major bare ground and vegetation cover categories (0%, between 0% and 100%, and100%). The first two density classes (0: 0% vegetation cover and 1: < 100% vegetation cover) plotted to the left of the second primary ordination axis, while density class 2 (i.e. 100% vegetation cover, low density) plotted to the right (Figure 36). Bare ground and total vegetation cover affected preservation and visibility of manifestations, and are represented by the horizontal spread of these three density classes.

The other three vegetation density classes (all 100% vegetation cover, but with low (LD), medium (MD) and high (HD) density, respectively) plotted, from bottom to top, to the right of the second primary ordination axis (Figure 36). These vegetation density classes explained vertical spread of manifestation data. Rather than affecting preservation and visibility of manifestation, classes 2-4 summarized vegetation height and total vegetation cover, which indicated an increase in structural heterogeneity (i.e. potential niches to be filled).

Manifestations were representative of animal activity when visibility and preservation of manifestations (measured as vegetation density) were similar within pairs of sites. Two pairs of sites (PGL and YR) had matching vegetation densities. Manifestations at EN were similar to NR for both pairs of sites.

At the burned pair of sites (PGL), variation in vegetation structure and, thus, variation in manifestation data were low. Although significant, differences in bare ground (< 7%), moribund vegetative cover (< 3%) and vegetation height (< 9cm) were small. Thus, preservation and visibility of manifestations (i.e. horizontal spread) and structural heterogeneity (i.e. vertical spread) were similar at PGL.

At the unburned pair of sites (YR), variation in manifestations was high. As YR had 100% vegetation cover, visibility and preservation of manifestations (i.e. horizontal spread) were similar. However, there was a large (~17cm), significant difference in vegetation height, which corresponded with higher structural heterogeneity at EN YR.

In addition to visibility and preservation of manifestation, horizontal spread of manifestation data represented the continuum from live/green to dead vegetation cover. Bare ground and live vegetative cover are highest on the far left, while dead vegetation cover is highest on the far right (Figure 37). Vegetation density classes successfully captured relative amounts of bare ground, but not ratio of dead and live vegetation cover.

For the two pairs of sites (RGL and BP) with different vegetation densities, a combination of elevated vegetation height and live vegetation cover explained differences between EN and NR. In addition to visibility and preservation of manifestations, relative amounts of live vegetative cover and structural heterogeneity (i.e. vegetation height) might have influenced animal activity.

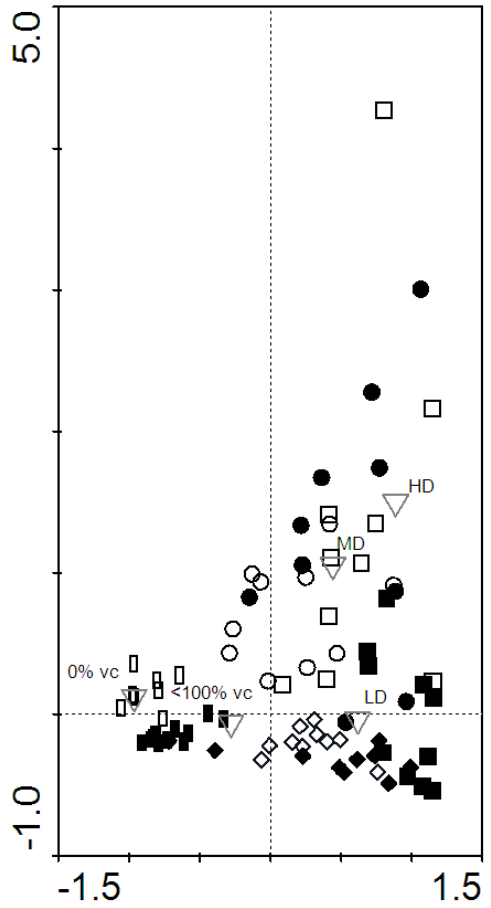

Figure 36 Patterns in the Correspondence Analysis of manifestations were strongly influenced by bare ground and vegetation density. The first two density classes (0% vc: 0% vegetation cover and < 100 % vc: < 100% vegetation cover), which were both a function of bare ground, plotted horizontally to the left of the second primary ordination axis. The other three density classes (all 100% vegetation cover, LD, MD and HD) plotted to the right of the second primary ordination axis. Different symbols indicated different pairs of sites: ○ EN RGL, ● NR RGL, □ EN YR, ■ NR YR, ▯ EN PGL, Î NR PGL, ◇ EN BP and ◆ NR BP. See Table 2 for a description of pairs of sites and Table 14 for an explanation of environmental variable abbreviations.

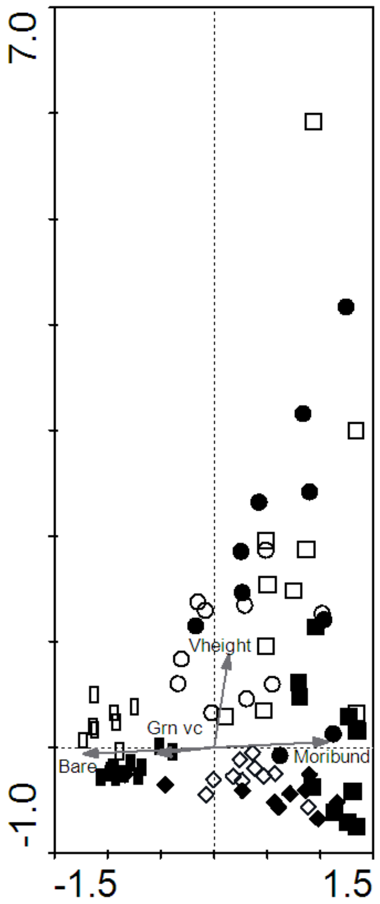

Figure 37 Other environmental variables (EVs) contributed in explaining manifestation patterns on the Correspondence Analysis. Bare ground increased towards the left, and leaf litter and moribund vegetative growth towards the right. Vegetation height increased diagonally towards the top right. Different symbols indicated different pairs of sites: ○ EN RGL, ● NR RGL, □ EN YR, ■ NR YR, ▯ EN PGL, Î NR PGL, ◊ EN BP and ♦ NR BP. See Table 2 for a description of pairs of sites and Table 14 for an explanation of EV abbreviations.

1st pair of sites: EN PGL vs. NR PGL

At the first natural pair of sites (PGL), the two primary ordination axes explained 51.9% of variation in manifestations (Table 22). The difference between EN and NR SUs was small (ANOSIM, R = 0.225, p<0.021; Table 20). Most (seven out of 10) EN SUs plotted to the right of the second primary ordination axis, while all NR SUs plotted to the left. Three EN and three NR SUs grouped in the bottom-left quadrant (Figure 38).

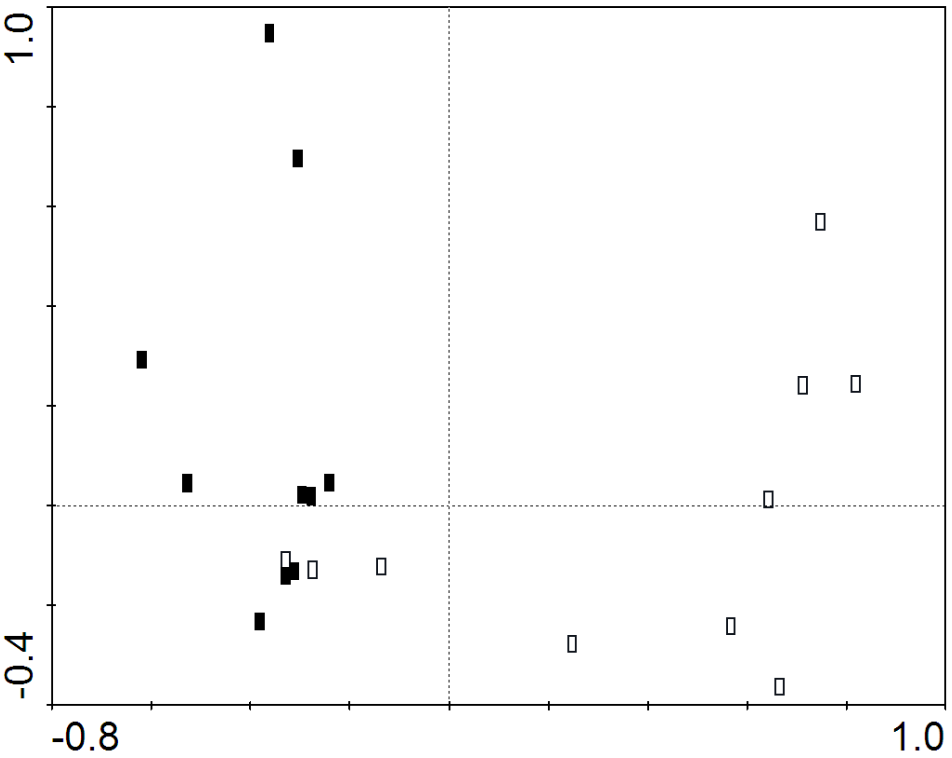

Figure 38 Based on Correspondence Analysis of manifestations at the first natural pair of sites (PGL), Ecological Network (▯) and Nature Reserve (Î) sampling units were different. See Table 2 for a description of pairs of sites.

Table 22 A summary of the eigenvalues and the cumulative variation of the ordination axes of the Correspondence Analysis drawn for manifestations at the first natural pair of sites (PGL).

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.925	0.829	0.806	0.703	
Cumulative percentage variance					
of species data:	37.4	51.9	62.2	71.2	
of species-environment relationship:	45.4	59.4	68.9	75.2	
Sum of all eigenvalues					0.571
Sum of all canonical eigenvalues					0.403

When EVs were added to the CA, the two primary ordination axes explained 59.4% of variation in the manifestation-EV relationship (Table 22). Vegetation height, bare ground and moribund vegetative cover increased towards the bottom-right, and associated with EN SUs. Green vegetative cover increased towards the top-left corner, and associated with NR SUs (Figure 39).

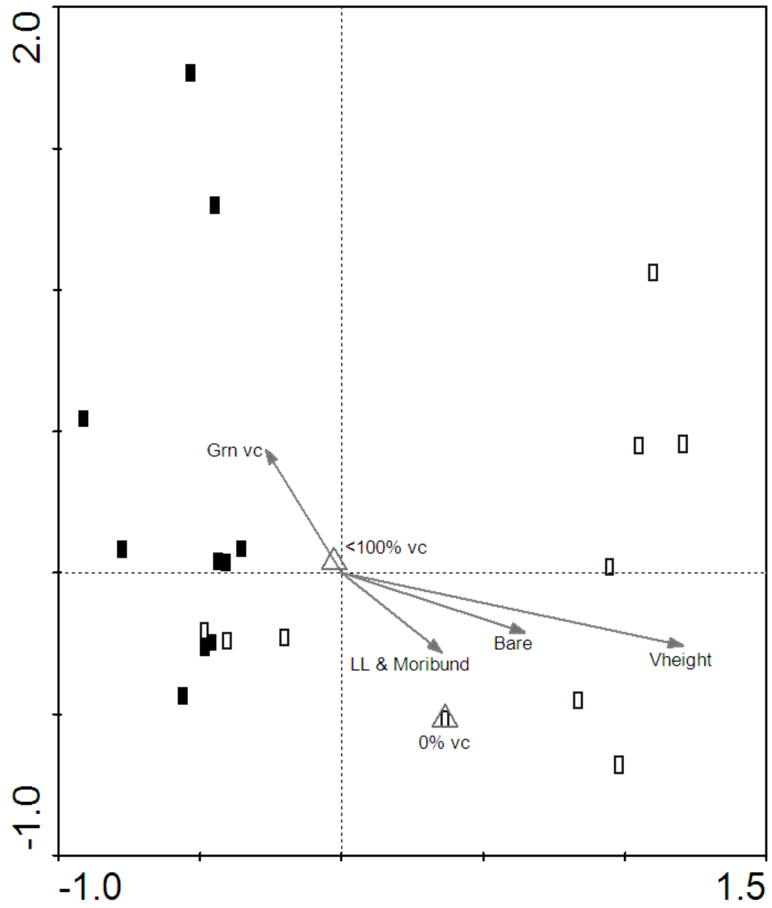

Figure 39 Environmental variables (EVs) at the first natural pair of sites (PGL) explained manifestation patterns. Vegetation height, bare ground, and leaf litter and moribund vegetative growth increased towards the bottom-left, and associated with Ecological Network sampling units (SUs). Green vegetation cover associated with Nature Reserve SUs. See Table 2 for a description of pairs of sites and Table 14 for an explanation of EV abbreviations.

2nd pair of sites: EN BP vs. NR BP

Manifestations in EN SUs were different from NR SUs at the other natural site (BP) (ANOSIM, R = 0.324, $p<0.01$; Table 20). Based on the two primary ordination axes of CA that explained 52.6% of variation in manifestation data (Table 23), EN and NR SUs grouped separately (Figure 40). Most (eight out of 10) EN SUs plotted in the bottom-right quadrant, while NR SUs were spread over the other three quadrants.

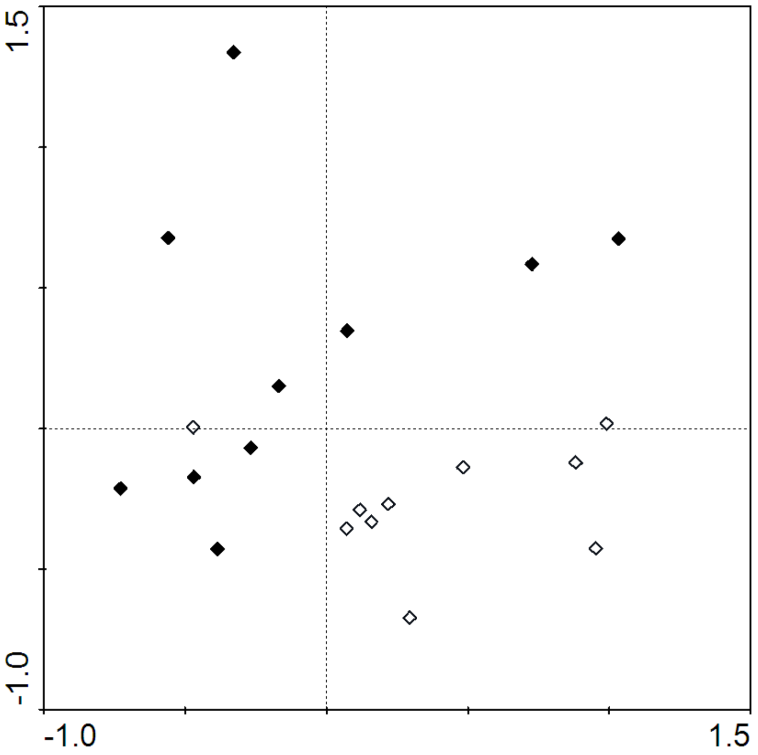

Figure 40 Based on Correspondence Analysis of manifestations at the second natural pair of sites (BP), Ecological Network (◇) and Nature Reserve (◆) sampling units grouped separately. See Table 2 for a description of pairs of sites.

Table 23 A summary of the eigenvalues and the cumulative variation of the ordination axes of the Correspondence Analysis drawn for manifestations at the other natural pair of sites (BP).

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.835	0.926	0.745	0.778	
Cumulative percentage variance					
of species data:	28.8	52.6	70.0	79.2	
of species-environment relationship:	29.1	58.6	72.6	80.6	
Sum of all eigenvalues					0.894
Sum of all canonical eigenvalues					0.618

The two ordination axes of CA explained 58.6% of the manifestation-EV relationship (Table 23). Moss and bare ground (i.e. density class 1 = < 100% vegetation cover) associated with EN SUs. The other two EVs measured in vegetation quadrats (green vegetation cover and moribund vegetative growth) associated with NR SUs. Leaf litter and moribund vegetative cover increased diagonally towards the bottom-left corner, maximum vegetation height diagonally towards the top-left corner, and green/live vegetation cover increased directly upwards. Density class 2 (i.e. 100% vegetation cover, low vegetation density) associated with NR SUs (Figure 41).

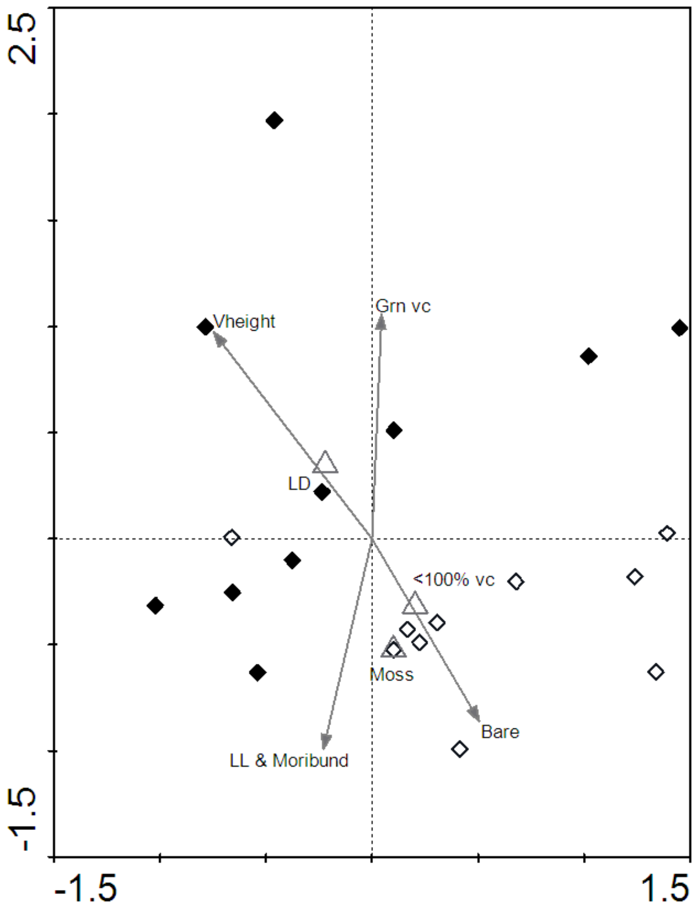

Figure 41 At the second, natural pair of sites (BP), high maximum vegetation height, green/live vegetative cover, and leaf litter and moribund vegetative cover associated with Nature Reserve sampling units (SUs) (♦), while bare ground associated with Ecological Network SUs (◊). See Table 2 for a description of pairs of sites and Table 14 for an explanation of environmental variable abbreviations used on the graph.

3rd pair of sites: EN RGL vs. NR RGL

Manifestations at the older, rehabilitated pair of sites (RGL) was very similar in EN and NR SUs (ANOSIM, R = 0.17, p<0.05; Table 20). Cumulative variation in manifestation data explained by the two primary ordination axes of CA equaled 33.2%. Five NR SUs plotted in the bottom-left quadrant with three EN SUs (Figure 42). Three EN SUs plotted in the bottom-right quadrant, and four EN SUs in the top-right quadrant. Two NR SU plotted to the right of the second ordination axis, with one above the first primary ordination axis and one below. Three NR SUs plotted in the top-left quadrant (Figure 42).

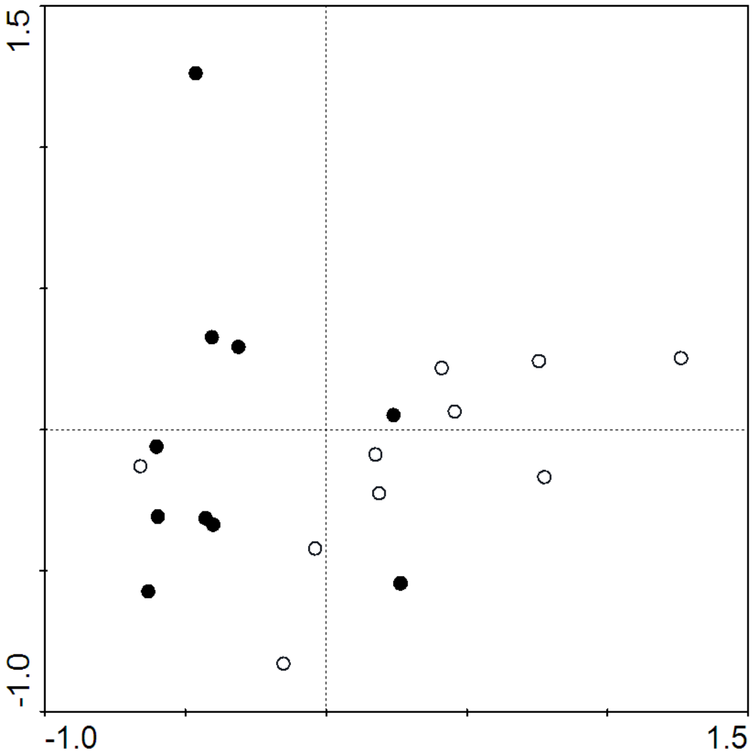

Figure 42 Manifestations in Ecological Network (○) and Nature Reserve (●) sampling units at the older, rehabilitated pair of sites (RGL) did not differ much. See Table 2 for a description of pairs of sites.

Table 24 A summary of the eigenvalues and the cumulative variation of the ordination axes of the Correspondence Analysis drawn for manifestations at the older, rehabilitated pair of sites (RGL).

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.898	0.800	0.816	0.891	
Cumulative percentage variance					
of species data:	18.4	33.2	46.7	56.7	
of species-environment relationship:	20.9	34.1	46.8	58.0	
Sum of all eigenvalues					1.527
Sum of all canonical eigenvalues					1.088

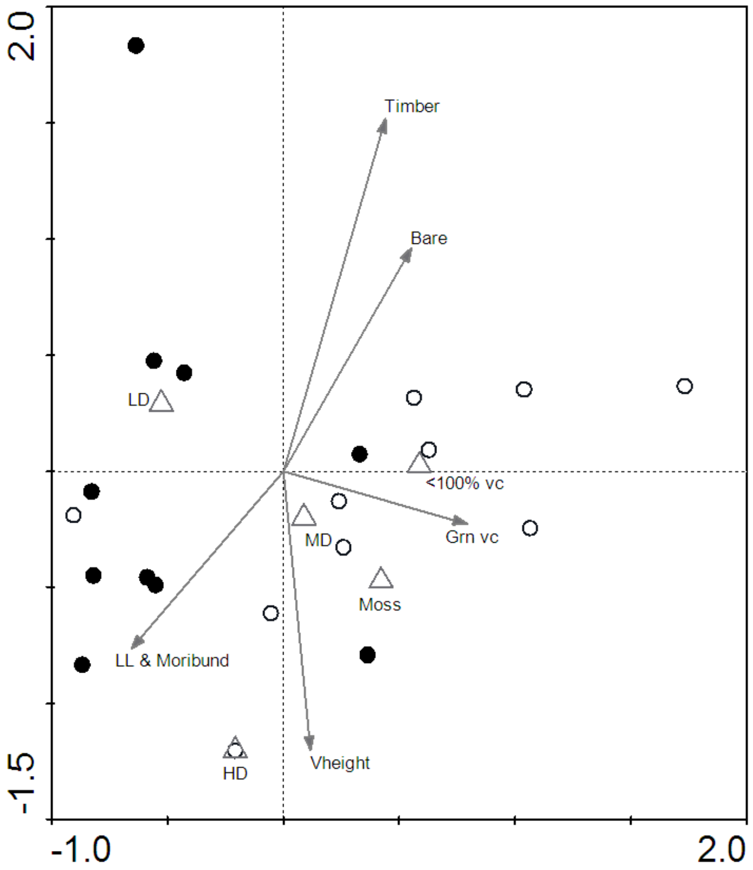

Figure 43 Environmental variables (EVs) did not greatly contribute to an understanding of manifestation patterns on Correspondence Analysis graph at the older, rehabilitated pair of sites (RGL). Density classes ascended from the first primary ordination axis on the right (<100% vegetation cover) downwards to the bottom-left quadrant (HD). Ecological Network sampling units (SUs) (○) associated with these density classes. Nature Reserve SUs (●) associated with high leaf litter and moribund vegetative cover, which increased towards the bottom-left corner. See Table 2 for a description of pairs of sites and Table 14 for an explanation of EV abbreviations.

Although most EVs had a strong effect on manifestations, they did not contribute to an explanation of manifestation patterns as the two primary ordination axes of CA only accounted for 34.1% of variation in the manifestation-EV relationship (Table 24). Leaf litter and moribund vegetative growth, and bare ground formed a continuum from bottom-left to top-right. Leaf litter and moribund vegetative growth was highest in the bottom-left corner, while bare ground increased towards the top-right. Vegetation density classes 1, 3 and 4 (i.e. <100% vegetation cover, and 100% vegetation cover, but medium and high density) plotted in an ascending order from the first primary ordination axis on the right toward the bottom-left quadrant. EN SUs arranged on this vegetation density continuum, which could be influenced by the bare ground-moribund growth continuum. Green vegetation cover increased at an angle towards the right, and vegetation height increased downwards. They both associate with EN SUs (Figure 43).

4th pair of sites: EN YR vs. NR YR

At the younger, rehabilitated pair of sites (YR), the difference in manifestations in EN SUs compared to NR SUs was small (ANOSIM, R = 0.197, p=0.01; Table 20). Based on the two primary ordination axes that explained 39.6% of variation in manifestation patterns (Table 25), EN and NR SUs grouped separately (Figure 44). Five EN SUs plotted in the bottom-right quadrant with three NR SUs. One EN SU shared the top-left quadrant with three NR SUs. Four EN SUs plotted in the top-right quadrant, and four NR SUs in the bottom-left quadrant.

Upon inclusion of EVs, cumulative variation explained by the two primary ordination axes of CA was 41.7% (Table 25). Green/live vegetation cover increased towards the top-left corner, while moribund vegetative growth increased towards the bottom-right. NR SUs arranged from top-left to bottom-right on this green-moribund vegetative growth continuum (Figure 45). In addition to this continuum, manifestations at EN SUs were influenced by higher maximum vegetation height, higher vegetation density, more bare ground and more timber (Figure 45).

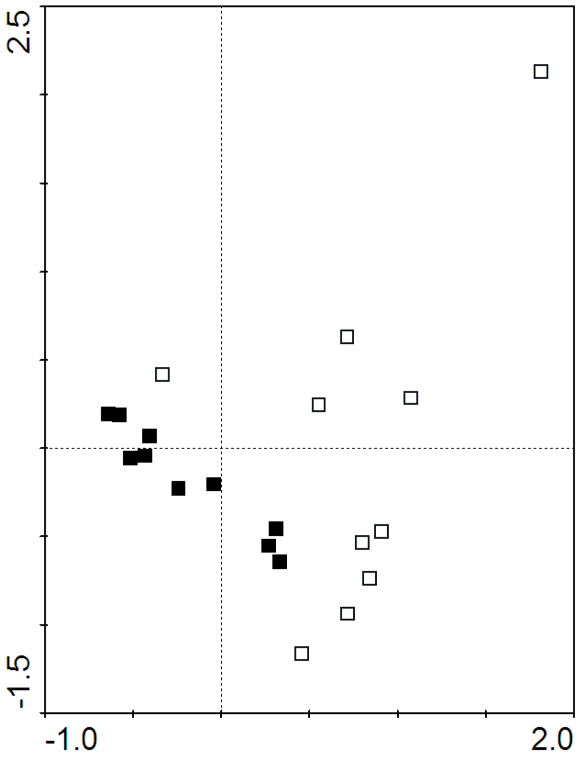

Figure 44 Correspondence Analysis of manifestations at the younger, rehabilitated pair of sites (YR) showed that Ecological Network sampling units (SUs) (□) were different from Nature Reserve SUs (■). See Table 2 for a description of pairs of sites.

Table 25 A summary of the eigenvalues and the cumulative variation of the ordination axes of the Correspondence Analysis drawn for manifestations at the younger rehabilitated pair of sites (YR).

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations:	0.958	0.856	0.865	0.955	
Cumulative percentage variance					
of species data:	25.2	39.6	51.9	61.2	
of species-environment relationship:	28.7	41.7	53.1	63.6	
Sum of all eigenvalues					1.551
Sum of all canonical eigenvalues					1.253

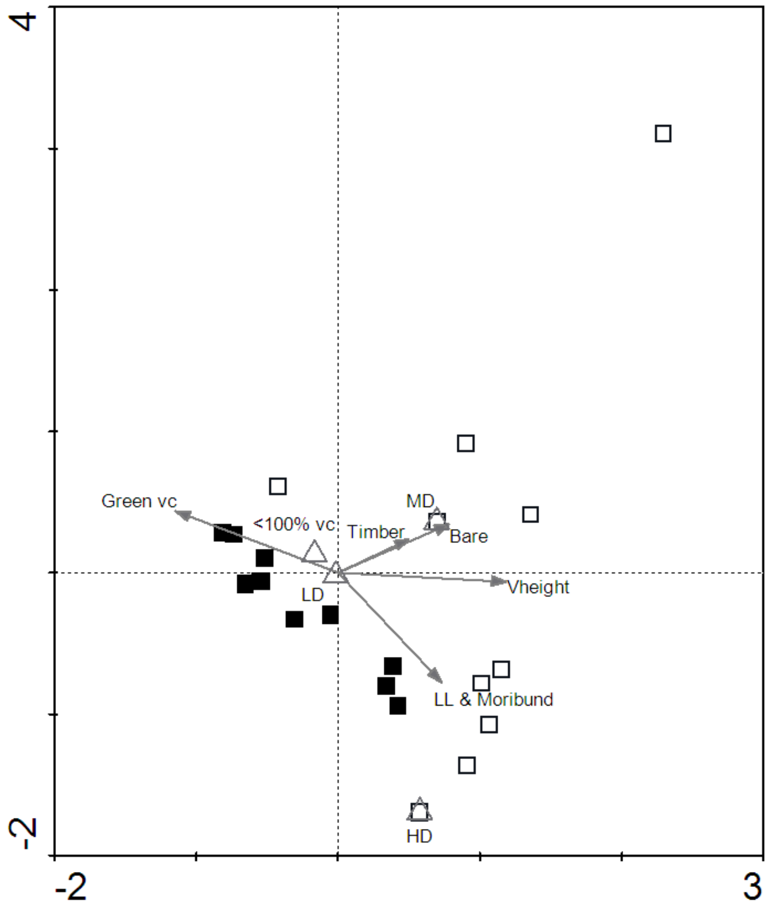

Figure 45 At the younger, rehabilitated pair of sites (YR), leaf litter and moribund vegetative growth increased towards the bottom-right corner, and green/live vegetative cover towards the upper-left corner. Nature Reserve sampling units (SUs) (■) arranged on this green vegetation cover-moribund vegetative growth continuum. Ecological Network SUs (□) were influenced by higher maximum vegetation height, more bare ground and more timber. See Table 2 for a description of pairs of sites and Table 14 for an explanation of environmental variable abbreviations used on the graph.

Fungi

Instead of CA, results on fungi and animal (bird and mammal) species will be reported using MDS, because MDS, combined with ANOSIM, is better in resolving differences in species composition between pairs of sites when the number of observations are few. Fungi were observed only in rehabilitated pairs of sites (RGL and YR) where they contributed to the decomposition of stumps and old timber logs.

1st pair of sites: EN RGL vs. NR RGL

Fungi species composition in the EN was similar to NR for the older, rehabilitated pair of sites (RGL) (ANOSIM, $R = 0.37$, $p<0.01$). Although EN and NR SUs separated, five NR SUs and three EN SUs overlapped on the MDS (Figure 46). While fungi were found in all EN SUs, there were fungi in only nine out of 10 NR SUs.

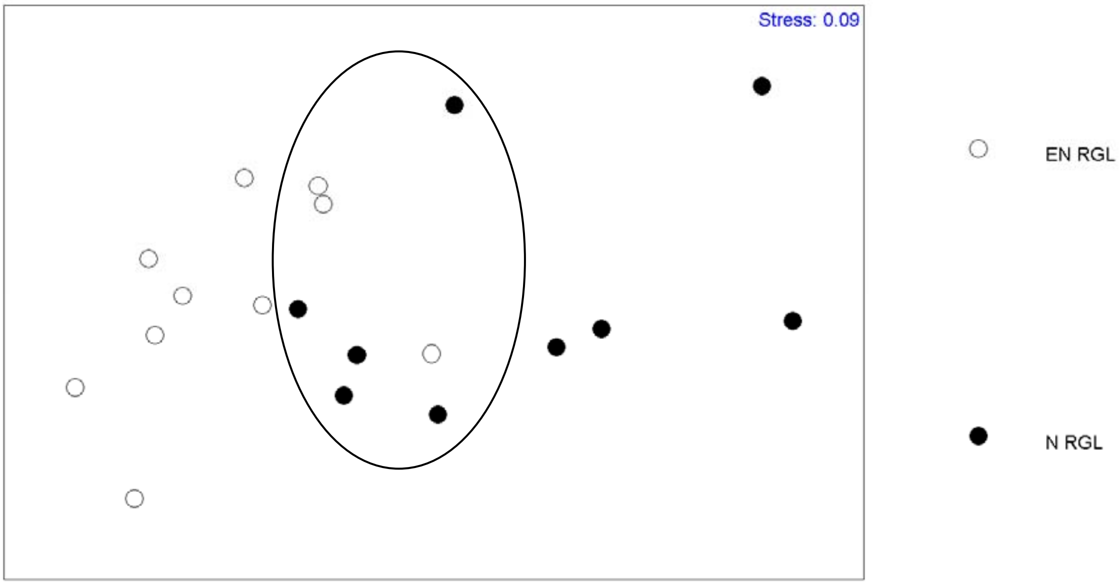

Figure 46 MDS of fungi species composition at the older, rehabilitated pair of sites (RGL) showed overlap between Ecological Network (○) and Nature Reserve sampling units (●).

2^{nd} pair of sites: EN YR vs. NR YR

There were fewer fungi in the younger, rehabilitated pair of sites (YR) than at the older one. In addition, there were five EN SUs with fungi compared to only four in the NR. Species composition between EN and NR (ANOSIM, R = 0.431, p=0.014) differed, which caused EN and NR SUs to separate on the MDS (Figure 47). There were two groups, top and bottom, that were different. Within these groups, EN SUs clustered separately from NR SUs Figure 47).

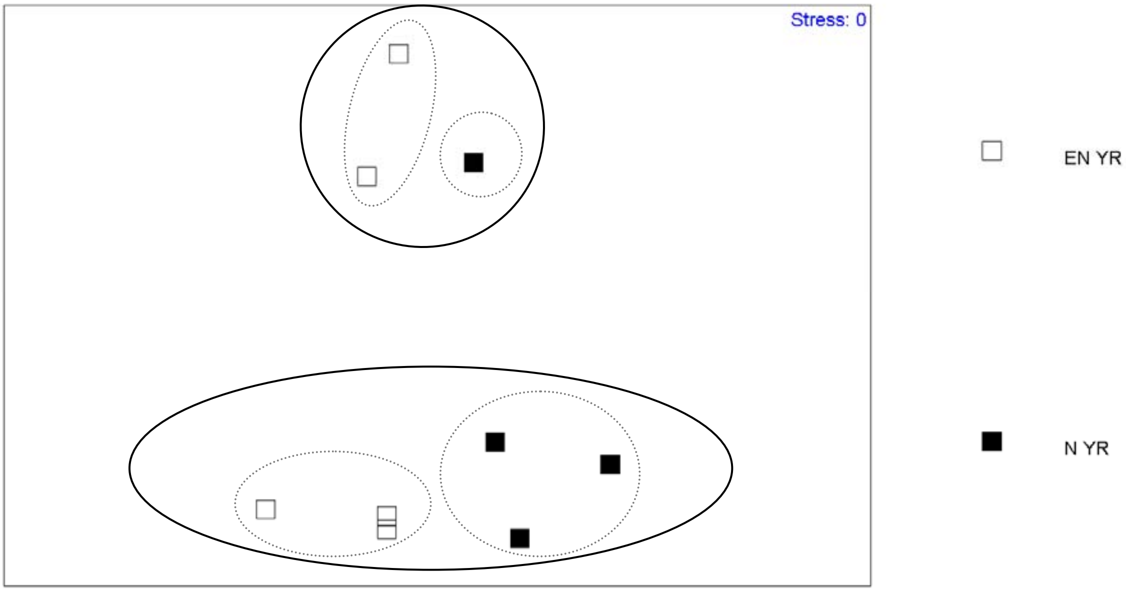

Figure 47 Fungi species assemblage at Ecological Network (EN) sampling units (SUs) (☐) of the younger, rehabilitated pair of sites (YR) differed from Nature Reserve (NR) SUs (■). There are two groups (top and bottom). Within these groups, EN and NR SUs clustered separately.

Vertebrates

When bird and mammal data were pooled, animal species composition in EN did not differ significantly from that in the NR (ANOSIM, R = -0.25, p=0.914). MDS showed two groups. At the first group, one rehabilitated and one natural NR site (NR PGL and NR RGL) clustered. At the other group, one rehabilitated EN site (EN YR) and one natural, NR site (NR BP) clustered (Figure 48).

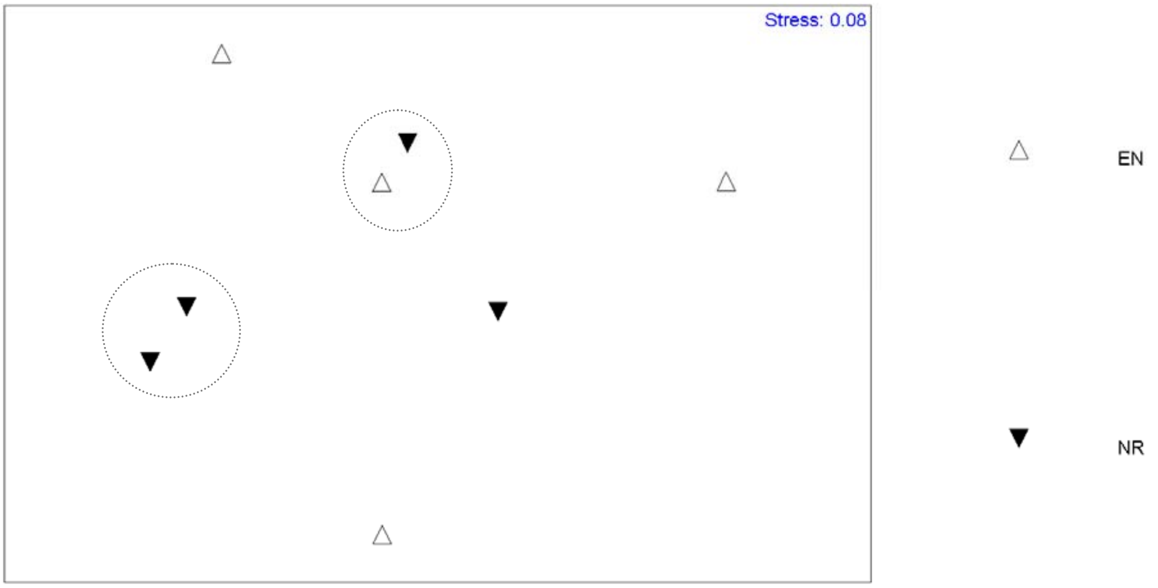

Figure 48 Animal (bird and mammal) species composition at Ecological Network (▽) and Nature Reserve (▼) sites.

Discussion

Habitat heterogeneity (e.g. different, successive grassland plant communities with different attributes) has two dimensions – vertical (or structural heterogeneity) and horizontal (or spatial heterogeneity). Habitat heterogeneity is partly caused by topography (including drainage patterns), soil type and disturbances. Topography and soil type are mostly deterministic of large-scale spatial heterogeneity, while natural disturbances are capable of shaping the structural and spatial heterogeneity of an ecosystem at different temporal and spatial scales (Bond & Keeley 2005).

South African grasslands are consumer (i.e. grazing and fire), and not resource (i.e. soils and climate) controlled (Bond & Keeley 2005), with habitat heterogeneity being shaped by different fire regimes (i.e. fire frequency, intensity and severity, as well as season, type and extent of fire across a landscape) (Bond & Keeley 2005). In view of these points, many differences recorded here between Ecological Network (EN) and Nature Reserve (NR), both for environmental variables (EVs) and for measurements of biodiversity, are likely to be influenced by local disturbance regimes.

Overall comparison of environmental variables

As environmental variables (EVs) were interrelated, it was possible to collectively explain certain combinations of EVs by a single factor. For example, leaf litter and moribund vegetative growth, vegetation height and vegetation density were all determined by vegetation age i.e. time since last fire. That single factor is at least partly the result of area-specific grassland management practices.

All EVs fluctuate within a naturally dynamic system. Fluctuations might occur over short (management-related), longer (ecological adaptations) and very long periods (evolutionary adaptations). Here, however, it is likely that differences between the EN and NR are due to management and ecological adaptations, rather than evolutionary adaptations, as forestry in the study area has been in existence for only a few decades.

Despite choice of pairs of sites that appeared similar, vegetation structure (i.e. bare ground, green/live vegetative cover and vegetation height) differed overall between EN and NR, and also, specifically for two natural pairs of sites (BP and PGL). Differences found in vegetation structure are explained by drought, grazing pressure, local fire regime and area-specific animal behavior.

Drought

Increased bare ground might be due to drought. Drought has two causes: reduction in precipitation and a reduction in accessible ground water (Kienzle & Schulze 1992; le Maitre *et al.* 1999). The first operates at the regional spatial scale, and does not differentiate between pairs of sites, less than 50 km apart. Thus, if drought caused more bare ground in EN, relative to NR, a reduction in accessible ground water is more likely to be the reason than an overall reduction in precipitation.

Ground water becomes less accessible when the water table retracts to deeper soil layers. Water-table depth is determined by precipitation, water extraction (by vegetation through transpiration) and lateral water flow through the aquifer (Kienzle & Schulze 1992). Eucalyptus plantations have deep rooting systems, and high transpiration rates. Thus, a plantation could create a groundwater depression area below the plantation similar to a cone of depression around a borehole (Rawlins & Kelbe 1990). Soil permeability (i.e. relative clay content) and soil structure influences the spatial extent of the depression area (Kienzle & Schulze 1992).

Both natural pairs of sites (BP and PGL) had dominant grass cover. Unlike eucalypt trees, grass roots are shallow i.e. they extract water from the top layers in the soil profile (Walker *et al.* 1981). When "plantation-induced drought" (i.e. groundwater depression by plantations) is coupled with a naturally, dry year (i.e. low precipitation), grasses may start to die off. This might explain more bare ground in EN than NR for these two pairs of sites. In contrast, natural NR sites were probably not impacted by "plantation induced drought", as they were buffered from the effect of plantation by 4 km of natural vegetation.

Green vegetative cover

Overall, green/live vegetation cover was lower in EN than NR. Specifically, there was a significant difference for two natural pairs of sites (BP and PGL). In addition to plantation-induced drought that could affect primary productivity of grasses in ENs, there were two other potential explanations: allelopathy and grazing.

Allelopathy

Eucalypt trees have an allelopathic (i.e. suppressive) effect on growth of understorey plants, including some grass species e.g. *Cynodon dactylon* (Babu and Kandasamy 1997). Allelochemicals released by trees might also affect neighbouring communities (Gill and

Prasad 2000). This effect, however, diminishes with increasing distance from eucalypt plantation boundary. At a distance of 7m from eucalypt trees, the effect on yields of field crops was neglible (Narwal and Sarmah 1992).

Since all EN SUs were positioned more than 30m from plantation boundaries, it is very unlikely that lower green vegetative cover was the result of allelopathic effects of eucalypt trees on grassland ENs.

Grazing

Herbivory by semi-resident game and regularly visiting game at these natural EN sites might explain the differences in green vegetative cover. iSimangaliso Wetland Park has the largest concentration of southern reedbuck in southern Africa (Stuart & Stuart 2007), with many individuals in the EN and among eucalypt plantations. The one natural EN site (EN PGL) was regularly visited by two family groups (~ 6 individuals each, including young) of southern reedbuck. At the second natural EN site (EN BP), a community of ~11 zebra and ~21 (including young) blue wildebeest individuals resided on a semi-permanent basis. Zebra and blue wildebeest species are grazers, and occur in social groups, ranging in size from 6 to 12 for zebra (Grubb 1981), and 2 to 25 for most breeding herds of blue wildebeest (Attwell 1982).

Population density, as the cause of high intensity grazing, is determined by population distribution and population size. Whereas population distribution might be altered by movement corridors, population size of generalist herbivores (e.g. zebra, blue wildebeest and southern reedbuck) would probably be influenced by additional feeding, shelter and breeding habitat (Newmark 1993) supplied by corridors.

The two natural EN pairs of sites were not connected to other grassland patches via high-quality grassland corridors or wide (>40 m), mowed firebreaks. If grazing pressure is to be reduced, semi-resident communities of grazers must voluntarily leave the area to graze in other grassland areas while population sizes are maintained constant. Although southern reedbuck and zebra readily moved through narrow (~10 m), mowed grassland corridors and eucalypt plantations, movement patterns of blue wildebeest herds depended on herd size. While large blue wildebeest herds (~80 individuals) preferred wide (~50 m) grassland corridors, smaller herds (~5 individuals) moved along roads through plantations. Vegetation structure influences blue wildebeest herd size in the lowlands of KwaZulu-Natal (i.e. Zululand) (Attwell 1982). While open, grassland habitat favored larger breeding herds, herd sizes tended to be small in heavily wooded habitat (Attwell 1982). Voluntary movement of large blue wildebeest herds between grassland areas requires wide grassland movement corridors between isolated grassland patches.

Connected and unconnected habitat patches did not affect population densities of most small mammal species, including a generalist mouse species (*Peromyscus gossypinus*), a generalist rat species (*Signodon hispidus*) (Mabry *et al.* 2003), a specialist vole species (*Clethrionomys gapperi*) and a generalist mouse species (*P. maniculatus*) (Mech & Hallett 2001). However, population density of one specialist mouse species (*P. polionotus*) was lower in connected habitat (Mabry *et al.* 2003). It is possible that different small mammal population densities were caused by differing habitat qualities, associated with corridors (Haddad & Baum 1999), rather than by connectivity per se.

Fire regime

Vegetation height, vegetation density, and leaf litter and moribund vegetative cover were influenced by fire regime. Specifically fire severity (i.e. ecosystem impact (Bond & Keeley 2005), measured as removal of combustible plant material) differed between EN and NR.

Overall, vegetation height and density were higher in EN than NR. Forestry operations preferentially burn on cooler days, when the fire hazard is lower. Cool fires have lower fire severity, which result in less complete removal of combustible plant material. Temporal fluctuations and spatial variability in the volume of combustible plant material (i.e. vegetation height, vegetation density, and leaf litter and moribund vegetative growth) are part of a dynamic ecosystem.

Implications of vegetation cover vs. bare ground ratio

Generally, more vegetation cover than bare ground is desirable, as it increases water infiltration, provides resources and habitat for above-ground organisms (e.g. small mammals in Peles & Barrett 1996) and, through ecosystem processes, such as decomposition, creates favorable conditions for below-ground organisms (e.g. earthworms and termites). Although dominant vegetation cover can be considered as ‘good’, it does not mean that bare ground is always ‘bad’. Small areas of bare ground are necessary for certain invertebrate species to complete their life cycle (Lu & Samways 2002) and for butterflies to bask in the sun (Pryke & Samways 2001).

Fire, molehills and diggings in grassland all increase bare ground cover, which reduce competition from perennial grass species (Collins & Uno 1985) and introduce recruitment possibilities (Overbeck *et al.* 2005) for non-mycorrhizal, short-lived herbaceous species (Overbeck *et al.* 2005; Kotanen 1995; Milton *et al.* 1997; Canals & Sebastia 2000; Collins & Uno 1985), characteristic of early-successional stages. Small-scale, animal-mediated disturbances not only increase plant species richness, but also change plant species composition (Canals & Sebastia 2000; Kotanen 1995; Milton *et al.* 1997).

The possibility that regeneration niches might be colonized by alien plant species cannot be excluded. Indeed, native and alien annual grasses responded positively to pig digging in Californian grassland (Kotanen 1995). Furthermore, 89% of seeds that germinated from bison (*Bos bison*) dung was an alien, annual grass species (*Bromus japonicus*) (Collins & Uno 1985). Because bison preferentially graze in recently-burned areas, alien propagules are dispersed to these 'new' areas (Collins & Uno 1985). Lastly, a study investigating the effect of livestock grazing on Australian subtropical grasslands found more native decreaser and more alien increaser plant species (McIntyre *et al.* 2003).

Overall comparison of plants

Plants are relatively sedentary, reliable indicators of past and present disturbances, and indicative of below-ground processes (e.g. lateral water flow in the aquifer). Therefore, differences in plant species richness and composition indicates localized seen (i.e. above-ground and current) and unseen (i.e. subterranean and historic) processes.

Overall, plant species richness was higher in NR than EN, at least for three of the four pairs of sites (BP, PGL and YR). Differences in species richness were small (<3 spp.) for two pairs of sites (BP and YR), but it was large (~12 spp.) for the other pair (PGL). This suggests that certain processes inherent to these ENs (e.g. management practices in the forestry plantation matrix) might have an impoverishing effect on plant species richness, which could have important implications for the long term conservation of biodiversity in these systems.

Plant species composition differed between pairs of sites (i.e. RGL vs. YR vs. PGL vs. BP). Therefore, different pairs of sites were considered different habitat types. Differences in species compositions between habitat types were, among others, due to different soil types, natural variation in moisture content (e.g. grassland with and without wetland elements), and different disturbance history (e.g. grazing and fire regimes, and vegetative recovery after clearing plantations). Differences between habitat types contributed to variation of plant species composition across the landscape and should be viewed separately from differences between EN and NR.

Differences between EN and NR within each pair of sites was due to causes intrinsic to respective areas. These causes may include, among others, differences in soil moisture content as a result of plantation-induced drought and lower fire intensity in grassland ENs.

Differences in plant species composition between EN and NR were smaller than differences observed between habitat types, and can contribute to landscape heterogeneity if differences between EN and NR do not exceed magnitude of natural fluctuations in the system. Habitat heterogeneity (i.e. variation in measured EVs and biodiversity at a landscape spatial scale) is desirable at various spatial (Samways *et al.* 2006) and temporal scales. Diverse and dynamic ecosystems sustain a higher variety of organisms, because more niches are available.

Natural processes, including topographical differences (e.g. drainage patterns) and variation in disturbance regime across the landscape, shape plant community composition in different habitat types. One pair of sites (PGL) was characterized by dominant woody shrub cover, while another (BP) was characterized by dominant herbaceous cover. In addition, dominant sedge cover, which is indicative of a shallow water table, characterized two pairs of sites (BP and YR).

In addition to growth forms, richness and composition of grass species differed between pairs of sites. Dominant grass species richness varied from four (PGL) to three (YR) to one (RGL and BP). Three grass species (*P. maximum*, *D. geminatum* and *M. repens*) did not associate with any specific pair of sites, but plotted in the bottom half of CA with three of the four EN sites (EN YR, EN RGL and EN BP). *P. maximum* and *D. geminatum* are shade-tolerant grass species that grow below eucalypt trees, while *M. repens* is a weedy pioneer species that plays an important role in stabilizing soil in disturbed areas (van Oudtshoorn 1992).

Differences in vegetation height and density between EN and NR are at least partly influenced by characteristics of the grass community. For example, bunch grasses were taller than lawn grasses, but lawn grasses provided denser vegetation cover than bunch grasses. In addition, some bunch grasses were taller and some lawn grasses were denser than other species with the same growth form. For example, *Chloris gayana* was taller than *P. maximum*, and *S. secundatum* was denser than *Cynodon dactylon*.

Three of the four pairs of sites were characterized by a set of EVs (i.e. volume of combustible plant material) that represented vegetation age. For example, a recently-burned pair of sites (PGL) was characterized by much bare ground, green vegetative cover and low vegetation density, while an older pair of sites (RGL) had much leaf litter and moribund vegetative cover, and elevated vegetation density and height.

Comparison of plants for pairs of sites

Natural pairs of sites

Habitat transformation affects landscape structure and species diversity at different spatial and temporal scales (Lindborg & Eriksson 2004). When relating present-day and past connectivity with current patterns in plant diversity, a time lag of between 50 and 100 years was found in the response of plant diversity to landscape structure (Lindborg & Eriksson 2004). The possibility of a time lag in biological responses of long-lived plant species to current context remains untested. However, plantations have existed for ~ 50 years. Since most grassland plant species do not live longer than 50 years (I. Johnson, pers. comm.), biological response of most grassland plant species to current landscape structure should be complete. Furthermore, historical context was found to be less important than current patch size and heterogeneity (i.e. soil type and topography) in shaping plant communities in Swedish semi-natural grassland (Oster *et al.* 2007). These two studies agree with aspects from this study i.e. the relative importance of connectivity (i.e. historical context), patch size (i.e. source vs. sink) and habitat heterogeneity in conserving plant diversity.

As with the Swedish semi-natural grasslands, both natural pairs of sites (BP and PGL) were remnant habitat patches within a transformed matrix. Assuming EN and NR originally had similar suites of plant species, differences in plant species richness and composition would be due to local extinction, colonization from different source habitats or shifts in plant communities caused by fire regime (Bond & Keeley 2005), grazing regime (McIntyre & Lavorel 2001; McIvor *et al.* 2005) and differential seed predation (Orrock & Damschen 2005; Orrock *et al.* 2003).

Differences in plant species richness and composition at PGL were very large. Within the framework of metapopulation dynamics, EN PGL was probably not large enough to sustain population size of individual plant species, which possibly led to local extinction in the past. Thus, at least for plant species, it functioned as a habitat sink. Furthermore, EN PGL was not connected to potential source habitat with high-quality grassland corridors. Thus, colonization would have been limited to seed dispersal of disturbance-tolerant plant species from the matrix. Matrix included eucalypt plantations, a staff housing complex, rehabilitated grassland and mowed firebreaks next to roads. All of these areas were either frequently disturbed (e.g. mowing) or had a history of intense disturbance (e.g. rehabilitated grassland was cleared of plantations).

Differential seed predation in connected NR PGL vs. unconnected EN PGL might have influenced soil-stored seed population. At least for palatable obligate seed producing grass species in South African savannas, seed longevity is very short (2-3 years) (O'Connor 1991). Therefore, seedbank size, especially for these obligate reseeders, depends on annual input of seeds (O'Connor 1991). However, seed predation of *T. triandra* in South African montane grasslands ranged between 70% and 98%. Ants (*Camponotus* and *Myrmicaria* species) were the main predators, but signs of seed predation by rodents were also detected (Everson *et al*. 2009).

Removal of seed was reported to be predator-specific i.e. invertebrates removed more seeds in unconnected habitat, while rodents removed more seeds in connected habitat patches (Orrock *et al.* 2003). These results are supported by another study that reported less predation of large-seeded *Prunus serotina* in unconnected habitat patches, while both large-seeded *P. serotina* and small-seeded *Rubus allegheniensis* suffered heavy predation in connected habitat patches (Orrock & Damschen 2005). In contrast to what was expected, mean small mammal burrow density (as a preliminary surrogate for small mammal population density) at the unconnected EN PGL (12.6) was significantly higher than at the connected NR PGL (7.1), but the total number of ant nests at EN PGL (60.9) was similar to NR PGL (59.7), as was expected.

Fire regime in EN PGL differed from NR PGL. There are three aspects of a fire regime that might explain observed differences, namely fire season, frequency, intensity and severity. Fire intensity is a measure of energy release (i.e. heat), and fire severity is a function of fire intensity, but specifically measures ecosystem impact (Bond & Keeley 2005). It is generally assumed that local fire regime selects for species that fit local conditions (Bond & Keeley 2005). Therefore, diverse fire regime should promote biodiversity. This assumption formed the basis of fire management in the Kruger National Park, South Africa (van Wilgen *et al*. 2008), but is poorly understood and untested (Parr and Andersen 2006). If the assumption is valid, differences in fire season, intensity, frequency and severity might cause a shift in plant species composition. However, it was found that effect of different fire regimes on species composition of South African savanna was small compared to its effect on vegetation structure and biomass (van Wilgen *et al*. 2007). Post-fire regeneration of reseeders is influenced by fire intensity and frequency. While some plant species need fire for seedling recruitment (Keeley & Fotheringham 2000), high fire intensity could damage soil-stored seeds, as seen in reduced seedling density in Californian shrubland (Keeley 1998).

Post-fire regeneration of resprouters is influenced by fire intensity (Keeley 1998) and severity. Fire severity is analogue to 'pruning' and stimulated new growth in resprouting plant species. However, high fire intensity damaged resprouting organs of shrub species in Californian shrubland, which resulted in poor post-fire regeneration (Keeley 1998).

Fire intensity was driven by fuel load volume (i.e. accumulation of plant material as influenced by post-fire age, grazing and rainfall) in Kansas tallgrass prairie (Gibson *et al.* 1990), while both fuel load volume and fire season (i.e. fuel moisture content) affected fire intensity in the Kruger National Park (Govender *et al*. 2006).

Fire frequency not only influenced fuel load volume, but also fuel load distribution (Figure 49). In Kansas tallgrass prairie, distribution of plant material was most homogenous in areas with a moderate fire frequency. In contrast, accumulation of plant material was very diverse in areas with a low fire frequency, and was patchy in areas with a high fire frequency. These variations in fuel load corresponded with spatial variation in fire intensity (Gibson *et al.* 1990). It is believed that not only fire intensity per se, but also variation in fire intensity drove spatial variation in plant species composition. Variation, however, declines as fire intensity increases (Keeley 1998; Gibson *et al.* 1990). Thus, high fire intensity has direct and indirect influences on the reseeding plant community. It directly damages soil-stored seeds, and indirectly affects spatial variation in plant community (Figure 49).

Fire frequency also has direct and indirect effects. Low fire frequency indirectly affects fire intensity through its effects on fuel load, while high fire frequency directly influences the native:alien plant ratio and possibly shrub encroachment in heavily-grazed areas where grass fuel load is insufficient to generate enough heat to kill woody species (Figure 49). For example, abundance of alien annual grasses and resprouting shrubs (Syphard *et al.* 2006) increased, while abundance of fire-cued shrub species decreased in areas with high fire frequency (Syphard *et al.* 2006). While shrub encroachment was reported to be advanced by high frequency, low intensity fires in South African savanna (Roques *et al.* 2001), woody encroachment was also reported for African savanna where a reduction in frequency of intense fires allowed establishment of *Acacia nilotica* seedlings (Skowno *et al.* 1999). Fire intensity, therefore, seems to have a larger influence on woody encroachment than fire frequency.

Although moderate fire frequency reduces variation in fire intensity with negative consequences for spatial variation in plant community, effects will probably be smaller than when high intensity fire kills plants or when alien plants replace native plants.

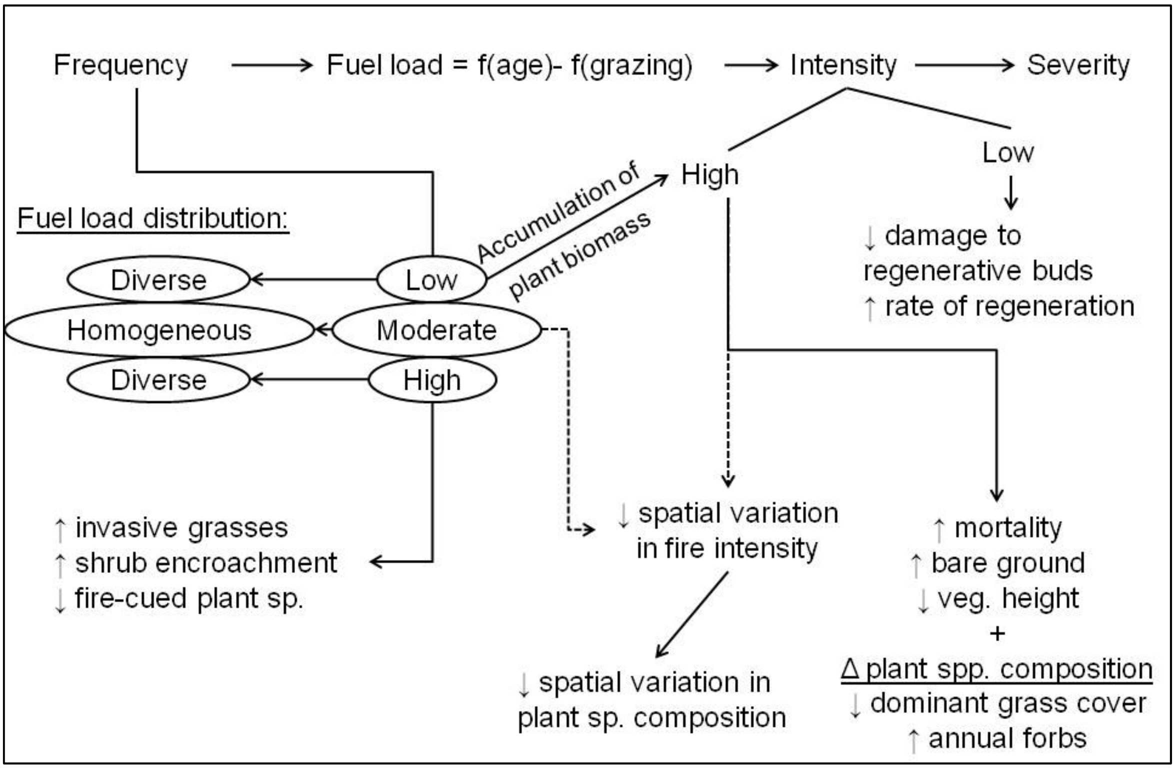

Figure 49 The effect of fire on vegetative regeneration of grassland. While fuel load influences fire intensity, fire frequency influences fuel load and fuel load distribution. Moderate fire frequency might cause a reduction in the spatial variation of fire intensity, but it has smaller negative effects than either low or high fire frequency.

In undisturbed Mediterranean grassland, plant species richness was low, and forbs, tall perennial and tall annual grasses dominated (Noy-Meir 1995; Noy-Meir *et al.* 1989). These grasses had a rapidly upward-growing sward in the growing season (Noy-Meir 1995). Interestingly, these are all traits that can describe EN PGL. It had low plant species richness, and was dominated by a tall, perennial grass species (*Digitaria* sp. 1) that grew rapidly after being burned. Although not dominant, a few herb species (e.g. *Scabiosa* spp.) also occurred in the area.

Furthermore, EN PGL had significantly more leaf litter and moribund vegetative cover, and higher vegetation height, which are all traits ascribed to undisturbed Mediterranean grassland (Noy-Meir 1995). However, EN PGL was disturbed i.e. burned and grazed. A possible explanation for this similarity between EN PGL and undisturbed grassland is very low disturbance intensity, i.e. fire severity and/or grazing intensity is too low to adequately remove plant biomass. This caused vegetation structure to resemble that of undisturbed grassland.

Generally, low fire intensity is recommended for grassland, as grasses grow optimally when fire severity is minimal (Bock & Bock 1978). High intensity fires were documented to reduce vegetation height, change plant species composition (i.e. reduce dominant grass cover, stimulate growth of other grasses and increase annual forbs) and create more bare ground (Bock & Bock 1978) (Figure 49). High-intensity fires might increase species richness, because of reduced competition from dominant species and more bare ground (i.e. open habitat) (Bock & Bock 1978). However, EN PGL already had more bare ground than NR PGL. Doubts exist over whether additional bare ground will result in increased species richness.

Post-fire regeneration in Californian shrubland was extensively investigated after a large wildfire (Keeley 1998). Vegetation recovered faster at inland than at coastal sites. Inland sites were dominated by annual herbs and had well-drained, sandy soils. Coastal sites' soils had high clay content (i.e. better water-holding capacity), and were dominated by perennial herbs (Keeley 1998). Interestingly here, NR PGL occurs in land type Ha44a, while EN PGL occurs in Ha 45a. Although soil types (Umtentweni, Mkambati, Vasi and Longlands) were similar up to a depth of 1200mm, there were differences in relative percentage clay content. EN PGL had 5-10% more clay than NR PGL. In addition, weathered rock limited root penetration at NR PGL, which was not the case at EN PGL. If it is assumed that green vegetation cover is representative of post-fire vegetation recovery, differences at PGL might be explained by soil differences and associated growth forms. Even though the sites appeared similar and soil types were similar, relative percentage clay content and depth limiting materials differed. This might explain differences in plant species composition and rate of vegetative recovery.

There were differences in plant species richness and composition at the other natural pair of sites (BP), but differences were small. Differences can be explained by different matrices (i.e. source habitats), different grazing regimes and variation in soil moisture content.

EN BP was the largest natural grassland area among the eucalypt plantations. Therefore, it had the potential to function as source habitat for some of the other grassland areas. However, there was no high-quality grassland area from which it could be colonized should some species go locally extinct. In contrast, NR BP was surrounded by natural grassland, including other seasonal wetland areas. Thus, there was only an outflow of propagules at EN BP, but an influx and efflux at NR BP.

Plant species richness differed significantly, but the difference was small (EN BP: ~5 spp. and NR BP: ~7 spp.). Although grazing intensity in EN BP and NR BP appeared to be similar, grazers rarely moved from EN BP. Similar to fire, different grazing regimes (i.e. low intensity vs. high intensity and ‘sustained’ vs. ‘sporadic’ grazing) can change species composition (Noy-Meir *et al.* 1989; O'Connor and Picket 1992). Lightly to moderately grazed subtropical grassland in Australia was characterized by tall forbs, tall grass and moderately leafy perennial grasses (McIntyre & Lavorel 2001; McIvor *et al.* 2005), which generally agrees with results from Mediterranean grassland (Noy-Meir *et al.* 1989). Mesic savanna grasslands areas in South Africa subjected to low grazing intensity had long-lived, palatable perennial grass species (O'Connor and Picket 1992). In contrast, heavily grazed subtropical grassland in Australia was characterized by annual grasses, low-growing perennial grasses and low-growing, mat-forming forbs (McIntyre & Lavorel 2001; McIvor *et al.* 2005) (Figure 50). Heavily-grazed mesic savanna grassland areas in South Africa had short-lived perennial grasses, unpalatable grasses and forbs (O'Connor and Picket 1992). Character traits of plant species at BP and heavily-grazed subtropical grassland in Australia were similar.

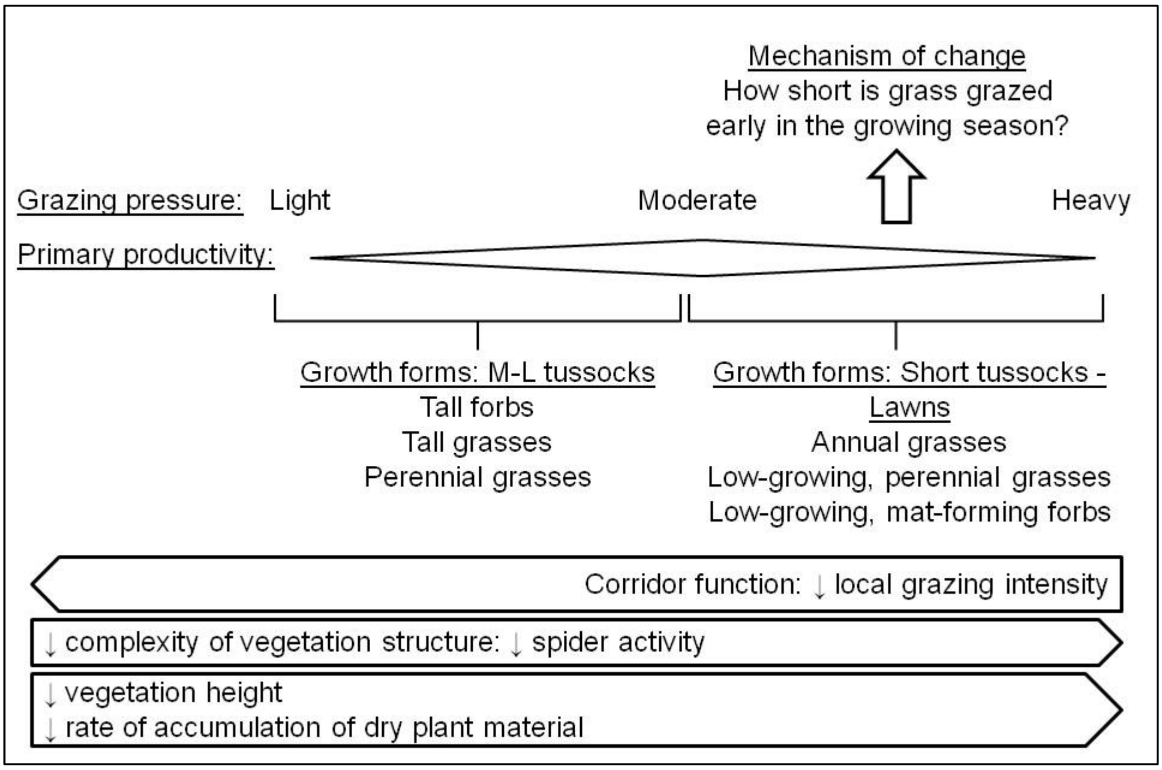

Figure 50 Vegetation structure changes with different grazing intensities. Grazing intensity at one natural pair of sites (BP) ranged between moderate and heavy.

Vegetation height was significantly lower in EN BP (~6 cm) than NR BP (~7.5 cm). Firstly, this reduction in height might be due to change in plant species composition (McIntyre & Lavorel 2001), which was a response to grazing pressure. Alternatively, it might be due to removal of grass inflorescences. If inflorescences were continually removed, seed production would decline (Collins & Uno 1985) and obligate reseeder species might be jeopardized. When coupled with drought and high variability in rainfall, sustained heavy grazing could cause local and/or regional extinction of palatable, obligate reseeding grasses in South Africa (O'Connor 1991). Interestingly, when grazing pressure varied from moderate to high, as in the case of BP, the major mechanism of grassland change in Meditteranean grassland was how short grass was grazed early in the growing season (Noy-Meir *et al.* 1989).

Water availability, as indicated by sedges and moss, at NR BP may have driven increased primary productivity, resulting in higher and more live vegetative cover. Spatial variation in soil moisture (e.g. drainage patterns) have driven plant communities in SQF (SGS Qualifor 2007) and probably caused differences in plant species composition at this natural pair of sites (BP). Differences in soil moisture might be explained by climatic drought (i.e.

reduction in precipitation as part of climatic cycle) or plantation-induced drought. Climatic cycles have been observed to cause fluctuations in relative amounts of sedge and grass cover, with sedges dominating in wet cycles and vice versa (R. van Wyk, pers. comm.). Associations of dominant sedge cover with NR BP, and dominant grass with EN BP further supports the 'plantation-induced drought' hypothesis.

Association of bare ground with EN BP might be explained by blue wildebeest territorial behavior. There were six times as many blue wildebeest diggings in EN BP (18) as in NR BP (3). Elevated bare ground might be explained by territorial behavior of blue wildebeest males, as territorial behavior involved digging and fighting. In 1982, blue wildebeest males in Zululand had atypical territorial behavior, presumably because the territorial network was incomplete (Attwell 1982). While blue wildebeest males normally display territoriality only when they were within their own territory, blue wildebeest males in Zululand always displayed territorial behavior, irrespective of whether they were in their own territory or not (Attwell 1982).

EN BP had high dry fuel loads and high grazing pressure, which are not easily reconciled. In Mediterranean grassland, grazing continually removed green plant material during growing season, resulting in reduced rates of plant material accumulation (Noy-Meir 1995). This was the case for EN BP. Plant biomass was continually removed, which resulted in reduced fuel load and, therefore, lower fire intensity. When the effect of grazing on fuel load (Noy-Meir 1995) is combined with foresters' guidelines to only burn on cool days with high humidity and no wind (L. Nel, pers. comm.), fire intensity was even further reduced at EN BP.

Fire severity is defined as a measure of ecosystem impact (Bond and Keeley 2005) or the degree of vegetation change induced by fire (Landmann 2003).Generally, fire intensity and fire severity is positively correlated i.e. warmer fires have a larger impact on vegetation and vice versa. When comparing grassland burned by a very hot fire with grassland burned by a cooler fire, amount of plant biomass remaining after the fire will be higher in the latter case. This was probably the case for EN BP, as low intensity fire did not remove plant biomass completely resulting in comparatively higher fuel loads even after being burned. Alternatively, differences in fuel load might be due to burning season. If NR BP was burned in late winter, and EN BP was burned after first spring rains, fire at EN BP would have scorched new growth, resulting in what was measured as 'leaf litter and moribund vegetative growth'.

In summary, most differences in plant species composition between EN and NR for natural pairs of sites can potentially be explained by patch quality/size, colonization from different matrices, fire regime (i.e. seedling recruitment and invasion), grazing pressure (i.e. shift from tall to short plant communities), soil moisture (i.e. sedge:grass cover ratio), soil type (i.e. clay vs. sand content), connectivity (i.e. seed dispersal and differential seed predation), mammal-specific behavior (i.e. blue wildebeest territorial diggings) and different growth forms (e.g. lawn vs. bunch grasses).

Rehabilitated pairs of sites

Rehabilitation of former plantation areas is similar to succession following volcanic eruption i.e. a change from bare ground → vegetation cover of remnant, generalist, shade-tolerant grass species (e.g. *P. maximum* and *D. geminatum*) that originally grew beneath plantation trees → full suite of natural grassland species. Total vegetation cover during earlier phases of the rehabilitation process was at least as important as plant species richness and composition in later phases, as it limited erosion. Indeed, it was found that erosion in Mediterranean shrubland, caused by high-intensity rain, changed the physiochemical structure of soil (De Luis *et al.* 2001). These changes influenced plant species composition and affected the resprouter:obligate reseeder ratio (De Luis *et al.* 2001). Plant species richness and composition during earlier phases of rehabilitation indicates *rate* of change and *direction* of change (i.e. successional trajectory), and could affect plant species composition in later stages.

At the younger, rehabilitated pair of sites (YR), plant species richness and composition at the EN differed from NR. Differences might be due to characteristics of source habitat, dispersal distance from source habitat, soil moisture, soil disturbances by animals (e.g. molehills and warthog grubbing) and large mammal grazing.

The surrounding matrix might have acted as a source of plant propagules for EN YR and NR YR, respectively. NR YR was surrounded with rehabilitated grassland and located ~500 m from natural grassland, while EN YR was adjacent eucalypt plantations, dry forest and thicket, and ~2 km from a large (~13 ha), natural grassland area. There is a possibility that plant communities of the rehabilitated grassland matrix, surrounding NR YR, would have been enriched with species from adjacent natural grassland, causing higher species richness and slightly different plant species composition than what would normally have been expected from rehabilitated grassland. Seed dispersal is the mechanism of colonization for plants, because seeds are generally plants' most mobile life stage. Assuming seed dispersal was successful, differences in species richness and composition might be explained by the 'spill-over effect' from surrounding matrices into sampled sites.

Connecting otherwise isolated habitat patches (e.g. EN YR) might facilitate migration (i.e. seed dispersal) between grassland patches. However, dispersal of two forb species (*Cirsium dissectum* and *Succisa pratensis*) in Dutch semi-natural grassland showed that corridors did not facilitate movement of wind-dispersed seeds between grassland patches (Soons *et al.* 2005). This might be explained by the direction of the corridor relative to the direction of prevailing wind. Seed dispersal of an annual grass species (*Rhinanthus minor*) with large, wind-dispersed seeds were in the direction of prevailing winds (Coulson *et al.* 2001).

If EN YR was successfully connected to nearby natural grassland patches, dispersal distance would still jeopardize successful colonization, as chances of successful seed dispersal decreases as distance between source habitat and 'new' grassland increases. It has been suggested that large mammal grazers disperse seeds of some grassland species (Janzen 1984) over long distances. Indeed, awassi sheep have been used as dispersal agents of legumes in an attempt to rehabilitate degraded grassland in Syria (Ghassali *et al.* 1998). In contrast, sheep grazing at an experimental site in the United Kingdom (UK) did not affect seed dispersal at all (Coulson *et al.* 2001).

Studies investigating dispersal of plants by large mammals in the Succulent Karoo, South Africa, found that domestic stock and wild animals dispersed a variety of taxa (including Aizoaceae, Mesembryanthemaceae, Chenopodiaceae and Poaceae) (Milton and Dean 2001; Haarmeyer *et al.* 2010). In addition, browsing herbivores and bat-eared foxes dispersed seeds of fleshy-fruited shrubs (Milton and Dean 2001). In renosterveld, however, indigenous ungulates did not contribute to rehabilitation of old fields, as they dispersed mainly lawn grasses such as *Cynodon dactylon* (38%) and alien pasture grasses (31%), which were not representative of species occurring in remnant patches of renosterveld (Shiponeni and Milton 2006).

Although seed dispersal through grazing was found to be largely facultative, it might be important for long-distance dispersal of some small-seeded grassland plant species (Collins & Uno 1985). Thus, if corridors direct movement of vertebrates from one grassland patch to another, seeds of some plant species, including some aliens, should follow the same route.

An experimental approach to comparing the effect of mowing and grazing on dispersal of wind-adapted seeds in the UK found that mowing dispersed more seeds over larger distances in the mowing direction (Coulson *et al.* 2001). As road verges in SQF functioned as firebreaks that were regularly mowed, mowing direction from source habitat to EN YR might expedite rate of colonization.

If sedge cover (*C. natalensis*) and green vegetative cover were indicative of higher soil moisture, NR YR was wetter than EN YR. While NR YR only suffers from climatic drought (i.e. reduction in precipitation as part of wet and dry cycles), EN YR was subjected to both climatic and plantation-induced drought. Thus, it would have been drier at EN YR. This will select for drought-resistance in newly-colonized plant species by limiting the number of ‘wet’ microsites, which could cause a shift towards drought-resistance in EN plant communities.

Warthog diggings at NR YR (26) exceeded that of EN YR (1) by far. In addition, there were nearly four times as many mole hills in NR YR (312) than in EN YR (79). Although digging for food and molehills are disturbances with small spatial extents, it created a mosaic of different successional stages in the plant community, affecting plant species richness and composition. Similar to warthog diggings, grubbing by introduced feral pigs in Californian coastal prairie revegetated rapidly, but plant species composition and richness was different from undisturbed grassland matrix (Kotanen 1995). The same applied to other small-scale animal disturbances, such as molehills, in semi-natural grasslands (Milton *et al.* 1997; Canals & Sebastia 2000).

Initially, grazing pressure appeared to be similar at YR. However, evidence suggests that grazing intensity might have been slightly higher at NR YR, as it had more green vegetative cover and reduced vegetation height. In the Serengeti, productivity in moderately grazed grassland was twice that of ungrazed areas, provided there was enough soil moisture (McNaughton 1979). Furthermore, grazing by large mammals reduced grass height and activated tillers, which resulted in a flat, dense canopy, also known as a grazing lawn (McNaughton 1984). One dominant grass species at NR YR was *S. secundata*, which is an alien lawn grass species often found in grazing lawns. As NR YR was historically visited by hippopotamus on a regular basis, vegetation structure might have been shaped by this large mammal species. Due to climatic drought, the pan depression at NR YR dried up, leading to hippopotamus emigration (B. Hart, pers. comm.).

In addition to moderate grazing pressure, differences in vegetation height might have been an artifact of grass growth forms (i.e. lawn vs. bunch grasses). In contrast with the lawn grass species at NR YR, dominant grass species at EN YR (*P. maximum* and *D. geminatum*) were both bunch grasses. As these two species are both shade-tolerant species that originally grew beneath plantations, their presence might be explained by colonization from the plantation matrix.

EN YR was characterized by patches of predominantly dead plant material, interspersed with bare ground. Although the exact reason for patchy vegetation distribution is unclear, the same pattern was documented in annually-burned sandhill grassland, Florida (Gibson *et al.* 1990) and North-American tallgrass prairie (Collins & Uno 1985). Patchy vegetation distribution might be (1) typical of early successional stages, as both burning and plantation-clearing effectively reset succession. Alternatively, patchy vegetation distribution might (2) be due to competition for moisture (e.g. Karoo veld), (3) be the result of selective grazing (Adler *et al*. 2001) or (4) reflect mycorrhizal islands that exist in recently-disturbed plant communities (Gange *et al.* 1993), especially since mycorrhizal infections can promote seedling establishment of some grassland plant species (van der Heijden 2004).

Lastly, vegetation patches might have been created by foraging of small mammals. Predator avoidance was identified as one of the major determinants of small mammal behavior in South American shrublands and grasslands, as predators restrict movement of small mammals to protective cover e.g. dense vegetation cover or timber piles (Jaksic 1986). This was also the case for South Africa, where scarcity of diurnal small mammals in communual rangeland in Namaqualand was attributed to lack of vegetative cover in which small mammals could avoid their predators (Joubert and Ryan 1999). Intense herbage removal around these grass shelters creates zones of bare ground (Jaksic 1986), as was documented in this study.

These possibilities are not mutually exclusive, as some mycorrhizal fungi are dispersed by mycophagous animals. Although this phenomenon is mainly applicable to forest ecosystems (e.g. Johnson 1996; Malajczuk *et al.* 1987; Maser *et al.* 1978; Pyare & Longland 2001), ~21% of small mammal individuals in Oregon rangeland had hypogeous (i.e. animal-dispersed) mycorrhizal fungi spores in their guts (Maser *et al.* 1988). In addition, it was found that burrow activity of *Paratomys brantsii* created small patches of increased fertility that facilitates plant colonization on old mine dumps in the west coast of South Africa. Burrow mound soils had a higher pH, lower electrical conductivity and a five-fold increase in microbial activity when compared to control soils on the mine dump (Desmet and Cowling 1999). Although wind and water are the main dispersers of grassland mycorrhiza, small mammals might be locally important (Maser *et al.* 1988).

At the other rehabilitated pair of sites (RGL), plant species richness and composition was similar, which implied similar successional trajectories. As for the previous rehabilitated pair of sites, plant species richness and composition was mostly affected by characteristics of source habitats. Small differences in green cover might be explained by differences in soil moisture.

EN RGL and NR RGL had similar matrices (i.e. coastal lowland forest, eucalypt plantations and rehabilitated grassland in different stages of succession). Furthermore, rehabilitated grassland matrices had similar plant species composition, probably driven by similar historical and current disturbance regime. If 'new' grassland areas assume plant species richness and composition of source habitats (i.e. rehabilitated grassland matrices), plant species richness and composition should be similar at RGL. This was the case.

However, there were small differences in plant species composition, dead : green vegetation cover ratio and vegetation distribution at RGL. Patches of green vegetative cover associated with EN RGL, while evenly-distributed, dry vegetation cover associated with NR RGL. These differences were probably created by spatial orientation of old timber logs that were left in-field after the 2005 wildfire. Old timber logs were scattered at EN RGL, but stacked in piles at NR RGL. Decomposing logs affect the water balance even at early stages of decomposition (i.e. first two years). In Pacific Northwest old-growth forests, ~40% of rain falling through forest canopy ran off decomposing conifer logs, ~25% was absorbed and evaporated later, and ~30% leached from the bottom of logs (Harmon & Sexton 1995). Furthermore, logs reduce evaporation of soil moisture and are poor conductors of heat (e.g. wood chips in gardens), which renders them effective microclimate regulators.

Area affected by old timber logs was larger at EN RGL, as can be seen by patches of green vegetative cover. In contrast, evenly-distributed dry plant cover at NR RGL might be due to vegetation die-back caused by large fluctuations in soil surface temperature when coupled with low soil moisture in the absence of decomposing logs.

In addition, scattered timber logs and pine stumps at EN RGL might have provided shelter for small mammals from their predators (e.g. Jaksic 1986). If this was the case, intense foraging around timber logs would have enforced patchy vegetation and bare ground distribution. This explanation is supported by one observation of a small mammal nest inside a partially decomposed pine stump. Preference of small mammals for timber logs (Tallmon & Mills 1994) and how their abundance correlate with amount of timber logs (Carey & Johnson 1995) have been studied for a number of small mammal species (e.g. *Clethrionomys californicus*, *C. gapperi*, *Neurothrichus gibbsii*, *Peromyscus maniculatus* and *Sorex throwbridgii*) in natural and managed forest. There is a strong positive correlation between amount of coarse woody debris (e.g. timber logs) and small mammal abundance. Amount of coarse woody debris also influenced reproduction success of *P. gossypinus* (Loeb 1999). Small mammal species richness and composition was not affected by amount of timber logs (Loeb 1999).

Different fire intensities might explain differences in plant species composition. During the 2005 wildfire, fire was probably hotter in EN RGL, as there was lateral heat transfer from burning plantations to burning grassland. This was not the case for NR RGL, as it was not surrounded with plantations. Higher fire intensity at EN RGL might have affected plant species composition, as hot fire can damage seed population (Noy-Meir 1995). However, fire intensity fails to account for differences observed in vegetation distribution (patchy vs. even) and dead:alive vegetation cover ratio.

In summary, differences in plant species richness and composition at rehabilitated pairs of sites (YR and RGL) were mainly caused by characteristics of source habitat/matrix, dispersal distance, soil moisture, warthog diggings, mole hills, large mammal grazing patterns, microhabitats created by timber logs, mycorrhizal islands and small mammal population dynamics.

Overall comparison of manifestations

Manifestations were representative of animal activity. However, chances of seeing any manifestation type were dependent on abundance and preservation of that manifestation type. Preservation was influenced by vegetation structure (e.g. vegetation density), local weather conditions (e.g. wind and rain), soil moisture content and clay content.

Overall consideration of manifestation data showed only small differences between EN and NR for each pair of sites. Variation in manifestation data was larger at unburned pairs of sites (RGL and YR) than at recently-burned pairs of sites (BP and PGL). Burning reduced variability in vegetation structure. Vegetation structure, in turn, influenced visibility and preservation of manifestations, as well as activity of small mammals (e.g. Bock & Bock 1978; Cook 1959; Crowner & Barrett 1979) and spiders (Duffey 1962).

It was not possible to separate effect of fire on vegetation structure from the effect of vegetation structure on visibility or preservation of faunal manifestations. Generally, burning caused a reduction in small mammal populations, mostly through a reduction in food and shelter from predators (Cook 1959; Crowner & Barrett 1979). However, small mammal diversity was not adversely affected by burning South African grasslands. Rather, it was higher in burned grassland 6 months after fire than in unburned grassland (Yarnell *et al*. 2007). After fire, recovery of most small mammal populations was restricted by recovery of vegetation cover in which they can avoid predators (Cook 1959; Yarnell *et al*. 2007). Following grass cover establishment, abundance of seed-eating small mammal species (*Perognathus* spp., *Dipodomys* spp., *Mus musculus* and *Reithrodontomys megalotis*) and grass-dwelling small mammal species (e.g. *Microtus californicus*) was governed by food availability (Bock & Bock 1978; Cook 1959).

Comparisons of specific manifestations

Spider activity

It was not possible to determine which spider species was responsible for construction of which spider web. Therefore, all spider-related manifestations (i.e. spider webs, burrows, tunnels or nests) were pooled for each site. Spider activity was, thus, not representative of a single species, but rather of spiders in general.

Overall, there was no significant difference in the overall number of spider webs/burrows/nests for any of the pairs of sites. This is the case in spite of differences in vegetation structure (e.g. vegetation height, cover and density), as shaped by different grazing and burning regimes.

Vegetation structure was found to influence spider activity in other studies. There are three effects of grazing animals (defoliation, treading and manuring), which all affect vegetation structure (Morris 2000). A detailed study on the effect of vegetation structure and microclimate on spider communities in limestone grassland, UK, found that 90% of all spiders were affected by vegetation structure (Duffey 1962). In addition to vegetation structure, web-spinning spiders were influenced by food supply and microclimate (i.e. fluctuations in temperature, humidity and light intensity) (Duffey 1962). Structural complexity of different habitat types had an effect on functional groups of spiders in South African savannas (Whitmore *et al*. 2002). Both vegetation structure and microclimate were influenced by burning and grazing.

Molehills

Winnowing is the transportation of subsurface soil to the soil surface (Paton *et al*. 1995). Here, I specifically referred to the role of molerats in this process.

Overall, there were significantly more molehills in NR (21.6) than in the EN (8.8). Of all mole species in South African, the common mole-rat (*Cryptomys hottentotus*) was most probably responsible for the molehills. This species is vegetarian, and feeds on subterranean storage organs, such as fleshy roots, bulbs, tubers and underground grass stolons (Avery 2004). It has been found evolution of social cooperative behavior in African mole-rats (Bathyergidae) is driven by (1) geophytes density, (2) months per year with rainfall greater than 25mm and variation in rainfall (Faulkes *et al*. 1997). Most probably, all three variables contributed to differences in number of molehills between EN and NR.

Firstly, food availability might be lower in ENs, as leaf litter in eucalypt plantations generally has low palatability (Haynes *et al.* 2003). It was shown that digestible energy available from geophytes in an area greatly influenced burrow construction in Cape mole-rats (*Georychus capensis*) (Du Toit *et al*. 1985). In the UK, where moles mainly fed on earthworms, number of molehills reflected abundance of earthworms (Edwards *et al.* 1999).

Secondly, differences in molehill density might be explained by differences in soil moisture content. It was reported that *Cryptomys hottentotus* does not push up new mounds in the dry season, but merely “redistribute the loose soil in abandoned tunnels” (Genelly 1965).

Lastly, mole-rat activity might have been influenced by the vibrations of chainsaws in tree harvesting operations. Individuals of social Namib Desert golden mole (*Eremitalpa granti namibensis*) and solitary Cape mole-rat (*Georychus capensis*) communicated with vibrations e.g. drumming with hind legs on burrow floor (Narins *et al.* 1997). In addition, it was found that the blind mole-rat (*Spalax ehrenbergi*) used echolocation to identify objects that it would have to avoid when tunneling (Kimchi & Terkel 2003; Kimchi & Terkel 2002). Without the ability to identify obstructions from a distance, the high energy expenditure of tunneling could potentially lead to mortality. However, most vertebrates are able to detect direction from which vibration comes (Gridi-Papp & Narins 2008). Thus, mole-rats might respond behaviorally and move overland away from the source of vibration. This makes them vulnerable to predation.

Small mammal burrow entrances

Overall, there was a significantly larger amount of small mammal burrow entrances in EN (5.8) than in NR (3.2). This was the case for all pairs of sites, but the difference was significant only for one pair of sites: PGL. Since there were differences in relative clay content at PGL, it is possible that it influenced burrowing activity of small mammals. Small mammal burrows were found to be influenced by bulk density and texture of soil (Laundre & Reynolds 1993). Burrow density, length, depth, volume and complexity of four out of five small mammals (*Spermophilus elegans*, *Microtus montanus*, *P. maniculatus* and *Dipodomys ordii*) were affected by the relative amounts of sand and clay content (Laundre & Reynolds 1993).

Alternatively, differences in small mammal burrow entrance density might reflect occupancy of EN and NR by different small mammal species. For example, pouched mouse (*Saccostomus campestris*) burrows typically only have one entrance (Ellison 1993), while striped mouse (*Rhabdomys pamilio*) burrows have two to three entrances and highveld gerbil (*Tatera brantsii*) burrows have four to seven entrances and several blocked entrances (Bronner 1992).

Alternatively, differences in small mammal burrow density might be a reflection of small mammal population density. In this case, it was assumed that small mammal population density at EN was approximately twice that of NR. This might be due to cover provided by eucalypt plantations for small mammals from their predators. In Australia, use of eucalypt plantations by reptiles, ground-dwelling mammals and birds, relative to agricultural land and remnant vegetation, was investigated. Eucalypt plantations were used more frequently than open, agricultural pastures, but less frequently than native, remnant vegetation (Hobbs *et al.* 2003). In addition, higher small mammal population density might be due to invasion of alien small mammal species that is more tolerant to disturbance and habitat fragmentation than native small mammal species (e.g. Barnett *et al.* 1977; Bennet 1990).

Ant nests

Similar to spider webs, it was not possible to identify different ant species' nests. Therefore, all types of ant nests were pooled for each site. 'Ant nests' are, therefore, not representative of the activity of any specific ant species, but rather of ants in general.

There was no difference in the number of ant nests recorded in the EN and NR, overall or for any specific pair of sites. In Chihuahuan desert grassland, there was no difference in the number of seasonal or 'persistent' ant nests between burned and unburned areas four months after fire, even though grass cover was reduced (Killgore *et al.* 2009). Even though there were differences in ant assemblages between burned and unburned areas, fire regime (fire frequency, fire season and time since last fire) did not influence ant assemblages in mopane woodland, *Terminalia* woodland and *Acacia* woodland, Kruger National Park, South Africa (Parr *et al.* 2004). Changes in ant assemblages were linked to fire-induced changes in vegetation structure and habitat cover, rather than specific aspects of a fire regime (Parr *et al.* 2004).

Overall comparison of fungi

There was no significant difference in fungi species richness, generally between EN and NR, or for any specific pair of sites. However, wood-decay fungi species richness was highest at the older, rehabilitated pair of sites (RGL). RGL had many timber logs, and all fungi were recorded on these timber logs or stumps. In Swedish forests, amount of coarse woody debris (CWD) and size of logs were found to increase fungi species richness (Edman *et al.* 2004).

Differences in fungi species composition at YR might be due to different matrices. In Finland, fungi species composition was strongly influenced by fungi species composition and abundance of surrounding areas (Edman *et al.* 2004), because most spores of wood-decay fungi settle near the fruiting body (Malloch & Blackwell 1992; Stenlid & Gustafsson 2001). Specifically, two distinct groups might be the result of colonization from different vegetation types in those matrices. For example, EN YR and NR YR were both previously planted under pine trees and were within close proximity of indigenous forest. Thus, the one group might be remnants from pine plantations, while the other dispersed from nearby indigenous forest.

Spatial orientation of timber logs at RGL affected moisture containment and, thus, microclimate of different areas. In northern Finland, microclimate directed fungi community development (Renvall 1995). Furthermore, wood-decay species composition in pristine forest was influenced by stage of decomposition, history of fungal infections preceding tree-felling, log diameter and amount of bark (Renvall 1995). These results agree with results on microfungal communities of two tree species, Canada, where stage of decomposition influenced species composition through its effect on wood porosity and, thus, log moisture (Lumley *et al.* 2001).

Comparison of vertebrate species richness and abundance for pairs of sites

Although not significant, vertebrate (bird and large mammal) species richness and abundance were higher in NR than EN. The difference in vertebrate species richness was relatively small (~2 spp.), but there was a large difference in abundance.

Of all recorded animals, more than 60% of all individuals and 75% of all species were birds. Bird species composition and density were found to change in response to habitat quality in the midlands of KwaZulu-Natal (Lipsey & Hockey 2010). They identified five major habitat types based, among others, on relative percentage grass cover, forb cover, woody plant cover and bramble cover (Lipsey & Hockey 2010). Three bird communities associated with these habitat types. Grassland specialist bird species were found in large open areas of high-quality grassland that has been burned within two years prior to sampling (Lipsey & Hockey 2010). Density of habitat generalist bird species did not vary between habitat types, but they generally associated with less-open areas that had a high proportion of edge habitat (proximity to plantations) and have not been burned recently (i.e. tall grass cover) (Lipsey & Hockey 2010). Non-grassland species associated with low-quality grassland habitat in narrow corridors between plantations (Lipsey & Hockey 2010).

Fragmentation of grassland habitat by commercial forestry might increase total species richness at the regional spatial scale, because large, open grassland areas in nature reserves provided habitat for grassland bird species, while corridors among commercial plantations provided suitable habitat for habitat generalist and woodland-associated bird species (Fairbanks 2004; Wethered & Lawes 2005). However, while regional species richness might increase, conservation of grassland specialist bird species might be jeopardized.

Although not significant, species composition in the EN was similar to the NR. In this study, all recorded vertebrate species were highly mobile. Most large mammal species used wide (~ 40 m), mowed road verges to move between EN sites, and between EN and NR. Use of movement corridors by large, mobile taxa has been reported previously (Haddad *et al.*

2003) even though evidence for the importance of physical connectivity was not found for South African grassland birds (Lipsey & Hockey 2010).

Management recommendations

The results here suggest that SiyaQhubeka Forests (including the EN) function as a buffer zone for core habitat in iSimangaliso Wetland Park. Whether it is viewed in this manner by conservation bodies will affect management objectives, which, in turn, will influence management recommendations for the EN.

Ideally, the EN should be managed as a shifting mosaic, where foci of high-intensity disturbances move through the EN. For example, discretely burned patches will promote intensive grazing, as large herbivores concentrate on newly-burned grassland areas. Burning different patches over consecutive years should create a mosaic of disturbance foci, where different patches represent different successional stages (Fuhlendorf & Engle 2004). It remains to be tested whether it is possible to manage movement of large herbivores by burning discrete patches in the EN.

Implementation of a shifting mosaic will affect other taxa. For example, burning season influenced grasshopper assemblages. Winter burns were more beneficial for grasshopper species richness and abundance than spring burns (Chambers & Samways 1998).

Although this matter requires a more thorough investigation into effect of different fire regimes on grassland ENs among forestry plantations, high-intensity fires might be detrimental to flora and some fauna at EN BP. In Arizonian grassland, combination of high-severity burns, heavy grazing and trampling resulted in permanent loss of plant cover, especially dominant sacaton (*Sporobolus airoides*) grass cover (Bock & Bock 1978). In addition, a combination of heavy grazing and fire, as well as a combination of fire and drought had a negative effect on small mammal diversity in South African sub-arid grassland near Pilanesberg (Yarnell *et al*. 2007). Large mammals will most probably return to EN BP once it has burned, because mammals preferred grazing in recently-burned areas (Archibald *et al*. 2005). This agrees with findings on the North American Great Plain, where large mammals spent up to 75% of their time grazing in a third of the land that has been burned during the year before sampling (Fuhlendorf & Engle 2004). The return of large mammals should not be prevented at BP, as this could cause a reduction in the abundance of lawn grasses that probably contribute most to their diet. When heavily-grazed *Cynodon* lawns in subtropical Australian grassland were rested from grazing, the abundance of *Cynodon* spp. declined and the abundance of forbs increased (McIvor *et al.* 2005).

The negative impact of grazing intensity on fire frequency in African savanna (Roques *et al.* 2001) should be taken into account when deciding on fire intervals. Grazing is a selective form of plant biomass consumption. It continually removes green biomass with consequences for plant material accumulation (Noy-Meir 1995). The decision to burn or not to burn should not be based exclusively on vegetation age (i.e. time since last fire), but should take amount and distribution of the fuel load into account.

Moderate fire frequency (i.e. ~ 3 yrs) should be maintained in the grassland EN areas. High fire frequency directly affects chances for invasion (Syphard *et al.* 2006; Keeley *et al.* 2003), shrub encroachment (Roques *et al.* 2001) and the abundance of fire-cued plant species (Syphard *et al.* 2006). In contrast, low fire frequency (>5 yrs) results in high fire intensity (Gibson *et al.* 1990), which negatively affects regeneration of resprouter and reseeder plant communities through its effect on resprouting organs and soil-stored seeds (Keeley 1998).

Around wetland EN areas (e.g. EN BP), timber harvesting cycles should be synchronized with wet and dry climatic cycles. Climatic drought is measured at a temporal scale, while plantation-induced drought is measured at a spatial scale. Generally, management practices cannot change the dynamics of climatic drought. However, plantation-induced drought can be alleviated by harvesting of eucalypt plantations. If ‘dry periods’ of climatic drought and plantation-induced drought, respectively, are synchronized, one might be able to sustain fluctuations of soil moisture in wetland habitat. Fluctuations in soil moisture form part of the dynamics in wetland habitat. Without dynamics, a system loses its resilience and, consequently, its ability to adapt to local conditions by changing plant species composition (e.g. sedges vs. grasses).

Conclusion

The aim of this study was to determine how representative grassland biodiversity in the Ecological Network (EN) is compared to that of the adjacent Nature Reserve (NR). Answering this research question required comparisons of biodiversity measures between the EN and NR. These biodiversity measures were species richness and composition of plants, fungi, vertebrates (large mammals and birds) and faunal 'manifestations' (e.g. dung, tracks and molehills). A comparison of environmental variables (EVs) was included, as EVs should at least partly explain differences observed between the EN and NR.

Overall, there were significantly more plant species in the NR than in the EN. In addition, there were differences in plant species composition for each of the four pairs of sites. However, when all pairs of sites were considered, differences within each pair of sites (EN vs. NR) were smaller than differences between habitat types.

When each pair of sites was considered separately, there was a distinction between factors causing differences between EN and NR in natural grassland and rehabilitated grassland, respectively. In natural grassland, differences in biodiversity patterns were probably caused by (1) soil type (i.e. higher clay content in the EN), (2) matrix characteristics (e.g. disturbance regime in immediate surroundings), (3) patch size, (4) habitat quality, (5) patch isolation (i.e. proximity to other grassland areas), (6) soil moisture content, as influenced by plantation-induced drought in the EN, (7) disturbance regime (e.g. grazing intensity and burning frequency) and (8) differential seed predation.

It is assumed that there is a natural influx and efflux of individuals from different species in space and over time in natural grassland. Furthermore, it is assumed that movement of individuals through ENs depended on habitat quality at the EN sites, other suitable habitat patches within the surrounding matrix and functional connectivity between different patches. If the EN sites fulfilled in the habitat requirements of the species for its entire lifecycle, it would not be necessary for the species to move from the area in search of alternative resources. Patch quality, however, depended on edge effect, which increased as patch size and width decreased. One edge effect of plantations on grassland plant community at the EN sites, as gleaned from scientific literature, could potentially be the effect of plantations on soil moisture i.e. plantation-induced drought. If plantation-induced drought was the cause for lower green vegetation cover at EN sites, neither natural EN sites were large enough to escape the effect of plantation-induced drought. Plantation-induced drought would have affected primary productivity negatively and might have eliminated drought-sensitive plant species. This selection pressure, together with potential differences in seed predation by larger small-mammal populations at EN sites, might have caused a shift in seed bank and, therefore, plant species composition.

Although the EN sites showed edge effects, other grassland patches within the EN were either smaller or had a history of intense disturbance (i.e. cleared of plantations within the last five years). Size and historical disturbances resulted in lower habitat quality. Thus, natural EN sites had comparatively higher habitat quality than the surrounding matrix. Since high-quality habitat patches might potentially act as sources for lower quality patches, there was probably a continuous flow of propagules from natural EN sites to nearby grassland patches in the EN.

Local disturbance regime shaped local plant communities and vegetation structure in natural grassland. Differences in vegetation structure suggested that fire regime at natural EN sites was different from that at NR. Fire intensity is determined by fuel load, while differences in fuel load are determined by fire frequency and grazing pressure. Therefore, differences in fire intensity could be explained by differences in grazing pressure and/or fire frequency. Although grassland areas in the EN and NR were burned every two years, natural grassland areas in the EN were often chronically grazed. As grazing reduced fuel load, fire intensity was lower in the EN. Low-intensity grassland fires can be considered as desirable, as it results in fast vegetative regeneration. However, practices that result in low-intensity fire (i.e. high fire frequency or heavy grazing) might explain the differences observed in plant species composition.

In the rehabilitated grassland, processes driving differences in biodiversity patterns between EN and NR can be divided into two categories, dispersal and establishment, which together determine successful colonization. The dispersal processes that probably shaped plant communities were (1) degree of isolation (i.e. dispersal distance and dispersal vectors) and (2) vegetation types in the matrix that function as source populations for ‘new’ grassland areas. Establishment processes relate to factors influencing propagules *after* they arrived at a site. Here, they were (1) soil moisture content, as influenced by plantation-induced drought at EN sites, (2) disturbance regime (e.g. grazing intensity and soil disturbances caused by molehills and warthog diggings) and (3) small mammal population dynamics (e.g. foraging behavior and seed predation).

Rehabilitated grassland was colonized by plants and fungi from the immediate surroundings. Therefore, rehabilitated grassland assumed characteristics of the surrounding matrix. The probability that ‘new’ grassland will become similar to natural grassland decreased as the distance between rehabilitated and remnant, natural grassland increased. The main vector for seed dispersal in the Grassland Biome is wind. However, wind was not always a successful dispersal vector in the EN, because the corridors were not designed according to the direction of the prevailing wind. Other dispersal vectors (e.g. large mammals and mowing) might be more successful.

Soil moisture content, disturbance regime and small mammal population dynamics probably influenced succession of plant communities in rehabilitated grassland. This came about for three reasons. Firstly, only those species that are drought-tolerant will survive in the EN. While the grassland community in the NR suffered only climatic drought, grassland communities in the EN suffered both climatic and plantation-induced drought. Secondly, there was at least double the amount of molehills and warthog diggings in the NR than in the EN. Although soil disturbances caused by molehills and warthog diggings were of small spatial extent, they influence succession of plant communities. Thirdly, small mammal population density in the EN was higher than in the NR. Small mammal population size is limited by vegetation cover in which they can hide from their predators. Foraging behavior around dense vegetation patches create bare zones (i.e. patchy vegetation distribution) that was seen in the EN. This will probably jeopardize survival of newly-colonized seedlings.

However, patchy vegetation distribution in rehabilitated grassland ENs was not explained by small mammal foraging behavior alone. Spatial orientation of old timber logs (i.e. scattered in the EN vs. stacked in the NR) created microhabitat favorable for sustained vegetative growth and for small-mammal reproduction. Thus, these factors reinforced patchy vegetation distribution.

There was not any significant differences in species richness, species composition or abundance of bird and large mammals between EN and NR. This could probably be explained by high mobility of birds and large mammals.

The aim of this study was to evaluate grassland ENs against their primary objective – biodiversity conservation. This approach required a comparison of species richness and composition between grassland ENs and similar habitat in adjacent nature reserves. There were differences between ENs and nature reserves. However, these differences were large for only one of the four pairs of sites. Therefore, we conclude that grassland ENs contribute to biodiversity conservation in the commercially-productive landscape. It is recommended that this landscape approach to conservation is explored in other commercial land uses.

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