Land cover and climate change threats to savanna and grassland habitats in KwaZulu-Natal

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A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

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February 2017 in Johannesburg, South Africa

Declaration

I declare that this thesis is my own, unaided work, unless otherwise specified within the text. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg, South Africa. It has not been submitted before for any other degree or examination at any other University.

DJewitt

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17th day of February 2017 in Johannesburg

“Here be dragons”

Image adapted from www.jmtheoret.deviantart.com

Abstract

Global change, specifically land cover change and climate change, are recognised as the leading drivers of biodiversity loss worldwide. Habitat loss has resulted in a loss of biodiversity and led to significant declines in species populations. Climate change is altering species distributions, ecosystem composition and phenology. Conservation planning is required to offset these dynamic threats to species persistence into the future.

Plants form the basis of trophic structure and functioning and may not be able to track changing environmental conditions as well as mobile species. They thus represent an essential starting point for understanding climate change and habitat loss impacts. The patterns and processes which generate and maintain floristic diversity must be explored before global change impacts on these communities can be assessed and planned for at a landscape scale.

This thesis investigates the environmental variables structuring indigenous plant community composition, pattern and turnover in grassland and savanna systems in KwaZulu-Natal. The threats posed by land cover change and climate change are explored and a coarse-grained landscape connectivity map developed to impart maximum resilience in order to maintain floristic diversity in the era of anthropogenically induced global change.

The environmental variables correlated to floristic pattern and turnover were temperature, soil fertility and precipitation variables. The orientation of the temperature gradient conflicts with the soil fertility gradient, hence species with particular soil requirements will be hampered in their efforts to track the temperature gradient. The gradients were non-linear with turnover highest on dystrophic soils in warm and drier summer regions.

The major drivers of land cover change were cropped agriculture, timber plantations (agroforestry), rural and urban development, dams and mines. The drivers of change differed according to land tenure type. The average rate of habitat loss in the province over an 18 year period was 1.2% per annum, levels which are considered unsustainable. A target level of 50% of natural habitat remaining is recommended.

Environmental domains were identified using the environmental correlates of plant community composition. These were used to investigate climate change impacts using a collection of downscaled climate models. Conditions suiting savanna species are set to increase at the expense of conditions suiting grassland species raising significant challenges for the conservation of grasslands. Indices of habitat intactness and climatic stability were used to develop a vulnerability framework to guide conservation actions to mitigate global change impacts on floristic diversity.

Building on the insights gained from the study, a connectivity map linking protected areas was developed, that if implemented, will maximise the opportunity to maintain floristic diversity into the future. The spatial location of the corridors was prioritised based on broad scale climatic refugia, high turnover areas and important plant areas for endemic and threatened species. The corridors were aligned along the major climatic gradients driving floristic pattern. The corridors represent the most natural and cost-effective way for species to adapt to climate change and persist in the landscape.

This thesis provides new insights into two global threats facing plant communities in KwaZulu-Natal and provides a suite of products that inform dynamic conservation planning and directs appropriate conservation action. The results may be used to inform policy and legislation.

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Disclaimer

This thesis consists of a sequence of content chapters that have been prepared for publication in a range of scientific journals. This has meant that formatting styles vary between chapters, with some degree of overlap to ensure publishable papers. Author contributions, areas of overlap and specific Journals have been specified in Chapter 1.

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List of Abbreviations

Asp	Aspect
Base	Soil base status
CART	Classification and Regression Tree analysis
CBD	Convention on Biological Diversity
CCAM	Conformal-cubic atmospheric model
CEC	Cation exchange capacity
Clay	Soil clay percentage
Depth	Soil depth categories
Drain	Soil drainage
EKZNW	Ezemvelo KwaZulu-Natal Wildlife
FrstDur	Median number of days of frost duration
FrstMedS	Median start date of the first frosts
GDM	Generalised dissimilarity modelling
Geol	Geology
IPCC	Intergovernmental Panel on Climate Change
iSWP	iSimangaliso Wetland Park
ITB	Ingonyama Trust Board
KZN	KwaZulu-Natal
LULCC	Land-use and land-cover change
MAP	Mean annual precipitation
MAT	Mean annual temperature
MDP	Maloti Drakensberg Park
MdRnFeb	Average median rainfall in February

MdRnJuly	Average median rainfall in July
MedAP	Median annual precipitation
MnAnEvap	Mean annual potential evaporation
MnTmpJul	Average minimum temperature in July
MxTmpFeb	Average maximum temperature in February
NLC	National land-cover
NMS	Nonmetric multidimensional scaling
PA	Protected Area
PAW	Profile plant water availability
PC1Heat	Thermal principal component
PC2Moist	Moisture, soil and solar radiation principal component
PCA	Principal Component Analysis
pH	Soil pH
RCP	Representative Concentration Pathways
Rflge10mm	Rainfall days ≥ 10 mm
Rflge2mm	Rainfall days ≥ 2 mm
SICZ	South Indian Convergence Zone
SR_Feb	Average solar radiation in February
SR_July	Average solar radiation in July
Struct	Soil structure
WHS	World Heritage Site

CHAPTER 1

1. General Introduction: Conservation in the face of global change

1.1 Study Rationale and Introduction

Here be dragons! This phrase was originally used on the Lenox Globe, the second or third oldest known terrestrial globe ca. 1510, but the term is colloquially associated with medieval map makers who supposedly used the term to indicate dangerous or unexplored territories at the edges of their known world (Blake, 1999). Indeed, the Ebstorf map from the thirteenth century has the dragon (*Draco species*) in the extreme south-eastern part of Africa and Giovanni Leardo's map (1452) shows "*Dixerto dexabitado p. chaldo e p. serpent*" in southernmost Africa (M. Hoogvliet in Blake 1999), suggesting the southern and south-eastern parts of Africa may be a stronghold for dragons. Long dismissed as creatures of legend and fantasy, recent research is, however, indicating that anthropogenic impacts on the world may unintentionally be paving the way for the resurgence of dragons (Hamilton, May and Waters, 2015).

KwaZulu-Natal (KZN) is an east coast province of South Africa and may thus be at particular risk of a resurgence of dragons given the anthropogenic impacts on the landscape and natural habitat, and the historical mapped locations of dragons. Certainly the rapid, cumulative anthropogenic impacts are moving us towards uncharted and dangerous territory for the regions biodiversity, deserving the map label of 'Here be dragons' because the future landscape is likely to be very different from the current known landscape. It is thus essential that the major anthropogenic threats to the regions biodiversity be researched so that their impact may be planned for and mitigated as far as possible.

The primary drivers of global terrestrial biodiversity loss are land-use change and climate change (Sala et al., 2000). Habitat loss, and the resulting fragmentation of natural habitat, is currently recognised as the major driver of biodiversity loss (Fahrig, 2003; Millennium Ecosystem Assessment, 2005; Joppa et al., 2016) but climate change is likely to exacerbate this loss, especially in future (Reyers, 2001; Meadows, 2006; Sala and Jackson, 2006; Dawson et al., 2011; Mantyka-Pringle et al., 2012). Global change refers to the accumulative and interactive effects of changes in atmospheric composition, climate, land use and biological diversity (Walker and Steffen, 1997; Chapin et al., 2000) but also includes threats such as fragmentation, alien invasive species, nitrogen deposition and overexploitation of natural resources (Sala et al., 2000; May, 2010). Other agents of environmental change include pollution, ocean rise, extreme climatic events, carbon fertilisation, pests and diseases (O'Connor, 2010).

These threats have caused, and will continue to cause, an acceleration in species extinction rates and is a direct product of increasing human population numbers as well as an increasing impact per person or consumption patterns (Toth and Szigeti, 2016). The global human population is only expected to stabilise at approximately nine billion people by around 2050, hence these anthropogenic threats are expected to exert further pressure on remaining biodiversity (May, 2010). The consequences of biodiversity loss are altered ecosystem processes and resilience of ecosystems to environmental change, with significant consequences for the ecosystem services on which humans depend (Chapin III et al., 2000).

A central tenet of ecology and biogeography is to understand the factors driving community composition patterns and variation across spatial scales (Arellano et al., 2016) and along environmental gradients (Pausas and Austin, 2001; Kraft et al., 2011). Given global change impacts on species loss, there is an increased need to understand the factors that drive biodiversity patterns in order to predict how these patterns may be altered in future (Thomas et al., 2004; Fitzpatrick et al., 2011), to assess threats to species persistence (Yates et al., 2010) and to plan to mitigate these threats. Countries that are signatories to the Convention on Biological Diversity (CBD), such as South Africa, are required to plan for conserving biodiversity into the future. The central principles of conservation planning are representivity and persistence (Margules and Pressey, 2000). However, maintaining species persistence in a dynamic world of rapid land use and climate change is challenging (Pressey et al., 2007).

KwaZulu-Natal is a species rich province owing to the complex mix between geomorphological history, varied climate and species lineages that are prone to diversification (Cowling and Hilton-Taylor, 1997). There are strong ecological gradients over limited distances with pronounced variations in topography, altitude, geology, soils, temperature and precipitation which further contribute to high levels of biodiversity. However, the region has high human population growth rates (Statistics SA, 2012), is experiencing high rates of habitat loss (Jewitt, 2012) and is predicted to experience climate change impacts (IPCC, 2014), that threaten the regions rich biodiversity.

It is thus imperative that the patterns and drivers of biodiversity, specifically floristic communities, in the province be understood, and the primary drivers of biodiversity loss *viz.* land use change and climate change impacts, are assessed and quantified, and plans developed to mitigate these threats. Given the environmental heterogeneity and diverse vegetation, KZN provides a useful case study at the scale at which conservation planning is undertaken and implemented by a regional conservation authority. The research focuses on plant community composition because plants form the basis of trophic structure and functioning. Plant communities are effective predictors of arthropod assemblage composition, which is significant because arthropods make-up approximately two-thirds of the world's diversity (Schaffers et al., 2008). Plants are sedentary and may be limited in their ability to track changing environmental conditions compared to mobile species such as vertebrates, and thus represent an essential starting point for investigating climate change impacts in KZN.

There are no other studies that have investigated the land use and climate change threats to floristic composition in this region and at this scale. This research gap needs to be filled for the following reasons:

> *i)* The environmental gradients correlated with floristic composition and related to the ecological and evolutionary processes which generate and maintain diversity, are not known in this region;
>
> *ii)* The rapid rate of habitat loss (Jewitt, 2012) places an urgency on identifying and conserving appropriate areas to ensure continued representivity and persistence of floristic diversity;
>
> *iii)* Climate change impacts require conservation plans that will allow most species to naturally adapt and track changing environmental conditions (Pearson and Dawson, 2005);
>
> *iv)* There are constitutional (Constitution of the Republic of South Africa, section 24), legal (e.g. National Environmental Management Act, Act No. 107, 1998) and international mandates (e.g. Convention on Biological Diversity) requiring planning and conservation of the landscape and species; and
>
> *v)* Adequate target amounts of natural habitats are required to support floristic communities into the future. In addition, rural communities rely directly on natural resources for fuel, construction materials, food and medicine (Makhado et al., 2009) and human well-being is dependent on the services provided by ecosystems (Chapin III et al., 2000; Rands et al., 2010). Hence sufficient amounts of well-connected natural areas are required to sustain these demands.

This thesis aims to address these issues in a manner intended to provide spatial products that can inform conservation planning initiatives in KZN.

1.2 Background literature

1.2.1 A landscape approach to dynamic conservation planning

Some of the main delivery mechanisms of conservation projects are now based on landscape-scale conservation initiatives (Ellis et al., 2011; Shreeve and Dennis, 2011). This entails the coordinated conservation and management across a range of habitats, for many species across large natural and semi-natural areas. Often conservation attention is focussed on rare species but there is growing evidence that widespread species are declining rapidly (Shreeve and Dennis, 2011). Common species most at risk are those specialised on widespread environmental conditions, as they are vulnerable to a wide range of drivers of environmental change (Lindenmayer et al., 2011). It is the common species however that perform key functional and ecological roles in the landscape (Lindenmayer et al., 2011) and thus their conservation is essential.

The broader landscape (the matrix) consists of a mix of anthropogenically altered landscapes, semi-natural and natural landscapes (Mackey et al., 2010). Protected Areas (PAs) are patches of natural habitat embedded in the landscape matrix. The landscape matrix is important to biodiversity conservation as much biodiversity resides outside of PAs (Goodman, 2006). Species may need to live or move through the matrix (Brady et al., 2009) and transformed landscapes may severely impact the ability of many species to survive (Heller and Zavaleta, 2009). Negative human impacts may cross protected area boundaries and influence native species and ecological processes (Hansen and DeFries, 2007), hence matrix management is essential (Brady et al., 2009). Further land cover and land use change will lead to isolated PAs. Climate change is predicted to alter species distributions, hence existing PA effectiveness in species conservation may be reduced in future (Beier and Brost, 2010). Thus PAs cannot be managed in isolation and a landscape approach to conservation is required (Sanderson et al., 2002; Rands et al., 2010) which specifically includes the retention and protection of large natural landscapes (Worboys et al., 2015) and a well-connected landscape (Beier and Brost, 2010).

Conserving biodiversity over large extents requires planning (Schwenk and Donovan, 2011) and is challenging considering the vast array of species, ecosystems and anthropogenic threats that must be considered (Poiani et al., 2000). A structured and systematic approach to conservation planning is useful to deal with this complexity and has been widely applied globally (Margules and Pressey, 2000; Cowling and Pressey, 2003). The essence of a systematic conservation plan is representivity (represent the full variety of biodiversity) and persistence (the long term survival of biodiversity) (Margules and Pressey, 2000). In order to operationalise these goals, they need to be translated into quantitative targets. Targets allow for the measurement of the conservation value of different areas and the achievement towards these goals (Margules and Pressey, 2000). Conservation goals aimed at maintaining representative and viable samples of ecosystems and species will be challenged by dynamic change brought about by climate change and other anthropogenically caused changes in species abundance and distribution (Hannah et al., 2002; Pressey et al., 2007). Climate change induced changes in species distributions may produce new community assemblages, which poses problems for strategies based on conserving representative and target amounts of communities or vegetation types. Biodiversity conservation must therefore focus on conserving dynamic, multiscale patterns and processes that sustain species and their supporting processes and natural systems (Poiani et al., 2000). Conservation plans need to offset threats to species persistence in order to maintain species and genetic diversity (Thuiller et al., 2008). Ways need to be found to reduce the drivers of biodiversity loss such as habitat transformation and to predict the consequences of environmental change (Sutherland, 2006). In this way priority areas for future conservation may be determined (Gaston, 2006).

1.2.2 KZN study area

Southern Africa has the richest flora in the world amongst areas of comparable size, with high levels of species endemism (80%) (Goldblatt, 1978). KwaZulu-Natal is a province on the east coast of South Africa (Figure 1) and encompasses an area of 94 697km^2. The province has more than 6000 vascular plant species within 1258 genera, of which 16% are endemic and 11% rare and threatened (Scott-Shaw, 1999). The province contains part of the Maputaland-Pondoland-Albany biodiversity hotspot as well as centres of plant endemism such as Pondoland, Maputaland, Midlands and Drakensberg Alpine centres of endemism

(Mucina and Rutherford, 2006). Cowling and Hilton-Taylor (1997) suggest that the high levels of diversity arise from the geomorphological history of the subcontinent, the varied climate and species lineages that are prone to diversification. Historical climate fluctuations and persistence of refugia allowed species to persist and speciate. Steep ecological gradients exist due to prominent heterogeneity in climatic variables such as temperature and precipitation, altitude, geology, soils and topography, which further contribute towards the high levels of biodiversity.

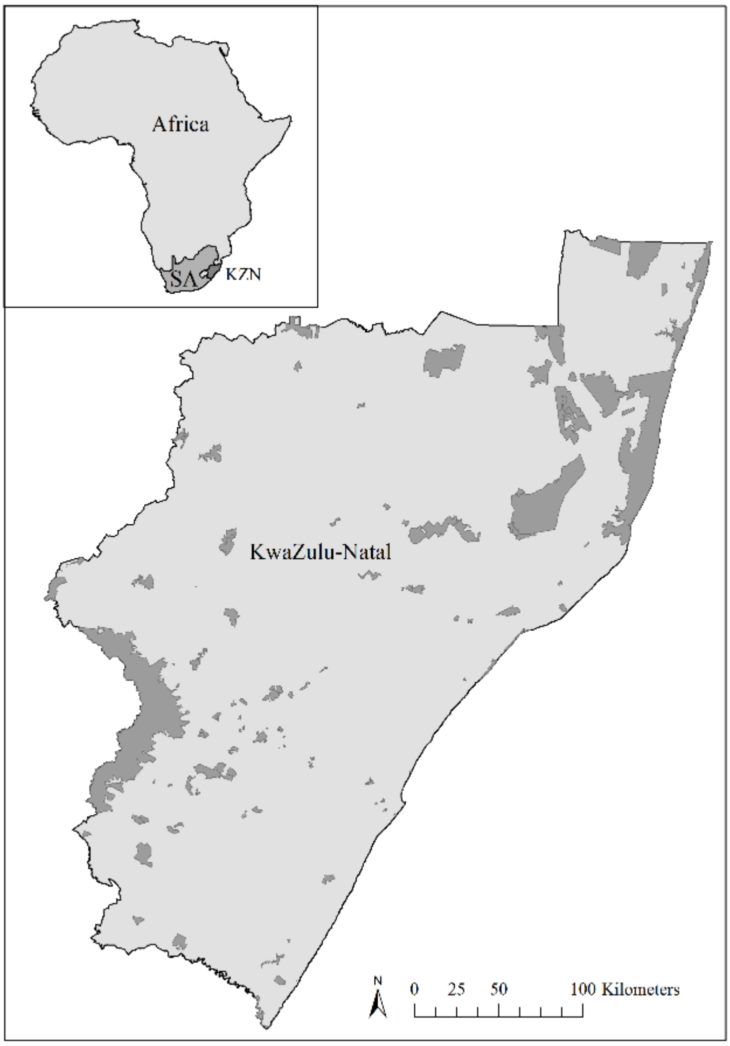

Figure 1 The location of KwaZulu-Natal (KZN), South Africa. Protected Areas are shown in dark grey in KZN and include two World Heritage Sites, provincial protected areas and Stewardship sites proclaimed as at October 2015.

The landscape ranges from the peaks of the Drakensberg escarpment at over 3000m in the west to the subtropical coastal landscape along the Indian Ocean in the east. The latitudinal gradient subtends 4° of latitude facilitating a mix of temperate species from the south and tropical species from the north. The geology consists primarily of base-poor granites and sandstones, and base-rich basalt, dolerite, mudstones, shales, rhyolite and tillite. The geology is orientated in an approximately north-south direction and is therefore confounded with the east-west orientation of the altitudinal gradient. The Maputaland region in the north-east of the province consists of geologically young sands (Partridge, 1997). The major biomes are represented by savanna, grassland, Indian Ocean Coastal Belt and forest systems (Mucina and Rutherford, 2006). The forest biome covers a small percentage of the province, as do wetlands, hence these azonal vegetation types are excluded from the analysis.

Latitude and altitude represent the two major temperature gradients in the province. Coastal mean annual temperatures (MAT) range from 20.3°C in the south (31°S) to 22.9°C in the north east (27°S); along the Drakensberg escarpment MAT decreases to 7.9°C (Schulze, 2006). The average minimum winter temperature (July) is lowest in the Drakensberg (-6.4°C) and southern escarpment, warming along the coast and Maputaland (13.5°C). The average maximum summer temperatures (February) are highest in north eastern KZN and the Thukela basin (32.6°C), whereas the Drakensberg escarpment has cooler average summer temperatures (18.1°C).

A complex precipitation gradient exists in the province, created by topography, orographic precipitation, mistbelts and oceanic influences. Mean annual precipitation (MAP) is highest along the Drakensberg and the coast (up to 1923mm.yr^{-1}) (Schulze, 2006). Drier regions include the Thukela river basin, north Zululand and western Maputaland (450-500mm.yr^{-1}). KZN receives mainly summer rainfall, although up to 50mm may fall during winter months associated with cold fronts moving across the country from the south. Snow may fall on the high lying areas in the west of the province. The Drakensberg, midlands and northern coastal regions may receive an average of 282mm of rain in February.

Biodiversity in the province faces large threats mostly in the form of human population growth and associated land transformations (Reyers, 2001). KZN has the second largest share of the national population (10.9 million people in 2015) after Gauteng (Statistics SA, 2015) and an average fertility rate of 2.81 (the average number of children born to a woman in her lifetime) (Statistics SA, 2011). Internal migration streams reveal that KZN experiences positive net migration (Statistics SA, 2011). This increasing population is leading to rapid urban expansion and increasing pressure on the natural resources and ecosystem services. Many rural communities live on communally owned land and are reliant on natural resources for food, fibre, fuel, and medicine (Shackleton et al., 2001). As a result there are likely to be increased levels of conflict between conservation and other land uses (Meadows, 2006; Di Minin et al., 2013). KZN receives a mean annual precipitation of 837 mm, making it one of the wettest province in the country (Schulze, 2006). Consequently, agriculture (consisting primarily of commercial and subsistence crops, sugar cane, timber plantations and orchards) is a major feature of the landscape. The average rate of habitat transformation within the province between 1994 and 2008 was 1.35% per annum or approximately 128 000ha.annum^{-1} (Jewitt, 2012).

The province has a range of PAs including two World Heritage Sites (iSimangaliso Wetland Park World Heritage Site and Maloti Drakensberg Park World Heritage Site), provincial protected areas managed by Ezemvelo KZN Wildlife and Stewardship sites proclaimed under the National Environmental Management: Protected Areas Act 57 of 2003. By October 2015 protected areas conserved 9% of the terrestrial landscape, excluding marine protected areas.

This biodiverse province, with strong ecological gradients makes a good case study to develop conservation planning tools to mitigate the major global threats to its floristic diversity.

1.2.3 The environmental correlates of floristic pattern

Understanding the environmental factors controlling floristic composition and pattern is critical for enabling conservation planning to ensure representivity and persistence (Margules and Pressey, 2000) into the future. Indeed a prerequisite for predicting how communities will change in the wake of global change requires an understanding of the processes that govern the pattern and assembly of communities (Guisan and Rahbek, 2011; Arellano et al., 2015). A broad array of biotic, disturbance (e.g. fire and herbivory), historical factors and processes combine to structure floristic communities (Cowling et al., 1997). Understanding these complex interactions, the ensuing spatial patterns and the associated environmental gradients, has long been a central research area of plant community ecology (Pausas and Austin, 2001). This understanding is also essential in order to be able to effect appropriate management, to track community responses over time or to restore the diversity and integrity of a community that has been degraded by anthropogenic influences (Hirst and Jackson, 2007).

A gradient analysis describes the distribution of species or communities in response to environmental gradients (Whittaker, 1973). Savanna and grassland ecosystems are largely nondiscrete in their boundaries and are defined by general, widespread elevational and climatic gradients (Poiani et al., 2000). At regional scales the distribution of vegetation is largely determined by climate (Lavorel, 1999), at landscape scales by land use and soil type, and at the site scale by soil type and biotic interactions (Pearson and Dawson, 2003). Land management practices such as fire and herbivory regimes may strongly influence vegetation communities (Cowling et al., 1997) but since these variables are important in both grassland and savanna systems, these factors are effectively held constant allowing for examination of regional and landscape drivers (Bredenkamp et al., 2002). Fire is so frequent in these systems that organisms are well adapted to it, and it can be considered an ‘included’ disturbance (Fairbanks, 2000).

Climate change may cause species to shift their ranges (Carvalo et al., 2011), so an analysis of distribution patterns of species along environmental gradients is critical for understanding species responses to climate change (Toledo et al., 2012; Gwitira et al., 2013). Plant species distributions in southern Africa are influenced by climate, in particular temperature and precipitation (Mucina and Rutherford, 2006). A distinct east-west gradient exists in the grassland biome from the mesic east to the arid west, along with a temperature gradient (O’Connor and Bredenkamp, 1997). Scholes (1997) reported that savanna vegetation patterns were determined by rainfall gradients. Fairbanks (2000) classified South African woodlands using mean monthly temperature, total plant-available water balance of soil, elevation, landscape topographic position and soil fertility.

Pressey (2007) suggests that climatic gradients be identified and incorporated into systematic conservation plans in order to promote range adjustments by species. Local and macroclimatic gradients act as surrogates for evolutionary and ecological processes and are easier to incorporate into conservation plans (Cowling et al., 2003; Rouget et al., 2003, 2006). Few studies have quantified the environmental correlates of plant composition with the aim of facilitating conservation planning. Available studies on vegetation-environment relations in the province have been limited to local landscapes and protected areas, the largest regional study being the Perkins (1997) analysis covering 14 400km^2. Responses of most species to climate operate well beyond this spatial scale, hence the necessity of the current study. In addition to protecting species, habitats and landscapes, conservation efforts should focus on representing geographic and environmental gradients so that evolutionary and ecological processes may persist in the long term (Fairbanks and Benn, 2000).

The steep environmental gradients over short distances within KZN provide an ideal ecological setting for this study. There are marked altitudinal and latitudinal gradients which affect temperature and precipitation ranges. The variation in geology affects the derived soil types. Whilst patterns in floristic composition are unlikely to have a single primary cause (Gaston, 2000), compositional variation is likely to be strongly coupled to climatic variation and soil properties (Virtanen et al., 2006) at this scale.

In this study an analytical framework is presented to identify the major environmental gradients correlated with floristic composition in the region. The gradients correlated to floristic composition are identified at the provincial scale, an appropriate scale for conservation planning in the province.

1.2.4 Mapping landscape beta diversity

Beta diversity (β) was defined as “the extent of change of community composition, or degree of community differentiation, in relation to a complex gradient of environment, or a pattern of environments” (Whittaker, 1960) or more simply “between-habitat diversity” (Whittaker, 1972). The efforts to understand and describe beta diversity patterns has resulted in a multitude of beta diversity definitions, leading to multiple concepts, mathematical expressions and analysis methods (Koleff et al., 2003; Legendre et al., 2005; Anderson et al., 2011; Szava-Kovats and Pärtel, 2014). Beta diversity indices link site (alpha) diversity and regional (gamma) diversity. It may refer to variation within a given extent or turnover along an environmental, temporal or spatial gradient (Anderson et al., 2011).

Beta diversity indices may be used to distinguish species nestedness (species loss) from turnover (species replacement) (Baselga, 2010) and to infer the processes that structure ecological communities (Kraft et al., 2011). Beta diversity indices serve as collective properties of biodiversity and may be used as high-order surrogates in place of modelling individual species distributions, especially where biological data is lacking (Austin, 1999;

Margules and Pressey, 2000; Ferrier, 2002). This facilitates the use of sparse or spatially biased datasets (Ferrier, 2002).

Traditional methods of gradient analysis assume that compositional turnover occurs at a constant rate along a gradient, but in reality this is not often observed (Ferrier et al., 2007). If turnover rates do vary along ecological gradients, then identifying areas of high species turnover will increase the spatial efficiency of including matrix species in the conservation planning process and maximise overall species representivity and persistence (Ferrier, 2002). This complements conservation plans based only on threatened or endemic species or vegetation types. Understanding beta diversity variation along a gradient provides insights into potential climate change responses of communities (Fitzpatrick et al., 2013), as areas of high turnover are vulnerable to climatic variability (McKnight et al., 2007).

In this study the rate of species turnover along and between geographic and environmental gradients is assessed and landscape beta diversity spatially mapped in order to inform conservation planning in the region.

1.2.5 The threat of land cover change

The major driver of biodiversity loss is habitat destruction, and the resulting fragmentation of natural habitat (Fahrig, 2003; Millennium Ecosystem Assessment, 2005; Joppa et al., 2016). The impacts of habitat loss are numerous and can be drivers of irreversible ecological shifts, altering vegetation structure, species composition, and their disturbance regimes, precipitating ecological cascades (Pardini et al., 2010). Habitat loss leads to reductions in species response diversity and functional redundancy which reduces ecosystem resilience (Laliberté et al., 2010). Differing land uses directly and differentially affect biodiversity integrity (O’Connor, 2005; O’Connor and Kuyler, 2009). Functional diversity, especially of animal communities, may be reduced by land use intensification, which can negatively impact ecosystem services through the loss of diversity and species traits (Flynn et al., 2009). Land use and land cover change have the ability to influence climate and weather conditions from local to global scales (Pielke et al., 2002), potentially exacerbating climate change. Other impacts include potential soil erosion, loss of ecosystem services, the disruption of socio-cultural practices and the promotion of natural disasters such as flooding (Foody, 2002; Kindu et al., 2013).

The best documented macroecological pattern is the positive relationship between the numbers of species occurring in an area relative to the size of an area (Gaston, 2006). The species-area relationship (SAR) is well studied in ecology and states generally that as sampling area increases, the number of species recorded increases (Triantis et al., 2012) or describes how the number of species relates to area (Thomas et al., 2004). Grassland and savanna systems are large continuous systems. Habitat loss and fragmentation are creating islands of habitat patches in a sea of anthropogenically transformed landscape. The biota of these systems are most likely ill-adapted at surviving in small patches of habitat. The loss of habitat areas will lead to a decline in the number of species able to persist in that habitat patch and the further habitat patches are from each other the less likely they are to support long-term viable populations of species.

Research has shown that the amount of natural habitat remaining in the landscape is important for persistence of species. With less than 30%-50% of the landscape remaining natural, the probability of the landscape supporting viable species populations declines rapidly and is termed a persistence threshold. Below these levels, habitat arrangement becomes a critical factor in explaining population size and persistence (Flather and Bevers, 2002; Fahrig, 2003). Thus both habitat amount and the geometry of habitat are important in ensuring population persistence once a landscape passes through the persistence threshold.

Habitat loss may lead to a significant decline in the number of species but the extinction of species may involve a time lag (Sang et al., 2010). Thus the number of species in recently altered habitats may reflect past habitat availability and the species that may eventually go extinct represent an extinction debt. The extinction of species tends to be disproportionately weighted towards large-bodied species in many higher taxa, and species in the upper trophic levels are likely to be eliminated before those species in the lower trophic levels (Dobson et al., 2006). The resulting fragmentation limits species migrations and gene flow (Heller and Zavaleta, 2009). For migratory species, landscape modification outside of the province may impact their survival (Sheehan and Sanderson, 2012), despite adequate habitat within the province.

Habitat loss and fragmentation effects on plant species are scale-dependent and taxon-specific (Yu et al., 2012). Species composition patterns are related to the complexity of the habitat shape and the perimeter to area ratio. Fragmentation effects on species composition and diversity depends on both the pattern of fragmentation of the landscape and the degree of habitat loss. (Yu et al., 2012). However, it is important to note habitat area in itself is no guarantee of population viability as land-management practices may degrade the habitat and exacerbate declines (With et al., 2008).

Taxon-specific responses to the functional consequences of habitat loss are expected (Rosenlew and Roslin, 2008). European studies on habitat loss impacts on plant community changes found that plant species with traits such as animal dispersal mechanisms, annual life cycles or a strong competitive ability for light enabled species to cope with habitat loss (Marini et al., 2012). Saar et al. (2012) found that plant traits that made local populations more prone to extinction in calcareous grasslands included species that lacked clonal growth, had shorter life spans, produced fewer seeds per shoot, were self-pollinated, adapted to lower soil nitrogen and had higher light requirements. Anthropogenic impacts lead to the decline of rare species, increasing levels of alien species and an increase in the abundance of generalist species (Socolar et al., 2016).

Societal responses to economic opportunities, mediated by institutional factors, are the main drivers of land-cover change (Lambin et al., 2001). KZN is experiencing a rapid rate of habitat loss (Jewitt, 2012) and large scale land cover change is evident in other parts of South Africa (Coetzer et al., 2010) raising questions generally about sustainable resource extraction, ecosystem functioning and biodiversity conservation. Understanding the patterns, processes and impacts of land-use and land-cover change is essential in order to guide biodiversity conservation, especially in light of other global threats such as climate change (Heller and Zavaleta, 2009). In order to do this, up-to-date and accurate information on land cover and land use is critical for conservation planning (Fairbanks et al., 2000).

Given the complex nature of KZN, and differing land tenure systems in place, it is essential to understand the drivers, patterns and processes of land cover change to facilitate biodiversity conservation. Using quantitative analytical techniques that address known inadequacies of conventional transition matrices (Pontius et al., 2004; Aldwaik and Pontius, 2012) and that specifically assist in identifying the underlying processes of landscape change, this study characterises the systematic land-cover changes occurring in KZN. This is achieved using three provincial land-cover maps of the province (2005, 2008 and 2011) that are directly comparable. The extent and rates of habitat loss are determined using a series of national (1994, 2000) and the provincial land-cover maps.

1.2.6 The threat of climate change

Carbon dioxide levels have increased to the highest levels yet in the last 800 000 years and pre-industrial levels have increased by 40% (IPCC, 2013). It is expected that global atmospheric carbon dioxide levels will range between 421-936 ppm by the end of this century dependent on future emission scenarios (IPCC, 2013). These increases in CO_2 stem primarily from net land use change emissions and fossil fuel emissions, and it is considered most likely that the observed global warming is due to anthropogenic influences (IPCC, 2013). Climate change scenarios, or the Representative Concentration Pathways (RCPs), predict global surface temperature is likely to exceed 1.5 ^{o}C for all RCP scenarios by 2100 and warming will continue beyond 2100. Hot extremes are expected to increase whilst cold extremes will diminish (IPCC, 2013). Precipitation predictions are less certain but it is likely that the El Niño Southern Oscillation will intensify precipitation variability in the region.

The fourth assessment report predicted significant warming (1-3^{o}C) in the region with changes in precipitation being variable. Along the east coast of South Africa, precipitation is not predicted to decrease significantly and may even increase, although the intensity of rainfall events and intervals between rainfall events are likely to increase (IPCC, 2007). Nationally, range shifts are predicted to take place in an easterly direction, hence species will move into one of the most transformed and populous landscapes in South Africa (van Jaarsveld and Chown, 2001).

Climate change is likely to alter both temperature and precipitation. Median temperature is expected to increase by 3-4°C across the southern African sub-region (Christensen et al., 2007). It is predicted that heavy precipitation events will increase in frequency along with heat waves and hot extremes. Tropical cyclones will become more intense but are expected to occur less frequently in South Africa. Future precipitation effects are less well known as drying is expected in the southwest winter rainfall regions but model predictions are less clear in KZN due to strong orographic forcing in the region. The relative importance of temperature and precipitation need to be understood in order to undertake conservation planning to mitigate the effects of climate change. The effects of changes in extreme climatic conditions will differ from changes in mean climatic conditions. Plant water relations will be influenced by the extremes of precipitation and temperature events whereas plant phenology will be affected by changing mean conditions (Reyer et al., 2013).

Numerous Global Circulation Models are used to predict future climatic trends. These are downscaled in order to assist planning at a regional scale. One such dataset is based on the dynamic downscaled models of southern Africa researched by Engelbrecht et al. (2009). They predict that the subtropical high-pressure belt will intensify in the south of the subcontinent resulting in a displacement of the frontal rain systems to the south. They predict lower rainfall over the south-eastern subcontinent due to mid- and upper-level highs being more prominent over the central and eastern parts of southern Africa, especially in spring and autumn. The Indian Ocean High is predicted to intensify over the south-western Indian Ocean in mid-summer which results in more frequent cloud bands associated with the South Indian Convergence Zone (SICZ) over the south eastern subcontinent, resulting in generally wetter conditions in this region. Despite the predicted increases in summer rainfall, eastern SA is predicted to become drier. This contrasts with general perceptions that SA will become wetter in the east and drier in the west. However, rainfall models are notoriously variable (Jury, 2012).

Land-use change, resulting from increased human populations and corresponding conversion of natural habitat to agriculture, silviculture and living space, overshadows climate change as a driver of biodiversity loss (Wessels et al., 2003; Noss et al., 2011; Verburg et al., 2011). However, climate change is anticipated to become one of the greatest drivers of biodiversity loss in the future (Heller and Zavaleta, 2009). Climate change is likely to produce shifts in the distributions and abundances of species (Thomas et al., 2004) and hence the composition of habitats (Berry et al., 2002). Paleoecological evidence shows that species migrated to track their environmental niches (Collingham and Huntley, 2000). Thus there is a need to incorporate gradients into landscape planning so that species may track their environmental niche (Manning et al., 2009). Physical geography, habitat fragmentation and land use patterns, will restrict the potential of species to migrate and track changing climates and will thus increase their susceptibility to climate change. Landscape characteristics (e.g. landscape heterogeneity, the distribution, size and isolation of patches) and species traits (e.g. dispersal ability, population growth rates) will influence the rate at which species are able to disperse through the landscape (Collingham and Huntley, 2000). Habitats outside of protected areas are often inhospitable to the survival of many species (Heller and Zavaleta, 2009) because of human infrastructure and its associated stressors such as unsustainable resource use, hunting, invasive species, vehicles and environmental pollution. With high rates of human population growth and associated development, anthropogenic transformation of the landscape will continue.

Impacts on vegetation composition and structure are continuous and do not have an identifiable or predictable end point. Ecosystems will not shift as intact entities as species response is individual based on their competitive abilities and recovery from disturbance (Walker and Steffen, 1997). Range shifts, as a result of species tracking suitable climates, will lead to changes in species composition and relative abundance (Manning et al., 2009). These species interactions may alter feedbacks which can create cascading effects in an ecosystem. Thus novel assemblages of species, which have not existed in the past, will arise due to extinctions of species, changes in abundance values and invasions by new species. However, predicting the consequences of novel conditions is particularly difficult (Sutherland, 2006). Ecosystems will become substantially reorganized containing early successional, generalist or weedy species. Slow processes, such as soil nutrient dynamics, species composition changes and long-lived plants, regulate ecological responses, hence climate change impacts may take decades or centuries to emerge (Luo et al., 2011). Novel assemblages of species challenge the preservationist view still widely held in conservation (Manning et al., 2009).

Climate change is already having multiple effects on species and ecosystems including, but not limited to, species distribution shifts along elevational gradients, phenological changes, decoupling of plant-pollinator relationships, effects on demographic rates, population size reductions, range restricted species extinctions, direct loss of habitat from sea-level rise, and the spread of invasive species and diseases (Mawdsley et al., 2009). Climate change is expected to bring about a disruption of ecological matches such as spatial and temporal synchrony of occurrence, morphological and physiological interdependencies (Schweiger et al., 2010). Areas at high latitudes, high elevations and protected areas with abrupt land-use boundaries will be particularly vulnerable to climate change effects (Sala et al., 2000).

Major impacts on biodiversity in southern Africa are expected to be the invasion of grasslands by savanna tree species and an increase in bush encroachment. Up to 80% of animal species and 44% of plant species would experience alteration to their geographic ranges (van Jaarsveld and Chown, 2001). Studies on animal impacts in South Africa were varied, although most range shifts were predicted to follow the east-west precipitation gradient, and move towards the east (Erasmus et al., 2002). Climate change is likely to shift the environmental niche of species outside of existing protected areas (Shaw et al., 2012), highlighting the importance of enabling species to migrate through the landscape to more suitable climes. These range shifts however, are likely to increase conflicts between conservation and other land uses (Erasmus et al., 2002).

The speed at which species will be able to track changing climes is varied and will undoubtedly be confounded by anthropogenically altered landscapes. Schwartz (1992) demonstrated that migration rates of trees (based on Holocene tree migration rates of an average of 10-45km per century up to a maximum of 200km per century) in response to climatic warming, could decline by an order of magnitude where habitat availability is less than 50%. Hence tree species may fail to track suitable environmental niches. Migration lag is problematic with plants because it could threaten carbon storage and biodiversity (Corlett and Westcott, 2013). Based on maximum dispersal distances of between 50-1500m and time to plant maturity of between 1-30 years, it is estimated that plant movement will range between 1.7-1500m.year^{-1} in unfragmented landscapes and without considering species interactions. However these velocities are probably most suited to species with good colonizing ability and well-dispersed generalists e.g. pioneer and ruderal species (Corlett and Westcott, 2013).

Plant species range expansions will be affected by species interactions. There are two main patterns of range expansion viz. ‘jump dispersal’ and ‘diffusion dispersal’ (Wilkinson, 2011). ‘Jump dispersal’ is where species colonise new areas over long distances, often with inhospitable habitat in between. This may be facilitated by animal species, for example the spread of *Trillium* seeds by deer over large geographies (Vellend et al., 2003) or via rare events by air or water currents. ‘Diffusion dispersal’ refers to the gradual spread of species in suitable habitat. Species may fail to establish in new areas because of competition from existing species.

Refugia are habitats that some species can retreat to, persist in and potentially expand from, in changing climates (Keppel et al., 2011). By protecting climate refugia and ensuring linkages in the landscape, especially along the major environmental gradients identified in the province, natural processes and features that mitigate the effects of climate change are supported (Hansen et al., 2009). Species may be able to persist in isolated populations in climatic refuges until conditions improve, hence research to identify potential refugial areas under changing climates, is needed. Conserving projected refugia does not guarantee the viability of the ecosystem and therefore should not be the only criteria used for identifying important conservation areas (Groves et al., 2012). Areas of high topographic diversity create a range of microclimates in close proximity that may serve as refugia.

For conservation plans to be fully effective, planners must fully integrate the effects of climate change into their plans (Hansen et al., 2009). Climate change mitigation has been difficult to achieve worldwide (Yates et al., 2010), therefore sound predictions of future climate change impacts on biodiversity are required to guide conservation planning. Protecting the wide array of biodiversity in this province requires a coarse filter approach, especially since little is known of the specific biology of many of the species making their conservation especially difficult. A generic tool is needed to guide decision making for the majority of this diversity (Saxon et al., 2005). Approaches to incorporate climate change into conservation plans include protecting climate refugia, conserving the geophysical stage, enhancing landscape connectivity, and sustaining ecosystem functioning and processes (Groves et al., 2012). Common climate change adaptation recommendations are to increase the protected area network and link protected areas to increase connectivity in the landscape (Hannah et al., 2007; Heller and Zavaleta, 2009; Lawler 2009; Mawdsley et al., 2009; Ackerly et al., 2010; Beier and Brost, 2010).

In this study, an approach for understanding climate change impacts on floristic communities is presented. The identified environmental correlates of the floristic communities are used to define current environmental domains. An ensemble of future modelled climates are used to track future environmental domains to identify climatically stable areas (potential macro-refugia) and areas of greatest change (potential novel communities). A vulnerability framework based on habitat intactness, climatic stability and potential rate of climate change is developed in order to guide appropriate conservation actions.

1.2.7 Planning for the maintenance of floristic diversity in the face of land cover and climate change

Global terrestrial biodiversity loss is driven primarily by land-use change and climate change (Sala et al., 2000). Habitat loss and the resulting fragmentation of landscapes leads to reductions in response diversity and functional diversity, which reduces ecosystem resilience (Laliberté et al., 2010). In order for species to track the climates to which they are adapted, they will need to disperse through transformed and fragmented landscapes (Pearson and

Dawson, 2005), or adapt *in-situ*. However, transformed landscapes are often inhospitable to species survival (Heller and Zavaleta, 2009) and the new land-use may present a barrier to the movement of the species (Pearson and Dawson, 2005). The ability of species and communities to adapt to a new climatic regime will depend on factors which can influence or constrain their movement. At a community level, each constraint e.g. land use, can act as a filter which reduces the number of species which can pass through to a potentially new habitat made available by climate change (Millennium Ecosystem Assessment, 2005). Existing protected areas may fail to protect species in future because of altered species distributions (Monzón et al., 2011). Thus it is essential to retain and protect unfragmented, large natural landscapes for maintaining biodiversity into the future (Worboys et al., 2015) and to manage landscapes to assist species to track changing conditions (Pearson and Dawson, 2005).

The most widely cited climate change adaptations are to increase connectivity in the landscape and increase the number of protected areas (Hannah et al., 2007; Heller and Zavaleta, 2009; Lawler 2009; Mawdsley et al., 2009; Ackerly et al., 2010; Beier and Brost, 2010). Similarly, corridors mitigate the effects of land use change (Worboys et al., 2015). It is further suggested that the matrix be ‘softened’ to make it more permeable to species trying to cross the matrix to a suitable habitat patch (Mawdsley et al., 2009; Rands et al., 2010; Gillson et al., 2013). These are *in-situ* solutions and as such are probably the least expensive conservation options and also the best to facilitate the natural processes that support biodiversity.

The best prospect for communities and species to naturally adapt to climate change is to ensure linkages exist in the landscape so that species can shift their distributions. Good connectivity can improve the ecological integrity of protected areas, thus enhancing ecosystem resilience (Groves et al., 2012). Linkages keep populations and ecosystems connected, facilitate access for species with different life cycle habitat requirements, facilitate species with large home ranges and helps to maintain ecological processes. According to island biogeography theory and metapopulation theory, species able to use linkages such as corridors or stepping stones have a greater capacity to persist in fragmented habitats (Bennet 2003). Species richness can be increased with increasing connectivity between patches (Rösch et al., 2013).

Corridors may assist the movement of species through inhospitable environments. Dispersal movements benefit small populations by supplementation of individuals or for recolonization of locally extinct patches. They also assist in the maintenance of ecological processes such as seed dispersal, pollination, predation, and promote genetic viability. Corridors help to restore the natural flow and interchange of plants and animals across the landscape (Bennet, 2003).

There has been a degree of criticism levelled against the efficacy of corridors due to a lack of scientific evidence showing the benefits of corridors (Simberloff, 1992), the possibility that negative effects may outweigh the positive effects and that they may not be a cost effective option. However, this controversy has waned and the importance of landscape connectivity is now widely accepted (Crooks and Sanjayan, 2006; Worboys et al., 2015). Further, the precautionary principle applies as evidence has shown that the isolation of populations and communities through habitat loss has a detrimental effect. It is recognised however that connectivity may not be beneficial in all circumstances (Worboys et al., 2015), or may have negative effects. For example, corridors tend to be linear features and thus are prone to edge effects. Community composition is altered along road edges, with effects extending up to 25-30m, often containing more exotic than native species (Gieselman et al., 2013). This may be mitigated by maximising the width of the corridor.

Habitat amount and quality are vital components for population viability. Large areas and high-quality habitats provide source populations and locations for colonization (Hodgson et al., 2011). Habitat patches are embedded in an anthropogenically modified landscape or matrix. The matrix influences species abundance and population sizes in fragmented habitat patches, and can be even more important in population viability than corridors (Watling et al., 2011). A matrix that is less harmful to organisms will better support their dispersal or movement.

Along with connectivity and viability, climatically under-represented areas need to be included in conservation planning priorities. However, the ability to include these areas decreases as habitat loss and degradation increases. In order to preserve flexibility in conservation planning, strategic planning is required. Once original habitat amount is diminished, climatic biases are likely to exist and they will be more difficult to mitigate (Pyke, 2004). Climate change will act in concert with other stressors such as habitat transformation and invasive species. Ecosystems and species that are already stressed by these factors will be less resilient to climate change (Hansen et al., 2009).

The spatial prioritisation of the location of corridors in the landscape is essential if maximum ecological resilience (*sensu* Holling 1973) is to be achieved. Ecological resilience is enhanced by high levels of biodiversity which would include high levels of functional and response diversity, heterogeneous landscapes, the maintenance of natural disturbance regimes such as fires and maintaining the capacity for processes such as dispersal, colonization, migration and spatial subsidization (Cumming, 2011). Incorporating important plant conservation areas identified via a systematic conservation planning approach (Margules and Pressey, 2000) would ensure that threatened or endemic plant species and vegetation types may be included in the corridors.

Environmental gradients define the distribution of species (Lawler, 2009). Maintaining linkages between areas of the dominant environmental drivers, such as temperature and precipitation, will allow species to move along these gradients as the climate changes, and maximise climatic suitability into the future (Pearson and Dawson, 2005). Nuñez et al. (2013) suggested using a coarse filter approach to identify linkages for movement between areas of low human impact and spatial gradients. Corridors based on gradients and land-use patterns will be robust to the uncertainty in direction and magnitude of climate change.

Incorporating areas of high turnover maximises the representation of diversity in conservation plans (Ferrier, 2002; Pressey, 2004), specifically of common species. These areas may further enhance the resilience of plant communities under global change (Fitzpatrick et al., 2013), as high turnover areas are where species ranges are vulnerable to climate change (McKnight et al., 2007). Incorporating environmental gradients and areas of high beta diversity help to preserve the ecological and evolutionary processes that create and maintain diversity.

Where macro-refugial areas for plant communities are known, these areas should be incorporated into the corridors in order to maximise species persistence into the future and minimise climate change impacts. Areas where an ensemble of climate change models concur, reduces the uncertainty of climate change predictions and may be used to enhance conservation adaptations strategies (Jones-Farrand et al., 2011).

Protected areas should be functionally connected to allow for the movement of species and genes (Noss et al., 2011). New protected areas should be placed in areas anticipated to be important for biodiversity in the future and to cater for species of high conservation value (Heller and Zavaleta, 2009), while still maintaining the current configurations of diversity which secures the source populations. The spatial distance between existing and new protected areas should be minimized to facilitate species migration. The full range of bioclimatic variability needs to be captured across the landscape. Areas of high endemism, high genetic diversity, ecotones and refugia should be protected.

Based on these principles, this study develops a spatially explicit connectivity map to serve as a decision support tool at coarse scales, to impart landscape resilience to land-cover and climate change. Protected areas are linked using the lowest cost distance to maximise plant dispersal opportunities. A biological underpinning of floristic composition that supports ecological and evolutionary processes by using climatic gradients correlated to floristic composition and areas of high beta diversity, broad-scale climate refugia and important plant conservation areas, in order to maximise the persistence potential of floristic diversity in the face of global change. The corridors attempt to retain large natural and semi-natural landscapes so that species may respond naturally to climate change and limit further habitat loss.

1.3 Research aims, objectives and outline of the thesis

The primary aim of the study is to develop an understanding of the most important drivers determining indigenous plant community composition, pattern, and turnover in grassland and savanna systems in KZN. The threats posed by climate change and land-cover change to these communities are investigated and a guide to impart maximum resilience to floristic diversity developed. The research aims to facilitate conservation planning for floristic diversity.

Five broad objectives result from this:

1.3.1 Objective 1: To analyse the relations between phytosociological data and environmental variables with the aim of identifying the dominant environmental correlates and gradients of floristic composition, in order to facilitate future conservation planning.

The specific questions addressed are:

1. Across KZN, what are the dominant environmental gradients most associated with plant species composition, recognizing the province has steep gradients over short distances?

2. Which environmental variables delimit floristic community pattern?

1.3.2 Objective 2: To assess how the rate of species turnover varies along and between environmental and geographic gradients and to map beta diversity in the province.

The specific question and output addressed are:

1. How does the rate of species turnover vary along and between environmental and geographic gradients?

2. Develop a map of beta diversity of plant communities in KZN to guide conservation planning.

1.3.3 Objective 3: To understand the amounts, rates, drivers, patterns and processes of land cover change in KZN for biodiversity conservation.

The specific questions addressed are:

1. What are the drivers, patterns and processes of land-cover change in KZN and across different land tenure systems between 2005, 2008 and 2011?

2. What is the extent and rate of natural habitat loss between 1994 and 2011?

1.3.4 Objective 4: To understand climate change impacts on vegetation communities using the major environmental correlates of floristic composition to map current and future environmental domains using an ensemble of regional climate models, with the aim of identifying regions expected to experience the greatest (potential novel communities) and least (potential macrorefugia) degree of climate change by 2050.

The specific questions addressed are:

1. What and where are the major environmental domains in KZN, determined using the three primary climatic and edaphic correlates of floristic composition in KZN?

2. How will the environmental domains change in KZN by 2050, determined using an ensemble of climatic models based on the A2 emission scenario?

3. Which areas of the province are expected to experience the least and greatest magnitude of change?

4. Which environmental domains are the most vulnerable in terms of climate change, habitat loss and mean magnitude of change?

1.3.5 Objective 5: To prioritise the spatial location of a coarse-grained, spatially explicit connectivity map to serve as a decision support tool to impart landscape resilience for floristic diversity to land-cover and climate change. The aim is to use a biological underpinning of floristic composition that supports ecological and evolutionary processes by using climatic gradients correlated to floristic composition, areas of high beta diversity, broad-scale climate refugia and important plant conservation areas, in order to maximise the persistence of floristic diversity in the face of global change.

The specific output is:

1. A corridor map that maximises the retention of large natural and semi-natural landscapes to allow species to respond to climate change and limit further habitat loss.

1.4 Structure of the thesis

The thesis is comprised of five content chapters (Chapters 2-6) with an introductory and concluding chapter (Chapters 1 and 7 respectively). Chapter 1 describes the rationale for the study, a literature review and the thesis aims and objectives. A detailed overview is provided of the study area. The content chapters have been written in the format of scientific journal articles.

The content chapters and their publication details are as follows:

- Chapter 2 is published in Austral Ecology (Jewitt et al., 2015a). This chapter investigates the gradients correlated to floristic composition in KZN.

- Chapter 3 is published in Biodiversity Conservation (Jewitt et al., 2016). This chapter investigates the levels of beta diversity in KZN.
- Chapter 4 is published in the South African Journal of Science (Jewitt et al., 2015b). This chapter explores land cover change in KZN.
- Chapter 5 is published in Applied Geography (Jewitt et al., 2015c). This chapter explores climate change impacts for floristic communities in KZN.
- Chapter 6 explores conservation planning solutions to mitigate land cover and climate change impacts to maintain floristic diversity into the future.

The order of the chapter presentation in this thesis does not match the time-line of journal acceptance. Due to the requirements of publishing scientific articles, there is an unavoidable degree of repetition, especially with respect to the study site description, motivations for the study and literature review.

1.4.1 Author contributions

The published chapters 2-6 have multiple co-authors. The following list includes a description of the contributions of each author:

- D Jewitt: Primary author, conducted all data collation and analysis, responsible for paper concepts and the write-up
- PS Goodman: PhD Co-supervisor, provided guidance with regard to theoretical approach for the thesis and commented on various drafts of all papers / chapters
- TG O’Connor: PhD Co-supervisor, provided guidance with regard to theoretical approach for the thesis and commented on various drafts of all papers / chapters
- BFN Erasmus: PhD Co-supervisor, provided guidance with regard to theoretical approach for the thesis and commented on various drafts of papers / chapters
- ETF Witkowski: PhD Co-supervisor, provided guidance with regard to theoretical approach for the thesis and commented on various drafts of all papers / chapters
- WW Hargrove: Assisted with running the *k*-means clustering algorithm and commented on the paper in chapter 5 (climate change)
- DM Maddalena: Assisted with running the *k*-means clustering algorithm and commented on the paper in chapter 5 (climate change)

1.4.2 Nota bene

The provincial boundary used for this research in some instances included the currently disputed Matatiele region in the southwest which is currently administered by the Eastern Cape Province, but which was previously administered by KZN. This region is included for planning purposes only, but does lead to a situation where the province size reported or mapped varies amongst the published papers.

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CHAPTER 2

2. Floristic composition in relation to environmental gradients across KwaZulu-Natal, South Africa

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Floristic composition in relation to environmental gradients across KwaZulu-Natal, South Africa

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Abstract Conservation planning in the face of global change is still in its infancy. A suggested approach is to incorporate environmental gradients into conservation planning as they reflect the ecological and evolutionary processes generating and maintaining diversity. Our study provides a framework to identify the dominant environmental gradients determining floristic composition and pattern. Nonmetric multidimensional scaling was used on 2155 sampling plots in savanna and grassland habitat located across the province of KwaZulu-Natal, South Africa (94 697 km^2), a floristically rich region having steep environmental gradients, to determine the dominant gradients. Hierarchical cluster analysis was used to group similar plots which were then used in a Classification and Regression Tree analysis to determine the environmental delimiters of the identified vegetation clusters. Temperature-related variables were the strongest delimiters of floristic composition across the province, in particular mean annual temperature. Frost duration was the primary variable in the Classification and Regression Tree analysis with important implications for savanna/grassland dynamics. Soil properties (base, pH status) and moisture variables accounted for most of the variation for the second and third axes of floristic variation. Given that climatic and edaphic variables were well correlated with floristic composition, it is anticipated that a changing climate will have a marked influence on floristic composition. We predict warmer temperatures may facilitate the spread of frost sensitive savanna species into previously cooler, grassland areas. Species associated with specific soil types will not easily be able to move up the altitudinal gradient to cooler climes because geology is aligned in an approximately north-south direction compared with increasing altitude from east-west. Future conservation planning should take cognisance of these gradients which are surrogates for ecological and evolutionary processes promoting persistence.

Key words: climate change, conservation planning, multivariate analysis, ordination, vegetation type.

INTRODUCTION

The central tenets of conservation planning are representivity and persistence (Margules & Pressey 2000). Much attention has been aimed at ensuring representivity but factors promoting persistence in a dynamic world are less well documented (Pressey *et al.* 2007). Planning for evolutionary and ecological processes which maintain and generate biodiversity (Balmford *et al.* 1998), and planning for threats such as climate change need to be enhanced (Heller & Zavaleta 2009).

Conservation planning for climate change adaptation is still in its infancy (Midgley *et al.* 2003). Species shift their ranges as climate changes and hence research effort has focused on species distribution modelling (Carvalho *et al.* 2011; Toledo *et al.* 2012) but these consider only a restricted set of species, often because of a paucity of data for many species. In highly diverse areas, it is impracticable to model individual species responses. Other efforts focus on biome level modelling but this is too coarse for detailed conservation planning (Midgley *et al.* 2003). Pressey (2007) calls for the identification and incorporation of climatic gradients to promote range adjustments by species and indeed some authors have incorporated macroclimatic and local gradients into their plans as surrogates for ecological and evolutionary processes (Cowling *et al.* 2003; Rouget *et al.* 2003, 2006) but they do not explicitly identify environmental correlates to a broad range of floristic species. Investigations based on a limited number of species are inadequate for conservation planning as they cannot be assumed

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to reflect a broader vegetation response. Our study provides a framework for meeting this deficit. An understanding of the main environmental gradients that affect species composition is required if gradients are to be used as surrogates (Sætersdal & Gjerde 2011).

Understanding floristic spatial patterns and their environmental gradients has long been a central tenet of plant community ecology (Pausas & Austin 2001). A gradient analysis describes the distribution of vegetation in response to environmental gradients (Whittaker 1973). It is generally accepted that vegetation distribution is determined by climate at regional scales (Lavorel 1999), land use and soil type at landscape scales, and soil type and biotic interactions at the site scale (Pearson & Dawson 2003). Plant species distribution within the southern African subcontinent is influenced by climate, specifically precipitation and temperature (Mucina & Rutherford 2006). The grassland biome has a distinct east-west rainfall gradient and a temperature gradient (O'Connor & Bredenkamp 1997) while spatial variation in rainfall is a key determinant of savanna vegetation patterns (Scholes 1997).

KwaZulu-Natal (KZN) is a province of South Africa that is species rich, containing portions of the Maputaland-Pondoland-Albany biodiversity hotspot and four centres of plant endemism (Drakensberg Alpine, Midlands, Pondoland, northern KZN) (Mucina & Rutherford 2006). There are more than 6000 vascular plant species, representing 1258 genera, and high levels of endemism (16%) in an area of 94 697 km^2 (Scott-Shaw 1999). The high levels of alpha diversity within KZN arise from a complex interplay of geomorphological history of the subcontinent, climate and species which originate from lineages that are prone to diversification (Cowling & Hilton-Taylor 1997). Pronounced variation in altitude, topography, geology, soils, precipitation and temperature has created steep ecological gradients, occurring over short distances, further contributing towards the high levels of biodiversity. Given the pronounced environmental variation and diverse vegetation, the province provides a useful case study for developing the analytical framework.

The necessity for understanding the spatial floristic ecology in KZN is critical, given rapid global change which will pose new challenges for the understanding and management of the landscape. Concern exists around high rates of human population growth (Statistics South Africa 2012), climate change impacts (Intergovernmental Panel on Climate Change 2007a) and habitat loss (Jewitt 2012), among others. These effects may lead to dramatic changes in the biotic structure and composition of communities, which in turn may alter ecosystem functioning (Hooper *et al.* 2005) and the floristic spatial patterns found in KZN, thus challenging conservation plans aiming to achieve representivity of current vegetation associations. Hence the relative importance of environmental variables in structuring floristic community pattern at the provincial scale, the scale used for conservation planning in KZN, needs to be understood so that future anthropogenic impacts may be planned for and mitigated.

Few studies globally have identified the environmental gradients associated with plant species composition with the aim of facilitating conservation planning in the face of climate change, despite the fact that climate change will alter plant species distributions through range expansion or contraction. We present an analytical framework to identify the dominant environmental gradients most associated with current floristic composition, using a floristically rich region as a case study. This community analysis identifies the environmental gradients that act as coarse-filter ecological and evolutionary surrogates once incorporated into a conservation plan. In particular, we address the following main questions: (i) Across KZN, what are the dominant environmental gradients most associated with plant species composition, recognizing the province has steep gradients over short distances? (ii) Which environmental variables delimit floristic community pattern?

METHODS

Study area

The landscape ranges from subtropical climates on the coast of the Indian Ocean in the east to the alpine climates of the Drakensberg escarpment at about 3000 m. The province subtends 4° of latitude (Fig. 1) providing a melting pot for tropical species from the north and temperate species from the south. The geology consists primarily of base-rich dolerite, basalt, rhyolite, shales, mudstone and tillite, and base-poor granites and sandstones. Geological types run approximately in a north-south direction and are thus confounded with altitude. The north-eastern parts of KZN in Maputaland consist of geologically young sands (Partridge 1997). Four biomes are represented in KZN: grasslands, savanna, Indian Ocean Coastal Belt and forests (Mucina & Rutherford 2006).

There are two strong temperature gradients relating to latitude and altitude. Along the coast, mean annual temperature decreases from 22.9°C in Maputaland (27°S) to 20.3°C on the southern coast (31°S), and altitudinally mean annual temperature decreases from the coast to 7.9°C along the Drakensberg escarpment. The average minimum temperature in July is lowest in the Drakensberg (–6.4°C) and southern escarpment, with warmer minimum temperatures along the coast, Zululand and Maputaland (13.5°C). The highest average maximum temperatures during February occur in Maputaland, Zululand and the Thukela basin (32.6°C), with

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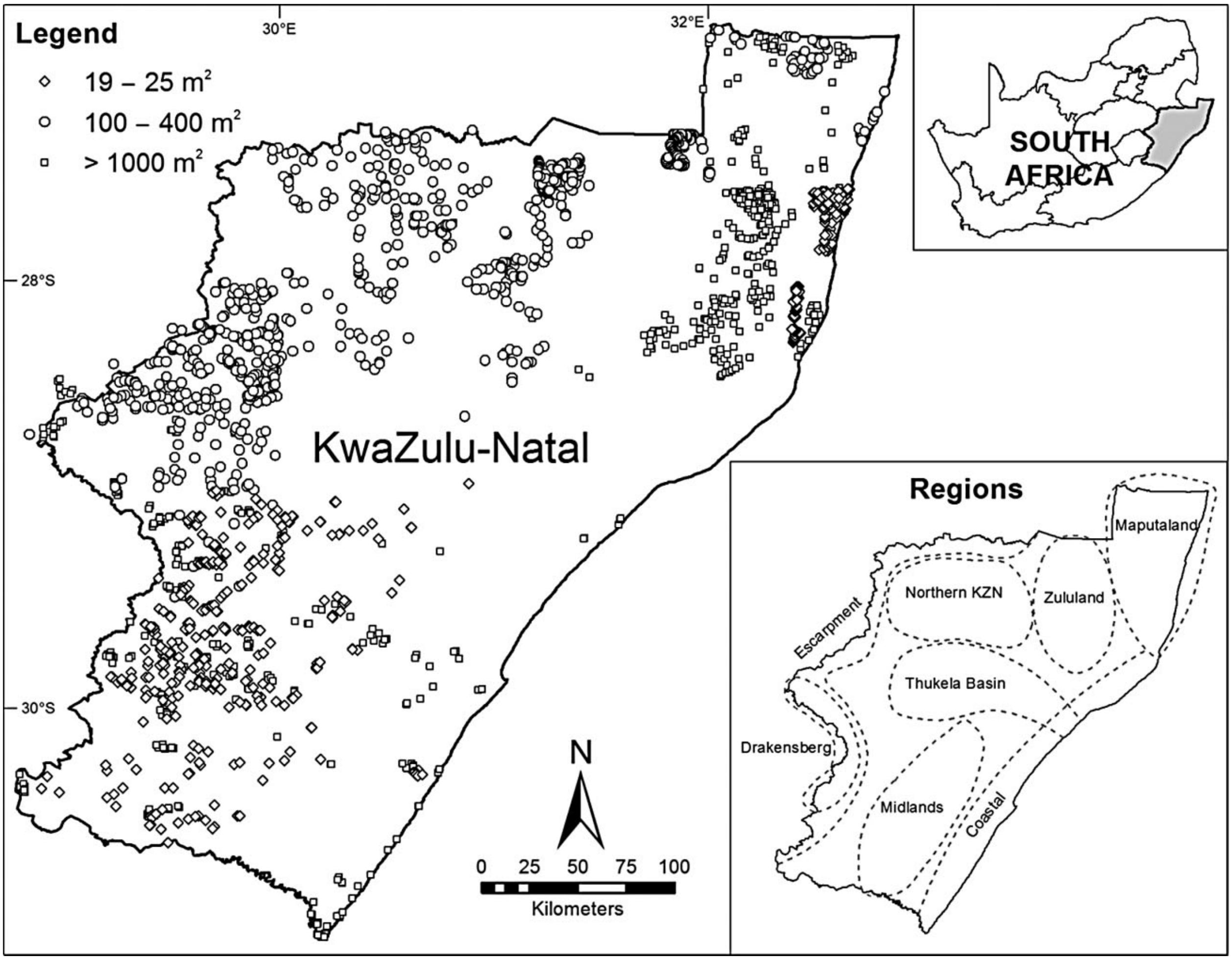

Fig. 1. The study area and location of vegetation plots of different sizes. The inset on the bottom right shows regions referred to in the text.

the Drakensberg having cooler average maximum temperatures of 18.1°C.

The precipitation gradient is more complex, having rain shadow effects created by the topography. The coastal and Drakensberg escarpment areas receive the highest mean annual precipitation (up to 1923 mm $year^{-1}$), with the midlands creating an orographic precipitation and mistbelt area. Some of the driest areas in KZN occur in the west of Maputaland, north Zululand and the Thukela river basin (450–500 mm $year^{-1}$). KZN receives mainly summer rainfall. Winter precipitation is low throughout, although up to 50 mm may fall during a winter month along the coast or as snow in the Drakensberg. The highest average summer rainfall in February occurs in the Drakensberg (282 mm), midlands and the coastal region north of the Thukela River.

Data collection and preparation

Vegetation sample plot (relevé) data from a number of previous studies were collated and used in this analysis (Goodman 1990; Van Wyk 1991, 1992; Eckhardt *et al.* 1996a,b,c; Perkins 1997; James 1998; Robbeson 1998; Matthews *et al.* 1999, 2001; Ngwenya 2003; Ströhmenger *et al.* 2003; O'Connor 2005; and unpublished data from the following researchers: P. S. Goodman, unpubl. data, 2002; E. Granger, unpubl. data, 2008; C. Halkett-Sidall, unpubl. data, 2007; D. Jewitt, unpubl. data, 2004, 2005, 2006, 2007, 2008, 2010; R. Scott-Shaw, unpubl. data, 2006, 2007, 2008, 2010; R. Uys *et al.*, unpubl. data, 2004, 2005, 2006 and N. Van Rooyen, unpubl. data, 2008). These datasets were collected for various objectives, at different temporal and spatial scales. The clumped nature of some of the samples (Fig. 1) results from size restrictions in the study areas of each study. Gaps in coverage are a result of land transformation within KZN or a lack of collection in certain regions.

The sample plot sizes varied from 19 m^2 to ≥1000 m^2. Larger plot sizes were often associated with savannas which needed to be larger given the physiognomic structure of trees *versus* grassland plants. Using Procrustean analysis, the authors confirmed (Appendix S1) that similar ordination results are obtained across the range of plot sizes available in the sample for this study, which was also shown elsewhere (Peres-Neto & Jackson 2001; Otýpková & Chytrý 2006). Hence, data from different plot sizes were combined. The complete dataset consisted of 2260 plots (Fig. 1) and 2636 species. McCune *et al.* (1997) demonstrated

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Table 1. Summary of the 51 variables used in the analyses

Environmental variable	Code	Reference
Mean annual temperature	MAT	Schulze and Maharaj (2007a)
Average minimum temperature in July	MnTmpJul	Schulze and Maharaj (2007b)
Average maximum temperature in February	MxTmpFeb	Schulze and Maharaj (2007c)
Median start date of the first frosts	FrstMedS	Schulze and Maharaj (2007d)
Median number of days of frost duration	FrstDur	Schulze and Maharaj (2007d)
Average solar radiation in February	SR_Feb	Schulze 2007b
Average solar radiation in July	SR_July	Schulze 2007b
Mean annual precipitation	MAP	Schulze and Lynch (2007a)
Median annual precipitation	MedAP	Schulze and Lynch (2007b)
Average median rainfall in February	MdRnFeb	Schulze and Lynch (2007b)
Average median rainfall in July	MdRnJuly	Schulze and Lynch (2007b)
Geology (9 categories)	Geol	kznsoil25v109_wll.zip†
Soil Clay percentage (<15%, 15–35%, ≥35%, no data)	Clay	kznsoil25v109_wll.zip†
Soil Depth categories (Shallow, deep, unknown)	Depth	kznsoil25v109_wll.zip†
Soil base status (dystrophic, mesotrophic, meso-eutrophic, eutrophic, unknown)	Base	kznsoil25v109_wll.zip†
Soil structure (weak, weak-moderate, moderate, strong, unknown)	Struct	kznsoil25v109_wll.zip†
Soil drainage (moderate, well drained, unknown)	Drain	kznsoil25v109_wll.zip†
Soil pH (acid, acid-neutral, neutral, neutral-alkaline, unknown)	pH	kznsoil25v109_wll.zip†
Profile plant water availability	PAW	Schulze and Horan (2007)
Mean annual potential evaporation	MnAnEvap	Schulze and Maharaj (2007e)
Aspect	Asp	90mv3_w31.zip†
Slope	Slope	90mv3_w31.zip†
Rainfall days ≥ 2 mm	Rflge2mm	Schulze 2006
Rainfall days ≥ 10 mm	Rflge10mm	Schulze 2006

†Indicates GIS layers developed by the Biodiversity Conservation Planning Division, Ezemvelo KZN Wildlife, P.O. Box 13053, Cascades, Pietermaritzburg, 3202, South Africa. Categorical variables have their class descriptions in parentheses from which dummy variables were created.

that scores on compositional gradients are relatively consistent across multiple observers, even where there was considerable variation in species capture by the different observers. This was due to the statistical redundancy of information provided by different species. Hence, it was concluded that the various datasets from disparate authors could be combined and used for this analysis. The combined dataset provided the best available coverage of points across KZN and its environmental gradients.

Only presence/absence data were used because they represent the most useful information for analyses of datasets with high beta diversity over large areas (Greig-Smith 1983), and because abundance data can be misleading in ordination analyses (Wilson 2012). Unidentified specimens and specimens identified only to genus level were discarded and all subspecies or varieties were taken back to the species level of identification ($n = 120$). All alien plant species ($n = 81$) were removed as were species that only occurred as singletons ($n = 520$) or doubletons ($n = 272$) (Tóthmérész 1994). Removing rare species reduces noise in the dataset and enhances the detection of relationships between community composition and environmental variables (McCune & Grace 2002). An outlier analysis was performed using PC-ORD (McCune & Mefford 2006, MjM Software Design, Gleneden Beach, OR, USA) and the outlier plots ($n = 105$) were deleted. Outlier plots are those with extreme values which can significantly influence multivariate analyses as they can obscure the information carried by the remainder of the data (McCune & Grace 2002). The technique calculates the frequency distribution of distances of each plot to every other plot and flags the outliers. The cleaned dataset comprised 2155 plots from grassland and savanna, containing 1643 species. All forest and wetland vegetation types, which cover a small percentage of KZN, were excluded from the analysis.

Only plots with site coordinates were used. Environmental variables for the analysis were extracted from spatial layers using the site coordinates and included climatic (Schulze 2007a), edaphic and geological variables. Gradients tested included variables that were considered important in plant species distributions such as temperature, light, moisture and soil characteristics which influence water and nutrient availability (Stevens 2006). Climate shapes vegetation and soil patterns both directly and indirectly. Where possible, variables with direct effects on plants and proximal predictors were used (Pausas & Austin 2001). Categorical variables were transformed into dummy binary variables, thus 51 variables were included in the analyses (Table 1). The climatic data were mapped at a 1 min of a degree latitude by longitude grid (Schulze 2007a). The soil and geology data were mapped at 1:250 000. The geological categories were grouped into lithologically similar types to reduce the number of categories from 34 to 9.

Data analysis

The analysis sought to identify the major environmental correlates of floristic composition using ordination techniques.

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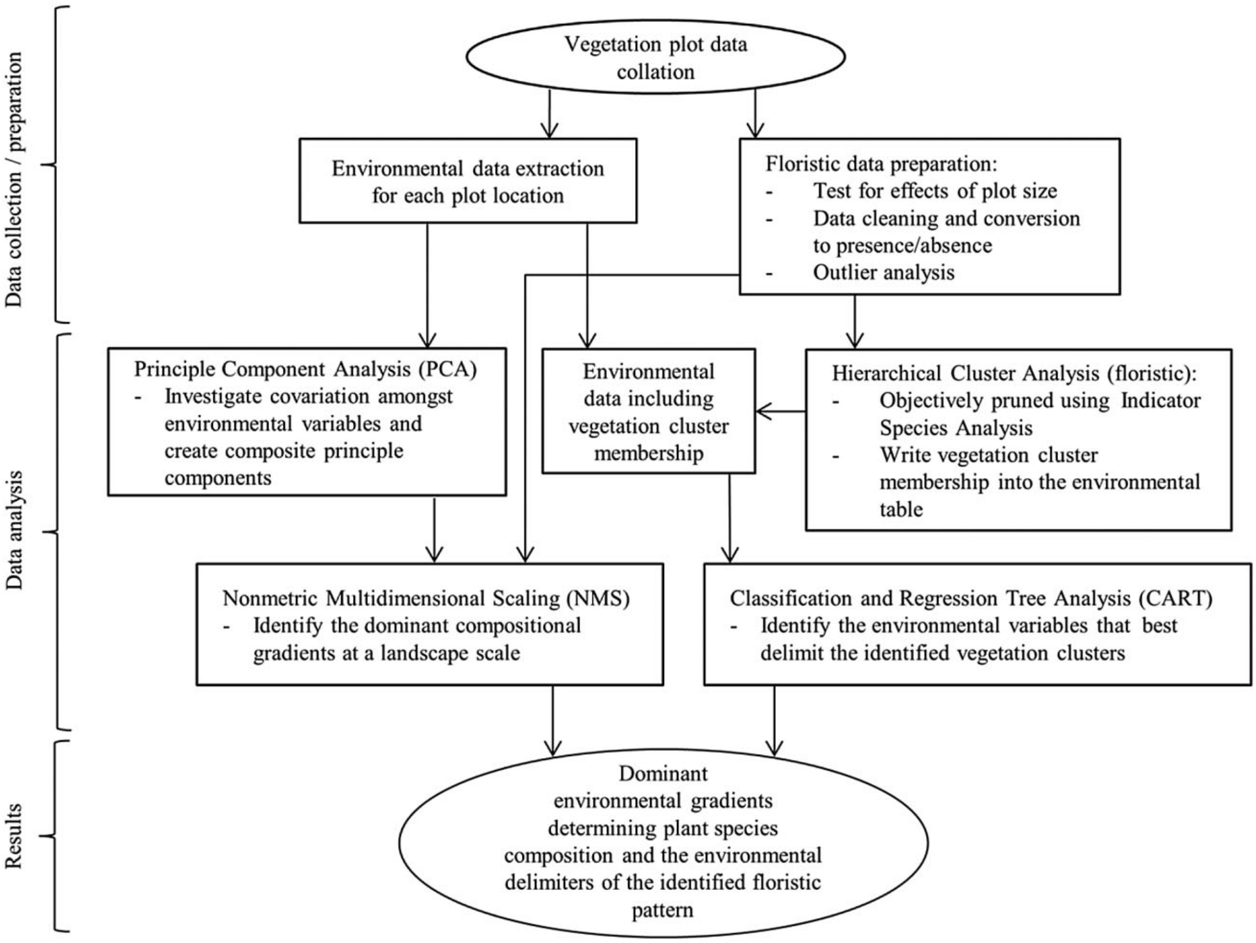

Fig. 2. A flowchart detailing the workflow undertaken in this analysis.

In order to elucidate the pattern of floristic communities, a hierarchical cluster analysis was conducted and these groups written to the environmental table. This was used in Classification and Regression Tree (CART) analysis to identify the environmental delimiters of the identified vegetation clusters (see Fig. 2 for analysis workflow).

Principal component analysis (PCA in package PC-ORD) was used to understand the covariation among environmental variables. It further allowed the initial large set of intercorrelated environmental variables to be reduced to principal components that could be related to floristic gradients (McCune & Grace 2002).

The dominant compositional gradients for the cleaned dataset were extracted using nonmetric multidimensional scaling (NMS) in PC-ORD (McCune & Mefford 2006). The Sørensen distance measure was used as it is an effective measure of sample or species similarity and is a semimetric distance measure useful in community ecology (McCune & Grace 2002). Five hundred iterations were run with random starting coordinates. The stability criterion was set to 0.000001. A Monte Carlo test was run to evaluate whether the NMS was extracting stronger axes than expected by chance (250 runs). The dimensionality of the data was determined by plotting the stress, or measure of fit, to the number of dimensions. Several runs were used for the final analysis to ensure the solution was stable.

Vegetation types were identified using hierarchical cluster analysis in PC-ORD. The Sørensen distance measure was used with the flexible beta linkage method ($\beta = -0.25$). The linkage method, or sorting strategy, was chosen because it takes advantage of the inherent flexibility in the combinatorial equation, is compatible with the Sørensen distance measure and because the user can control the space-distorting properties ($\beta = -0.25$ is space conserving) or degree of chaining (McCune & Grace 2002). The vegetation type membership was written to the environmental data table which could then be used in CART to identify environmental delimiters. The decision on where to prune the dendrogram was based on running an indicator species analysis (Dufrêne & Legendre 1997) in PC-ORD. A perfect indicator should always be faithful and also exclusive to that group (McCune & Grace 2002). The indicator species analysis was run for each cluster identified in the hierarchical cluster analysis. The resulting *P*-values, from the Monte Carlo test of significance of the observed maximum indicator value for each species (1000 permutations), were averaged across all species for all clusters. Similarly, the total number of significant indicators for each cluster was calculated. These were plotted against each other and the cluster which yielded the smallest average *P*-value and the highest number of significant indicators determined the level at which to prune the dendrogram.

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CART was run in STATISTICA (Statsoft Inc. 2012, STATISTICA version 11. www.statsoft.com) in order to explore the differences among the vegetation clusters identified by hierarchical cluster analysis, to determine the delimiters associated with the environmental gradients and to compare these to the gradients identified in the NMS correlations (Vayssières *et al.* 2000; Austin 2002; Thuiller *et al.* 2003). CART is a nonparametric method that partitions the dataset recursively into homogenous subsets (Urban 2002). Categorical variables were included in this analysis and the response codes used were the groups identified in the hierarchical cluster analysis. The criteria for predictive accuracy included the Gini goodness of fit measure, equal misclassification costs and the prior probabilities (which adjusts the importance of misclassification for each class). The stopping rules included pruning on misclassification and a minimum group size of 10% of the overall subset group size. V-fold cross validation was performed.

RESULTS

PCA

Temperature variables accounted for the most variation on the first axis (50.8%) and a combination of moisture, soil and solar radiation accounted for the most variation on the second axis (27.5%). Mean annual temperature, minimum July temperature and maximum February temperature were strongly negatively correlated with the first axis, while frost duration and median start date of first frosts were positively correlated with the first axis. On the second axis, plant available water, mean annual precipitation, median annual precipitation and weakly structured soils were positively correlated, and solar radiation and soil base status were negatively correlated. Hence composite variables were created for the first two axes, the first being a thermal principal component (PC1Heat) and the second a moisture, soil and solar radiation principal component (PC2Moist). These principle components were then correlated against the ordination axis plot scores obtained from using NMS along with the other environmental variables.

NMS

A three-dimensional solution was recommended for the dataset. The coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional spaces had a cumulative $r^2 = 0.662$ (axis $1 = 0.344$, axis $2 = 0.194$ and axis $3 = 0.123$). The stress level of 20.45% for the three-dimensional solution, which is relatively high, was considered acceptable as stress tends to increase with increasing sample size (McCune & Grace 2002). The stability was 0.064 and $P < 0.004$ for all axes. The first axis was rotated to the strongest variable (mean annual temperature) to improve interpretability. Using individual variables, those that correlated most strongly with the NMS axes were mean annual temperature, soil base status (dystrophic soils) and solar radiation in February for the three axes respectively (Fig. 3 and Table 2). The strong mean annual temperature gradient ($r^2 = 0.719$) ranged from 7.9°C to 22.9°C and differed by a factor of 3 across KZN. Using composite variables, the PC1Heat correlated well with the first axis and PC2Moist correlated well with the second axis. The Maputaland plots are separated in ordination space, as a result of the geologically young sands occurring in the area. These areas correlated to the more dystrophic and acidic soils of KZN and axis 2.

Determination of vegetation types and their delimiters

Based on finding the lowest average P across all clusters and highest number of significant indicator species for each cluster, the hierarchical cluster dendrogram was objectively pruned at 23 biologically meaningful vegetation clusters.

The CART analysis serves to define the environmental variables that best delimit the vegetation clusters, effectively identifying vegetation types. CART identified 34 vegetation types (Fig. 4). Given the strong correlation between floristic composition and environmental gradients, vegetation types may be inferred from areas lacking vegetation plot data. This predictive ability of CART explains why more vegetation types were defined in CART than in the hierarchical cluster analysis. The importance of the CART analysis, however, lies in the identification of the environmental variables that best delimit vegetation clusters rather than the final number of vegetation types. Further, the CART analysis serves to explain compositional variation at finer scales whereas the ordination analysis explains compositional variation at a broad scale.

The primary split in the CART tree was for frost duration of 21.5 days. Other important environmental variables included the maximum temperature in February, Plant available water, mean annual evaporation, median rainfall in February and July, solar radiation in February and July and median annual precipitation. Soil variables were not used in the classification while geology and slope only became important at finer scales. The recursive nature of the CART analysis highlights the importance of both temperature and moisture gradients at different scales.

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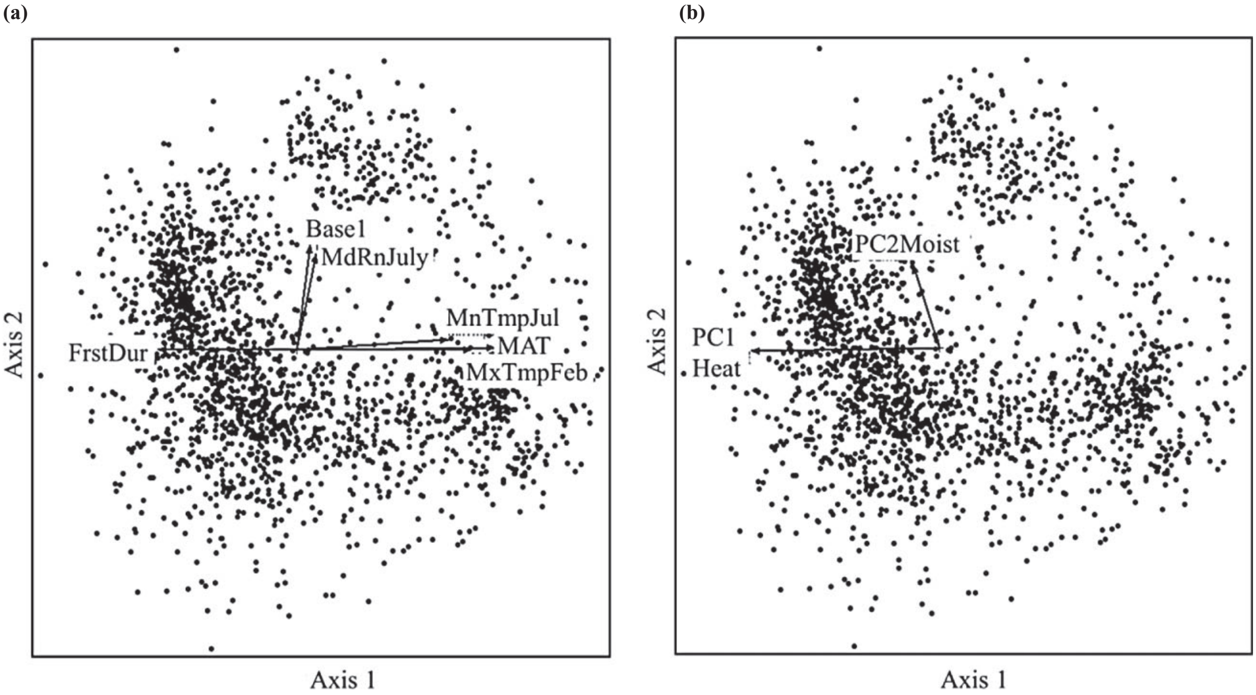

Fig. 3. Nonmetric multidimensional scaling (NMS) ordination of plot scores with the main environmental correlations. Axis 1 correlates with a temperature gradient increasing from left to right. Axis 2 correlates with a gradient from dystrophic, acidic, sandy soils in the top right and to more alkaline soils in the bottom right, as well as a moisture gradient increasing from bottom to top. (a) Individual variables. (b) Composite variables. The ordination results are only depicted in two dimensions because of the large number of data points.

Table 2. Pearson (r) and Kendall (tau) correlations between the nonmetric multidimensional scaling (NMS) axes and the environmental variables

	Axis 1			Axis 2			Axis 3	
	r	tau		r	tau		r	tau
MAT	0.848	0.654	Base1 (dystrophic)	0.560	0.410	SR_Feb	0.331	0.220
PC1Heat	−0.830	−0.620	PC2Moist	0.551	0.377	SR_July	0.304	0.242
MxTmpFeb	0.790	0.619	pH 1 (acidic)	0.551	0.402			
MnTmpJul	0.750	0.500	MdRnJuly	0.528	0.308			
FrstDur	−0.708	−0.558	PAW	0.516	0.327			

Codes for variables are given in Table 1.

Overall interpretation

The primary gradient accounting for floristic composition in KZN is temperature. Mean annual temperature provided the best positive correlate but the variables indicating stress periods for the plants, such as minimum July temperature, maximum February temperature and frost duration, were also useful in the analysis. Frost duration was the best negative correlate which corresponds with the primary branch of the CART analysis.

The secondary gradient accounting for floristic composition in the province was more complex and involved combinations of soil properties, moisture and variables which combine aspects of temperature, moisture and soil properties such as plant available water and mean annual evaporation. Again, the variables indicating a stress period for the plants such as precipitation in the coldest and driest month, and precipitation in hottest month were useful indicators. Only at much finer scales in the CART analysis did variables such as solar radiation, slope and geology become

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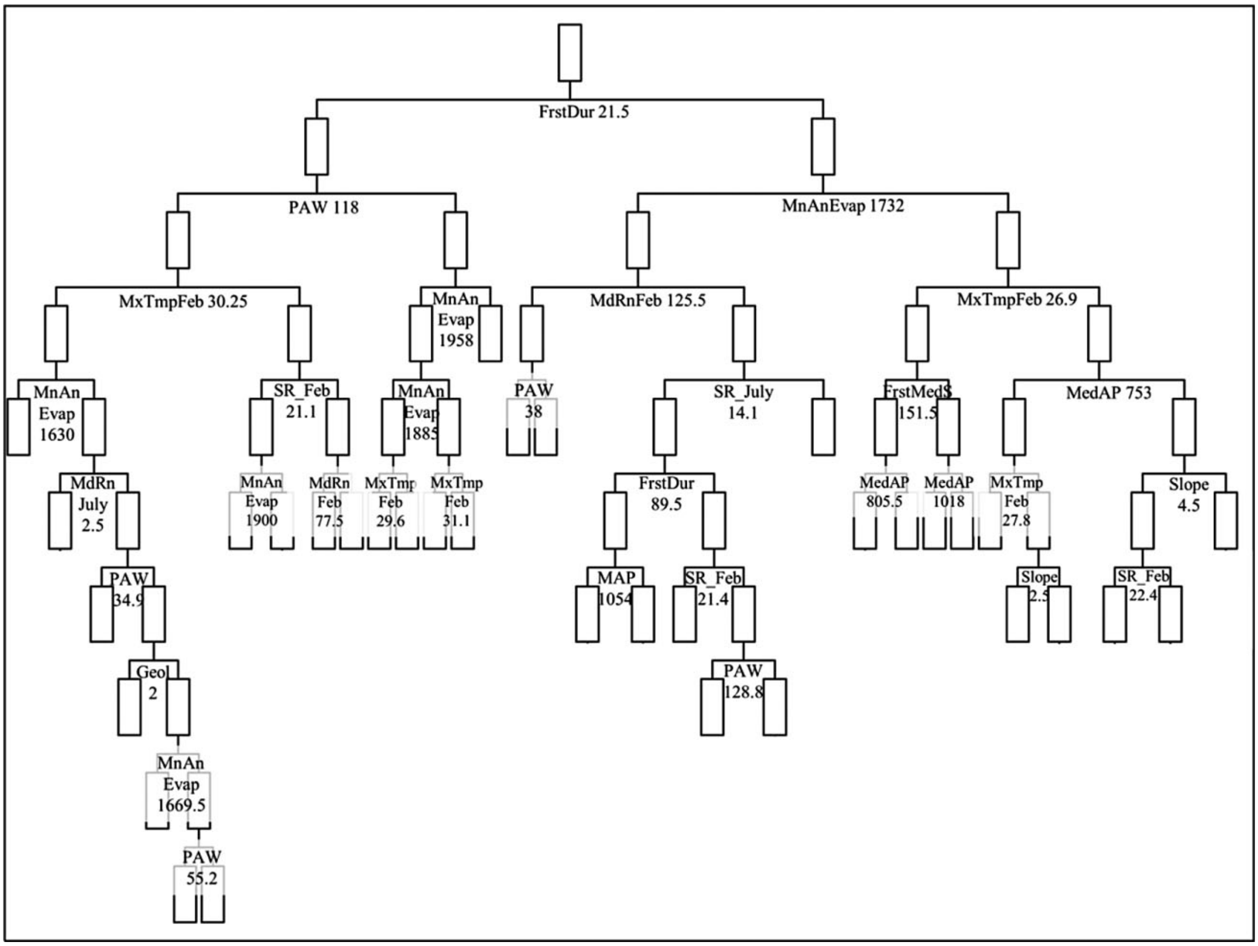

Fig. 4. The Classification and Regression Tree (CART) model for the dataset. Thirty-four vegetation types were identified. Amounts less than or equal to the threshold value are on the left of each branch and amounts greater than the threshold on the right.

important. Aspect was never a good correlate at the provincial scale.

DISCUSSION

Overview

Our study answers the call to promote persistence and dynamic threat considerations in conservation planning (Pressey *et al.* 2007) and thus to identify climatic gradients to facilitate the spatial adjustments of species resulting from climate change (Pressey 2007). This study provides a framework to identify the dominant environmental gradients driving floristic composition and delimiting floristic pattern. These drivers act as surrogates for the ecological and evolutionary processes which generate diversity but are also critically important for ensuring the persistence of this diversity, especially in the face of threats such as climate change. The framework adopts a top-down, coarse-filter approach using floristic composition instead of individual species, which was considered appropriate given the redundancy of species responses to environmental gradients and the paucity of species-specific information, yet still provides an appropriate scale for conservation planning.

Temperature variables were the most important correlates, followed by soil properties and moisture variables. The greater importance of temperature over soils is because climate varies over large spatial scales compared with smaller scale soil variations which act as environmental filters within homogenous climatic regions (Toledo *et al.* 2012). The CART analysis identified the environmental delimiters of the vegetation clusters in relation to specific environmental gradients. It showed how the environmental variables were related in a complex manner and relevant at more than one scale.

Given that climatic and edaphic variables were well correlated with floristic composition in KZN, it is anticipated that a changing climate will have a marked influence on floristic composition. Impacts of

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changing mean climatic conditions are likely to differ from changes in extreme climatic conditions. Plant phenology is largely affected by changing mean climate whereas plant water relations are vulnerable to extremes driven by temperature and precipitation (Reyer *et al.* 2013) which have more immediate effects on cellular processes and plant physiology.

Temperature: grassland to savanna?

Our study highlighted the importance of mean annual temperature as an environmental correlate of floristic composition. Mean annual temperature was a good proxy for maximum and minimum average monthly temperatures. Future climate predictions suggest a 3–4°C increase in average temperature (Christensen *et al.* 2007) across the African subregion by 2100, so at the very least major changes in plant phenology are expected. Heat waves and hot days and nights are expected to become more frequent (Intergovernmental Panel on Climate Change 2007b) so maximum temperatures in the hottest months will further impact floristic composition. Extreme events in future climate scenarios may override mean annual temperature as the primary environmental correlate dependent on the severity of the event.

The CART analysis identified frost duration as the primary environmental delimiter. This is significant as frost is a major regulator on the distribution of tropical savanna species (Smit 1990; Bredenkamp *et al.* 2002), and can limit plant growth and reproduction (Inouye 2000). Climate predictions suggest less frost occurrence (Intergovernmental Panel on Climate Change 2007b). Hence a decrease in the number of frost days is likely to enable frost-sensitive savanna species to invade previously cooler, grassland areas and even small changes in the occurrence might have large impacts on vegetation structure. Interactions between cold temperatures and fire limit tree growth in grasslands, probably because of slow plant growth which prevents trees escaping the fire trap (Wakeling *et al.* 2012). A changing frost duration period, apart from influencing future species composition, is also likely to alter nutrient cycling from warming soils, in particular soil organic carbon (Matzner & Borken 2008).

Precipitation and water balance

The precipitation gradient, although strong and differing by a factor of four, was not as significant for floristic composition as the temperature gradient. This may be due to the complexity of the gradient resulting from topographically induced rain shadow effects, orographic precipitation and oceanic influences; hence, precipitation effects were important at local scales. Rainfall events in winter were significantly correlated to NMS-axis 2 which is important because rainfall primarily occurs in summer in KZN so a winter precipitation event provides essential soil moisture during a typically dry period. Variables influencing plant water availability such as mean annual evaporation were more important than precipitation in the CART analysis highlighting the importance of water balance to plants. For example, available plant water for the same mean annual precipitation differs significantly from the sandy Maputaland plains to the Drakensberg; hence, localized impacts can be expected. Byrne (2012) predicted greater impacts on plant community structure in more mesic grassland communities because of greater changes in the dynamics of soil water.

Climate change predictions do not clearly suggest a marked increase in precipitation, with models differing in overall precipitation amount (Intergovernmental Panel on Climate Change 2007b), but do indicate greater intensity of individual rainfall events and longer duration between rainfall events. Strong orographic forcing may result in locally different future precipitation patterns in this study region. Longer interduration rainfall events will increase the stress periods and water balance for plants. Cleland *et al.* (2013) predicted that rare and annual species will show the greatest temporal variability in species composition in response to rising interannual variability in precipitation. If variable but more intense precipitation events are coupled with more extreme temperature events which will alter plant water availability, a greater impact on floristic composition can be expected.

Soil disjunctions

The analysis highlighted the importance of climatic variables but also showed the importance of soil and geology variables at local landscape scales. Plants will need to respond to increasing temperature by mostly migrating up the altitudinal gradient to cooler climes. However, altitude in KZN is confounded with geology in that different geological types align in an approximately north-south direction compared with increasing altitude from east-west. Thus, a change in soil type may block the movement of plant species to new climes. Specifically, the distinct floristic vegetation types associated with the dystrophic, acidic soils of Maputaland will be most at risk as soil types at higher elevation are base rich. Future research should focus on identifying species that have specific soil

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requirements as these will be most at risk from climate change.

Other influences on floristic composition

The climatic variables are not, however, the only drivers of community composition. Rainfall influences composition both directly through the water balance and indirectly through the fire regime. Grasslands and savannas in the area are not at equilibrium with climate in the sense that the region is warm and wet enough to support a forest biome (Bond 2008). One of the major factors preventing the succession to forest is fire, which was not studied in this analysis. However, because fire is important in both grassland and savanna, this factor is in effect held constant, allowing for examination of the other variables (Bredenkamp *et al.* 2002). Should overall precipitation increase, more biomass production is expected which may alter the frequency and intensity of fire events. Further investigation is required to determine if the altered fire regimes would be sufficient to counter the combined effects of increased CO_2 and reduced frost occurrence on savanna species.

A concomitant global factor influencing species composition is atmospheric CO_2 concentrations. Some savanna tree seedlings and saplings have demonstrated the ability to rapidly recharge root starch reserves thus allowing them to escape the fire trap under elevated CO_2 conditions (Kgope *et al.* 2010). However, CO_2 concentrations are considered spatially uniform and thus were not specifically addressed in this analysis.

Conservation planning implications

Pressey (2007) suggested that steep, short gradients are likely to be the easiest to maintain whereas long gentle gradients may present challenges. This is illustrated by the two World Heritage Sites occurring in KZN, the Maloti Drakensberg Park World Heritage Site (MDP) and the iSimangaliso Wetland Park (iSWP) in Maputaland covering 233 484 ha and 214 792 ha (terrestrial aspect only) respectively. The MDP has a large altitudinal range of 2242 m but iSWP only has a range of 475 m. Given the average lapse rate of 6.4°C km^{-1}, the MDP would seem best suited to providing a landscape allowing species to migrate up the altitudinal gradient to cooler climes. However, the geology changes from nutrient-poor sandstone at lower levels to relatively nutrient-rich basalt at the top, and presents steep cliffs which may act as barriers to species migration. The iSWP with its relatively low altitudinal range and flora adapted to specific sandy soils would be at great risk from climate change. The opportunity for these species to track environmental niches along latitudinal gradients to the south are further limited by land transformation (Jewitt 2012).

Often small protected areas do not accommodate the length of gradients required for the migration of flora in response to climate change, and many occur in transformed landscapes. Thus there is an urgent need to enhance regional connectivity between existing protected areas and critical biodiversity areas outside of protected areas along climatic (usually altitudinal) gradients. New protected areas need to be established across the full range of identified gradients.

Ecological gradients promote diversification and speciation, and steeper gradients lead to more variation (Freedman *et al.* 2010). The incorporation of the identified climatic gradients into conservation plans, such as through least-cost paths (Rouget *et al.* 2003), will facilitate persistence objectives in planning processes. These gradients present a mechanism by which species may naturally and most cost-effectively adapt to climate change. The presence of disjunctions, for example soil or habitat transformation, along an environmental gradient may limit the migration potential of some species which may then require assisted migration if they are to persist under future climate regimes.

CONCLUSION

Our study provides a framework to identify environmental gradients correlated to floristic composition and pattern with the specific aim of promoting persistence and dynamic threat considerations in conservation planning. These gradients act as surrogates for ecological and evolutionary processes which generate and maintain diversity and are complementary to existing conservation approaches.

The framework presented here could be usefully applied in other regions with steep environmental gradients, especially other austral countries sharing similar topography to KZN. The identified gradients elucidate potential climate change impacts and could guide the identification of climatic refugia. Identifying areas expected to be the most stable under future climate predictions are critical for the conservation of current floristic communities. Areas experiencing the greatest magnitude of change are more likely to experience novel community assemblages. These impacts will need to be further studied in conjunction with the impacts of large-scale habitat transformation and

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fragmentation which could present barriers to climate tracking responses and migration dynamics of species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Procrustean analysis to determine ordination differences between plot sizes.

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Chapter 2

Appendix 1 Appendix S1: Procrustean analysis to determine ordination differences between plot sizes

Using a subset of the data which had nested vegetation sampling based on modified Whittaker plots (Stohlgren *et al*. 1995), Procrustean Analysis was used to determine if there were significant differences between resulting ordinations of differing plot sizes (Peres-Neto and Jackson 2001; Otýpková and Chytrý 2006). The PROTEST program (Jackson 1995; www.zoo.utoronto.ca/jackson/pro1.html) was used for this analysis. Two datasets were used, one with plot sizes ranging from 1m^2, 10m^2 and 100m^2 (O'Connor 2005) and a second with plot sizes of 1m^2, 100m^2 and 1000m^2 (R. Uys *et al*. unpubl.), where n = 16 and n = 129 respectively, run for 999 permutations.

Ordinations on the dataset were conducted using Nonmetric Multidimensional Scaling, (NMS) described in more detail in the main article. Results indicated that the ordination results across the different plot sizes were more similar than expected by chance ($P < 0.001$) (Table 1), indicating that irrespective of plot size, similar ordination results were obtained. The greatest deviations in the ordination patterns were between the extremes of the plot sizes e.g. 1m^2 – 1000m^2, but were still statistically significant. Otýpková and Chytrý (2006) reported similar findings. The analysis in the accompanying paper uses a minimum plot size of 19m^2, significantly larger than the minimum of 1m^2 plot size of the Procrustean Analysis, which would serve to reduce potential differences in ordination patterns.

Additionally, NMS ordinations for the full dataset of the main paper were tested on three subsets of similarly sized plots (19m^2 – 25m^2, 100m^2 – 400m^2 and greater than 400m^2), all of which yielded similar ordination and correlation results. Differences which arose between the analyses were due to the differing spatial distribution of the plots in the province, which affected the gradient lengths. Based on the results of the Procrustean Analysis which indicated that similar ordination results are obtained irrespective of the plot sizes and the NMS ordination tests on subsets of the data based on plot size ranges which yielded similar results, the data of varying plot sizes were combined into one dataset for analysis and reporting in the main paper. By combining the datasets, the best geographic coverage of points across the province was achieved and thus the greatest gradients were covered. Larger plot sizes were often associated with plots sampled in savannas which needed to be larger given the physiognomic structure of trees versus grassland plants.

Table 1. Procrustean analysis results for the Nonmetric Multidimensional Scaling ordination for the Uys dataset with plot sizes of 1m^2, 100m^2 and 1000m^2 and the O'Connor dataset with 1m^2, 10m^2 and 100m^2.

Study	Plot size (m^2)	m12	*P*-value
Uys	1 versus 100	0.4953	0.001
Uys	1 versus 1000	0.6322	0.001
Uys	100 versus 1000	0.4179	0.001
O'Connor	1 versus10	0.4790	0.001
O'Connor	1 versus 100	0.4006	0.001
O'Connor	10 versus 100	0.2613	0.001

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CHAPTER 3

3. Mapping landscape beta diversity of plants across KwaZulu-Natal, South Africa, for aiding conservation planning

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ORIGINAL PAPER

Mapping landscape beta diversity of plants across KwaZulu-Natal, South Africa, for aiding conservation planning

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Abstract Collective properties of biodiversity, such as beta diversity, are suggested as complementary measures of species richness to guide the prioritisation and selection of important biodiversity areas in regional conservation planning. We assessed variation in the rate of plant species turnover along and between environmental gradients in KwaZulu-Natal, South Africa using generalised dissimilarity modelling, in order to map landscape levels of floristic beta diversity. Our dataset consisted of 434 plots (1000 m^2) containing 997 grassland and savanna matrix species. Our model explained 79 % of the null deviance observed in floristic dissimilarities. Variable rates of turnover existed along the major environmental gradients of mean annual temperature, median rainfall in February, and soil cation exchange capacity, as well as along gradients of geographical distance. Beta diversity was highest in relatively warm, drier summer regions and on dystrophic soils. Areas of high beta diversity identify areas that should be included in conservation plans to maximise representation of diversity and highlight areas best suited to protected area expansion. Biome transition areas in high beta diversity areas may be susceptible to climate variability. Including beta diversity turnover rates in regional conservation plans

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will help to preserve evolutionary and ecological processes that create and maintain diversity.

Keywords Compositional turnover · Environmental gradients · Generalised dissimilarity modelling · Processes

Introduction

A central theme in ecology is understanding spatial patterns in diversity along gradients (Kraft et al. 2011). Patterns in species diversity arise because of environmental conditions, historical evolutionary diversification and processes that control the survival or extinction of species such as biotic interactions and stochastic events (Ricklefs 2006; D'Amen et al. 2015). Often multiple processes and scales interact in a complex community assembly process (Ricklefs 2004). The central tenet of conservation planning requires knowledge of both the pattern and the processes that maintain this variation in diversity (Margules and Pressey 2000), an understanding which becomes critically important if global change impacts are to be mitigated (D'Amen et al. 2015). Often this is achieved by modelling individual species distributions or mechanistic niche models (Fitzpatrick et al. 2011). However, in under-sampled regions or highly diverse systems, a paucity of biological data may limit the ability to model individual species distributions. In these cases, higher-order surrogates such as environmental classes or vegetation types are used (Margules and Pressey 2000).

A refinement of the use of surrogates is to model the collective properties of biodiversity, such as alpha (α) or beta (β) diversity, through the integration of biological and environmental data and the use of predictive modelling (Austin 1999; Ferrier 2002). By modelling collective properties of biodiversity rather than individual species, more effective use may be made of datasets with sparse or biased spatial coverages (Ferrier 2002). Research efforts in this regard have focussed on modelling species richness but species richness indices cannot meet the representivity requirements of conservation planning (Ferrier 2002). This requirement is better met by information on the patterns of compositional dissimilarity, such as beta diversity (Ferrier 2002).

Beta diversity was originally defined as "the extent of change of community composition, or degree of community differentiation, in relation to a complex gradient of environment, or a pattern of environments" (Whittaker 1960), or "between-habitat diversity" (Whittaker 1972). There has been a resurgence of attempts to understand beta diversity patterns, leading to multiple concepts, mathematical expressions and analysis methods (Koleff et al. 2003; Legendre et al. 2005; Anderson et al. 2011; Szava-Kovats and Pärtel 2014), often with authors making use of multiple beta diversity indices in their analyses (Apgaua et al. 2014). Beta diversity provides a link between alpha (site) diversity and gamma (regional) diversity and may refer to both turnover (directional) in community structure along a spatial, temporal or environmental gradient and variation (non-directional) within a given extent (Anderson et al. 2011), i.e., variation among study units (Legendre and Legendre 2012). Beta diversity indices are often used to infer the processes that structure ecological communities (Kraft et al. 2011) and to disentangle species turnover (species replacement) from nestedness (species loss) (Baselga 2010).

Several techniques have been developed for analysing beta diversity, the appropriateness of which are dependent on the nature of the data and questions being asked. Generalized dissimilarity modelling (GDM) analyses and predicts spatial patterns of community composition turnover between all pairs of sites as a function of both environmental and geographic separation (Ferrier et al. 2007). The advantages of this statistical technique is that it can analyse beta diversity across large regions containing large numbers of species, and specifically addresses two issues of nonlinearity associated with large-scaled, high diversity data sets. The first issue concerns the curvilinear relationship between observed compositional dissimilarity and increasing environmental or spatial separation of sites. Because many compositional dissimilarity indices are constrained between 0 and 1, the dissimilarity index asymptotes at 1 despite further increases in the separation of sites (Ferrier et al. 2007). GDM addresses this issue by using generalised linear modelling with a link function defining the relationship between compositional dissimilarity and environmental distances between sites, and a variance function that defines how the variance of the predicted compositional dissimilarity depends on the predicted mean (Ferrier et al. 2007). The second issue concerns the assumed constant rate of compositional turnover along a gradient, which is often not observed in reality (Ferrier et al. 2007). This is addressed by fitting nonlinear, monotonically constrained functions directly to the environmental variables and the nonlinear shape of the response is achieved by fitting linear combinations of I-spline basis functions which are equivalent to polynomial regression terms (Ferrier et al. 2007).

KwaZulu-Natal (KZN) is a province of South Africa occurring on the east coast of the country. It is floristically rich (Scott-Shaw 1999) and has steep environmental gradients. However, it is facing rapid loss of natural habitat (Jewitt et al. 2015b). Conservation planning using all facets of diversity are required if this diversity and the processes that maintain it, are to be conserved into the future. In particular, identifying areas of rapid species turnover and their environmental correlates will aid conservation planning by increasing the spatial efficiency of capturing common species in the planning process which would complement traditional plans based on vegetation types or threatened and endemic species distributions only. It thus complements species richness targets, strengthens the efficiency of achieving overall representivity and persistence of species and identifies areas where climate change impacts are likely to result in high species turnover. It also holds promise for identifying possible conduit areas for species movement in response to climate change. Jewitt et al. (2015c) identified the dominant environmental gradients associated with floristic composition in the province using nonmetric multidimensional scaling on 2155 plots and 1643 species. The dominant drivers were mean annual temperature, soil base status and moisture variables. However, their study did not specifically identify the rate of change in species composition along those gradients, and their analysis assumed a linear response of species turnover along the gradient.

In this paper we aim to assess how the rate of species turnover varies along and between environmental and geographic gradients, and to spatially map beta diversity at landscape scales in the province using GDM, as a further informant to the provinces systematic conservation plan.

Methods

Study area

KwaZulu-Natal has more than 6000 vascular plant species and high (16 %) levels of endemism in an area of 94,697 km^2 (Scott-Shaw 1999). It has steep environmental gradients occurring over short distances. Mean annual temperature, soil base status and precipitation variables have been shown to be the best correlates of floristic composition across KZN (Jewitt et al. 2015c). The temperature gradient is particularly strong, due in part to an altitudinal range of over 3000 m from the Indian Ocean coast in the east to the alpine climes of the Drakensberg escarpment in the west, and a latitudinal gradient from 27 to 31°S, giving rise to a range in mean annual temperature of 7.9–22.9 °C. Geological substrates vary from base-rich dolerite and basalt to geologically young, dystrophic sands in the north east (Partridge 1997). The geological substrates are aligned in approximately north–south directions which are thus confounded with the east–west altitudinal gradient. The region receives summer rainfall but the precipitation gradient is complex due to topographical induced rain shadows, orographic rainfall, and mistbelt areas. Snow may occur on the highlands during winter. The landscape matrix, the broader terrestrial landscape mix of natural, semi-natural and altered landscapes (Worboys et al. 2015) consists of extensive grassland and savanna systems interspersed with smaller azonal areas of forest and wetlands (Mucina and Rutherford 2006). The altered landscapes consist of extensive agriculture, timber plantations, the built environment, mines and dams (Jewitt et al. 2015b).

The data

The floristic data consisted of presence/absence data collated from multiple plot (relevé)-based studies of vegetation (Goodman 1990 and unpublished data from the following researchers: P.S. Goodman, unpubl. data 2002; E. Granger, unpubl. data 2008; D. Jewitt, unpubl. data 2004, 2005, 2006, 2007, 2008, 2010; R. Scott-Shaw, unpubl. data 2006, 2007, 2008, 2010; R. Uys et al., unpubl. data 2004, 2005, 2006). The plot sizes were all 1000 m^2, occurring in grassland, savanna and Indian ocean coastal belt biomes, representing 50 vegetation types (Mucina and Rutherford 2006) (Supplementary information 1). All species occurring in the plots were recorded, and specimens identified to species level included in the analysis. Species richness ranged from 14 to 117 species per plot with a mean of 56 (Fig. 1. A colour version of this figure is available in Supplementary information 2). Plots occurring in wetland and forest biomes were excluded from the analysis. Plot shapes were either rectangular or circular. Whilst plot shape may yield slightly different floristic composition results (Houeto et al. 2013), this was not considered significant at the geographic scale at which this analysis was conducted. This dataset provided the greatest coverage of points across the province and thus was best suited for making conservation planning recommendations. Other plot based data sets exist for the province but the plot sizes varied from 19 to over 1000 m^2 and were limited in provincial extent. Given the sensitivity of beta diversity measures to plot size (Lennon et al. 2001; Koleff et al. 2003) and extent of area (Legendre and Legendre 2012), they were excluded from this analysis.

An outlier analysis was performed on the plot data using principal component analysis (PC-ORD) (McCune and Mefford 2006, MjM Software Design, Gleneden Beach, OR,

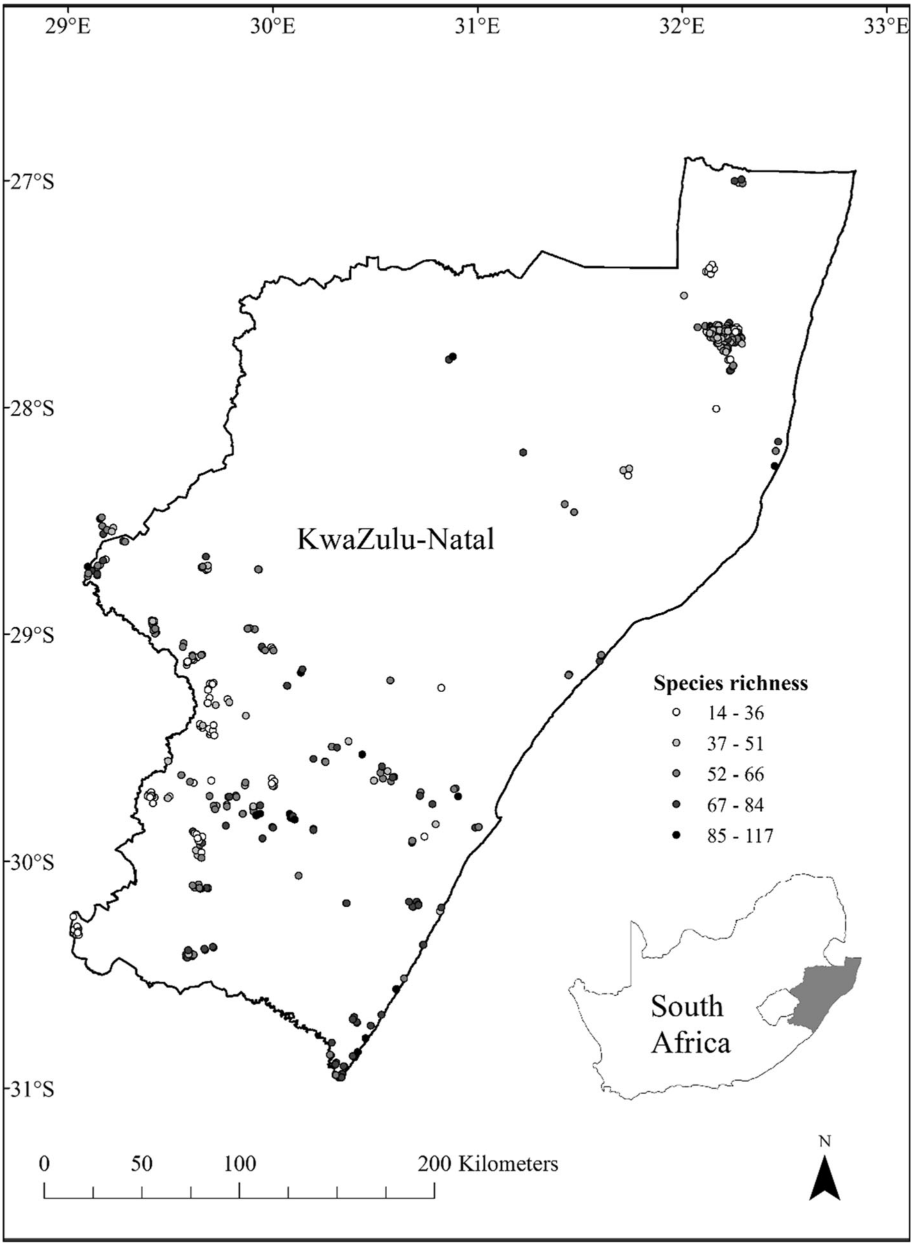

Fig. 1 The location of the 1000 m^2 vegetation plots in KZN, South Africa. The range of species richness values are shown for each plot

USA). The technique identifies outliers based on the frequency distribution of dissimilarity distances of all plots to each other. Nine outlier plots were deleted. In order to reduce noise in the dataset and enhance the detection of community composition and environmental relationships (McCune and Grace 2002), species that only occurred once or twice were removed ($n = 641$). Abundance values were converted to presence/absence data, as this provides useful information for the analysis of large, high diversity datasets (Greig-Smith 1983). The cleaned dataset consisted of 434 plots with 997 species and was used to construct a site-by-species matrix.

Environmental variables known to influence plant species distributions by affecting water and nutrient availability (Stevens 2006) were extracted from geographical information system layers to create a site-by-environmental variable matrix. In particular, continuous variables with direct effects on plants were used (Austin 1999; Pausas and Austin 2001). The choice of variables was informed by the floristic gradient analysis conducted in the province by Jewitt et al. (2015c), specifically the use of the PC-ORD to identify correlated variables, and the exclusion of variables not relevant at this scale of analysis. The initial 13 environmental variables included mean annual temperature (Schulze and Maharaj 2007a), average maximum temperature in February (Schulze and Maharaj 2007b), average minimum temperature in July (Schulze and Maharaj 2007c), frost duration, median start date of the first frosts (Schulze and Maharaj 2007d), mean annual potential evaporation (Schulze and Maharaj 2007e), mean annual precipitation (Schulze and Lynch 2007a), median rainfall in February, median rainfall in July, median annual precipitation (Schulze and Lynch 2007b), profile plant available water (Schulze and Horan 2007), soil cation exchange capacity (ISRIC 2013) and altitude (Shuttle Radar Topography Mission (SRTM 30 m) http://www2.jpl.nasa.gov/srtm/). The environmental dataset included geographical coordinates of the plots. The resolution of the climatic data was approximately 1 arc minute.

Statistical modelling

Generalized dissimilarity modelling (Ferrier et al. 2007) was used to determine the contribution of environmental variables and geographic separation in explaining beta diversity. The analysis was performed in R version 3.2.2 (R Core Team 2015) using the GDM package (version 1.1.5) (Manion et al. 2015). The default of three I-spline basis functions per environmental predictor was used, with both the Bray–Curtis diversity measure (Bray and Curtis 1957) and Jaccard index (Jaccard 1912). The plotted functions provide an indication of the importance of each environmental variable (the maximum height of the I-spline) and the slope of the function indicates the variable rate of species turnover or beta diversity along the gradient (Fitzpatrick et al. 2013). The I-spline plots represent partial regression fits i.e. the contribution of an environmental variable whilst holding the other variables constant. A full description of the technique and the interpretation thereof can be found in Ferrier et al. (2007) and a useful explanation in Fitzpatrick et al. (2011) and in Fitzpatrick and Keller (2015).

Initially all variables were included in the model in order to determine which variables contributed the most to beta diversity. Based on the PC-ORD performed in the Jewitt et al. (2015c) analysis, correlated environmental variables were identified. Thereafter the three most significant, uncorrelated environmental variables were retained and the model rerun with geographic space included as a predictor. I-splines were plotted to gauge the magnitude and rate of turnover along each environmental gradient and the contribution of geographic separation. The slope values for each I-spline were calculated (relativized by the maximum value of each axis to create values ranging between 0 and 1) and used to reclassify the relevant environmental gradient in ArcGIS 10.3 (ESRI 2014) to spatially depict beta diversity along the gradient. The summed coefficients of the I-splines indicated the contribution of each predictor to the model. These were used to weight the significant environmental layers before summing them to create a beta diversity map of the province.

Results

The Bray–Curtis model explained 79 %, and the Jaccard model explained 78.3 %, of the null deviance observed in floristic dissimilarities (Fig. 2). Both models reached the same conclusions, hence only the Bray–Curtis model is detailed further as it explained slightly more of the null deviance observed in floristic dissimilarities. Patterns of species turnover in KZN were dependent on geographical separation, and 3 major environmental variables, viz. mean annual temperature, median rainfall in February, and soil cation exchange capacity (Fig. 3). In all instances the fitted I-splines were non-linear, indicating variable rates of turnover along each gradient. Based on the summed coefficients of the I-splines, which indicate the importance of the gradient to beta diversity, mean annual temperature was the most important predictor variable across KZN (2.25), followed by median rainfall in February (0.81) and cation exchange capacity (0.3). Turnover along the temperature gradient from low temperatures upwards was relatively constant until mean annual temperatures reached 18.1 °C, where-after turnover rates increased steeply. Turnover along the precipitation gradient was highest where median rainfall in February was below 107 mm. Where rainfall in February exceeded this value, turnover remained relatively constant. Similarly, turnover was highest at low (<14 cmol kg^{-1}) soil cation exchange capacity. Geographical separation was an important predictor of beta diversity with a summed coefficient of 1.35.

The weighted environmental layers were combined and mapped to represent the spatial distribution of beta diversity within the province (Fig. 4). Our analysis showed that geographical separation was the second most important predictor of beta diversity after mean annual temperature. However, we chose to exclude it from the development of the beta diversity map of the province, preferring to use variables directly meaningful to plants (Austin 1999) and since distance is correlated with increasing environmental dissimilarity was not included in the mapping. We recognise though that distance is an important modifier of beta diversity.

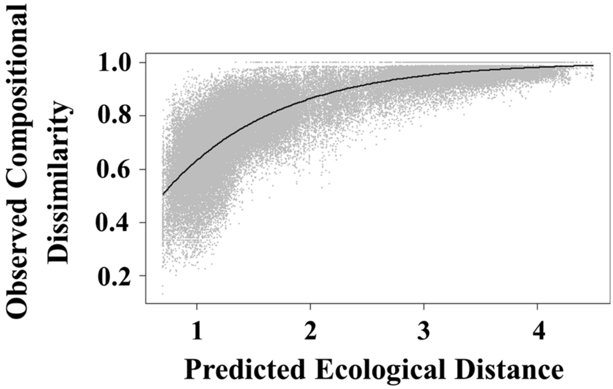

Fig. 2 The plotted inverse link function for the model indicating where observed compositional dissimilarity equals predicted values, indicating the overall fit of the model

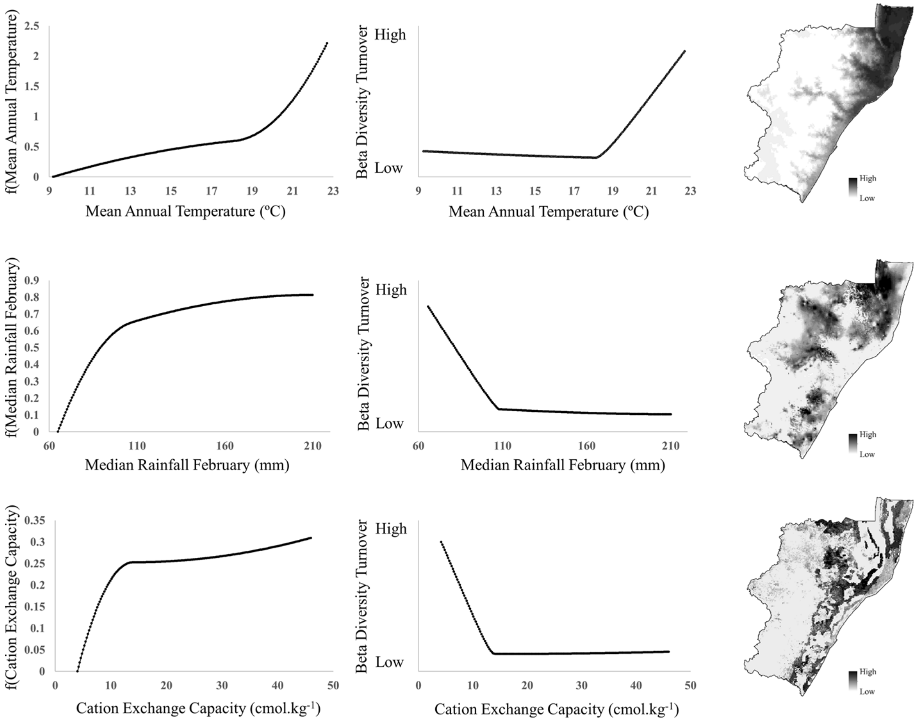

Fig. 3 The fitted I-spline functions (*left column*), slope graphs (*middle column*) and spatial depiction of beta diversity (*right column*) for mean annual temperature (*first row*), median rainfall in February (*second row*) and soil cation exchange capacity (*third row*). The turnover of species is lower in *light areas* compared to *dark areas*

Discussion

Beta diversity and environmental gradients

Our study shows that beta diversity varies along gradients, consistent with other studies (Ferrier et al. 2007; Fitzpatrick et al. 2011, 2013; Laidlaw et al. 2016). Mean annual temperature was the strongest predictor of plant beta diversity in the province, followed by median rainfall in February and soil cation exchange capacity. Beta diversity was higher in relatively warm, drier summer regions and on dystrophic soils.

The province shows a pronounced range in mean annual temperature of 15 °C. There is both an altitudinal gradient and a lesser latitudinal gradient. The floristic composition changes from savanna and tropical wooded coastal grassland systems in the warmer northern and eastern parts of the province to mesic temperate grassland systems in the cooler western parts of the province. Beta diversity was highest above 18.1 °C. Climate change predictions suggest a 3–4 °C increase in mean temperature in the region by 2100 (Christensen et al. 2007), hence changes in the spatial distribution of species and beta diversity can be expected.

KwaZulu-Natal receives summer rainfall and the areas of lowest summer rainfall were characterised by the highest beta diversity. The amount of rainfall received in February is important because it coincides with the hottest summer months and is thus critical for plant

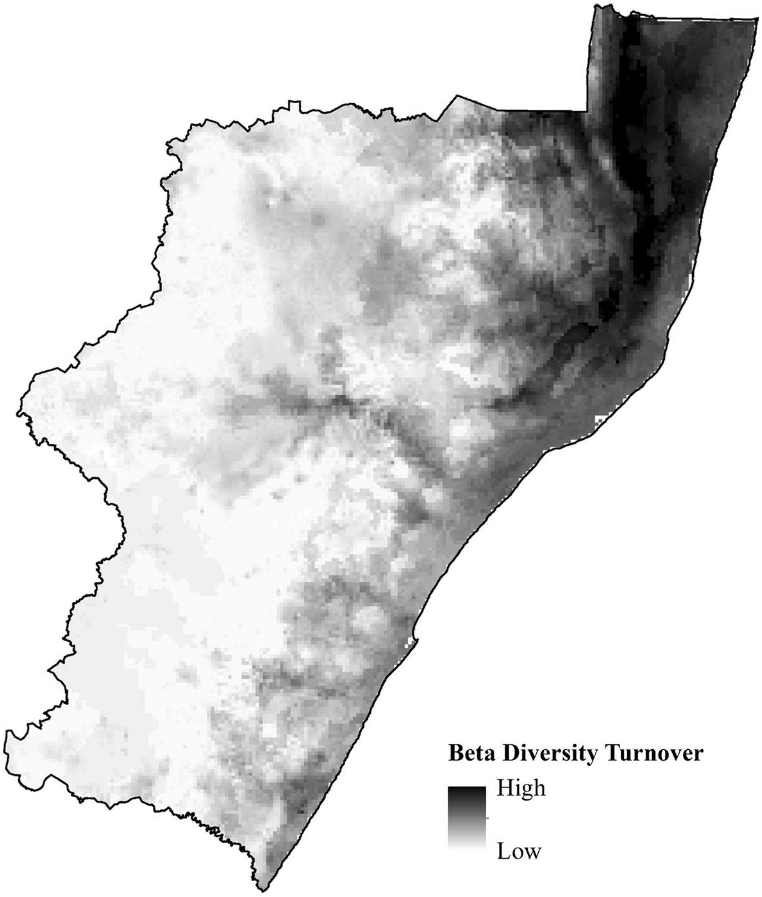

Fig. 4 The map of beta diversity in KZN. *Darker colours* represent higher turnover rates than *lighter colours*

growth. The precipitation gradient is complex due to oceanic, orographic and rain shadow effects, creating localised effects (Jewitt et al. 2015c). Climate change predictions for precipitation are varied, however an overall drying effect is expected in the province (Jewitt et al. 2015a).

Cation exchange capacity is a measure of soil fertility and nutrient retention capacity, and is closely related to soil base saturation. Generally the higher the cation exchange capacity the higher the soil fertility. The dystrophic soils in the north east of the province yielded higher levels of beta diversity. An analysis of the beta diversity components in the Fynbos of South Africa found that the strong soil fertility gradient in the region was related to plant endemism (Cowling 1990; Simmons and Cowling 1996), highlighting the importance of soil fertility on floristic composition. Similarly, Harrison (1999) found beta diversity differed significantly by soil type in Northern Californian meadows, and Paoli et al. (2006) highlighted potential dispersal limitations related to soil factors in tropical rain forest trees in Indonesia. In KZN, the strong north–south orientation of geology and the resulting soils, conflicts with the strong east–west temperature gradient (Jewitt et al. 2015c), which may pose problems for plant species with specific soil requirements trying to track the temperature gradient with climate change. This suggests that species with good dispersal ability and a wide tolerance of soil cation exchange capacities will persist better under future climate change scenarios.

Mapping the beta diversity along the significant environmental gradients, and incorporating the variation in rate of turnover along the gradients, allowed for the creation of a floristic beta diversity map of the province. The GDM method permits an objective basis for weighting and scaling the environmental variables (Ferrier 2002). The method also integrates beta (environmental turnover) and gamma (geographical) diversity.

Beta diversity and sample points

Our study would benefit from additional strategic sample points along the various environmental gradients, for example higher up the altitudinal gradient and the central and north-western parts of the province. An appropriate spatial design for the analysis was lacking in that data from disparate studies was combined to create the biological dataset. However, this is often the case with real world conservation initiatives, yet despite this, our model explained high levels of the null deviance observed in floristic dissimilarities. This is because GDM relies on patterns of compositional turnover in space rather than on species distributions themselves and is therefore less limited to sampled environments and can be extrapolated beyond the sampled areas (Fitzpatrick et al. 2011). However, additional sampling points may facilitate the detection and incorporation of other important environmental gradients in the model. The distribution of our data points highlights the clumped nature of points in protected areas and identifies gap areas that should be sampled in future. Opportunities to sample in these gap areas may be lost due to anthropogenic transformation of the landscape (Jewitt et al. 2015b).

Implications of beta diversity for conservation planning

The identification of areas of high beta diversity in the province, used with areas of high species richness, will maximise representation of diversity in regional conservation plans (Ferrier 2002). Preserving species-environment relationships are required to create and maintain beta diversity (Legendre et al. 2005). Understanding how beta diversity changes along and between environmental gradients also provides insights as to how communities may respond under environmental change (Fitzpatrick et al. 2013), and is an important first step towards identifying potential climate change refuge areas. High beta diversity areas are areas where species ranges are susceptible to climatic variability (McKnight et al. 2007). This would include biome transitions between the grassland, savanna and Indian ocean coastal belt biomes of KZN, and centres of plant endemism such as Pondoland on the south coast of the province.

Climate change adaptation strategies recommend increasing connectivity between protected areas in the landscape and increasing the protected area estate (Hannah et al. 2007; Beier and Brost 2010). Beta diversity maps may facilitate the identification of future sites for protected area expansion, as it is the rate of species turnover that informs the optimal placement of conservation areas (McKnight et al. 2007). High beta diversity values imply that conservation should target multiple, closely spaced sites (Ratter et al. 1997; Socolar et al. 2016) but the optimal reserve configuration requires fine-scale turnover maps. Since species distributions are defined by environmental gradients (Lawler 2009), the orientation of connectivity linkages along environmental gradients may facilitate maximum climatic suitability in future (Pearson and Dawson 2005). Hence, future conservation sites should include the major environmental gradients driving beta diversity, and areas of high beta diversity. Similarly, habitat corridors linking existing protected areas and critical biodiversity areas should follow major environmental gradients.

Land use change will influence habitat configuration and habitat amount, which will alter the ability for species to disperse and track changing environmental conditions. Given the rapid rate of conversion of natural areas to anthropogenic land classes in KZN, and the high levels of fragmentation of the natural landscape (Jewitt et al. 2015b), future research should focus on understanding the implications of land use change on beta diversity. Socolar et al. (2016) explain that initial anthropogenic impacts may lead to an increase in beta diversity due to localised species losses or the invasion of alien species. Further anthropogenic impacts may lead to the loss of rare species and an increase in the dominance of generalist species and alien invader species leading to the homogenisation of communities and lower beta diversity values. Finally, at very low community assemblage abundance, the neutral component of beta diversity may again slightly increase beta diversity. Hence caution needs to be applied in interpreting beta diversity changes in future. Even without further loss of habitat, plant extinction debt, which has a slow response to habitat fragmentation (Piqueray et al. 2011), may result in changed beta diversity values. Changes in land use management may alter biodiversity values across natural areas e.g. between protected areas and communal lands (Shackleton 2000).

Few studies have attempted to map floristic beta diversity in savanna and grassland systems, with most studies only identifying the correlates of beta diversity. Shackleton (2000) found beta diversity correlated to mean annual precipitation in savanna areas in South Africa. Uys et al. (2004) found that patterns of beta diversity in montane grasslands in South Africa were related to burning interval. In the Wisconsin area of the United States of America, savanna areas were found to have higher beta diversity levels than forests or prairies (Leach and Givnish 1999). Ratter et al. (1997) investigated the conservation planning implications of high beta diversity values in the Brazilian savannas (cerrado). Given the value of beta diversity in understanding the functioning of ecosystems, and for understanding possible implications for biodiversity conservation in the face of global change (Legendre et al. (2005), we recommend that further studies, particularly in grassland systems, be undertaken to evaluate and map beta diversity to facilitate conservation planning. Plants in particular have been found to have the highest beta diversity values amongst taxonomic groups (Soininen et al. 2007), and because they underpin habitat functioning and structure, represent an important starting point for facilitating conservation planning efforts.

Conclusion

Our study assessed the rates of plant species turnover along and between environmental and geographic gradients using GDM, and created a floristic beta diversity map of KZN to inform conservation planning by creating a complementary measure to species richness to efficiently guide the prioritisation and selection of important conservation areas to maximise overall species representivity and species persistence. Including beta diversity in regional conservation plans will help to preserve evolutionary and ecological processes that create and maintain diversity. The beta diversity map can further be used to enhance resilience of plant diversity in the face of global change.

Our research adds to the growing body of scientific literature on beta diversity, used here to elucidate the environmental drivers structuring floristic communities, and refines the current understanding of rates of species turnover along gradients, specifically in grassland and savanna systems. This approach may be used in other regions with steep environmental gradients and community based biological data to enhance regional conservation planning efforts.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Chapter 3

Appendix 2 Supplementary Information 1: Map of the grassland and savanna vegetation types of KwaZulu-Natal (KZN)

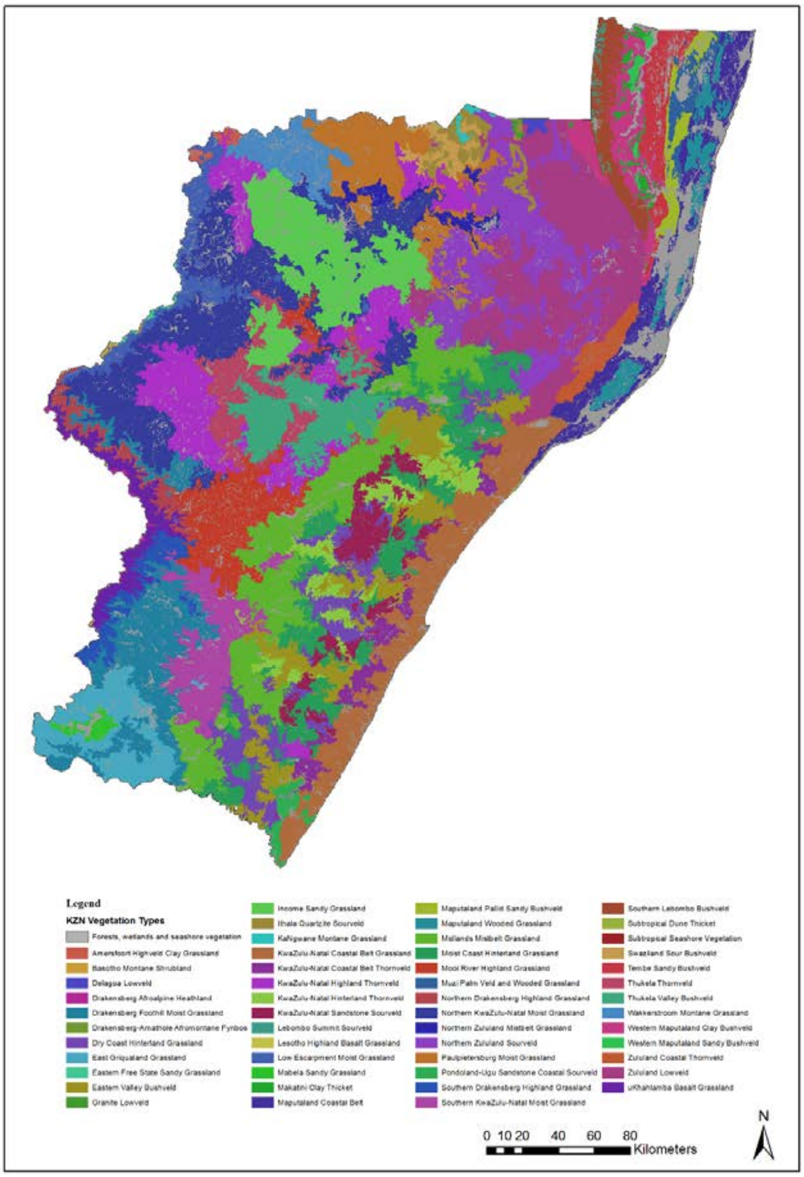

Fig. 1 Map of the savanna and grassland vegetation types of KwaZulu-Natal (KZN), adapted from Mucina and Rutherford (2006)

Reference

Mucina L, Rutherford MC (2006) The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria

Appendix 3 Supplementary Information 2: Fig. 1 with the species richness values shown in colour

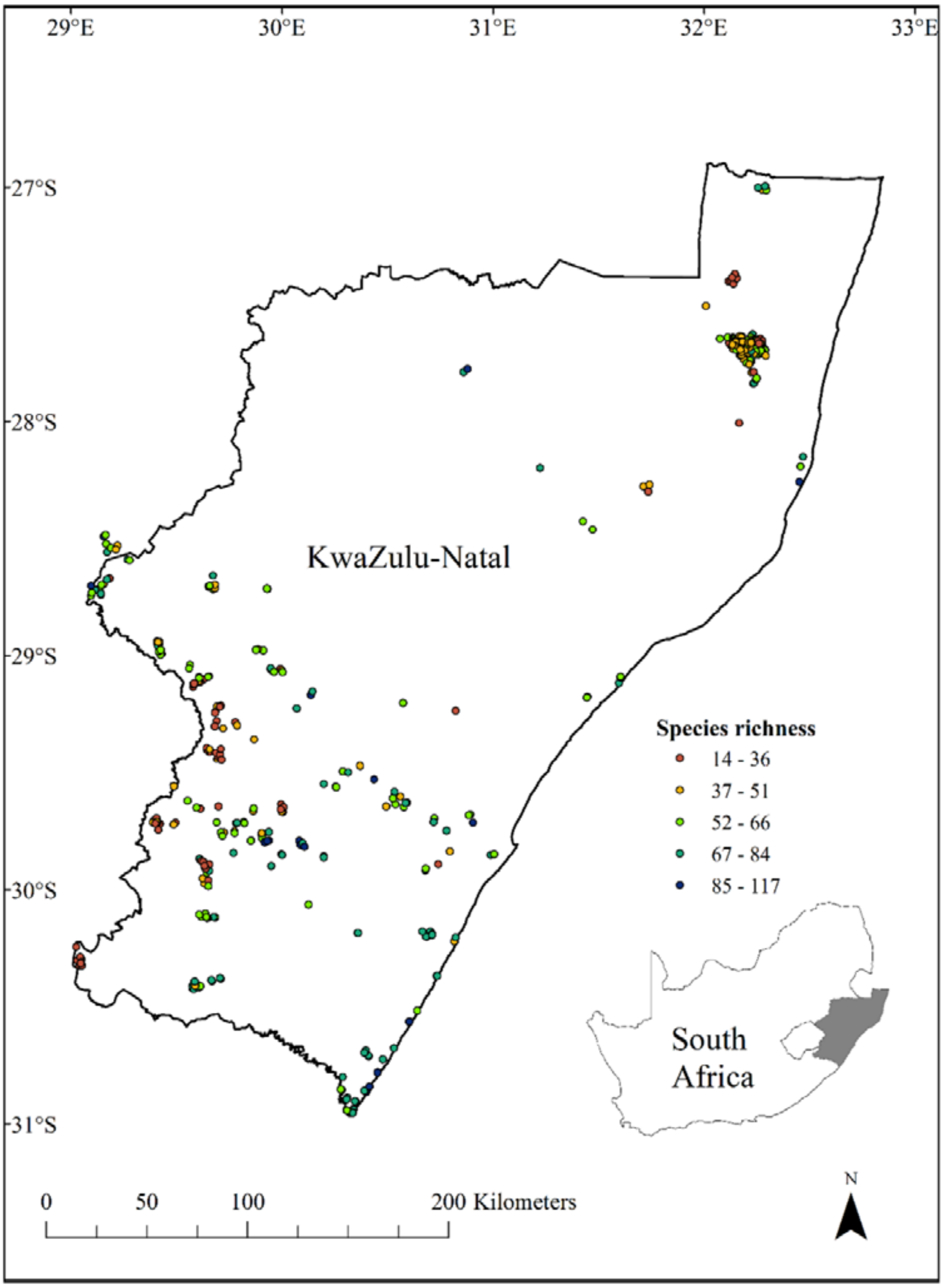

Fig. 1 The location of the 1000m^2 vegetation plots in KwaZulu-Natal (KZN), South Africa. The range of species richness values are shown for each plot

CHAPTER 4

4. Systematic land cover change in KwaZulu-Natal, South Africa: implications for biodiversity

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Systematic land-cover change in KwaZulu-Natal, South Africa: Implications for biodiversity

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Land-cover change and habitat loss are widely recognised as the major drivers of biodiversity loss in the world. Land-cover maps derived from satellite imagery provide useful tools for monitoring land-use and land-cover change. KwaZulu-Natal, a populous yet biodiversity-rich province in South Africa, is one of the first provinces to produce a set of three directly comparable land-cover maps (2005, 2008 and 2011). These maps were used to investigate systematic land-cover changes occurring in the province with a focus on biodiversity conservation. The Intensity Analysis framework was used for the analysis as this quantitative hierarchical method addresses shortcomings of other established land-cover change analyses. In only 6 years (2005–2011), a massive 7.6% of the natural habitat of the province was lost to anthropogenic transformation of the landscape. The major drivers of habitat loss were agriculture, timber plantations, the built environment, dams and mines. Categorical swapping formed a significant part of landscape change, including a return from anthropogenic categories to secondary vegetation, which we suggest should be tracked in analyses. Longer-term rates of habitat loss were determined using additional land-cover maps (1994, 2000). An average of 1.2% of the natural landscape has been transformed per annum since 1994. Apart from the direct loss of natural habitat, the anthropogenically transformed land covers all pose additional negative impacts for biodiversity remaining in these or surrounding areas. A target of no more than 50% of habitat loss should be adopted to adequately conserve biodiversity in the province. Our analysis provides the first provincial assessment of the rate of loss of natural habitat and may be used to fulfil incomplete criteria used in the identification of Threatened Terrestrial Ecosystems, and to report on the Convention on Biological Diversity targets on rates of natural habitat loss.

Introduction

Land-cover change and habitat loss are widely recognised as the major drivers of biodiversity loss in the world.[1-3] These changes not only fragment the landscape but alter biogeochemical cycles, climate, ecosystem processes and ecosystem resilience, thereby changing the nature of ecosystem services provision and human dependancies.[4-6] These losses and changes pose significant challenges for meeting biodiversity conservation goals and targets.

KwaZulu-Natal (KZN), a province situated on the eastern seaboard of South Africa, has a complex landscape, both in terms of its physical and biological diversity,[7] and the varied use and ownership of the landscape. The KZN landscape ranges from mountain climes of the Drakensberg escarpment of over 3000 m in the west to the subtropical climes of the Indian Ocean in the east (Figure 1) in an area of 93 307 km^2. KZN is the wettest of South Africa's provinces with a mean annual precipitation of 837 mm.[8] Consequently, agriculture – consisting primarily of sugar cane, orchards, commercial and subsistence crops, and timber plantations (agro-forestry) – represents major features of the landscape. The species-rich natural vegetation consists of mesic grasslands, savannas, forests and wetlands, and contains portions of the Maputaland-Pondoland-Albany biodiversity hotspot and the Midlands, Maputaland, Pondoland and Drakensberg Alpine centres of endemism.[9]

KwaZulu-Natal is the second most populous province in the country[10] with a mid-year population estimate of approximately 10.8 million people in 2011[11] (0.9 people per hectare). The province is experiencing a loss of natural habitat,[12] which has profound ecological consequences for this species-rich area. Similarly, the loss of natural capital and environmental degradation has socio-economic consequences for the many, mainly rural, inhabitants reliant on natural resources for fuel, fibre, food and medicine.[13] Many rural communities live on communally owned land, for which the drivers of change may differ from those on privately or state-owned land. It is thus important to quantify and understand the processes driving land-use and land-cover change (LULCC) in the province, and across different land tenure systems.

The availability of remotely sensed imagery has facilitated the monitoring of LULCC worldwide. In South Africa, two national land-cover (NLC) maps have been developed from satellite imagery based on *circa* 1994 (NLC 94)[14] and 2000 (NLC 2000)[15] conditions, but they are not directly comparable. Ezemvelo KZN Wildlife, the provincial conservation authority, has facilitated the development of three KZN land-cover maps based on 2005,[16,17] 2008[18,19] and 2011[20,21] conditions as part of its biodiversity monitoring mandate. These provincial data sets are valuable because they were developed using similar methodology, have similar legend categories and are mapped at the same resolution (20 m), making temporal comparisons more precise than less standardised land-cover maps. This series of five land-cover maps offers a valuable long-term period of 17 years within which to analyse land-cover change and rates of habitat loss within the province.

Understanding the patterns, processes and impacts of LULCC is essential in order to plan effectively for biodiversity conservation, especially in the face of other agents of global change such as climate.[22] Common methods of analysing land-cover change involve computing transition matrices between two points in time.[23] However, this method does not adequately account for category persistence, which tends to dominate the landscape. Failure to account for category persistence may mask important signals of land change.[24] The static state of the landscape between two time periods means that the signal of change is small in light of the overwhelming signal of persistence. Similarly, a lack of net change in a traditional analysis does not necessarily mean a lack of change on the landscape, because there could be location changes or swapping among categories. Thus an analysis that considers transitions of categories in terms of gains, losses, net change and swapping is insightful about patterns and processes of landscape change. Pontius et al.[24] developed a framework to account for these deficiencies. Further improvements to this method of analysis were developed in the Intensity Analysis framework[23] which was designed to analyse several points in time for the same study area. For each time interval, the method investigates the extent and speed of change and categorical gains and losses, whilst specifically considering the size and intensity of those changes and determining the intensity and variation of land-cover transitions from the categories available for the transitions. The framework thus identifies the underlying processes of the landscape transformations.

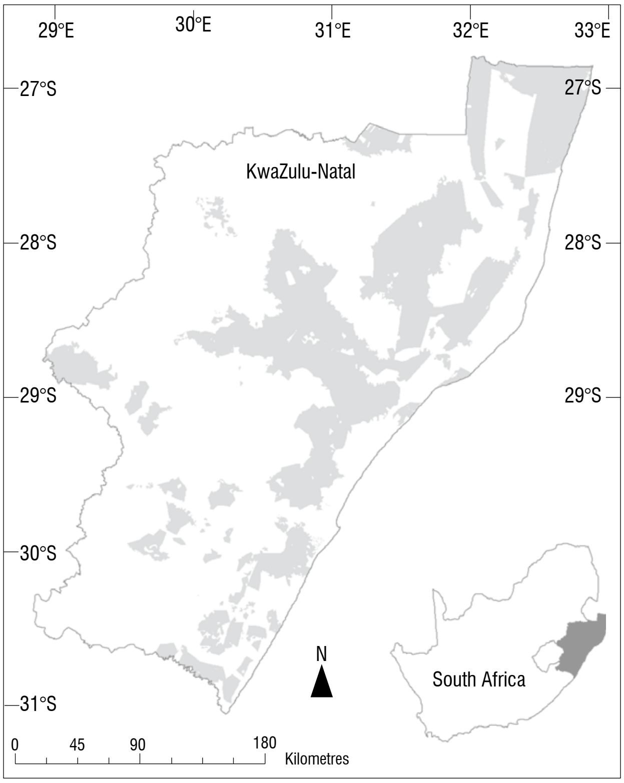

Figure 1: The location of KwaZulu-Natal, South Africa. The Ingonyama Trust Board administered areas are shown in grey, and were used as a proxy for communal areas.

Given the complex nature of KZN, it is essential to understand the drivers, patterns and processes of change for biodiversity conservation as the nature of the changes will have different management and policy implications. Using a quantitative method that addresses known inadequacies of conventional LULCC analyses and specifically assists in identifying the underlying processes of landscape change, and using the unique land-cover data set now available, should markedly improve our understanding of LULCC in KZN for conservation planning. Consequently, we have used the Intensity Analysis framework to characterise the systematic land-cover changes occurring in KZN using the three provincial land-cover maps (2005, 2008 and 2011). Differences in the pattern, rates and intensities of change are compared between land tenure systems (communal versus private and state-owned areas). In addition, the extent and rate of natural habitat loss are determined (from 1994 to 2011).

Methods

Communally owned lands

The historical legacy of the country has created three major land tenure systems in the province: communal, private and state-owned properties. The Ingonyama Trust was established in 1994 (*KwaZulu Ingonyama Trust Act No. 3 of 1994*) to hold land in title for members of communities in the province. The Ingonyama Trust Board (*KwaZulu-Natal Ingonyama Trust Amendment Act No. 9 of 1997*) administers the affairs of the Trust and the trust land and oversees the development of approximately 2.8 million hectares of communally owned land. The Ingonyama Trust Board (ITB) jurisdictional area was used as a proxy for communally owned land. Land-cover change differences were investigated between the ITB areas and the other land tenure systems (non-ITB).

Land-cover maps

Five land-cover maps were used in the analysis of land-cover change (Table 1). The details of methods used to develop these maps are dealt with in their associated documentation.[14-16,18,20] The methods in brief are as follows:

- The 1994 land-cover map was manually digitised from hard copy Landsat Thematic Mapper imagery based on 1994–1995 conditions, at a 1:250 000 scale but incorporating smaller features wherever feasible.[14]

Table 1: Land-cover map accuracy statistics, minimum mapping unit and number of classes for the national, KwaZulu-Natal (KZN) and aggregated class KZN land-cover maps. Initially nine categories were used in the analysis using the aggregated class maps, whereafter an 'abandoned' category was added and used in the Intensity Analysis.

Land-cover map	Overall map accuracy (%)	90% Confidence limits		Kappa index	Minimum mapping unit (ha)	Number of classes
		Low	High			
National 1994[12]	79.40	78.50	80.40	74.80	25	31
National 2000[13]	65.80	65.10	66.52	57.00	1–2	49
KZN 2005[4,5]	83.06	81.26	84.86	81.55	0.25	43
KZN 2008[6,7]	78.92	77.24	80.60	78.14	0.25	47
KZN 2011[8,9]	83.51	81.95	85.07	82.92	0.25	47
Aggregated classes KZN 2005	92.18	90.86	93.50	–	0.25	9;10
Aggregated classes KZN 2008	92.43	91.32	93.55	–	0.25	9;10
Aggregated classes KZN 2011	89.39	88.05	90.73	–	0.25	9;10

- The 2000 land-cover map was classified from multi-temporal Landsat 7 Enhanced Thematic Mapper imagery based on 2000–2003 conditions, although KZN formed part of phase 1 which used the earlier dated imagery.[15]
- The 2005 KZN land-cover map was developed from SPOT 2/4 imagery.[16,17] Certain post-classification modifications were made to improve the map, including the use of externally sourced data and expert edits.
- The 2008[18,19] and 2011[20,21] KZN land-cover maps were developed from SPOT 5 imagery. These maps represented temporal updates to the 2005 land-cover map.

The map accuracies ranged from 65.8% for the NLC 2000 to 83.5% for the provincial 2011 land-cover map (Table 1). Aggregating the classes of the provincial maps used for the change analysis significantly improved the map accuracies – up to 92.43% for the aggregated 2008 KZN land-cover map. The Kappa index for the provincial maps was high with the strength of classification agreements deemed 'substantial' and 'almost perfect' as per accepted benchmarks.[25] The aggregation of all five maps into only two categories for the long-term rate of habitat loss analysis would similarly significantly improve the accuracy statistics. Thus confidence was placed in accurately detecting change rather than error in this analysis. The imagery used to develop the provincial land-cover maps was provided as part of the South Africa Government/SANSA/SPOT IMAGE Agreement to supply annual SPOT imagery for the country.[26]

Data analysis

Detailed provincial analysis 2005–2011

The three provincial maps were analysed for land-cover change between 2005 and 2011 using IDRISI Selva.[27] The maps excluded the highly dynamic coastal sand and rock category and were standardised to the 2008 vegetation extent of the seashore line. The provincial boundary for this analysis includes the currently disputed Matatiele region in the southwest which is currently administered by the Eastern Cape but which was previously administered by KZN, and is included here for planning purposes only. Minor corrections were made to known dam and mine category errors. The maps were reclassified into 9 aggregated categories (Table 2; Supplementary figure 1 online) from the initial 43–47 land-cover categories and the associated aggregated accuracy statistics calculated from the accuracy assessment contingency tables (Table 3). The users' accuracy exceeded 91% in almost all cases, but some categories had lower statistics in specific years. Aggregation of the categories served to improve the accuracy of the maps by eliminating errors among the more detailed land-cover categories (Table 1).

Based on initial analyses that detected changes, swapping and persistence[24] of categories in the landscape, an additional 'abandoned' category was created that specifically tracked changes of non-natural vegetation classes back into a semi-natural state at a future time point. It is imperative for conservation planning that these changes be tracked as this category does not hold the same biodiversity value as primary natural vegetation. Hence 10 categories were used in the Intensity Analysis.

The land-cover changes were examined using the modified transition (cross-tabulation) matrix and the hierarchical Intensity Analysis framework which uses statistical methods to identify the most important transitions and the signals of systematic processes related to the patterns of land change.[23,24] The relevant papers detail the methods used, hence they are not repeated in this paper but the equations and notation used are provided in the online supplementary material for ease of reference. These matrices were used to calculate the extent of gains, losses and swapping between categories. The Intensity Analysis considers the size of the category concerned and analyses the data at three levels of analysis, namely time interval, category gains and losses and transition intensities across available categories. The interval analysis determines the annual rate of change compared with a uniform change level across the temporal period of the analysis, and may be classed as slow or fast in comparison to the uniform change level. The category analysis investigates each time interval's intensities of gains and losses per category and the categorical changes can be classed as dormant or active changes in comparison with the uniform intensity level. The transition analysis investigates transitions between particular gaining and correspondingly losing categories and vice versa to examine how the size and intensity of the transition varies. The transitions can be classed as targeted or avoided by comparing the observed intensity of each transition with a uniform intensity level.

Longer-term analysis of the rates of habitat loss

In addition to the provincial maps, the earlier national land-cover maps were used to investigate the amounts and rates of habitat transformation since 1994. In order to render the legend categories congruent, two categories were created across all five land-cover maps, namely untransformed (natural features and vegetation) and transformed (anthropogenically altered landscapes such as built infrastructure, cropland, plantations, mining and dams). Once an area had become transformed it was not permitted to become a natural category again at a future time point, effectively excluding the 'abandoned' category and thereby identifying primary natural areas best suited for biodiversity conservation. Data was resampled to a 500-m pixel size associated with the minimum mapping unit of 25 ha of the NLC 94, the coarsest level of mapping detail. A logarithmic regression curve was fitted to the temporal sequence of estimated remaining natural habitat in an attempt to best describe past pattern, and forecast the most likely state in 2050.

Table 2: The aggregated land-cover categories and a description of the categories included in the aggregated class

Aggregated land-cover category	Description
Water	Natural open water occurring in pans, rivers, wetlands, mangroves and estuaries
Plantations	Agro-forestry including clear-felled timber and rehabilitated plantation areas
Agriculture	Irrigated and dryland agriculture including permanent orchards, pineapples, sugar cane, subsistence agriculture, commercial annual crops and old cultivated fields
Mines	Major surface-based mineral, rock and sand excavation and dumping sites including rehabilitated mine areas
Built	All major urban and built-up areas, rural or low density dwellings, sports fields and race tracks, smallholdings, national, main and district roads, railways and airfields
Natural vegetation	Natural vegetation including forests, dense bush, bushland, woodland, bush clumps, grasslands, Alpine heath and degraded natural vegetation
Sand or rock	Naturally occurring exposed bare rock and sand, excluding coastal rock and sand
Erosion	Non-vegetated areas resulting from primarily gully erosion processes
Dams	Artificially impounded water
Abandoned	Secondary vegetation areas arising from abandoned non-natural categories, e.g. abandoned agricultural fields. From a biodiversity conservation perspective this category is tracked and separated in analyses because once abandoned, biodiversity value is never restored to its original state

Table 3: Aggregated class accuracy statistics for the KwaZulu-Natal 2005, 2008 and 2011 land-cover maps

Year	Category	Users' accuracy (%)	Producers' accuracy (%)	90% Confidence limits		Omission error	Commission error
				Low	High		
2005	Water	95.3	89.0	84.7	93.3	0.1	0.0
	Plantations	93.1	97.1	94.3	99.9	0.0	0.1
	Agriculture	92.9	91.7	88.7	94.6	0.1	0.1
	Mines	100.0	75.0	46.9	100.0	0.3	0.0
	Built	93.0	76.8	70.2	83.4	0.2	0.1
	Natural vegetation	91.2	95.7	94.2	97.2	0.0	0.1
	Sand or rock	75.0	75.0	46.9	100.0	0.3	0.3
	Erosion	100.0	100.0	97.3	100.0	0.0	0.0
	Dams	100.0	100.0	–	100.0	0.0	0.0
2008	Water	96.2	91.5	87.4	95.5	0.1	0.0
	Plantations	84.9	96.1	93.0	99.1	0.0	0.2
	Agriculture	93.2	91.8	89.7	94.0	0.1	0.1
	Mines	91.4	86.5	79.1	93.8	0.1	0.1
	Built	94.6	91.6	87.8	95.3	0.1	0.1
	Natural vegetation	94.6	95.7	94.2	97.3	0.0	0.1
	Sand or rock	92.3	60.0	45.8	74.2	0.4	0.1
	Erosion	80.6	80.6	71.4	89.9	0.2	0.2
	Dams	84.4	97.4	93.9	100.0	0.0	0.2
2011	Water	93.7	83.1	78.0	88.3	0.2	0.1
	Plantations	95.2	89.9	85.7	94.1	0.1	0.0
	Agriculture	95.3	93.1	90.8	95.4	0.1	0.0
	Mines	100.0	68.6	58.4	78.7	0.3	0.0
	Built	93.8	88.3	84.9	91.7	0.1	0.1
	Natural vegetation	78.8	97.3	95.8	98.7	0.0	0.2
	Sand or rock	100.0	28.0	16.3	39.7	0.7	0.0
	Erosion	91.3	84.0	74.4	93.6	0.2	0.1
	Dams	100.0	100.0	98.2	100.0	0.0	0.0

Results

Detailed provincial analysis 2005–2011

The percentage landscape change in KZN was 7.74% between 2005 and 2008, but slowed to 2.69% between 2008 and 2011 (Table 4, Figure 2). The greatest losses occurred in natural vegetation with a net loss of 721 733 ha (7.6%) since 2005. The greatest gains were made by agriculture with a net gain of 496 152 ha (5.2%) over the analysis period. Natural vegetation and agriculture were involved in the largest changes in the landscape in part because they accounted for a large part of the landscape. Importantly the agriculture and natural vegetation categories displayed high levels of swapping in the landscape (1.28% and 0.99%, respectively, between 2005 and 2008), i.e. changing to or from various categories over time. Commercial agriculture increased from 7.7% to 9.0% of KZN, driven primarily by dryland cropping, whilst subsistence agriculture increased from 3.3% to 7.4% in extent over the analysis period. The built environment had a net gain of 111 485 ha (1.2%) followed by plantations with 46 157 ha (0.5%).

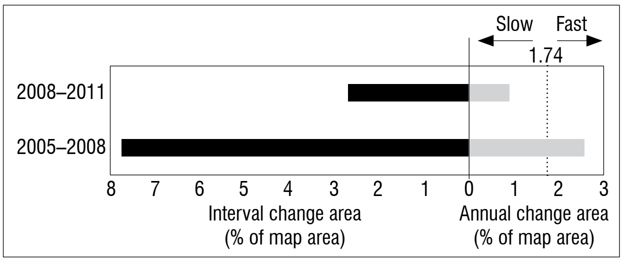

Figure 2: The landscape interval change occurring across KwaZulu-Natal between 2005–2008 and 2008–2011. The bars to the left (black) indicate the percentage area change occurring in the province in each interval, whilst the bars to the right (grey) represent the intensity of annual area of change within each time interval. Grey bars extending to the right or left of the vertical dashed line indicate a fast or slow change, respectively, relative to a uniform change across the analysis period.

Between 2005 and 2008 agriculture gained the most, followed by the built environment and plantations. Similarly, in the second time period (2008–2011), the major gains were made by agriculture and the built environment, but the gain in plantations slowed significantly. The natural vegetation category always showed the greatest losses. Figures 3 and 4 depict the annual size of the gain or loss, respectively, of a category on the left-hand side of the graph whilst the right-hand side indicates the intensity of the category gain and loss percentages relative to uniform change intensity across the landscape in general across the analysis period. Examining the intensity of the category gains and losses, which also considers the size of the category concerned, reveals that dams, mines and erosion were actively gaining categories in both time periods. The number of dams in the province increased from approximately 14 455 in 2005 to over 20 980 in 2011, representing a 45% increase in the number and a 26% increase in the extent of dams. Mining extent increased by 90% and erosion by 44%. In terms of losses, plantations was consistently a dormant category. The water and sand/rock categories were dynamic in nature.

Table 4: Percentage change in the aggregated land-cover categories in the KwaZulu-Natal landscape for 2005–2008 and 2008–2011. The gain in semi-natural vegetation (the change of non-natural vegetation classes back into a semi-natural state at a future time point) was tracked by the 'abandoned' category in the Intensity Analysis.

Category	2005–2008					2008–2011				
	Gain	Loss	Total change	Swap	Absolute value of net change	Gain	Loss	Total change	Swap	Absolute value of net change
Water	0.35	0.09	0.44	0.18	0.27	0.11	0.11	0.22	0.21	0.00
Plantations	0.71	0.22	0.92	0.44	0.49	0.18	0.18	0.36	0.36	0.00
Agriculture	4.92	0.64	5.56	1.28	4.28	1.26	0.30	1.56	0.60	0.96
Mines	0.04	0.00	0.04	0.01	0.03	0.01	0.00	0.02	0.01	0.01
Built	0.82	0.17	0.98	0.33	0.65	0.67	0.14	0.81	0.28	0.52
Natural vegetation	0.49	6.52	7.02	0.99	6.03	0.26	1.85	2.11	0.51	1.60
Sand or rock	0.01	0.03	0.04	0.03	0.02	0.02	0.06	0.08	0.04	0.04
Erosion	0.25	0.06	0.30	0.12	0.19	0.15	0.03	0.18	0.06	0.12
Dams	0.15	0.01	0.16	0.02	0.14	0.03	0.02	0.05	0.04	0.01
Total	7.74	7.74	7.74	1.69	6.04	2.69	2.69	2.69	1.05	1.63

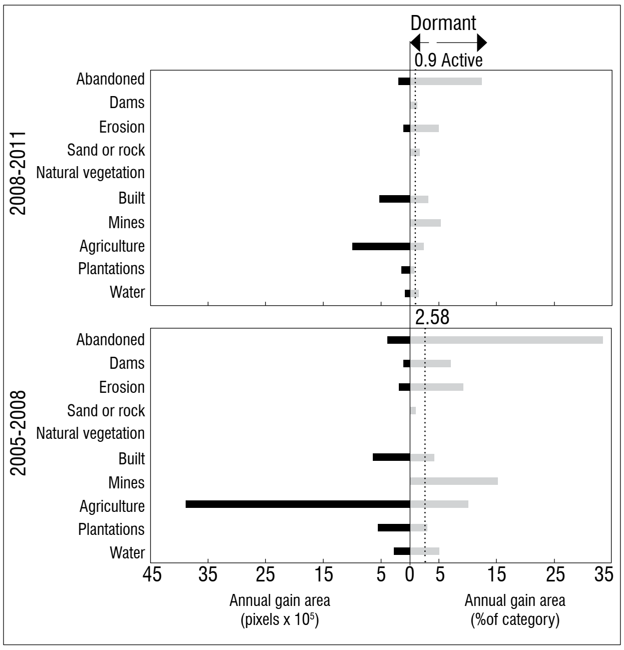

Figure 3: The gains per category for the 2005–2008 and 2008–2011 time intervals. The bars to the left (black) indicate the gross annual area gains per category. The bars to the right (grey) represent the intensity of the annual gains. Grey bars extending to the right or left of the vertical dashed line indicate active or dormant changes, respectively, relative to a uniform intensity across each analysis period.

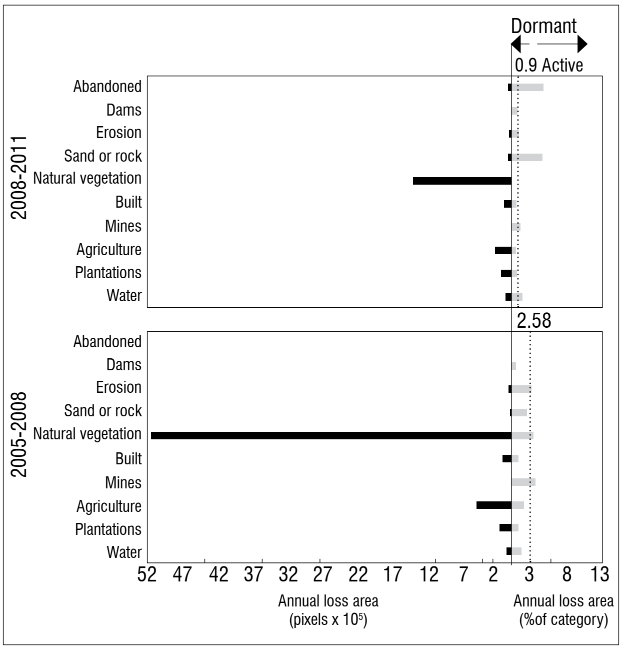

Figure 4: The losses per category for the 2005–2008 and 2008–2011 time intervals. The bars to the left (black) indicate the gross annual area losses per category. The bars to the right (grey) represent the intensity of the annual losses. Grey bars extending to the right or left of the vertical dashed line indicate active or dormant changes, respectively, relative to a uniform intensity across each analysis period.

Examination of the category transitions (Supplementary tables 2 and 3) reveals the abandoned category targeted agriculture, mines, built and dynamic natural categories such as erosion, sand and water. Agriculture targeted natural vegetation and erosion initially, but thereafter the abandoned, water, built and mine categories. The built areas targeted agricultural areas, but despite claiming an average of 7247 ha per annum of natural vegetation, cannot be said to have actively targeted this category, because of the large size and relative persistence of natural vegetation in the landscape. Erosion consistently targeted natural and abandoned vegetation and mines. Dams consistently targeted water, mines and erosion. Mines targeted natural and abandoned vegetation and dams.

The patterns of change in the communal (ITB) and non-communal (non-ITB) areas of the province followed similar patterns to those of KZN in that the rate of change slowed significantly in the second time period for both land tenure areas (Supplementary figures 2–7). A greater portion of the landscape changed in the ITB areas (10.84% and 3.41%) than in the non-ITB areas (6.45% and 2.39%) for both the first and second time periods, respectively. The major landscape differences between the ITB and non-ITB areas were that the communal areas practised a far greater degree of subsistence agriculture than commercial agriculture (30:1 versus 1:3 in non-ITB areas in 2008 with an increasing trend of subsistence agriculture). The ITB areas had a threefold higher proportion of low density settlements than high density settlements compared with non-ITB areas and the proportion of degraded natural vegetation was 50% higher in ITB areas than in non-ITB areas. The rate of increase in the built category was similar for both land tenure areas.

The ITB areas consistently gained in the abandoned, mining, agriculture, erosion and plantation categories, and the major losses stemmed from natural vegetation. The amount of swapping in the ITB landscape was 1.06% and 1.11%, respectively, in the first and second time periods. The non-ITB areas consistently gained in the agriculture, abandoned, built, dams, mining and erosion categories, and major losses stemmed from natural vegetation. The amount of swapping in the non-ITB landscape was 1.26% and 0.74%, respectively, in the first and second time periods.

Longer-term analysis of the extents and rates of habitat loss

In 1994, 73% of KZN was in a natural state. By 2011 this portion had decreased to 53% (Figure 5). The annual change percentage of the landscape decreased in each successive time period: 1.88% for 1994–2000, 1.05% for 2000–2005, 0.82% for 2005–2008 and 0.24% for 2008–2011. The average rate of habitat loss was 1.2% per annum between 1994 and 2011. A logarithmic regression function fitted the data well (adjusted $R^2=0.98$). Assuming habitat transformation continues in the same manner, it is estimated that by 2050, 45% of the landscape will remain in a natural state (Figure 6). Initially, the ITB areas had relatively more natural habitat than non-ITB areas; however, given the higher rate of change in the ITB areas, they are predicted to have less natural habitat remaining by 2050 than non-ITB areas.

Discussion

Biodiversity implications of land-cover changes

Landscape changes

The main drivers of change in the landscape were agriculture, timber plantations, built environments, mines and dams. Apart from the direct loss of natural habitat, these land covers all pose additional negative impacts for biodiversity remaining in these or surrounding areas. These effects may be direct (e.g. loss of habitat or extraction of water), indirect (e.g. pollution transported downstream), induced (e.g. associated industries and settlement) or cumulative (e.g. collective impacts on water quality and quantity).[28]

Land-cover change dynamics differed between ITB and non-ITB areas. The communal areas of the province experienced a proportionately greater degree of landscape change and development than private and state-owned areas. The ITB areas are predicted to have less natural habitat remaining than non-ITB areas in future which is problematic in that these communities rely heavily on natural resource use. Given the reliance on natural resources, the opportunity exists to promote the use of indigenous food and medicinal crops, which would benefit both biodiversity and lower the dependence on expensive agricultural inputs such as fertilisers. Low density settlement actively increased in ITB areas, posing challenges for service provision. Plantations actively increased in these areas compared with those in privately owned areas. There was a proportionally greater increase in the number of dams in the privately owned areas of the province.

Extensive land-use swapping occurred in the landscape, in particular between the agricultural and natural categories. Likely reasons for this swapping include agricultural field rotation common in subsistence

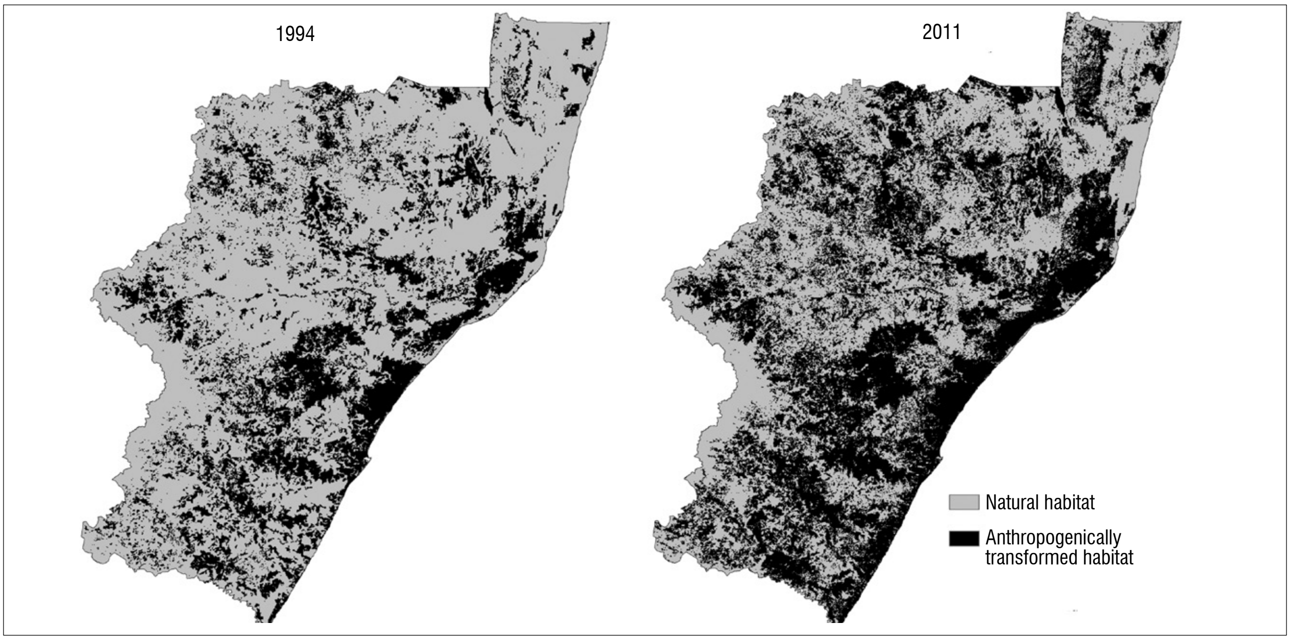

Figure 5: Accumulated transformation in KwaZulu-Natal from 1994 to 2011. The black areas represent anthropogenically transformed areas whilst the grey areas represent natural habitat.

farming and the abandonment of lands because of urbanisation, farm security issues, soil nutrient depletion, agricultural pests and diseases, invasive alien plants and economic factors. The transition analysis elucidated interesting change dynamics in the landscape, including, for example, swapping from built environments back to a natural environment, which is initially counter-intuitive. However, for diverse reasons, dwellings are often abandoned or become vandalised to the extent that vegetation overgrows the building foundations and it appears natural in later satellite images (Supplementary figures 8–22).

Agriculture

The average cultivated area per person in South Africa in 1960 was approximately 0.55 ha but this figure decreased to 0.3 ha by 1993.[29] In KZN in 2011, the commercial and subsistence agriculture equated to 0.14 ha per person, representing a significant decline over time despite a significant increase in agricultural extent. Increasing human populations will lower this ratio. Higher yields are possible from improved cultivars, irrigation, pesticide, herbicide and fertiliser use,[30] which may explain the smaller area required per person, but these inputs have negative impacts for biodiversity.

Agricultural expansion was pronounced prior to the 1960s. Policy instruments such as agricultural subsidies and minimum selling prices, were thought to have encouraged cultivation on marginal lands[29] which were later abandoned when subsidies were withdrawn. These old cultivated lands are still evident in the province but they are declining in extent, reverting primarily to agricultural use, in particular to subsistence and dryland cropping. However, these marginal areas are more prone to crop failure. The old croplands have altered soil structure, organic matter content and differing soil nutrient levels[31] and lack the full complement of native species, especially geophytic plants and those plants which rely on soil mycorrhizal associations, for example terrestrial orchids. It is not known how long it takes previously cultivated fields to return to a compositionally complete rangeland equivalent to primary rangelands, but it is estimated to be in excess of several decades.[32] This topic is worthy of further research.

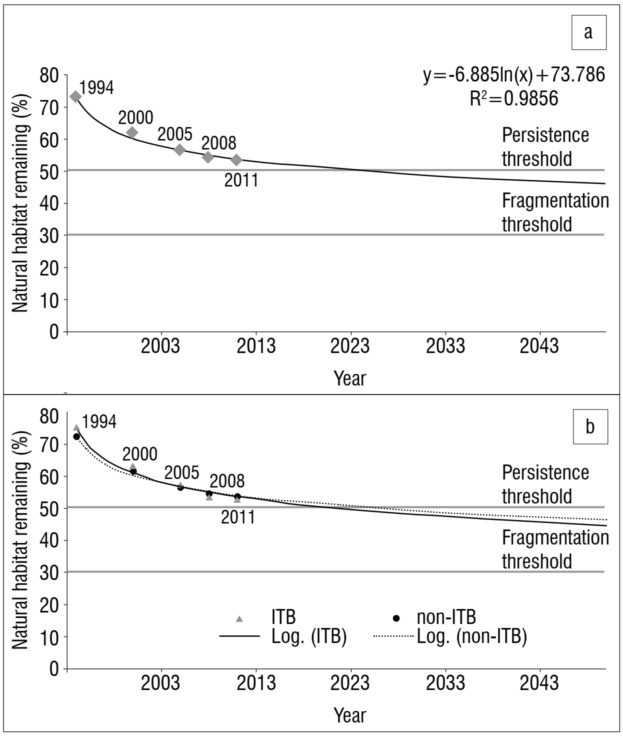

Figure 6: (a) Extrapolated rates of habitat loss in KwaZulu-Natal, assuming a business-as-usual scenario. The persistence threshold is reached once 50% of natural habitat is lost, beyond which there is a rapid decline in the probability of landscapes supporting viable populations. The fragmentation threshold is reached once 70% of natural habitat is lost, whereafter the spatial configuration of habitat patches becomes important for the persistence of remaining species.[43] (b) Extrapolated rates of habitat loss in the Ingonyama Trust Board (ITB) and non-ITB areas.

Plantations

Timber plantations occur primarily in the grassland and Indian Ocean Coastal Belt biomes. The extent of plantations has not increased significantly with a 46 000 ha increase in the first time period and a stabilisation in the second time period. The slowdown in the expansion of timber plantations in the second time period is most likely as a result of a reduction in the allocation of licences from the Department of Water Affairs and Forestry in terms of the *National Water Act No. 36 of 1998*, or because of economic factors associated with the industry. Indeed, certain catchments have been closed to new applications and a moratorium has been placed on others, pending further investigations on associated run-off reductions (Thambu D 2014, written communication, August 7). Plantations create acidic soils and an increase in available nitrate,[33] a situation for which many indigenous plant species are not adapted. Shading effects may promote shade-loving or forest species, but these species will be lost during rotational harvesting practices.[34]

Built environment

The built environment increased by 1.2% in KZN between 2005 and 2011. In particular there was an increase of the built environment in rural areas. Much of the province's biodiversity resides outside of protected areas in the rural landscape. Hence expansion in these areas poses threats for the remaining biodiversity. Sprawling urbanisation should be contained by the encouragement of higher-density settlements and the definition of an urban edge. An increase in the number of roads in rural areas is promoting development in remote areas, facilitating greater natural resource extraction and enhancing landscape fragmentation effects. Development in these areas reduces the opportunity for conserving large open spaces – which is one of the criteria used in protected area expansion plans.

Hydrological implications

The massive increase in the number of dams in the province is of significant concern for aquatic biodiversity and river health. The cumulative impacts of small dams reduces discharge, increases dissolved salts and alters macro-invertebrate indices.[35] Flow levels are reduced during dry periods, which causes hydromorphic grasslands to dry out and large trees to die back.[36] Larger dams and inter-basin transfer schemes significantly alter flow regimes and may lead to a dominance of livestock pest species.[37] Water extraction and pollution further negatively impact the ecosystem services that rivers and wetlands provide.

Mining

Mining extent almost doubled during the analysis period. The dominant form of mining affecting the change dynamics in the landscape is dune mining of titanium, iron, rutile and zircon, which occurs along the coast. The mobile nature of this form of mining creates a 'snail-trail' along the dune corridors with associated erosion, dam and abandoned category swapping. Mining impacts biodiversity principally via habitat loss, the alteration of ecological processes, pollution and the introduction of alien invasive species.[28]

Soil conservation

The extent of erosion is increasing in the province and creating degraded landscapes. Differing land-use practices may alter soil chemical and physical properties.[33] Ploughing, heavy grazing and burning deplete soil organic matter which affects soil water infiltration, retention and nutrient supply.[38] Dryland cropping, which is increasing in KZN, results in significant losses of soil organic matter. Lower soil organic matter results in lower water stable aggregates which are required to prevent soil erosion.[39] Future climate predictions suggest greater intensity of rainfall events and longer intervals between events.[40] Concomitant with the steep topography of KZN, soil erosion is thus likely to be exacerbated. Soil erosion has implications for biodiversity conservation, food security, soil conservation and water quality in terms of sedimentation and suspended sediment concentrations. Initiatives to prevent further soil erosion and degradation of natural vegetation are urgently required.

The implications of habitat loss

Extents and thresholds of habitat loss

This study highlighted the extensive loss of natural habitat occurring in the province, a massive 7.6% in only 6 years, which is of concern for biodiversity conservation and raises the question of whether this level of habitat loss is sustainable. At a national level the extent of transformed land in 2005 was 15.7%.[41] In KZN the picture is entirely different with 43% of land transformed in 2005, increasing to 46.4% by 2011. The changes in land cover, loss of habitat and the resulting fragmentation of the landscape have resulted in the loss of biodiversity and species population declines.[42] These losses will continue as more of the landscape is transformed by anthropogenic use as habitat is a finite resource, thus conservation efforts should focus on habitat preservation. As more natural habitat is lost, the opportunity costs associated with adding to the protected area estate increase. Certain areas in the landscape are unlikely to be transformed from their natural state because of, for instance, steep topography, protected areas or legislated development exclusion areas. Thus protected area expansion should focus on the areas most likely to experience a change to an anthropogenic category.

Flather and Bevers[43] identified a persistence threshold that exists once natural habitat is reduced below 50% of the total landscape for low degrees of patch aggregation. Beyond this level of transformation there is a rapid decline in the probability of landscapes supporting viable populations of organisms and a decline in habitat connectivity. The amount of natural habitat remaining in KZN is rapidly approaching this threshold. A target of no more than 50% of habit loss should be adopted to adequately conserve biodiversity in the province. Loss of habitat leads to a loss of ecological resilience and habitat specialist species.[44] This loss is of particular concern in this species-rich province and in the face of climate change for which ecological resilience is of paramount importance. A fragmentation threshold exists once 20–30% of natural habitat remains, whereafter the spatial configuration of habitat patches becomes important for maintaining population persistence.

Transformation of the landscape is creating ‘islands’ of protected areas in a matrix of anthropogenically transformed areas. This transformation is despite the province having good systematic conservation plans and data, which demonstrate that much of the biodiversity resides outside of protected areas. This situation calls into question the effectiveness of current conservation strategies and processes related to environmental authorisations. In light of extensive calls for further development in the province, a major rethink is required in order to determine how this development should be implemented. Effective management of the matrix is critical for the persistence of a vast majority of species that utilise these areas for breeding, foraging or migration.[45] New efforts to mainstream biodiversity into various land-use sectors are to be encouraged and supported.[46]

The science–policy interface

The Convention on Biological Diversity, to which South Africa is a signatory, has a target of halving (or where feasible bringing close to zero) by 2020, the rate of loss of natural habitat and significantly reducing degradation and fragmentation. The rates of habitat loss have declined in the province, but, given the recent global economic recession, caution needs to be exercised in interpreting the slowing rates as an achievement towards this target. Drivers such as changes in the economy, legislation, technological advances or even social resistance are likely to alter the rate of habitat transformation.

Some of the criteria used in the identification of Threatened Terrestrial Ecosystems (according to the *National Environmental Management: Biodiversity Act No. 10 of 2004* and the *National List of Ecosystems that are Threatened and in Need of Protection Act No. 1002 of 2011*) are incomplete because of data constraints. Specifically, criteria B – which examines the rate of loss of natural habitat – is not defined. Our data set and method of analysis provides the first provincial assessment of the rate of loss of natural habitat, and together with the Convention on Biological Diversity targets, could be used to fulfil this criterion of the legislation.

The main drivers of land-cover change are human responses to economic opportunities which are mediated by institutional factors.[6] Markets and policies constrain or encourage land-use change. Thus it is essential that decision- and policymakers are cognisant of the full implications that decisions and policy development may have on the rates of habitat loss. It is critical that a longer-term decision and planning framework, that is cognisant of constitutional and international agreements, be adopted. It is essential that conservation officials actively lead the way in biodiversity conservation, as stated eloquently by Noss et al.[47]:

> *The pro-growth norms of global society foster timidity among conservation professionals, steering them toward conformity with the global economic agenda and away from acknowledging what is ultimately needed to sustain life on Earth.*

Conclusions

The development of three directly comparable land-cover maps by Ezemvelo KZN Wildlife has permitted the first time-series analysis of LULCC in the province. The analysis elucidated the drivers, patterns and processes of land-cover change in KZN. The Intensity Analysis framework explicitly revealed change dynamics that other LULCC approaches would not have been able to do, by examining change at different levels of detail and considering category sizes and intensity of changes. This framework allowed a deeper understanding of systematic transitions in the province.

The challenge of conserving biodiversity in KZN is becoming increasingly difficult because natural habitat continues to be lost and the associated negative impacts and habitat degradation related to the identified land-cover drivers further threaten biodiversity. The provincial trends in habitat loss unfortunately follow global trends, but should this province, and South Africa, wish to lead the way in biodiversity conservation, some very important and difficult policy and legislative decisions need to be made now.

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Authors’ contributions

D.J. was the project leader, researcher and wrote the manuscript; P.S.G., B.F.N.E., T.G.O.C. and E.T.F.W. made conceptual and editorial contributions.

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Note: This article is supplemented with online only material.

Chapter 4

Appendix 4 Supplementary Information S1: Notations and equations

Online supplementary material to: Jewitt D, Goodman PS, Erasmus BFN, O'Connor TG, Witkowski ETF. Systematic land-cover change in KwaZulu-Natal, South Africa: implications for biodiversity. S Afr J sci. 2015;111(9/10), Art. #2015-0019, 9 pages. http://dx.doi.org/10.17159/sajs.2015/20150019

Table 1: Notation

J	Number of categories
i	Index for a category at an interval's initial time point
j	Index for a category at an interval's final time point
T	Number of time points
Y_t	Year at time point *t*
t	Index for the initial time point of interval $[Y_t, Y_{t+1}]$, where *t* ranges from *1* to *T*-1
P_{ij}	The proportion of the landscape that experiences a transition from category *i* to category *j*
P_{jj}	The proportion of the landscape that shows persistence of category *j*
P_{i+}	The proportion of the landscape in category *i* in time 1, which is the sum over all *j* of P_{ij}
P_{+j}	The proportion of the landscape in category j in time 2, which is the sum over all *i* of P_{ij}
S_j	The amount of swap for each category *j*
D_j	The absolute value of net change for category *j*
C_j	The total change for each category *j*
m	Index for the losing category for the selected transition
n	Index for the gaining category for the selected transition
C_{tij}	Number of elements (pixels) that transition from category *i* to category *j* during interval $[Y_t, Y_{t+1}]$
S_t	Annual intensity of change during interval $[Y_t, Y_{t+1}]$
U	Value of uniform line for time intensity analysis
G_{tj}	Annual intensity of gross gain of category *j* during interval $[Y_t, Y_{t+1}]$

L_{ti}	Annual intensity of gross loss of category *i* for time interval $[Y_t, Y_{t+1}]$
R_{tin}	Annual intensity of transition from category *i* to category *n* during interval $[Y_t, Y_{t+1}]$ where *i* ≠ *n*
W_{tn}	Value of uniform intensity of transition to category *n* from all non-*n* categories at time Y_t during time interval $[Y_t, Y_{t+1}]$.
Q_{tm}	Annual intensity of transition from category *m* to category *j* during time interval $[Y_t, Y_{t+1}]$ where *j* ≠ *m*
V_{tm}	Value of uniform intensity of transition from category *m* to all non-*m* categories at time Y_{t+1} during time interval $[Y_t, Y_{t+1}]$

Notation follows Pontius et al.[1] and Aldwaik and Pontius[2]

Equations

The equations follow Pontius et al.1 and Aldwaik and Pontius2. A program to facilitate the Intensity Analysis calculations is available from https://sites.google.com/site/intensityanalysis/.[2]

The amount of swap for each category *j*:

$$S_j = 2 \times MIN\left(P_{j+} - P_{jj,}\; P_{+j} - P_{jj}\right) \qquad \text{Equation 1}$$

Absolute value of net change for category *j*:

$$D_j = \left|P_{+j} - P_{j+}\right| \qquad \text{Equation 2}$$

Total change for each category:

$$C_j = D_j + S_j \qquad \text{Equation 3}$$

Annual intensity of change during interval $[Y_t, Y_{t+1}]$:

$$S_t = \frac{\left\{\sum_{j=1}^{J}\left[\left(\sum_{i=1}^{J} C_{tij}\right) - Ctij\right]\right\} / \left[\sum_{j=1}^{J}\left(\sum_{i=1}^{J} C_{tij}\right)\right]}{Y_{t+1} - Y_t} 100\% \qquad \text{Equation 4}$$

Value of uniform line for time intensity analysis:

$$U = \frac{\sum_{t=1}^{T-1}\left\{\sum_{j=1}^{J}\left[\left(\sum_{i=1}^{J} C_{tij}\right) - C_{tij}\right]\right\} / \left[\sum_{j=1}^{J}\left(\sum_{i=1}^{J} C_{tij}\right)\right]}{(Y_T - Y_1)} 100\% \qquad \text{Equation 5}$$

Intensity of gross annual gain of category j during interval $[Y_t, Y_{t+1}]$:

$$G_{tj} = \frac{\left[\left(\sum_{i=1}^{J} C_{tij}\right) - C_{tjj}\right] / (Y_{t+1} - Y_t)}{\sum_{i=1}^{J} C_{tij}} 100\% \qquad \text{Equation 6}$$

Intensity of gross annual loss of category *i* during interval $[Y_t, Y_{t+1}]$:

$$L_{ti} = \frac{\left[\left(\sum_{j=1}^{J} C_{tij}\right) - C_{tii}\right] / (Y_{t+1} - Y_t)}{\sum_{j=1}^{J} C_{tij}} 100\% \qquad \text{Equation 7}$$

Annual intensity of transition from category *i* to category *n* during interval $[Y_t, Y_{t+1}]$:

$$R_{tin} = \frac{C_{tin} / (Y_{t+1} - Y_t)}{\sum_{j=1}^{J} C_{tij}} 100\% \qquad \text{Equation 8}$$

Value of uniform intensity of annual transition to category *n* from all non-*n* categories at time Y_t during interval $[Y_t, Y_{t+1}]$:

$$W_{tn} = \frac{\left[\left(\sum_{i=1}^{J} C_{tin}\right) - C_{tnn}\right] / (Y_{t+1} - Y_t)}{\sum_{j=1}^{J}\left[\left(\sum_{i=1}^{J} C_{tij}\right) - C_{tnj}\right]} 100\% \qquad \text{Equation 9}$$

Annual intensity of transition from category *m* to category *j* during interval $[Y_t, Y_{t+1}]$:

$$Q_{tmj} = \frac{\left| C_{tmj} / (Y_{t+1} - Y_t) \right|}{\sum_{i=1}^{J} C_{tij}} 100\% \qquad \text{Equation 10}$$

Value of uniform intensity of annual transition from category *m* to all non-*m* categories at time Y_{t+1} during interval $[Y_t, Y_{t+1}]$:

$$V_{tn} = \frac{\left[\left(\sum_{j=1}^{J} C_{tmj}\right) - C_{tmm}\right] / (Y_{t+1} - Y_t)}{\sum_{i=1}^{J}\left[\left(\sum_{j=1}^{J} C_{tij}\right) - C_{tim}\right]} 100\% \qquad \text{Equation 11}$$

References

1 Pontius RG, Shusas E, McEachern M. Detecting important categorical land changes while accounting for persistence. Agric Ecosyst Environ. 2004;101:251–268.

2 Aldwaik SZ, Pontius RG. Intensity analysis to unify measurements of size and stationarity of land changes by interval, category, and transition. Landscape Urban Plan. 2012;106(1):103–114.

Appendix 5 Supplementary Information S2: Systematic KwaZulu-Natal land-cover transitions

Table 2: Transitions to land-cover categories across the two time intervals (2005-2008) and 2008-2011) in KwaZulu-Natal

		2005–2008			**2008–2011**		
Transitions to	**From**	**Transition Intensity (% of 2005 category)**	**Uniform Intensity (% of 2005 non-to category)**	**Transition**	**Transition Intensity (% of 2008 category)**	**Uniform Intensity (% of 2008 non-to category)**	**Transition**
Water							
	Plantations	0.00	0.06	Avoids	0.01	0.04	Avoids
	Agriculture	0.02	0.06	Avoids	0.02	0.04	Avoids
	Mines	0.01	0.06	Avoids	0.00	0.04	Avoids
	Built	0.00	0.06	Avoids	0.00	0.04	Avoids
	Natural Vegetation	0.07	0.06	Targets	0.04	0.04	Targets
	Sand or Rock	0.40	0.06	Targets	0.45	0.04	Targets
	Erosion	0.03	0.06	Avoids	0.05	0.04	Targets
	Dams	0.07	0.06	Targets	0.24	0.04	Targets
	Abandoned	0.00	0.06	Avoids	0.14	0.04	Targets
Plantations							
	Water	0.02	0.08	Avoids	0.02	0.04	Avoids
	Agriculture	0.09	0.08	Targets	0.03	0.04	Avoids
	Mines	0.00	0.08	Avoids	0.00	0.04	Avoids
	Built	0.04	0.08	Avoids	0.03	0.04	Avoids
	Natural Vegetation	0.09	0.08	Targets	0.04	0.04	Targets
	Sand or Rock	0.21	0.08	Targets	0.16	0.04	Targets
	Erosion	0.00	0.08	Avoids	0.00	0.04	Avoids
	Dams	0.00	0.08	Avoids	0.00	0.04	Avoids
	Abandoned	0.00	0.08	Avoids	0.42	0.04	Targets
Agriculture							

	Water	0.21	3.07	Avoids	1.41	0.55	Targets
	Plantations	0.62	3.07	Avoids	0.22	0.55	Avoids
	Mines	1.82	3.07	Avoids	1.15	0.55	Targets
	Built	0.20	3.07	Avoids	0.78	0.55	Targets
	Natural Vegetation	3.53	3.07	Targets	0.49	0.55	Avoids
	Sand or Rock	0.64	3.07	Avoids	0.15	0.55	Avoids
	Erosion	3.34	3.07	Targets	0.53	0.55	Avoids
	Dams	0.61	3.07	Avoids	0.48	0.55	Avoids
	Abandoned	0.00	3.07	Avoids	2.34	0.55	Targets
Mines							
	Water	0.00	0.00	Avoids	0.00	0.00	Avoids
	Plantations	0.00	0.00	Avoids	0.00	0.00	Avoids
	Agriculture	0.00	0.00	Avoids	0.00	0.00	Avoids
	Built	0.00	0.00	Avoids	0.00	0.00	Avoids
	Natural Vegetation	0.00	0.00	Targets	0.00	0.00	Targets
	Sand or Rock	0.00	0.00	Avoids	0.00	0.00	Avoids
	Erosion	0.02	0.00	Targets	0.00	0.00	Avoids
	Dams	0.00	0.00	Targets	0.02	0.00	Targets
	Abandoned	0.00	0.00	Avoids	0.01	0.00	Targets
Built							
	Water	0.03	0.39	Avoids	0.09	0.47	Avoids
	Plantations	1.24	0.39	Targets	0.36	0.47	Avoids
	Agriculture	0.93	0.39	Targets	0.88	0.47	Targets
	Mines	2.02	0.39	Targets	0.26	0.47	Avoids
	Natural Vegetation	0.33	0.39	Avoids	0.39	0.47	Avoids
	Sand or Rock	0.08	0.39	Avoids	0.09	0.47	Avoids
	Erosion	0.30	0.39	Avoids	0.47	0.47	Targets
	Dams	0.03	0.39	Avoids	0.18	0.47	Avoids

	Abandoned	0.00	0.39	Avoids	1.70	0.47	Targets
Natural Vegetation							
	Water	0.00	0.00	Avoids	0.00	0.00	Avoids
	Plantations	0.00	0.00	Avoids	0.00	0.00	Avoids
	Agriculture	0.00	0.00	Avoids	0.00	0.00	Avoids
	Mines	0.00	0.00	Avoids	0.00	0.00	Avoids
	Built	0.00	0.00	Avoids	0.00	0.00	Avoids
	Sand or Rock	0.00	0.00	Avoids	0.00	0.00	Avoids
	Erosion	0.00	0.00	Avoids	0.00	0.00	Avoids
	Dams	0.00	0.00	Avoids	0.00	0.00	Avoids
	Abandoned	0.00	0.00	Avoids	0.00	0.00	Avoids
Sand or Rock							
	Water	0.01	0.01	Targets	0.02	0.01	Targets
	Plantations	0.00	0.01	Avoids	0.00	0.01	Avoids
	Agriculture	0.00	0.01	Avoids	0.00	0.01	Avoids
	Mines	0.00	0.01	Avoids	0.01	0.01	Avoids
	Built	0.01	0.01	Avoids	0.00	0.01	Avoids
	Natural Vegetation	0.01	0.01	Targets	0.02	0.01	Targets
	Erosion	0.00	0.01	Avoids	0.00	0.01	Avoids
	Dams	0.00	0.01	Avoids	0.01	0.01	Targets
	Abandoned	0.00	0.01	Avoids	0.09	0.01	Targets
Erosion							
	Water	0.01	0.10	Avoids	0.03	0.06	Avoids
	Plantations	0.00	0.10	Avoids	0.00	0.06	Avoids
	Agriculture	0.14	0.10	Targets	0.05	0.06	Avoids
	Mines	4.13	0.10	Targets	0.55	0.06	Targets
	Built	0.00	0.10	Avoids	0.00	0.06	Avoids
	Natural Vegetation	0.11	0.10	Targets	0.07	0.06	Targets

	Sand or Rock	0.22	0.10	Targets	0.03	0.06	Avoids
	Dams	0.00	0.10	Avoids	0.01	0.06	Avoids
	Abandoned	0.00	0.10	Avoids	0.52	0.06	Targets
Dams							
	Water	0.45	0.01	Targets	0.01	0.00	Targets
	Plantations	0.00	0.01	Avoids	0.00	0.00	Avoids
	Agriculture	0.01	0.01	Avoids	0.00	0.00	Avoids
	Mines	0.37	0.01	Targets	0.04	0.00	Targets
	Built	0.00	0.01	Avoids	0.00	0.00	Avoids
	Natural Vegetation	0.01	0.01	Avoids	0.00	0.00	Targets
	Sand or Rock	0.00	0.01	Avoids	0.00	0.00	Avoids
	Erosion	0.02	0.01	Targets	0.00	0.00	Targets
	Abandoned	0.00	0.01	Avoids	0.01	0.00	Targets
Abandoned							
	Water	0.25	0.16	Targets	0.69	0.10	Targets
	Plantations	0.57	0.16	Targets	0.58	0.10	Targets
	Agriculture	1.53	0.16	Targets	0.11	0.10	Targets
	Mines	0.34	0.16	Targets	0.54	0.10	Targets
	Built	0.19	0.16	Targets	0.10	0.10	Targets
	Natural Vegetation	0.00	0.16	Avoids	0.00	0.10	Avoids
	Sand or Rock	0.48	0.16	Targets	5.86	0.10	Targets
	Erosion	0.58	0.16	Targets	0.33	0.10	Targets
	Dams	0.06	0.16	Avoids	0.23	0.10	Targets

Table 3: Transitions from land-cover categories across the two time intervals (2005-2008 and 2008-2011) in KwaZulu-Natal

		2005–2008			**2008–2011**		
Transitions from	**To**	**Transition Intensity(% of 2008 category)**	**Uniform Intensity (% of 2008 non-to category)**	**Transition**	**Transition Intensity (% of 2011 category)**	**Uniform Intensity (% of 2011 non-to category)**	**Transition**
Water							
	Plantations	0.01	0.01	Avoids	0.02	0.04	Avoids
	Agriculture	0.02	0.01	Targets	0.14	0.04	Targets
	Mines	0.01	0.01	Avoids	0.00	0.04	Avoids
	Built	0.00	0.01	Avoids	0.01	0.04	Avoids
	Natural Vegetation	0.00	0.01	Avoids	0.00	0.04	Avoids
	Sand or Rock	0.02	0.01	Targets	0.06	0.04	Targets
	Erosion	0.01	0.01	Avoids	0.04	0.04	Targets
	Dams	2.49	0.01	Targets	0.03	0.04	Avoids
	Abandoned	0.80	0.01	Targets	1.64	0.04	Targets
Plantations							
	Water	0.00	0.04	Avoids	0.01	0.02	Avoids
	Agriculture	0.06	0.04	Targets	0.02	0.02	Targets
	Mines	0.19	0.04	Targets	0.00	0.02	Avoids
	Built	0.20	0.04	Targets	0.06	0.02	Targets
	Natural Vegetation	0.00	0.04	Avoids	0.00	0.02	Avoids
	Sand or Rock	0.00	0.04	Avoids	0.01	0.02	Avoids
	Erosion	0.00	0.04	Avoids	0.00	0.02	Avoids
	Dams	0.01	0.04	Avoids	0.00	0.02	Avoids
	Abandoned	1.93	0.04	Targets	1.46	0.02	Targets
Agriculture							
	Water	0.12	0.25	Avoids	0.15	0.21	Avoids
	Plantations	0.39	0.25	Targets	0.25	0.21	Targets

	Mines	0.95	0.25	Targets	0.29	0.21	Targets
	Built	0.75	0.25	Targets	1.29	0.21	Targets
	Natural Vegetation	0.00	0.25	Avoids	0.00	0.21	Avoids
	Sand or Rock	0.02	0.25	Avoids	0.03	0.21	Avoids
	Erosion	1.07	0.25	Targets	0.71	0.21	Targets
	Dams	0.28	0.25	Targets	0.05	0.21	Avoids
	Abandoned	25.25	0.25	Targets	2.59	0.21	Targets
Mines							
	Water	0.00	0.00	Avoids	0.00	0.00	Avoids
	Plantations	0.00	0.00	Avoids	0.00	0.00	Avoids
	Agriculture	0.00	0.00	Targets	0.00	0.00	Targets
	Built	0.00	0.00	Targets	0.00	0.00	Avoids
	Natural Vegetation	0.00	0.00	Avoids	0.00	0.00	Avoids
	Sand or Rock	0.00	0.00	Avoids	0.00	0.00	Avoids
	Erosion	0.04	0.00	Targets	0.01	0.00	Targets
	Dams	0.01	0.00	Targets	0.00	0.00	Targets
	Abandoned	0.01	0.00	Targets	0.01	0.00	Targets
Built							
	Water	0.01	0.04	Avoids	0.01	0.10	Avoids
	Plantations	0.19	0.04	Targets	0.17	0.10	Targets
	Agriculture	0.11	0.04	Targets	0.46	0.10	Targets
	Mines	1.40	0.04	Targets	0.36	0.10	Targets
	Natural Vegetation	0.00	0.04	Avoids	0.00	0.10	Avoids
	Sand or Rock	0.09	0.04	Targets	0.03	0.10	Avoids
	Erosion	0.02	0.04	Avoids	0.02	0.10	Avoids
	Dams	0.07	0.04	Targets	0.03	0.10	Avoids
	Abandoned	3.52	0.04	Targets	1.39	0.10	Targets
Natural vegetation							

	Water	3.33	10.43	Avoids	1.77	2.18	Avoids
	Plantations	4.16	10.43	Avoids	1.56	2.18	Avoids
	Agriculture	17.69	10.43	Targets	2.05	2.18	Avoids
	Mines	15.77	10.43	Targets	6.89	2.18	Targets
	Built	2.65	10.43	Avoids	2.50	2.18	Targets
	Sand or Rock	1.06	10.43	Avoids	1.79	2.18	Avoids
	Erosion	8.62	10.43	Avoids	4.39	2.18	Targets
	Dams	1.80	10.43	Avoids	0.37	2.18	Avoids
	Abandoned	0.00	10.43	Avoids	0.00	2.18	Avoids
Sand or Rock							
	Water	0.19	0.02	Targets	0.21	0.05	Targets
	Plantations	0.09	0.02	Targets	0.07	0.05	Targets
	Agriculture	0.03	0.02	Targets	0.01	0.05	Avoids
	Mines	0.02	0.02	Avoids	0.00	0.05	Avoids
	Built	0.01	0.02	Avoids	0.01	0.05	Avoids
	Natural Vegetation	0.00	0.02	Avoids	0.00	0.05	Avoids
	Erosion	0.16	0.02	Targets	0.02	0.05	Avoids
	Dams	0.01	0.02	Avoids	0.00	0.05	Avoids
	Abandoned	0.78	0.02	Targets	6.30	0.05	Targets
Erosion							
	Water	0.01	0.04	Avoids	0.03	0.01	Targets
	Plantations	0.00	0.04	Avoids	0.00	0.01	Avoids
	Agriculture	0.18	0.04	Avoids	0.03	0.01	Targets
	Mines	1.04	0.04	Avoids	0.01	0.01	Avoids
	Built	0.03	0.04	Avoids	0.05	0.01	Targets
	Natural Vegetation	0.00	0.04	Avoids	0.00	0.01	Avoids
	Sand or Rock	0.00	0.04	Avoids	0.01	0.01	Avoids
	Dams	0.05	0.04	Avoids	0.01	0.01	Avoids
	Abandoned	1.01	0.04	Avoids	0.49	0.01	Targets

Dams							
	Water	0.01	0.00	Targets	0.04	0.00	Targets
	Plantations	0.00	0.00	Avoids	0.00	0.00	Avoids
	Agriculture	0.01	0.00	Targets	0.01	0.00	Targets
	Mines	0.06	0.00	Targets	0.30	0.00	Targets
	Built	0.00	0.00	Avoids	0.00	0.00	Targets
	Natural Vegetation	0.00	0.00	Avoids	0.00	0.00	Avoids
	Sand or Rock	0.00	0.00	Avoids	0.01	0.00	Targets
	Erosion	0.00	0.00	Avoids	0.00	0.00	Targets
	Abandoned	0.03	0.00	Targets	0.09	0.00	Targets
Abandoned							
	Water	0.00	0.00	Avoids	0.04	0.02	Targets
	Plantations	0.00	0.00	Avoids	0.11	0.02	Targets
	Agriculture	0.00	0.00	Avoids	0.07	0.02	Targets
	Mines	0.00	0.00	Avoids	0.33	0.02	Targets
	Built	0.00	0.00	Avoids	0.08	0.02	Targets
	Natural Vegetation	0.00	0.00	Avoids	0.00	0.02	Avoids
	Sand or Rock	0.00	0.00	Avoids	0.07	0.02	Targets
	Erosion	0.00	0.00	Avoids	0.21	0.02	Targets
	Dams	0.00	0.00	Avoids	0.01	0.02	Avoids

Appendix 6 Supplementary Information S5: 2011 Land-cover map

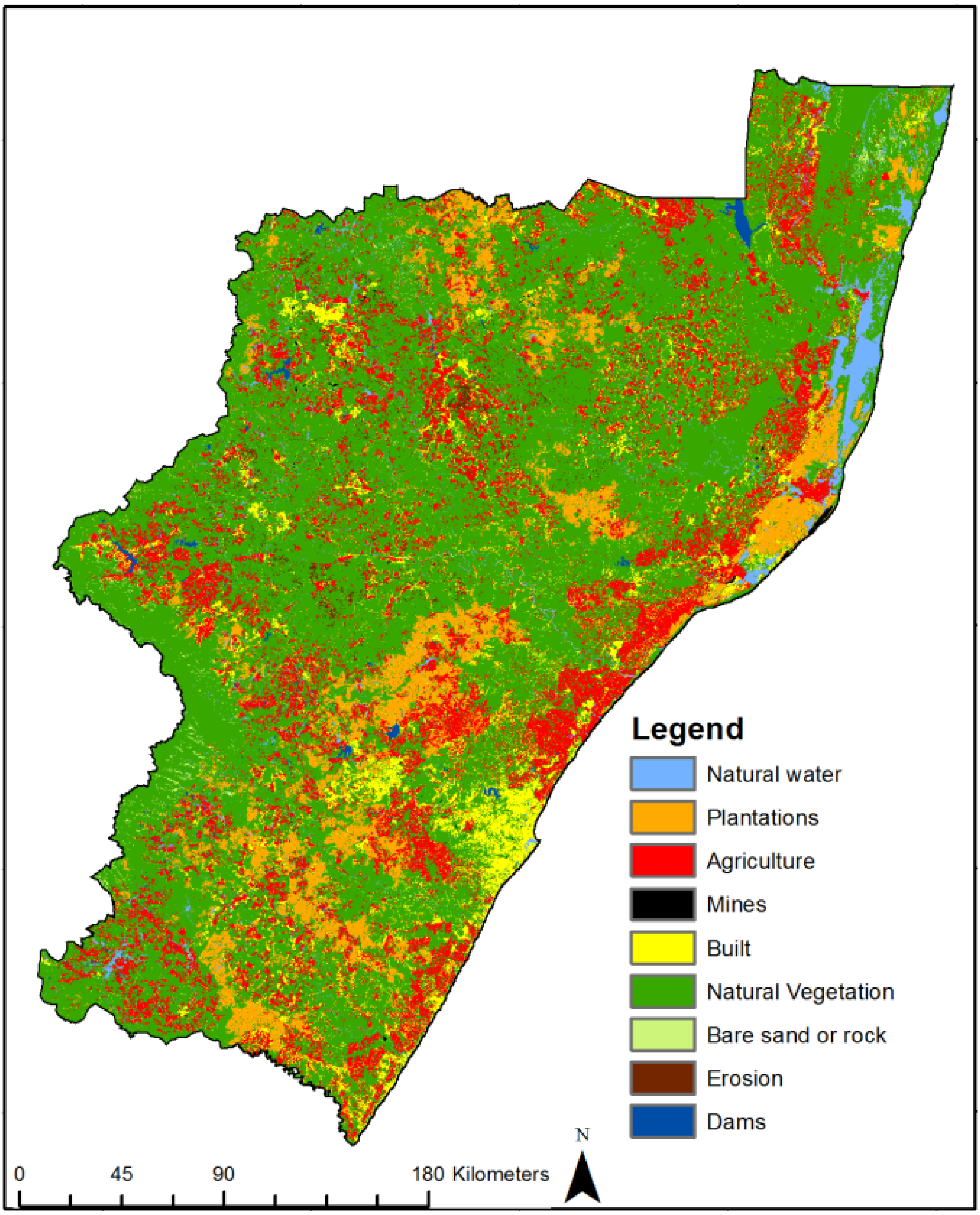

Figure 1: The 2011 KwaZulu-Natal reclassified land-cover map.

Appendix 7 Supplementary Information S3: The Ingonyama Trust Board (ITB) and non-ITB interval and categorical gain and loss graphs

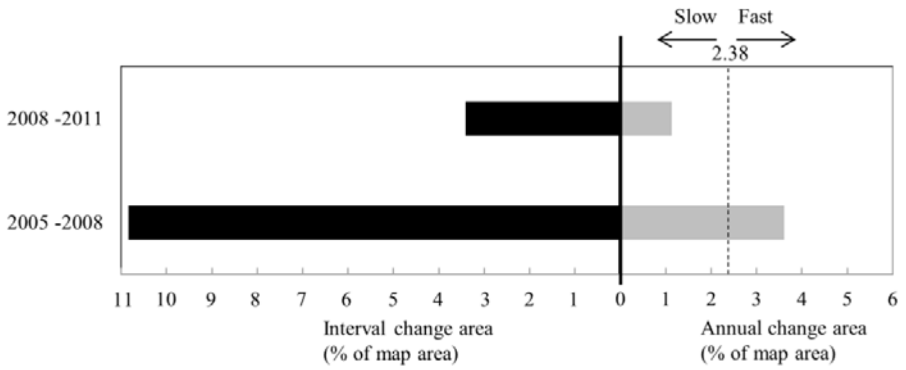

Figure 2: The landscape interval change occurring across the Ingonyama Trust Board (ITB) areas, representing communal areas, between 2005–2008 and 2008–2011. The bars to the left (black) indicate the percentage area change occurring in the ITB areas in each interval, whilst the bars to the right (grey) represent the intensity of annual area of change within each time interval. Grey bars extending to the right or left of the vertical dashed line indicate a fast or slow change, respectively, relative to a uniform change across the analysis period.

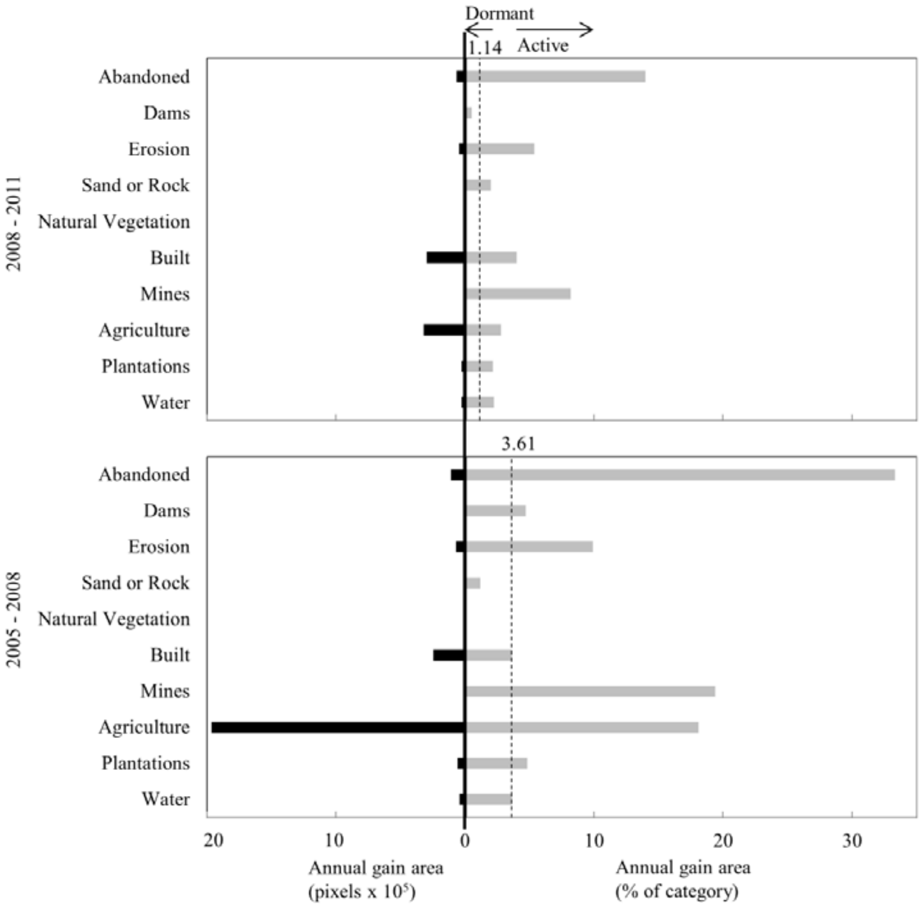

Figure 3: The gains per category for the 2005–2008 and 2008–2011 time intervals in the Ingonyama Trust Board (ITB) areas. The bars to the left (black) indicate the gross annual area gains per category. The bars to the right (grey) represent the intensity of the annual gains. Grey bars extending to the right or left of the vertical dashed line indicate active or dormant changes, respectively, relative to a uniform intensity across the analysis period.

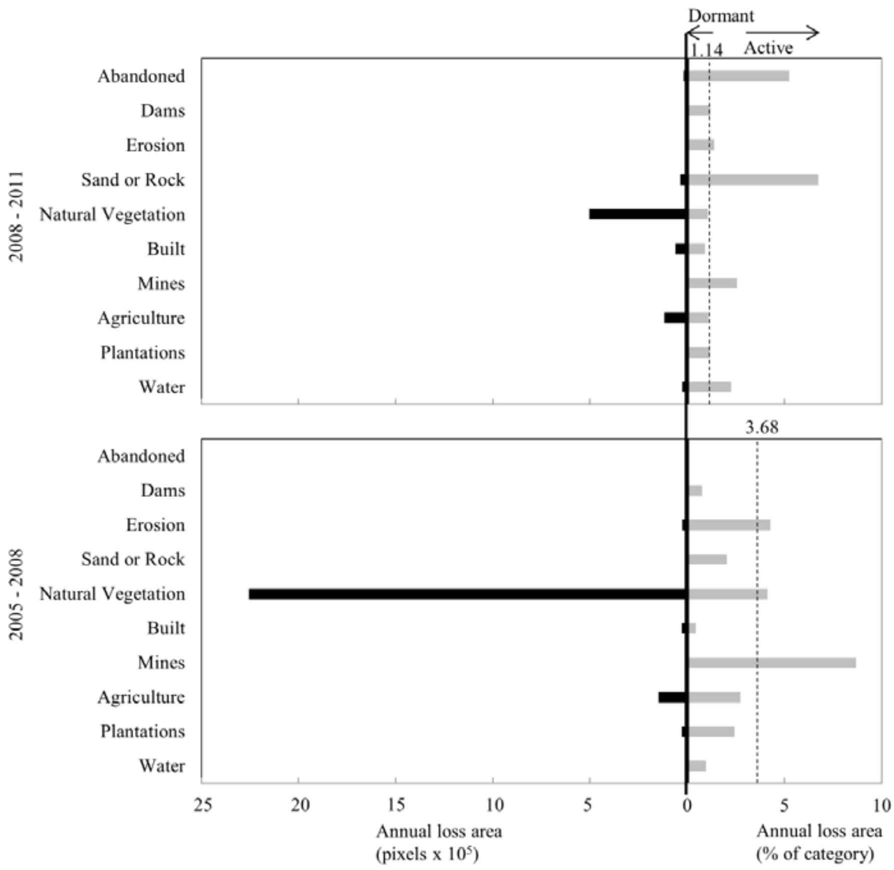

Figure 4: The losses per category for the 2005–2008 and 2008–2011 time intervals in the Ingonyama Trust Board (ITB) areas. The bars to the left (black) indicate the gross annual area losses per category. The bars to the right (grey) represent the intensity of the annual losses. Grey bars extending to the right or left of the vertical dashed line indicate active or dormant changes, respectively, relative to a uniform intensity across the analysis period.

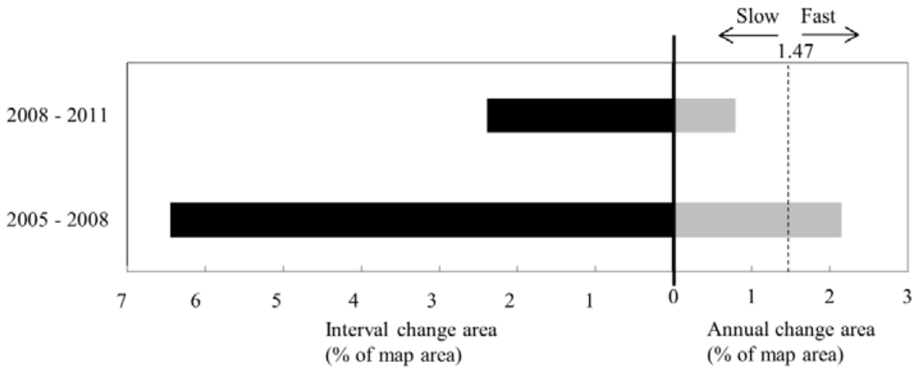

Figure 5: The landscape interval change occurring across non-Ingonyama Trust Board (non-ITB) areas, representing privately owned areas, between 2005–2008 and 2008–2011. The bars to the left (black) indicate the percentage area change occurring in the non-ITB areas in each interval, whilst the bars to the right (grey) represent the intensity of annual area of

change within each time interval. Grey bars extending to the right or left of the vertical dashed line indicate a fast or slow change, respectively, relative to a uniform change across the analysis period.

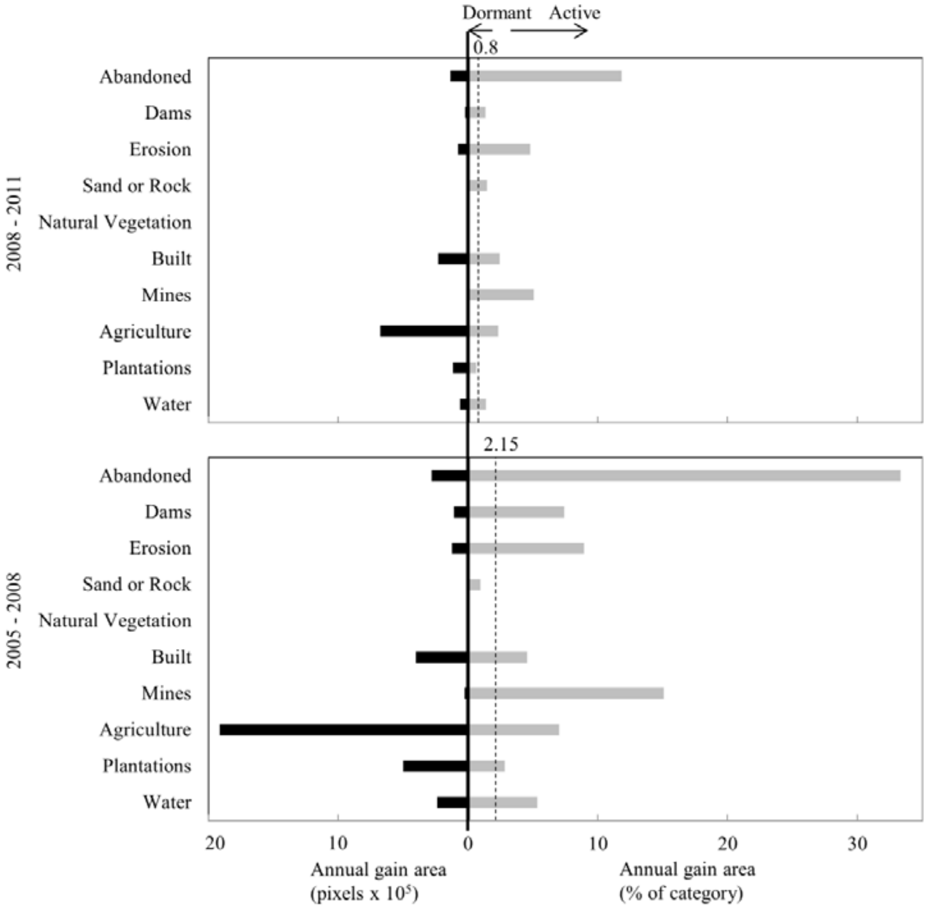

Figure 6: The gains per category for the 2005–2008 and 2008–2011 time intervals in the non-Ingonyama Trust Board (non-ITB) areas, representing privately owned areas. The bars to the left (black) indicate the gross annual area gains per category. The bars to the right (grey) represent the intensity of the annual gains. Grey bars extending to the right or left of the vertical dashed line indicate active or dormant changes, respectively, relative to a uniform intensity across the analysis period.

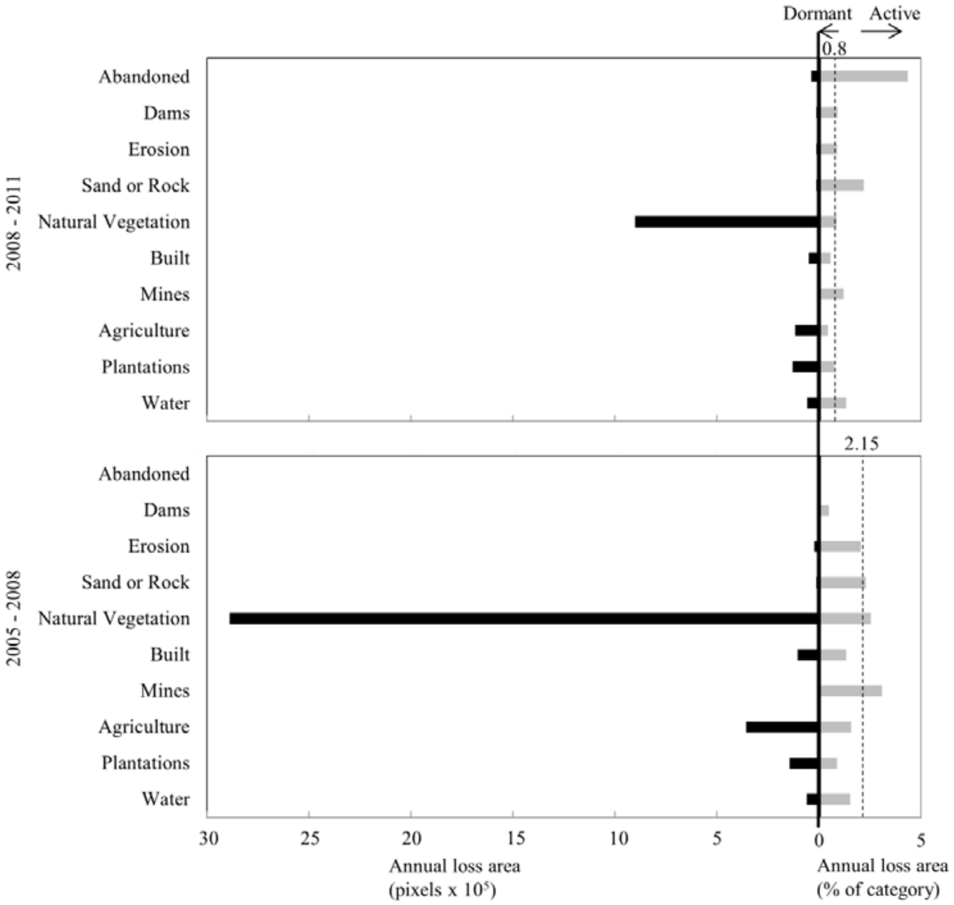

Figure 7: The losses per category for the 2005–2008 and 2008–2011 time intervals in the non-Ingonyama Trust Board (non-ITB) areas, representing privately owned areas. The bars to the left (black) indicate the gross annual area losses per category. The bars to the right (grey) represent the intensity of the annual losses. Grey bars extending to the right or left of the vertical dashed line indicate active or dormant changes, respectively, relative to a uniform intensity across the analysis period.

Appendix 8 Supplementary Information S4: Photographic examples of land-covers and transitions occurring in KwaZulu-Natal

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 8: A mosaic of current and fallow subsistence agricultural fields.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 9: Dune mining occurring along the north coast of KwaZulu-Natal (KZN). Active mining is occurring on the far right of the photograph with the dam, whilst rehabilitation of the mined dunes follows behind creating a ‘snail-trail’ effect as the mining progresses along the dune. The original dune forest is lost and either replaced by plantations, agriculture or natural vegetation dominated by *Acacia* thickets.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 10: An example of the Built category returning to natural vegetation (named Abandoned in this paper) as would be perceived on satellite imagery. This was an abandoned tea estate (the tea plants are lighter green in colour) which is now been invaded by alien invasive plants such as Bugweed (*Solanum mauritianum*) and wattle (*Acacia mearnsii*).

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 11: Extensive road infrastructure is being developed in rural areas leading to an expansion of dwellings, subsistence agriculture and associated development. This improved accessibility is increasing pressure on natural resources in terms of loss of habitat and extraction of natural resources.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 12: Numerous sports facilities are being developed in rural areas including soccer and netball fields.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 13: A rural subsistence production landscape, consisting of woodlots, sugarcane, maize and vegetable farming.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 14: Extensive erosion occurs in parts of KwaZulu-Natal.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 15: An example of an abandoned orchard. The farmhouse is derelict.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 16: The new Spring Grove dam which is part of inter-basin transfer scheme from the Mooi River to the Umgeni River to provide water to the Pietermaritzburg and Durban areas. These schemes alter hydrological flow regimes and impact aquatic diversity.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 17: A rehabilitated mine dump which could easily be interpreted as natural vegetation on a satellite image. These features are tracked in the time series analysis and remain as part of the accumulated transformation in the landscape and are thus not selected for biodiversity conservation purposes. Erosion associated with the mine can be seen on the right of the mine dump.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 18: An example of the illegal drainage of wetlands, usually for agricultural or housing purposes. In this instance the wetland is set to be rehabilitated.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 19: An example of old cultivated fields, most likely ploughed during the 1960's under inappropriate agricultural policy and subsidy schemes.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 20: An example of old cultivated fields in savanna systems. Depending on the resolution of the satellite imagery these areas may appear as natural vegetation on satellite images.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 21: Commercial timber plantations illustrating the fragmentation effects created on the original grasslands.

Photo: John Craigie, Ezemvelo KZN Wildlife

Figure 22: Extensive commercial sugarcane production.

CHAPTER 5

5. Climate-induced change of environmentally defined floristic domains: a conservation based vulnerability framework

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Climate-induced change of environmentally defined floristic domains: A conservation based vulnerability framework

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A B S T R A C T

Global climate change is having marked influences on species distributions, phenology and ecosystem composition and raises questions as to the effectiveness of current conservation strategies. Conservation planning has only recently begun to adequately account for dynamic threats such as climate change. We propose a method to incorporate climate-dynamic environmental domains, identified using specific environmental correlates of floristic composition, into conservation strategies, using the province of KwaZulu-Natal, South Africa as a case study. The environmental domains offer an approach to conservation that conserves diversity under current and future climates, recognising that the species constituting diversity may change through time. We mapped current locations of domains by identifying their positions in a multi-dimensional environmental space using a non-hierarchical iterative *k*-means clustering algorithm. Their future locations were explored using an ensemble of future climate scenarios. The HadCM2 and GFDL2.1 models represented the extreme ranges of the models. The magnitude of change in each environmental domain was calculated using Euclidean distances to determine areas of greatest and least stability for each future climate projection. Domains occurring in the savanna biome increase at the expense of domains occurring in the grassland biome, which has significant negative consequences for the species rich grasslands. The magnitude of change maps represents areas of changed climatic conditions or edaphic disjunctions. The HadCM2 model predicted the greatest overall magnitude of change across the province. Species with specific soil requirements may not be able to track changing climatic conditions. A vulnerability framework was developed that incorporated climatic stability and habitat intactness indices. The mean magnitude of change informed the potential speed of transition of domains between the vulnerability quadrants. The framework informs appropriate conservation actions to mitigate climate change impacts on biodiversity. The study explicitly links floristic pattern and climate variability and provides useful insights to facilitate conservation planning for climate change.

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1. Introduction

Global climate change is having marked influences on species distributions, phenology and ecosystem composition (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan, 2006). Ecosystems and biodiversity are further impacted by other concurrent stressors such as habitat loss, invasive species, overexploitation, pollution and disease (Mantyka-Pringle, Martin, & Rhodes, 2012). Over the next century, climate change as a result of increasing atmospheric CO_2 levels and other greenhouse gases is expected to become one of

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Abbreviations: CCAM, conformal-cubic atmospheric model; CEC, cation exchange capacity; IPCC, Intergovernmental Panel on Climate Change; KZN, KwaZulu-Natal; MAP, mean annual precipitation; MAT, mean annual temperature.

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the greatest drivers of biodiversity loss (Heller & Zavaleta, 2009), especially as climate change progresses towards the extremes.

These changes raise questions as to the effectiveness of current conservation strategies, which tend to focus on static spatial planning based on current conditions (Pressey, Cabeza, Watts, Cowling, & Wilson, 2007). Global change is turning ecosystems into rapidly changing landscapes (Hansen, Hoffman, Drews, & Mielbrecht, 2009). Thus temporal shifts in ecosystems and species need to be incorporated into conservation planning. Sound predictions of future climatic impacts on biodiversity are needed to guide adaptation and conservation planning efforts.

Much research has focussed on understanding climatic impacts on individual species using species distribution models (Erasmus, Van Jaarsveld, Chown, Kshatriya, & Wessels, 2002; Yates et al., 2010). However modelling all species occurring in diverse systems is not feasible and it is suggested instead that models are developed that predict climate effects on the distribution of communities (Yates et al., 2010), ecoregions (Hansen et al., 2009; Watson, Iwamura, & Butt, 2013) or environmental domains (Saxon, Baker, Hargrove, Hoffman, & Zganjar, 2005). Groves et al. (2012) recommend focussing conservation efforts on the geophysical environment (the metaphorical stage with the species as actors), as this maintains species diversity, and similarly, Beier and Brost (2010) recommend the use of land facets. The latter methods offer an approach to conservation that conserves diversity under current and future climates, recognising that the species constituting the diversity may change through time given their capacity to track appropriate conditions, phenological changes or physiological adaptation (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Building on these concepts we suggest that by identifying the specific environmental correlates defining current vegetation communities, the environmental domains of these communities may be identified, i.e. the environmental stage is identified. The environmental domains can then be modelled under future climate scenarios to understand how the domains may change and hence how communities are likely to respond, providing useful insights for dynamic conservation planning.

Jewitt, Goodman, Erasmus, O'Connor, and Witkowski (2015) examined the main environmental gradients correlated to floristic composition in KwaZulu-Natal (KZN) based on detailed vegetation sample plot (relevé) inventories. The study identified 23 major floristic communities in the province. The three primary correlates of floristic pattern were found to be temperature, soil base status and precipitation and can be used to define environmental domains. The study focussed on plant community composition because plants underpin trophic structure and functioning, and have been shown to be the most effective predictor of arthropod assemblage composition, a group which comprises almost two-thirds of the world's diversity (Schaffers, Raemakers, Sýkora, & ter Braak, 2008). Vertebrate species are mobile and thus may respond more readily to climate change compared to plants which are sedentary and thus lack motility other than through seed dispersal, as a means of adapting to climate change. Plant communities thus represent a good starting point to investigate dynamic climate changes.

The ability of species to track changing environmental domains will be hampered by habitat loss and land-cover change, which are recognised as major drivers of biodiversity loss (Jetz, Wilcove, & Dobson, 2007; Millenium Ecosystem Assessment, 2005; Vitousek, 1994). Indeed, in KZN an average of 1.2% per annum of natural habitat was transformed between 1994 and 2011, and it was estimated that by 2011 only 53% of the province remained in a natural state (Jewitt et al., in press). Climate change and habitat loss negatively interact contributing to the loss of biodiversity (Mantyka-Pringle et al., 2012). By considering the degree of habitat loss as well as climate stability (Watson et al., 2013), the vulnerability of environmental domains can be determined. By further considering the mean magnitude of change expected in each domain, the rate of change in each domain can be determined. We present a spatially explicit vulnerability framework using the environmental domains that can inform appropriate conservation actions and indicate where they are most appropriate.

We present an approach for understanding climatic impacts on vegetation communities by using the specific environmental correlates of these communities to define current environmental domains. Using edaphic factors assumed not to change significantly by 2050 and an ensemble of modelled future climates, future environmental domains are tracked and used to identify areas of climatic stability (potential macro-refugia) and instability (potential novel communities). We present a vulnerability framework that incorporates climatic stability, habitat intactness and the potential rate of climate change. These climate-dynamic environmental domains and the vulnerability framework will facilitate conservation planning for climate change. In particular we address the following questions: 1) What and where are the major environmental domains in KZN, determined using the three primary climatic and edaphic correlates of floristic composition in KZN? 2) How will the environmental domains change in KZN by 2050, determined using an ensemble of climatic models based on the A2 emission scenario? 3) Which areas of the province are expected to experience the least and greatest magnitude of change? 4) Which domains are the most vulnerable in terms of climate change, habitat loss and mean magnitude of change?

2. Materials and methods

2.1. Study area

KZN is a province of South Africa occurring on the eastern seaboard of the country (Fig. 1). It has a complex landscape, in terms of both biological and physical diversity. It is species rich having more than 6000 vascular plant species in an area of 93 307 km^2 and endemism levels of 16% (Scott-Shaw, 1999). It contains portions of the Maputaland-Pondoland-Albany biodiversity hotspot and the Drakensberg Alpine, Midlands, Pondoland and Maputaland centres of endemism (Mucina & Rutherford, 2006). KZN has a steep temperature gradient with mean annual temperatures (MAT) ranging between 7.9 °C and 22.9 °C, owing largely to an altitudinal gradient of over 3000 m from the Indian Ocean to the top of the Drakensberg escarpment. Similarly the province has a strong precipitation gradient with mean annual precipitation (MAP) ranging between approximately 450 mm–1900 mm. Cation exchange capacity (CEC) varies between 3 and 112 cmol kg^{-1} (ISRIC, 2013).

2.2. Analysis

The current climatic variables of MAT and MAP were derived from Schulze (2007) at a one arc minute resolution, averaged over a 30 year period (1961–1990). Using a multi-decadal range incorporates the inter-annual variability of the variables. The soil CEC data was obtained from ISRIC (International Soil Reference and Information Centre, 2013) at a 1 km resolution and averaged to a depth of 1 m. The current and future data were standardised to the same projection, resolution (1.8 km × 1.8 km) and normalised to a consistent range. All mapping work was done in ArcMap 10.2 (ArcGIS, 2013).

Future MAT and MAP data specific to KZN was calculated from climate models projected to 2050, averaged over a 20 year period (2041–2060). The future climate data were developed by the

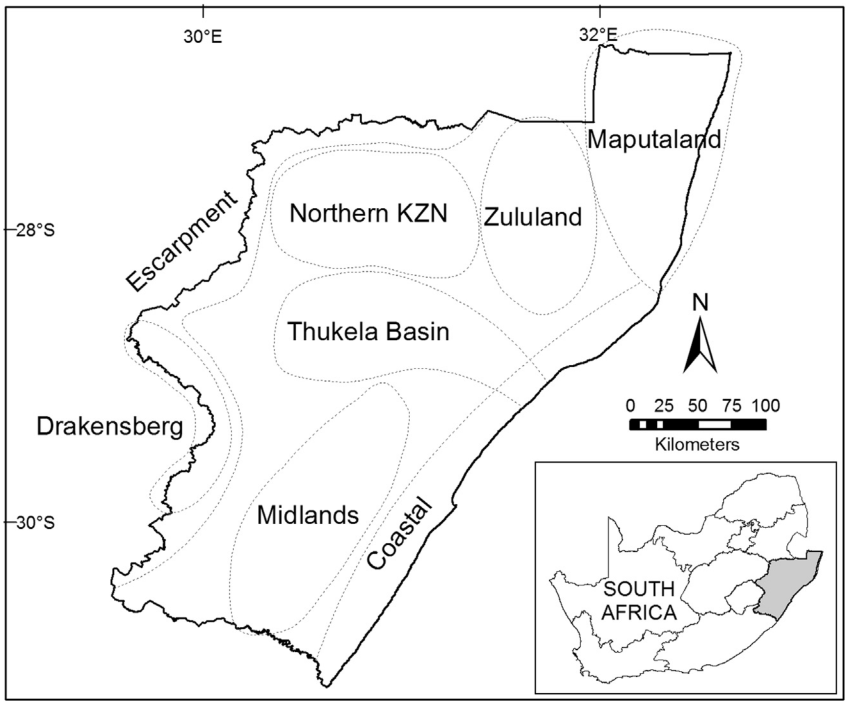

Fig. 1. The province of KwaZulu-Natal (KZN), South Africa with the regions referred to in the text.

Council for Scientific and Industrial Research (CSIR) (Engelbrecht, McGregor, & Engelbrecht, 2009; Engelbrecht et al., 2011). They used the conformal-cubic atmospheric model (CCAM), a variable-resolution global model, of the Commonwealth Scientific and Industrial Research Organisation (CSIRO) to perform dynamic downscaling which is suited to regional climate modelling. The model is good at simulating the present-day characteristics over Africa (Engelbrecht et al., 2009). The downscaling procedure forces the lower-boundary of the CCAM simulations (Engelbrecht et al., 2011) with the bias-corrected sea-surface temperature and sea-ice output of six different Coupled Global Climate Models that simulate the coupled ocean, atmosphere and land-surface processes, used in the Assessment Report Four (IPCC, 2007) of the Intergovernmental Panel on Climate Change (IPCC). The six models are CSIRO Mk 3.5, GFDL2.1 (GFDL cm2.1), GFDL2.0 (GFDL cm2.0), HadCM2, ECHAM5 and Miroc-Medres (Engelbrecht et al., 2011). All the projections are based on the A2 emission scenario of the Special Report on Emission Scenarios (SRES) (IPCC, 2000). The authors of the downscaled models recognise the need for more regional climate-change modelling studies including the use of different SRES (Engelbrecht et al., 2009; Engelbrecht et al., 2011), but at the time of this study such ensembles were not yet available. The horizontal resolution of the data is about 0.5° (approximately 60 km over southern Africa). The CCAM is problematic in that it generally overestimates rainfall totals over southern Africa, especially over and to the east of the eastern escarpment of South Africa, but this is also a problem of other Regional Climate Models (Engelbrecht et al., 2009). This modelling suite was specifically chosen rather than the later Assessment Report 5 models because they are dynamically downscaled, correlate well with current conditions and are specifically bias-corrected.

Data for each 1.8 km grid cell and environmental variable combination was written to a table. A multivariate geographic, non-hierarchical, iterative *k*-means clustering algorithm based on Euclidean distance was used to allocate each data point, including current and future variables, to an environmental domain (Hargrove & Hoffman, 2004; Saxon et al., 2005). The *k*-means clustering partitions *n* observations (grid cells) into *k* clusters (domains). The algorithm was coded in C and is dynamically load-balancing and fault-tolerant, and it performs both initial seed-finding and iterative cluster assignment in parallel. Domain seeds began initially with the most dissimilar seeds and each data point was assigned to the closest seed. After each iteration, the domain centroids were recalculated and each cell re-assigned to the new centroid until an acceptable convergence to an equilibrium classification or local optimum was obtained (<0.5% of cells changing). The final number of domains selected (23) was based on the number of floristic hierarchical clusters identified in KZN in the Jewitt, Goodman, O'Connor, and Witkowski (2015) analysis which identified the environmental correlates of floristic composition in the province using 2155 vegetation sample plots. The coordinates of the final domain centroids represent the domain's position in environmental space (Saxon et al., 2005) and is an index of their environmental similarity (Faith & Walker, 1996). The environmental domains were mapped back into geographic space.

The magnitude of predicted environmental change associated with the expansion or contraction of environmental domains was calculated by multiplying each individual current environmental domain reclassified to 0 and 1, by each predicted future domain for each climate model, to determine the nature of the environment changes over time. Since the domain centroids are located in environmental space, Euclidean distances can be used to calculate the magnitude of change associated with a grid cell changing from a current environmental domain type to a different future environmental domain. The Euclidean distances between current and future domain centroids were used to generate a dissimilarity matrix (Appendix A) which was used to generate a magnitude of change map for each future projection.

2.3. Development of the vulnerability framework

Other vulnerability frameworks consider exposure, sensitivity, adaptive capacity (Dawson, Jackson, House, Prentice, & Mace, 2011) or landscape conservation capacity and vulnerability to climate change (Gillson, Dawson, Jack, & McGeoch, 2013; Mazziotta et al., 2015). Our framework plots the Climate Stability Index against the Habitat Intactness Index thus representing two major agents of biodiversity loss, whilst also considering the mean magnitude of change expected in each domain, which is an indication of the potential speed of transition expected in each domain. The Climate Stability Index identifies the proportions of current domains that remain stable in future climate scenarios, i.e. where the magnitude of change is zero. The more stable an environmental domain is, the more robust it will be to climate change. The Habitat Intactness Index identifies the current levels of remaining natural vegetation in each domain based on the accumulated transformation as at 2011 (Jewitt et al., in press). The more natural habitat that remains in an environmental domain, the more likely it is that species will be able to naturally respond to changing climate.

The vulnerability framework places the environmental domains into quadrants that can inform appropriate conservation action (Fig. 2). Studies have shown that once 50% of the landscape is transformed a persistence threshold is reached, where after there is a rapid decline in the probability of landscapes supporting viable populations of organisms (Flather & Bevers, 2002). Hence a threshold of 50% of habitat intactness is applied. Similarly, a threshold of 50% is applied to the climate stability index. The conservation actions are climate adaptation strategies appropriate for biodiversity conservation (Gillson et al., 2013; Mawdsley, O'Malley, & Ojima, 2009). The least conservation effort is required in the top right quadrant which has sufficient remaining natural habitat and relatively large proportions of climatically stable areas, with conservation effort, resources and risk increasing towards the bottom left quadrant, which is high risk in that it is both climatically unstable and there is little natural habitat remaining. Quadrants are labelled 'Robust', 'Susceptible', 'Constrained' and 'Vulnerable' according to the degree of climatic stability and habitat intactness. Vulnerable domains require concerted conservation effort and resources if the species occurring in them are to persist into the future, a central tenet of conservation planning (Pressey et al., 2007). The likely speed of transition of domains between quadrants is indicated by overlaying the mean magnitude of change in each domain on the framework and serves to further prioritise domains requiring conservation effort.

3. Results

3.1. Climate models

The predicted change in MAP and MAT by 2050 compared to current conditions were graphed to determine which models predicted the greatest and least climate change in the province by 2050 (Fig. 3). The GFDL2.1 model predicted the lowest average temperature increase of 1.5 °C and was the only model to predict a slightly increased MAP (29 mm) in KZN. The HadCM2 model predicted an average 2.1 °C increase in MAT and a decrease of 90 mm in MAP in KZN. Since these two models represent the extremes of the predicted changes, only their results are presented for brevity. The GFDL2.1 model is good at representing large-scale current climate, including El-Niño, the drying of the African Sahel and seasonal predictions but is biased in the simulation of tropical climate and variability (www.gfdl.noaa.gov/model-development). The HadCM2 model overcomes difficulties associated with equilibrium and cold-start transient climate change experiments and captures the

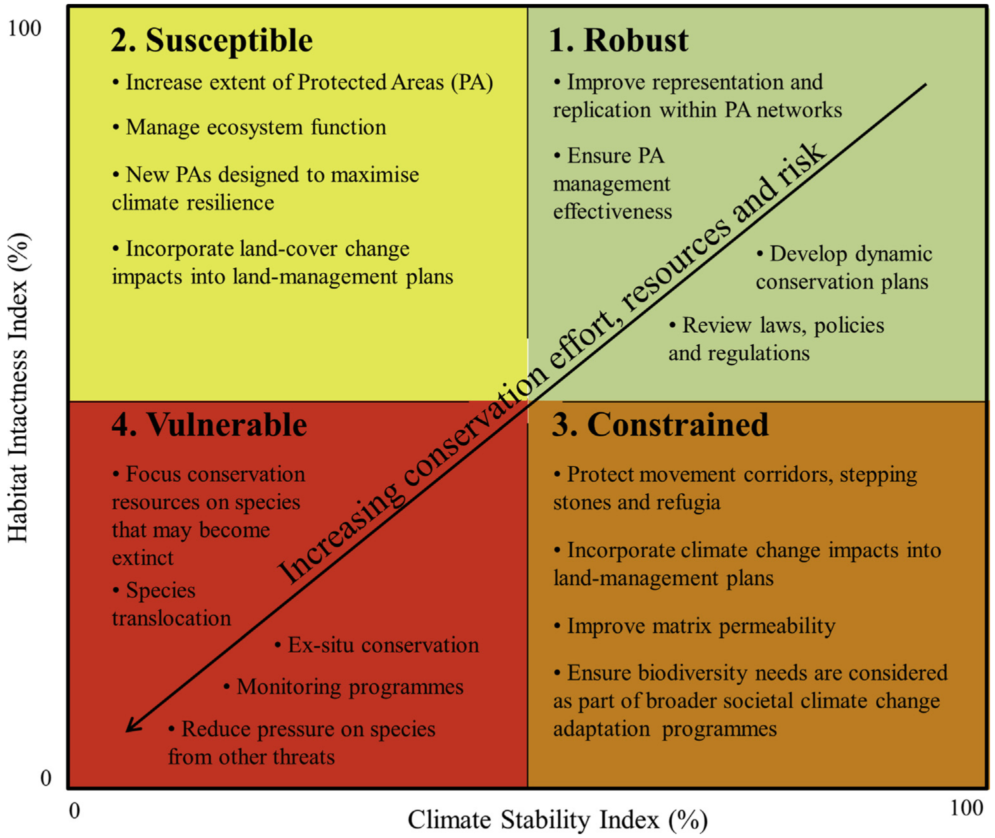

Fig. 2. The vulnerability framework with adaptation strategies appropriate for biodiversity conservation (Mawdsley et al., 2009).

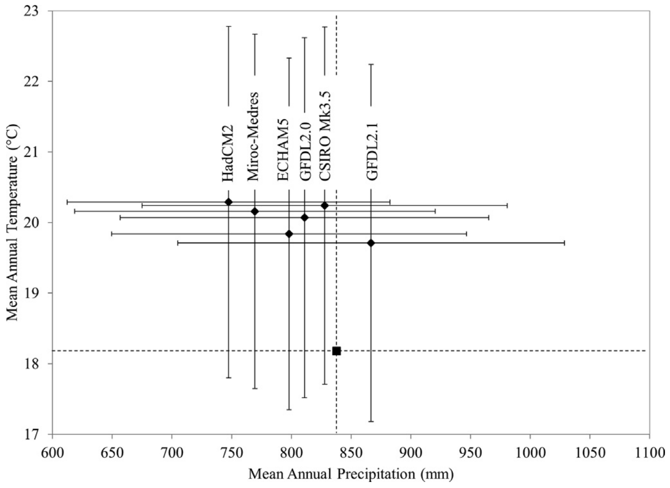

Fig. 3. The predicted change in mean annual precipitation (MAP) and mean annual temperature (MAT), with Standard Deviation bars (2041–2060), compared to current mean annual conditions, indicated by the dashed line and square symbol. Only the extremes of the models *viz.* HadCM2 and GFDL 2.1, are presented in this analysis.

observed signals of global-mean temperature changes well (www.ipcc-data.org).

3.2. *Environmental domains*

The mapped environmental domains (Fig. 4) showed marked changes by 2050. Domains 3, 12, 16, 17, 21 and 22 decrease in extent at the expense of domains 1, 4, 6, 7, 9, 10, 11, 13, 18, 19, which increase in extent (Table 1; Appendix B) in both models. The decreasing domains occur in the Midlands, low Drakensberg, Escarpment and northern KZN regions and all occur in the grassland biome (Appendix C). The increasing domains occur in Maputaland, Zululand and the Thukela basin regions and occur primarily in the savanna biome with the exception of domain 9 which occurs in grassland and domain 13 which occurs in the Indian Ocean Coastal Belt. Domains 2 and 8 remain stable across time. They represent the high altitude, cool and moist grassland domains of the high Drakensberg and are limited in extent. They remain stable given the high altitudinal range occurring in this region. Domains 5, 14, 15, 20 and 23 have variable responses across the models but occur along the coastal and south western (only domain 14) regions of the province. These differences arise due to the significantly drier conditions predicted along the coastal regions by the HadCM2 model. Temperature increases are ameliorated along the coast compared to inland areas. No domains disappear entirely during this analysis period and similarly no novel domains appear.

3.3. *Magnitude of change*

The magnitude of change maps indicate areas that will experience the greatest (darker shaded areas) or least stress (white coloured areas) from climate induced environmental change and thus where ecosystems and biodiversity will be at greater or lesser risk (Fig. 5). The HadCM2 model predicts the greater overall magnitude of change across KZN with large regions in south-western KZN and central Maputaland remaining stable but with large coastal changes. Both models predict changes in the western Thukela Basin and Northern KZN regions, and concur in part on changes in the Midlands and Zululand.

3.4. *Vulnerability framework*

In our case study (Fig. 6), domains 2, 3, 6, 8, 10, 18, and 19 consistently occur in quadrant one. They occur broadly in the Drakensberg, Midlands, parts of Zululand and western Maputaland. The size of the domain circles indicate the mean magnitude of change expected for each domain. For example, the mean magnitude of change for domain 8 in the HadCM2 model is large, thus it could potentially rapidly move to quadrant two. Consistent domains in quadrant two include 1, 4 and 21. They occur in the western Thukela Basin, northern KZN and eastern Zululand. There are no consistent domains in quadrant three as the HadCM2 model does not predict any domains in this quadrant given the large climatic changes predicted by this model. Domains 13, 15 and 20 occur in quadrant three in the GFDL2.1 model. Similarly domains 15, 20 and 23 also occur in the highly transformed, fragmented coastal parts of the province, although the models differ on the predictions of domain expansion and contraction. The most vulnerable domains are 17 and 23. These occur along the escarpment, Midlands and southern coastal regions. Species occurring in these domains are at high risk of local extirpation. The vulnerability framework results are represented spatially (Fig. 7).

4. Discussion

Our study gives an indication of the nature and extent of climate impacts in KZN using environmental domains. The current environmental domains were identified by specifically using previously identified environmental correlates of floristic community composition in KZN (Jewitt, Goodman, O'Connor et al., 2015). The nature of climate change was investigated by modelling the two extremes of an ensemble of future climate change scenarios. This provided an insight into how the environment is predicted to change, acknowledging that species will respond to climate change individualistically (Midgley, Hannah, Millar, Thuiller, & Booth, 2003). The study explicitly links floristic pattern and climate variability and provides useful insights to facilitate conservation planning for a changing climate.

The spatial distribution of the environmental domains shows where species with good dispersal ability would be able to disperse to in the increasing domains, assuming no barriers to species movements. Species restricted to diminishing domains may become stranded and would require a targeted conservation effort (Saxon et al., 2005). The models predicted conditions suiting savanna species would increase at the expense of current grassland areas. The grasslands in the province are both ancient and diverse in their suites of plant and animal species (Bond & Parr, 2010). Thus, predicted declines of grassland domains pose a significant risk to their unique biodiversity.

The magnitude of change maps highlight areas of greatest or least stress. This could be due to changed climatic conditions or a soil type disjunction. Geological formations in the province are broadly orientated in a north-south direction and are thus confounded with the east-west temperature gradient which decreases from the coast to the top of the Drakensberg Mountains. Thus species with specific soil requirements may not be able to track changing climatic conditions. The areas of stability (least stress) represent potential broad-scale macro-refugia areas. Refugia are areas that components of biodiversity can retreat to, persist in and potentially expand from in a changing climatic world (Keppel et al., 2011). Micro-refugia will exist in all domains based on the local topography, cold air drainage, prevailing wind directions and aspect (Ashcroft, 2010). The identification of broad-scale stable areas may guide the location of future protected areas which would limit climate change impacts on biodiversity. By incorporating

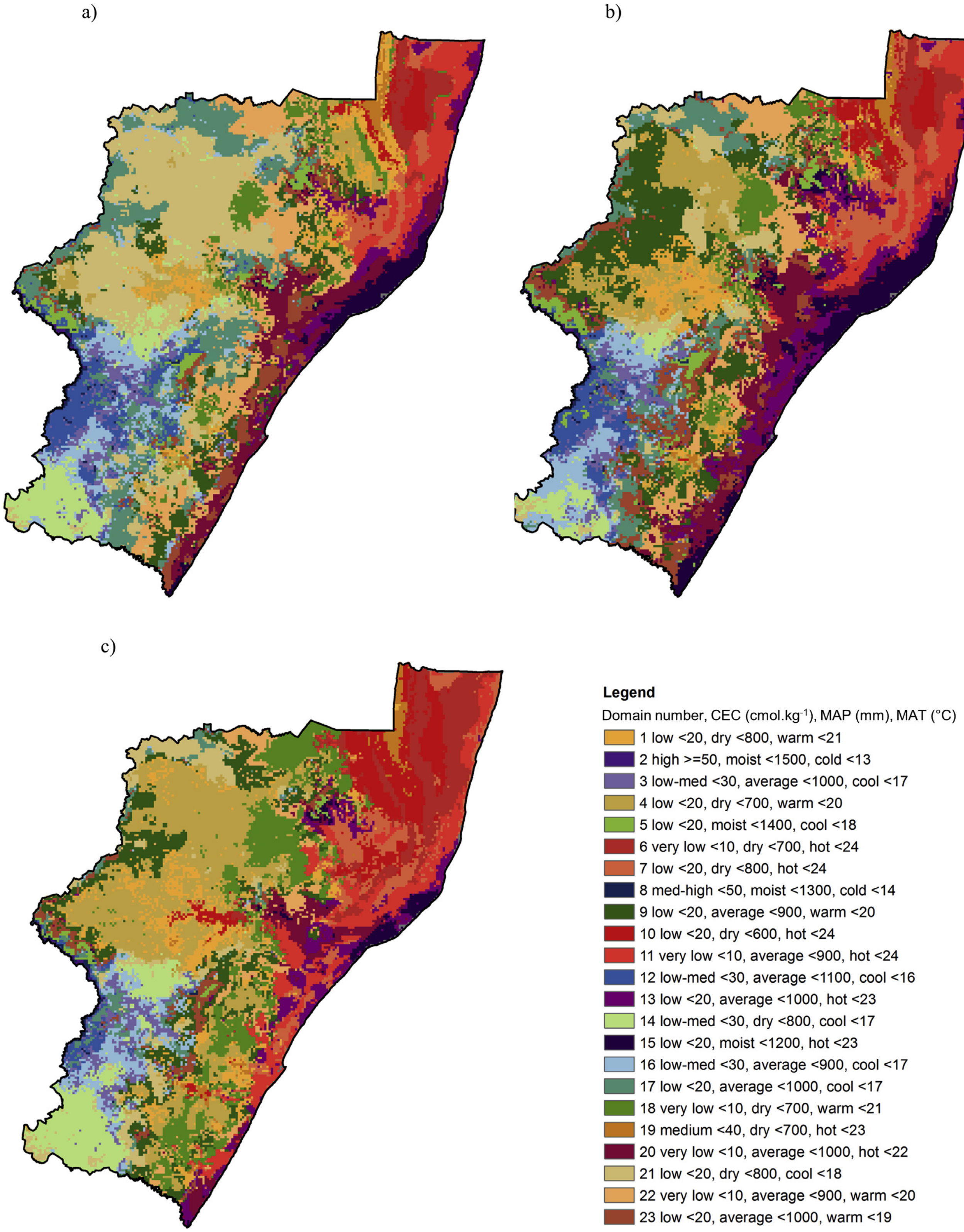

Fig. 4. The environmental domains of KwaZulu-Natal (KZN): a) Current (1961–1990) domains b) GFDL2.1 projected 2050 (2041–2060) domains c) HadCM2 projected 2050 (2041–2060) domains.

micro-refugia, climatically suitable areas for conservation corridors may be identified which could link existing protected areas, proposed protected areas and critical biodiversity areas identified through systematic conservation plans. These areas thus represent the most climate change resilient areas of the province.

The vulnerability framework informs appropriate conservation measures (Mawdsley et al., 2009). The suggested adaptation strategies are neither exhaustive nor exclusive to each quadrant, but

Table 1
Domain descriptions, current biome, spatial extent (ha) and percentage of surface area of KwaZulu-Natal, where IOCB refers to the Indian Ocean Coastal Belt.

Domain	Description (CEC (cmol kg^{-1}), MAP (mm), MAT (°C))	Current biome	Current		GFDL2.1		HadCM2	
			Area (ha)	Percentage (%)	Area (ha)	Percentage (%)	Area (ha)	Percentage (%)
1	Low <20, dry <800, warm <21	Savanna	372,694	3.9	403,153	4.3	563,662	6.0
2	High ≥50, moist <1500, cold <13	Grassland	16,085	0.2	16,427	0.2	14,716	0.2
3	Low-med <30, average <1000, cool <17	Grassland	250,859	2.7	247,094	2.6	217,320	2.3
4	Low <20, dry <700, warm <20	Savanna	303,221	3.2	663,595	7.0	1,725,209	18.3
5	Low <20, moist <1400, cool <18	Grassland	121,494	1.3	160,166	1.7	50,651	0.5
6	Very low <10, dry <700, hot <24	Savanna	178,305	1.9	236,827	2.5	634,847	6.7
7	Low <20, dry <800, hot <24	Savanna	213,897	2.3	398,020	4.2	466,809	4.9
8	Med-high <50, moist <1300, cold <14	Grassland	38,673	0.4	35,935	0.4	28,748	0.3
9	Low <20, average <900, warm <20	Grass/Savanna	499,322	5.3	1,213,225	12.9	821,365	8.7
10	Low <20, dry <600, hot <24	Savanna	151,610	1.6	249,147	2.6	584,196	6.2
11	Very low <10, average <900, hot <24	IOCB/Savanna	394,598	4.2	524,989	5.6	655,723	6.9
12	Low-med <30, average <1100, cool <16	Grassland	382,277	4.1	287,820	3.0	72,212	0.8
13	Low <20, average <1000, hot <23	IOCB/Savanna	256,334	2.7	511,984	5.4	328,546	3.5
14	Low-med <30, dry <800, cool <17	Grassland	462,702	4.9	196,443	2.1	518,829	5.5
15	Low <20, moist <1200, hot <23	IOCB	206,710	2.2	491,792	5.2	107,804	1.1
16	Low-med <30, average <900, cool <17	Grassland	497,953	5.3	437,377	4.6	302,878	3.2
17	Low <20, average <1000, cool <17	Grassland	1,068,801	11.3	561,608	6.0	188,230	2.0
18	Very low <10, dry <700, warm <21	Grass/Savanna	338,129	3.6	339,155	3.6	889,128	9.4
19	Medium <40, dry <700, hot <23	Savanna	77,687	0.8	99,933	1.1	118,071	1.3
20	Very low <10, average <1000, hot <22	Grass/IOCB/Savanna	540,732	5.7	657,777	7.0	236,485	2.5
21	Low <20, dry <800, cool <18	Grass/Savanna	1,836,093	19.5	417,527	4.4	423,003	4.5
22	Very low <10, average <900, warm <20	Grass/Savanna	818,970	8.7	645,114	6.8	299,798	3.2
23	Low <20, average <1100, warm <19	Grass/IOCB/Savanna	409,998	4.3	642,034	6.8	188,914	2.0

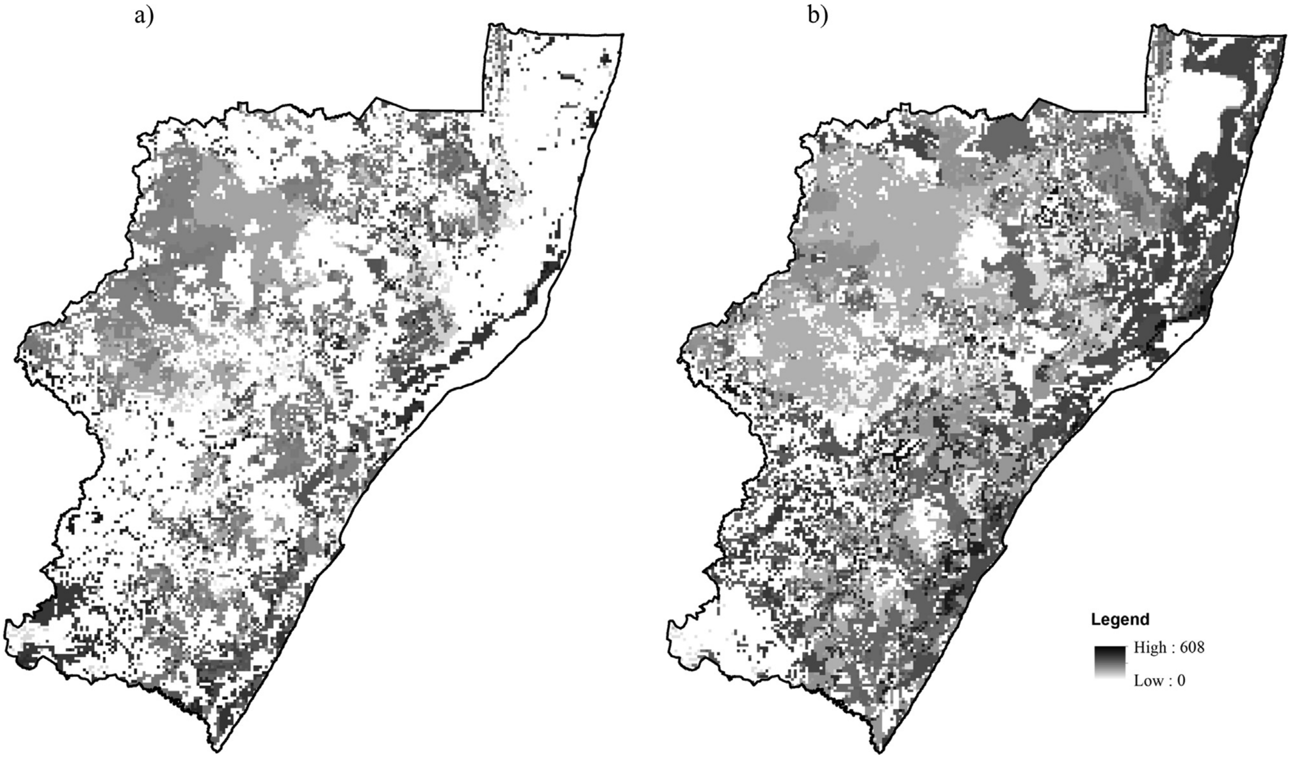

Fig. 5. The magnitude of change expected in a) the GFDL 2.1 climate model and b) the HadCM2 climate model. White areas indicate more stable areas, whereas darker areas indicate a greater magnitude of change.

rather represent a hierarchical scale of increasing conservation effort, risk and resources. For instance, appropriate legislation would benefit domains in all quadrants but if required, a monitoring programme may be developed for a threatened species even if the environmental domain occurs in the 'Robust' quadrant. The most appropriate conservation measure would depend on the conditions associated with each domain. For instance, domains 2 and 8 are considered 'Robust'. They occur in the Maloti Drakensberg Park World Heritage Site at high altitude. Thus they require effective protected area management in order to maximise resilience. Domain 13 is predicted to increase in extent in the future in both models. However this is one of the coastal domains, an area of the province that is highly transformed (Jewitt et al., in press). Thus whilst the environmental variables may permit a domain range

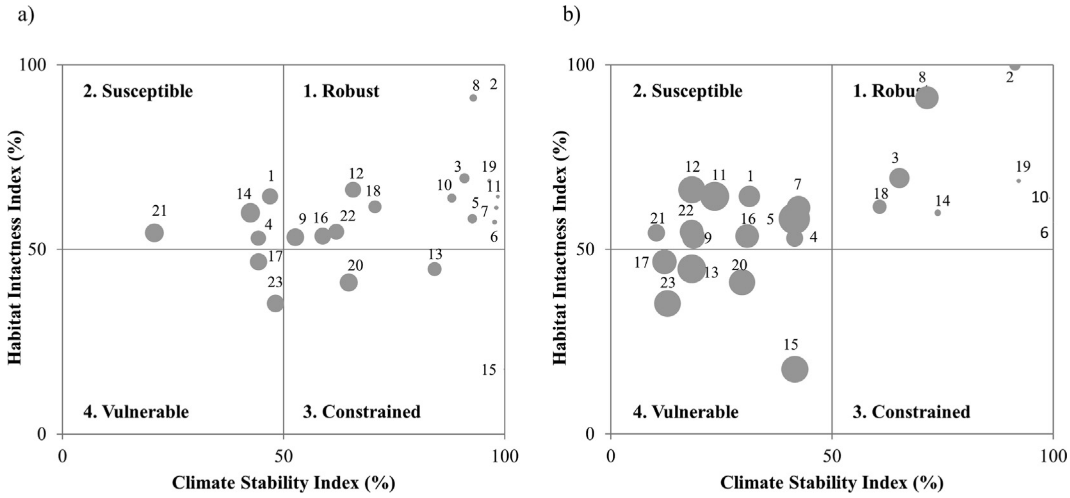

Fig. 6. The vulnerability framework for: a) the GFDL2.1 climate model, and b) the HadCM2 climate model. The Climate Stability Index reflects the percentage of the domains that remain stable in the future. The Habitat Intactness Index identifies the current levels of natural habitat remaining. The size of the circles indicates the relative mean magnitude of change expected in each domain.

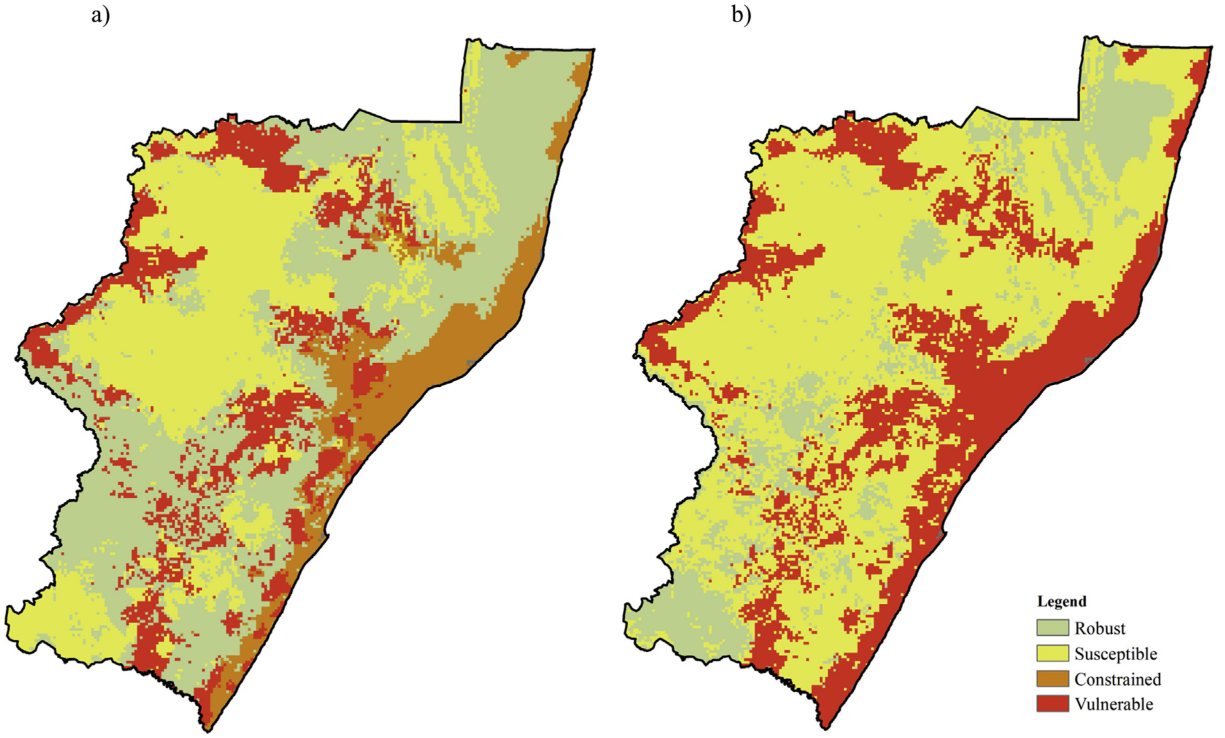

Fig. 7. The environmental domains ranked according to the vulnerability framework for: a) the GFDL2.1 climate model, and b) the HadCM2 climate model.

expansion, species occurring in this area occur in fragmented patches and so in reality would not easily be able to track these increasing domain ranges. Conservation measures that protect movement corridors and improve matrix permeability would be appropriate. The matrix surrounding protected areas consist of land-use practices that are often hostile to the survival of many species (Heller & Zavaleta, 2009), thus initiatives that mitigate these threats are beneficial to the species occurring there.

Species occurring in the 'Vulnerable' quadrant are at the most risk. Suggested conservation interventions include species translocations and *ex-situ* conservation. Assisted colonization is risky because of a lack of knowledge of the species biology of all species that may need to be translocated, an increased risk of the spread of pests and diseases, prohibitive costs (Hancock & Gallagher, 2014) and unknown consequences of introducing new species into communities (McLachlan, Hellman, & Schwartz, 2007). Reducing pressure on species from other threats may be more appropriate. *Ex-situ* conservation is a long-term activity, also with prohibitive costs (Cohen, Williams, Plucknett, & Shands, 1991). In future there may be no suitable habitat within which to re-establish species conserved through *ex-situ* conservation. Habitat loss is currently considered more significant than climate stability (Jetz et al., 2007) to biodiversity conservation, and it is also the threat that may be more easily influenced by conservation action locally (Watson et al., 2013), so securing habitat intactness should be prioritised.

Depending on the configuration of landscape transformation, an expanding domain could theoretically improve its habitat intactness index in future, but given the rapid rate of landscape transformation in the province this is unlikely, especially by 2050. If the current rates of habitat loss are not curtailed in line with the Convention on Biological Diversity (CBD) target of bringing the rate of habitat loss to zero by 2020, then the domains will move downwards in the framework.

The projections of climate change are uncertain and the models differ in their future predictions. By using an ensemble of climate models a range of possible responses to future climate change scenarios are produced. Where models concur, the uncertainty of the response is reduced and can increase the efficacy of proposed conservation adaptation strategies (Jones-Farrand, Fearer, Thogmartin, Thompson, Nelson, & Tirpak, 2011). Using adaptive management, the uncertainty associated with the effectiveness of the adaptation strategy may be evaluated (West et al., 2009) and fed back into conservation planning and management.

The future climate predictions made here are only until 2050. Far more extreme climatic change is expected by 2100 (Dawson et al., 2011; Mantyka-Pringle et al., 2012), hence diminishing domains may disappear entirely and novel domains may appear. The macro-refugia identified may not persist to the end of the century. Further research should be directed towards identifying and incorporating micro-refugia into conservation plans, and developing a network of potential conservation corridors using climatically stable areas that link protected areas and critical biodiversity areas. Should finer-scaled climatic models become available, the domains should be refined to better distinguish fine-scale heterogeneity in climate change.

5. Conclusion

By identifying climate-dynamic environmental domains that are explicitly linked to current floristic communities, the potential impacts of climate change on the biodiversity may be explored. This objective, coarse-filter approach facilitates conservation planning for common matrix plant species, and should be complemented by targeted fine-scale conservation plans for rare or threatened species. Beier et al. (2015) reviewed the use of abiotic surrogates for species representation in conservation planning and found them effective, particularly for plants and where the variables that most influence species turnover are used. Our technique may be successfully applied in regions where the environmental correlates of floristic communities are well known, or in areas where species information is scarce but the environmental gradients can be determined. The ensemble of future climate scenarios promotes an understanding of the range and degree of climate change impacts. Incorporating habitat loss, climate stability and magnitude of change into a vulnerability framework informs appropriate conservation actions to mitigate climate change impacts on biodiversity, facilitates dynamic conservation planning and highlights regions at most risk.

Author contributions

Debbie Jewitt: primary researcher and lead author,

Barend Erasmus: PhD supervisor and project advice,

Peter Goodman: PhD supervisor, statistical and project advice,

Tim O'Connor: PhD supervisor, statistical and project advice,

William Hargrove: assisted with running the *k*-means clustering algorithm,

Damian Maddalena: assisted with running the *k*-means clustering algorithm,

Ed Witkowski: PhD supervisor and project advice.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.apgeog.2015.06.004.

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Chapter 5

Appendix 9 Appendix A: Dissimilarity matrix based on Euclidean distances between domains

Appendix A Table A.1

Dissimilarity matrix based on Euclidean distances between domains.

Domain	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
1	0	761	189	43	593	107	26	511	99	139	77	337	202	17	404	141	190	25	96	243	15	114	283
2	761	0	572	804	168	868	735	250	662	900	684	424	559	777	357	620	571	786	857	518	746	647	478
3	189	572	0	232	404	296	163	323	89	327	112	149	15	204	216	48	2	214	285	55	174	75	95
4	43	804	232	0	636	64	69	554	142	96	120	380	245	27	447	184	233	18	53	286	58	157	326
5	593	168	404	636	0	700	567	82	494	732	516	255	391	609	189	452	403	618	689	350	578	479	309
6	107	868	296	64	700	0	133	619	207	32	184	445	309	92	512	248	297	82	11	350	122	221	391
7	26	735	163	69	567	133	0	485	73	165	51	311	176	43	378	115	164	51	123	217	13	88	257
8	511	250	323	554	82	619	485	0	412	650	434	174	310	527	108	370	322	537	608	268	497	398	228
9	99	662	89	142	494	207	73	412	0	238	23	238	103	115	305	42	91	125	196	144	85	14	184
10	139	900	327	96	732	32	165	650	238	0	216	476	341	123	543	280	329	114	42	382	154	253	422
11	77	684	112	120	516	184	51	434	23	216	0	260	125	93	327	64	113	102	173	166	62	37	206
12	337	424	149	380	255	445	311	174	238	476	260	0	136	353	67	196	148	363	434	95	323	224	54
13	202	559	15	245	391	309	176	310	103	341	125	136	0	218	202	61	13	227	298	41	187	88	82
14	17	777	204	27	609	92	43	527	115	123	93	353	218	0	420	157	206	10	81	259	31	130	299
15	404	357	216	447	189	512	378	108	305	543	327	67	202	420	0	263	215	430	501	161	389	291	121
16	141	620	48	184	452	248	115	370	42	280	64	196	61	157	263	0	49	166	237	102	126	27	142
17	190	571	2	233	403	297	164	322	91	329	113	148	13	206	215	49	0	215	286	53	175	76	94
18	25	786	214	18	618	82	51	537	125	114	102	363	227	10	430	166	215	0	71	268	40	139	309
19	96	857	285	53	689	11	123	608	196	42	173	434	298	81	501	237	286	71	0	339	111	210	380
20	243	518	55	286	350	350	217	268	144	382	166	95	41	259	161	102	53	268	339	0	228	129	40
21	15	746	174	58	578	122	13	497	85	154	62	323	187	31	389	126	175	40	111	228	0	99	269
22	114	647	75	157	479	221	88	398	14	253	37	224	88	130	291	27	76	139	210	129	99	0	170
23	283	478	95	326	309	391	257	228	184	422	206	54	82	299	121	142	94	309	380	40	269	170	0

Appendix 10 Appendix B: Environmental variable range and description

Appendix B

Table B.1

Environmental variable range and description.

Grouping	Cation Exchange Capacity (cmol.kg^{-1})	Description
1	<10	very low
2	<20	low
3	<30	low-medium
4	<40	medium
5	<50	medium-high
6	>=50	high
Grouping	Mean Annual Precipitation (mm)	Description
1	<600	dry
2	<700	dry
3	<800	dry
4	<900	average
5	<1000	average
6	<1100	average
7	<1200	moist
8	<1300	moist
9	<1400	moist
10	<1500	moist
Grouping	Mean Annual Temperature (°C)	Description
1	<13	cold
2	<14	cold
3	<15	cold
4	<16	cool
5	<17	cool
6	<18	cool
7	<19	warm
8	<20	warm
9	<21	warm
10	<22	hot
11	<23	hot
12	<24	hot

Appendix 11 Appendix C: The biomes of KwaZulu-Natal (KZN)

Appendix C

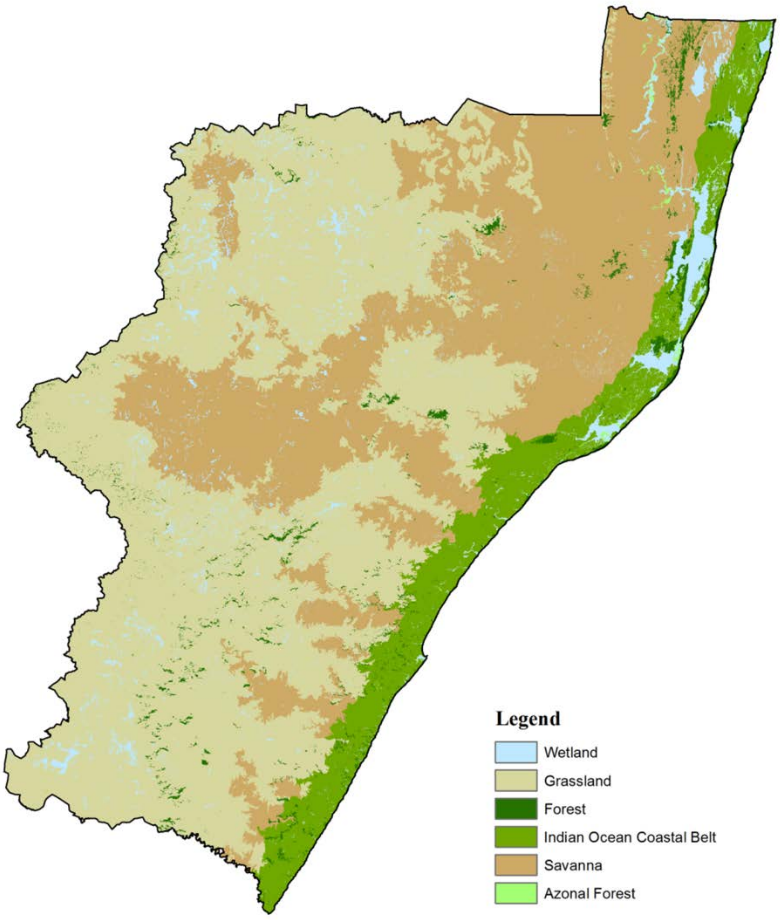

Fig. C.1. The biomes of KwaZulu-Natal (KZN).

CHAPTER 6

6. Planning for the maintenance of floristic diversity in the face of land cover and climate change

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6.1 Abstract

Context Habitat loss and climate change are primary drivers of global terrestrial biodiversity loss. Species will need to track changing environmental conditions through fragmented and transformed landscapes such as KwaZulu-Natal, South Africa. Landscape connectivity is an important tool for maintaining resilience to global change.

Objectives We develop a coarse-grained connectivity map between protected areas to aid decision-making for implementing corridors to maintain floristic diversity in the face of global change. The spatial location of corridors was prioritised using a biological underpinning of floristic composition that incorporated high beta diversity regions, important plant areas, climate refugia, and aligned to major climatic gradients driving floristic pattern.

Methods We used Linkage Mapper to develop the connectivity network. The resistance layer was based on land-cover categories with natural areas discounted according to their contribution towards meeting the biological objectives.

Results Three corridor maps were developed; a conservative option for meeting minimum corridor requirements, an optimal option for meeting a target amount of 50% of the landscape and an option including linkages in highly transformed areas. The importance of various protected areas and critical linkages in maintaining landscape connectivity are discussed, disconnected protected areas and pinch points identified where the loss of small areas could compromise landscape connectivity.

Conclusions This framework is suggested as a way to conserve floristic diversity into the future and is recommended as an approach for other global connectivity initiatives. A lack of implementation of corridors will lead to further habitat loss and fragmentation, resulting in further risk to plant diversity.

Keywords (10)

beta diversity, climate refugia, conservation planning, corridors, ecological processes, gradients, habitat, protected areas, resistance

6.2 Introduction

Global terrestrial biodiversity loss is driven primarily by land-use change and climate change (Sala et al 2000). Habitat loss and the resulting fragmentation of landscapes is currently recognised as the major driver of biodiversity loss (Fahrig 2003; Joppa et al 2016), and leads to reductions in response diversity and functional redundancy, which reduces ecosystem resilience (Laliberté et al 2010). However, climate change is expected to become a major threat in future (Dawson et al 2011). Species will need to track climates to which they are adapted, by dispersing through transformed and fragmented landscapes (Pearson and Dawson, 2005), or adapt to changing conditions *in-situ*. Transformed landscapes often jeopardise the survival of many species (Heller and Zavaleta 2009) and may present barriers to the movement of species (Pearson and Dawson 2005). Protected areas may fail to protect species in future because of the altered species distributions (Monzón et al 2011) and because the habitat within the protected areas is no longer suitable to support those species. The location of the protected areas may not be in the right location to assist species movement across transformed landscapes. Hence it is essential to manage landscapes to assist species in tracking changing conditions (Pearson and Dawson 2005).

KwaZulu-Natal (KZN) is a biologically diverse province on the east coast of South Africa. The province is undergoing rapid transformation, losing an estimated 1.2% of the natural landscape to anthropogenic transformation per annum, and by 2011 only 53% of the landscape remained in a natural state (Jewitt et al 2015b). The region is predicted to experience a 1.5 – 2.1 °C increase in mean annual temperature by 2050 and lower precipitation amounts (Jewitt et al 2015a). Given these threats and a broad objective of maintaining regional plant diversity and species persistence, it is essential that plans be made to mitigate these connectivity related threats as well as develop and implement meaningful targets for natural habitat retention.

Common climate change adaptation recommendations are to retain natural habitat linkages between existing protected areas to retain connectivity in the landscape, and increase the protected area estate to meet pre-set targets (Hannah et al 2007; Lawler 2009; Heller and Zavaleta 2009; Ackerly et al 2010; Beier and Brost 2010). Indeed, countries party to the Convention on Biological Diversity (CBD) should aim, amongst others, to a) have well connected systems of protected areas, b) increase terrestrial and inland water protection to 17%, and c) halve the rate of loss of natural habitats, by 2020. A well connected and large protected area system would aid species conservation (Hannah et al 2007), preserve ecosystem services, conserve environmental heterogeneity which is known to drive evolutionary processes and species richness (Monzón et al 2011), promote gene flow and assist species range shifts (Beier et al 2011). The question then is how do we best spatially prioritise the locations of linkages in the landscape to build ecological resilience (*sensu* Holling 1973) to climate change and efficiently identify important habitat areas required to maintain floristic diversity in future? Ecological resilience is enhanced by: high levels of biodiversity which would include high levels of response and functional diversity, heterogeneous landscapes, maintaining natural disturbance regimes (e.g. fire) and maintaining the capacity for broad-scale responses, for instance dispersal, colonization, and migration (Cumming 2011).

In the absence of biological data, and when planning for multiple species persistence, many authors suggest using abiotic variables as surrogates, such as conserving the geophysical stage (Groves et al 2012) or geophysical settings (Anderson et al 2014), using land facets (Beier and Brost 2010) or connecting climatically heterogeneous landscapes (Ackerly et al 2010). However, if biological information does exist, it would be better to incorporate this information into the framework. We suggest a biological framework for developing landscape connectivity for objectively defined plant communities, incorporating important environmental gradients, areas of high beta (β) diversity, predicted climate change impacts, and threatened and endemic plant locations.

We focus on plant communities at the landscape level because plants underpin habitat functioning and structure, and thus represent an essential starting point for understanding climate change impacts, particularly as they may not be able to follow changing environmental conditions as well as vagile species (Jewitt et al 2015a). Plants are good predictors of arthropod community composition, a group which makes up almost two-thirds of the world’s diversity (Schaffers et al 2008), hence plant communities may act as important surrogates for arthropod species. Further, habitat loss currently poses the greatest threat to plant diversity (Corlett 2016).

Environmental gradients largely define the distribution of species and ecosystems (Lawler 2009). Orientating corridor linkages along environmental gradients may assist with tracking climatic suitability into the future (Pearson and Dawson 2005). Corridors based on gradients and land-use patterns will be robust to the uncertainty in the direction and magnitude of climate change (Nuñez et al 2013). Habitat loss along environmental gradients has been found to cause homogenization along the gradient, leading to decreased adaptive phenotypic diversity (Freedman et al 2010). This may lead to a loss of diversity and reduces the ability of species to persist in changing environments. Hence protecting environmental gradients protects the genetic diversity required for adaptation and speciation (Beier and Brost 2010) in order to counter the threat of rapid environmental change leading to the domination by generalist species at the expense of specialist species (Bowers and Harris 1994).

Areas of high β-diversity are areas of high species turnover in space. Incorporating areas of high β-diversity facilitates conservation planning by capturing dominant species efficiently and thus maximises the representation of diversity in conservation plans compared to plans based only on rare and endangered species and communities (Ferrier 2002; Pressey 2004). Including these areas may assist in enhancing resilience of plant communities under global change (Fitzpatrick et al 2013), as high β-diversity areas are where species ranges are vulnerable to climate change (McKnight et al 2007). Similarly, these areas may help to preserve the ecological and evolutionary processes that create and maintain diversity (Kark and van Rensburg 2006). Hence landscape linkages should follow major environmental gradients correlated to plant composition and that drive β-diversity.

Techniques used to identify environmental gradients often exclude uncommon species as they may introduce noise to the results, and their exclusion assists in the detection of dominant relationships between environmental variables and community assemblages (McCune and Grace 2002). These rarer species are often of conservation importance however and should therefore be included in conservation initiatives. Incorporating areas containing threatened or endemic species adds to the species complement of the corridor analysis and builds a more holistic overview of plant conservation requirements.

Climate change is having marked influences on plant phenology and species distributions (Parmesan 2006). Where climate change impacts on plant communities have been studied, and climatic refugia identified, these areas should be incorporated so as to maximise species persistence into the future. Areas where an ensemble of climate change models concur, reduces the uncertainty of climate change predictions and may be used to enhance conservation adaptation strategies (Jones-Farrand et al 2011).

We aim to develop a coarse-grained, spatially explicit connectivity map to serve as a decision support tool for imparting landscape resilience for plant communities to land-cover and climate change, using KZN as a case study. The corridors will link protected areas using the lowest cost distance to maximise plant dispersal opportunities in order for plant communities to respond naturally to environmental change. We aim to prioritise the spatial location of the connectivity network using a biological underpinning of floristic composition that supports ecological and evolutionary processes and maximises species representation, in order to maintain floristic diversity in the face of global change. The implications of meeting different target amounts of natural habitat retention by changing corridor widths are explored.

6.3 Methods

6.3.1 Study area

KZN (Fig. 1) is floristically diverse containing over 6000 vascular plant species with high (16%) levels of endemism (Scott-Shaw 1999), with mesic grasslands, savannas, forests and wetlands. There are multiple gradients correlated to the floristic pattern observed in the province, primarily temperature, precipitation and soil gradients (Jewitt et al 2015c). There is a strong temperature gradient due to an altitudinal range of over 3000m over a distance of 160km from the top of the Drakensberg escarpment in the west to the warm Indian Ocean in the east, representing an approximate change of 15°C in mean annual temperature. The latitudinal gradient subtends 4° in latitude, representing a drop of approximately 2.6°C in mean annual temperature. The precipitation gradient is complex with oceanic and orographic influences and topographically induced rain shadows and mistbelt areas. The soils range from geologically young sandy soils in Maputaland to base-rich basalt, rhyolite, dolerite, mudstone, shales and tillite, and base-poor sandstones and granites (Partridge 1997).

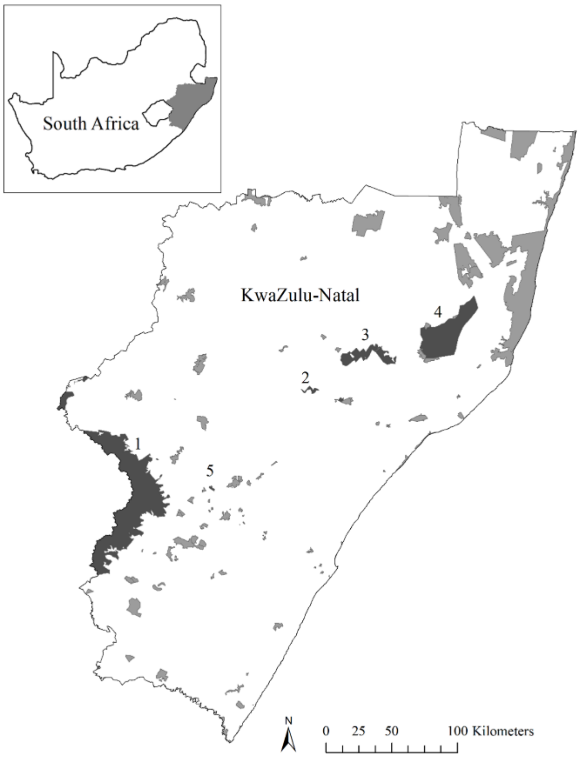
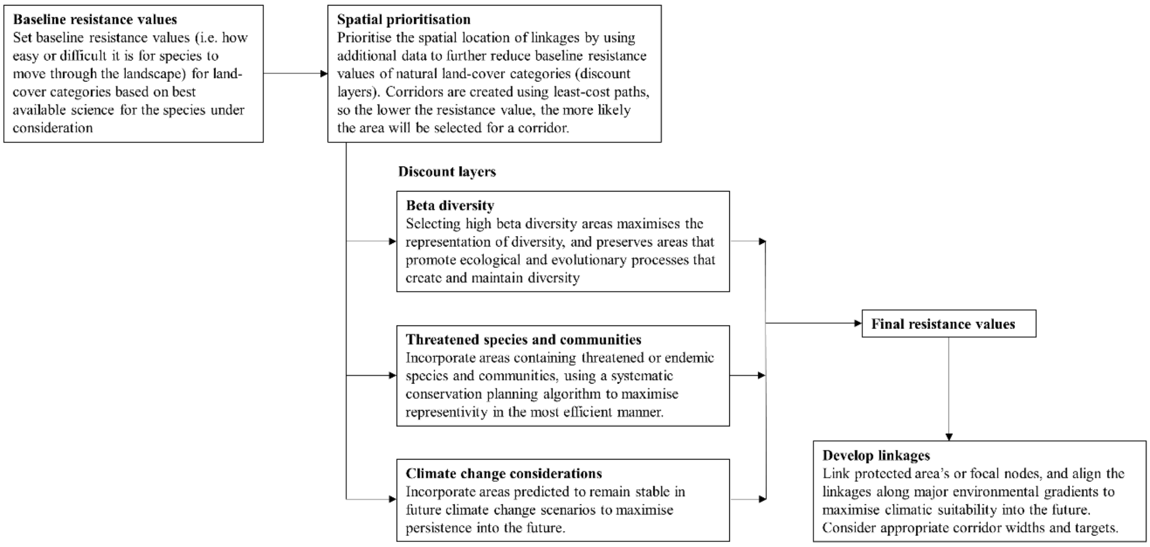


Figure 1 Study area of KwaZulu-Natal (KZN), South Africa, with the protected areas or focal nodes shown in grey. The most important protected areas for maintaining landscape connectivity are shown in dark grey, where: 1) Maloti Drakensberg Park World Heritage Site; 2) Qudeni Forest Reserve; 3) eMakhosini-Opathe Heritage Park; 4) Hluhluwe-iMfolozi Park; 5) Blue Crane Nature Reserve.

The province supports multiple forms of agriculture including commercial and subsistence crops, sugarcane, orchards and pineapples, as well as timber plantations. Agriculture expanded by 5% (496 152 ha), mining extent increased by 90%, and the number of dams increased by 45% with a 26% increase in extent, between 2005 and 2011 (Jewitt et al 2015b). The region is the second most populous in the country, with a population of approximately 10.9 million people in 2015 (Statistics South Africa 2015) or 1.17 people.ha^{-1}, which is increasing over time, and associated with an increase in the extent of the built environment (Jewitt et al 2015b). Hence transformation and fragmentation of the natural landscape is expected to intensify.

6.3.2 Framework overview

The approach adopted in this analysis is presented in Fig. 2. The first step involves developing a baseline resistance layer, developed from a land cover map. Resistance refers to the ability of a species to move across the landscape. Zero or low resistance (cost) allows free movement, high resistance (1000) allows restricted movement or may present an absolute barrier to movement (“NoData”) (Zeller et al 2012). Corridors are created using least-cost paths between protected areas, so the lower the resistance value, the more likely the area will be selected for a corridor. In order to prioritise the spatial location of the corridors, we discount natural vegetation categories (lower the resistance values) for areas of high β-diversity, threatened plant species and communities based on a systematic conservation plan and climate change refugia areas (the biological underpinning of the corridors). The data preparation section details the development of the baseline resistance values and discount layers.



Baseline resistance values
Set baseline resistance values (i.e. how easy or difficult it is for species to move through the landscape) for land-cover categories based on best available science for the species under consideration

Spatial prioritisation
Prioritise the spatial location of linkages by using additional data to further reduce baseline resistance values of natural land-cover categories (discount layers). Corridors are created using least-cost paths, so the lower the resistance value, the more likely the area will be selected for a corridor.

Discount layers

Beta diversity
Selecting high beta diversity areas maximises the representation of diversity, and preserves areas that promote ecological and evolutionary processes that create and maintain diversity

Threatened species and communities
Incorporate areas containing threatened or endemic species and communities, using a systematic conservation planning algorithm to maximise representivity in the most efficient manner.

Climate change considerations
Incorporate areas predicted to remain stable in future climate change scenarios to maximise persistence into the future.

Final resistance values

Develop linkages
Link protected area’s or focal nodes, and align the linkages along major environmental gradients to maximise climatic suitability into the future. Consider appropriate corridor widths and targets.

Figure 2 Flow diagram detailing the development of the resistance values, discount layers and corridor development.

6.3.3 Data preparation

Resistance layer

The 2011 land cover map of KZN (Ezemvelo KZN Wildlife and GeoTerraImage 2013; Ezemvelo KZN Wildlife 2013) formed the basis of the resistance layer required to develop the corridors. Minor known errors in the 2011 land cover map were corrected and historical cultivated fields (*circa* 1960/1970) added to the land cover map, to correct for known shortcomings in the land cover data due to historical agricultural practices (Supplementary Information 1). The historical cultivated fields were incorrectly identified as primary rangeland where they had not been converted to another land cover category. These secondary rangelands are depauperate in terms of the original plant species complement, especially in terms of geophytic plants and specialised species such as terrestrial orchids, and thus should not be prioritised for conservation planning.

The resistance values for the land-cover categories were informed by research related to the impact of land cover and land use on plant diversity:

- O'Connor (2005) investigated the impact of land use on plant diversity and community composition in the Highland Sourveld grasslands of South Africa using Whittaker plots. Kikuyu, ryegrass and *Eragrostis curvula* pastures were the most depauperate in species, followed by pine plantations, commercial and communal maize. These land uses supported mostly exotic or ruderal indigenous plant species and thus did not contribute to plant species conservation.
- O'Connor and Kuyler (2009) investigated the impact of land use on the biodiversity integrity of mesic grasslands in South Africa. Urban development had the greatest negative impact on landscape composition, followed by timber plantations, rural settlement under communal land tenure (due to the high levels of fragmentation and heavy grazing impact), irrigated crops, dairy, and dryland crops.
- The Biodiversity Intactness Index (BII) was a South African assessment that provided an indication of the average abundance of organisms (in this case we used the plant taxonomic group) relative to their reference populations across a range of land uses (Scholes and Biggs 2005). Urban, cultivated and timber plantation areas respectively were found to have the least fraction of original plant populations remaining.
- Anderson et al (2014) weighted land cover classes based on sensitivity analyses and expert opinion in north-eastern North America and similarly concluded that high and low intensity development and agricultural lands yielded the greatest resistance to movement through the landscape.

Based on these case studies, active cultivation, plantations, settlements, mines, rural subsistence and dam categories were interpreted as barriers to movement in the landscape and consequently set to “NoData” in the resistance layer (Table 1, resistance layer 1) i.e. corridors could not be established in these land cover types. The software excludes areas listed as “NoData” from corridor development. This resistance layer thus targeted primarily natural vegetation categories. A second resistance layer (Table 1, resistance layer 2) was created that relaxed some of the “NoData” categories such as rural dwellings, small holdings and dams, and lowered the resistance values of other anthropogenic land cover categories, in order to investigate the creation of linkages in highly transformed parts of the province.

Table 1 Resistance values, ranging between 300 – 1000, for the land cover categories and an indication of the natural categories that the discount layers were applied to. Once discounted for high β-diversity, important plant areas and climatically stable areas, the resistance values ranged between 10 – 1000, and were finally rescaled between 1 and 100. "NoData" values represent a barrier to movement in the landscape.

Code	**Land cover category**	**Discountable**	**Resistance layer 1**	**Resistance layer 2**
1	Natural Fresh Water		500	500
2	Plantation		NoData	NoData
3	Plantation clearfelled		NoData	NoData
4	Wetlands	Yes	400	400
5	Wetlands-mangrove		700	700
6	Permanent orchards (banana, citrus) irrigated		NoData	NoData
7	Permanent orchards (cashew) dryland		NoData	NoData
8	Permanent pineapples dryland		NoData	NoData
9	Sugarcane - commercial		NoData	NoData
10	Sugarcane - emerging farmer		NoData	NoData
11	Mines and quarries		NoData	NoData
12	Urban (Built-up dense settlement)		NoData	NoData
13	Golf courses/sports fields		NoData	900
14	Rural dwellings (Low density settlement)		NoData	800
15	Susbsistence (rural)		NoData	NoData
16	Annual commercial crops dryland		NoData	NoData
17	Annual commercial crops irrigated		NoData	NoData
18	Forest	No/Yes resp.	500	500
19	Dense bush (70-100cc)	Yes	400	400
20	Bushland (< 70cc)	Yes	350	350
21	Woodland	Yes	300	300
22	Grassland / bush clumps mix	Yes	300	300
23	Grassland	Yes	300	300
24	Bare sand		600	600
25	Degraded forest	No/Yes resp.	550	550
26	Degraded bushland (all types)	Yes	400	400
27	Degraded grassland	Yes	350	350
28	Old cultivated fields - grassland		800	600
29	Old cultivated fields - bushland		800	600
30	Smallholdings - grassland		NoData	700
31	Erosion		900	900
32	Bare rock		700	700
33	Alpine grass-heath	Yes	300	300
34	KZN national roads		1000	700

35	KZN main & district roads		900	600
36	Dams		NoData	800
37	Estuarine Water		700	600
38	Marine Water		NoData	NoData
39	Coastal Sand and Rock		NoData	700
40	Forest Glade	No/Yes resp.	400	400
41	Outside KZN Boundary		NoData	NoData
42	KZN Railways		900	700
43	Airfields		700	600
44	Old Plantation - high vegetation		800	600
45	Old Plantation - low vegetation		800	600
46	Rehabilitated mines - high vegetation		900	900
47	Rehabilitated mines - low vegetation		900	900
48	Historical fields		800	600

Other anthropogenic land cover class resistance values ranged between 600 and 1000 based on the supporting literature and expert opinion. Thin, linear features such as railway lines and roads were not made complete barriers to the dispersal of plant seeds. Historical agricultural fields were not considered barriers to plant dispersal and were thus included in the analyses. Baseline resistance values for natural vegetation categories ranged between 300 and 500. The natural vegetation values were further discounted depending on their position in the landscape and their contribution in terms of species turnover along environmental gradients, the presence of threatened plant species and vegetation types identified from a systematic conservation plan, and predicted climate change impacts. Equal weightings were given to the three discount layers, with each layer receiving a maximum discount of 100. Hence natural areas that met the maximum discount value of all three criteria would technically have a resistance value of zero. No areas met the maximum value for all three discount criteria, hence final resistance values ranged between 10 and 1000 with barriers set to “NoData”. The development of the discount layers are detailed below.

6.3.4 Discount layers

Gradients and β-diversity

Jewitt et al (2015c) identified the major environmental correlates of floristic composition in KZN and thereafter examined the rates of turnover along the gradients and mapped floristic β-diversity levels in KZN (Jewitt et al 2016). The gradient analysis consisted of 1643 species from 2155 plots (Jewitt et al 2015c), whilst the β-diversity analysis (Jewitt et al 2016) consisted of 997 grassland and savanna matrix species from 434 plots. Corridors were orientated in the direction of the major temperature gradients. Variable rates of turnover existed along the major environmental gradients, with the warm, drier summer regions and dystrophic soils exhibiting high levels of β-diversity. β-diversity values ranged from 4.73-33.8. Natural vegetation resistance values were discounted by 10 points for every 5 unit increase in turnover value (Supplementary Information 2). This resulted in a maximum discount of 100 for high β-diversity areas.

Plant systematic conservation plan

The development of the plant systematic conservation plan followed the framework developed by Margules and Pressey (2000) and used the C-Plan conservation planning software (Pressey et al 2005; Pressey et al 2008). The purpose of including conservation plan data was to maximise the representation of threatened and endemic plant species and vegetation types in the corridors. Irreplaceability scores were calculated based on vegetation types (n = 50), plant distribution points (n = 269) and plant species distribution models (n = 56) (Supplementary Information 3). Threatened vegetation types were weighted in the analysis. Plant species used in the systematic conservation plan were limited to savanna and grassland areas including damp areas and focussed on threatened and KZN endemic species. Forest and aquatic species were excluded, as forest and wetland biomes are small azonal components of the landscape compared to the dominant grassland and savanna vegetation types which will predominantly be used for landscape linkages. Plant red list status and nomenclature followed the Red List of South African Plants (SANBI 2015). Vegetation type status followed the provincial conservation targets and status, as developed by Ezemvelo KZN Wildlife, the mandated conservation organisation in the province (Jewitt 2014). Data was limited to species with at least 500 m spatial resolution accuracy. The planning units were based on sub-catchments with a mean size of 45 ha. Planning units that were 100% transformed, based on the accumulated transformation of the province (Jewitt et al 2015b), were excluded. Initially selected sites included protected areas managed by Ezemvelo KZN Wildlife and Stewardship sites proclaimed as protected areas as at October 2015 under the National Environmental Management: Protected Areas Act 57 of 2003.

Irreplaceability is a measure which reflects the importance of an area for meeting the achievement of the conservation goal (Pressey et al 2005). Irreplaceability values ranged between 0-1. Totally irreplaceable areas (1) were discounted by 100 points, class ‘002’ (0.6-

0.8) by 80 points, class ‘004’ (0.2-0.4) by 60 points and class ‘005’ (<0.2) by 50 points (Supplementary Information 4). There were no class ‘001’ and ‘003’ values.

Climate change

Jewitt et al (2015a) examined the projected impacts of climate change on environmental domains defined from the major floristic environmental gradient correlates. Predicted climates were represented by an envelope defined by the two most extreme scenarios for the area (Global Circulation Models HadCM2 and GFDL2.1) until 2050. Those environmental domains that experience no shift in location under future climates, are considered climatically stable areas and were discounted by 100 points (Supplementary Information 5).

6.4 Analysis

6.4.1 Final data resolution and resistance values

All data preparation analyses (rasters) were done at a pixel resolution of 20 m and across the extent of the land cover map. Once the final resistance layer was created, it was resampled to 100 m to enhance computational efficiency. Changing the resolution of the pixels has been shown to have minimal influence on connectivity results, provided that the resolution still captures relevant landscape elements such as barriers (McRae et al 2008). The final resistance values (Fig. 3) were rescaled between 1 and 100 (from 10 -1000) so that the cost-weighted distance of moving through the landscape was equal to Euclidean distance moved, in order to make the linkage statistics more meaningful (McRae and Kavanagh 2011). The edges of the study area (KZN) were buffered by 1 km to avoid boundary effects when creating the corridors (Koen et al 2010).

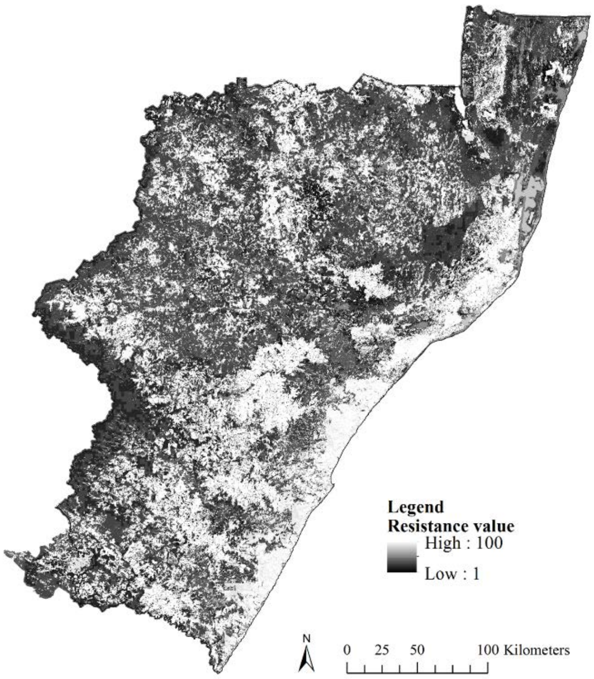


Figure 3 Final resistance values (resistance layer 1), rescaled between 1-100, discounted for important plant areas, climatically stable areas and high β-diversity areas. Lower resistance values are shown in darker shades.

6.4.2 Corridor creation

Linkage Mapper (McRae and Kavanagh 2011) was used to conduct the connectivity analysis. It uses the resistance map and a protected area vector layer to identify and create least-cost paths between the protected areas. Conefor Inputs was used to calculate the minimum Euclidean distances between all protected areas and proclaimed Stewardship sites (n=120, also referred to as focal nodes) using the nearest edge distance (Saura and Pascual-Hortal 2007). These distances are required by Linkage Mapper in order to create a table of pairs of protected areas and the distances between them. The maximum distance in the analysis was limited to 105 km which is the furthest distance between protected area closest neighbours. The network adjacency method was based on both Cost-weighted and Euclidean distances.

Several analyses were run, varying the input parameters, discount parameters and resistance values to explore corridor outputs and target amounts of habitat area. The first corridor output presented here used resistance layer 1, was not pruned and clipped to a cost-weighted width of 50 000. The corridor width is measured in cost-weighted distance units and can be used to vary the width of the corridor. The second corridor output used the same input parameters and resistance values (resistance layer 1) but was clipped to a 150 000 cost-weighted width. The third corridor output relaxed the resistance values (resistance layer 2) to allow for the creation of more corridors, especially in highly transformed areas. It was pruned to the nearest four focal node neighbours and clipped to a cost-weighted width of 50 000. In all cases, neighbouring constellations were connected and corridors that intersected core areas were dropped.

The Pinchpoint Mapper tool (McRae 2012a) and Centrality Mapper (McRae 2012b), both of which use Circuitscape (McRae et al 2013), were used to identify constrictions in corridors (pinch points) and to identify how important a link or protected area is for keeping the corridor network connected, respectively. These analyses were based on the first corridor output.

6.5 Results

The focal nodes conserve 9.08% of the landscape. The area of the province considered permeable to plant dispersal is 69% (as per resistance layer 1). In order to follow the major temperature gradient in the province, the corridors need to be orientated in approximately north-south and east-west directions. The first corridor output (Fig. 4), with a cost-distance width of 50 000, would conserve another 23% of the landscape, whereas the second corridor with a cost-distance width of 150 000, would conserve another 40.9%. Added to the protected areas, these represent 32% and 50% of the landscape respectively. The less transformed western parts of the province offer the greatest opportunity for corridor linkages, compared to the highly transformed south-eastern parts. In order to create linkages between focal nodes in this region, the resistance values needed to be relaxed (resistance layer 2), achieved by primarily adding in rural settlements and lowering some of the resistance values, as shown in corridor three (Fig. 4).

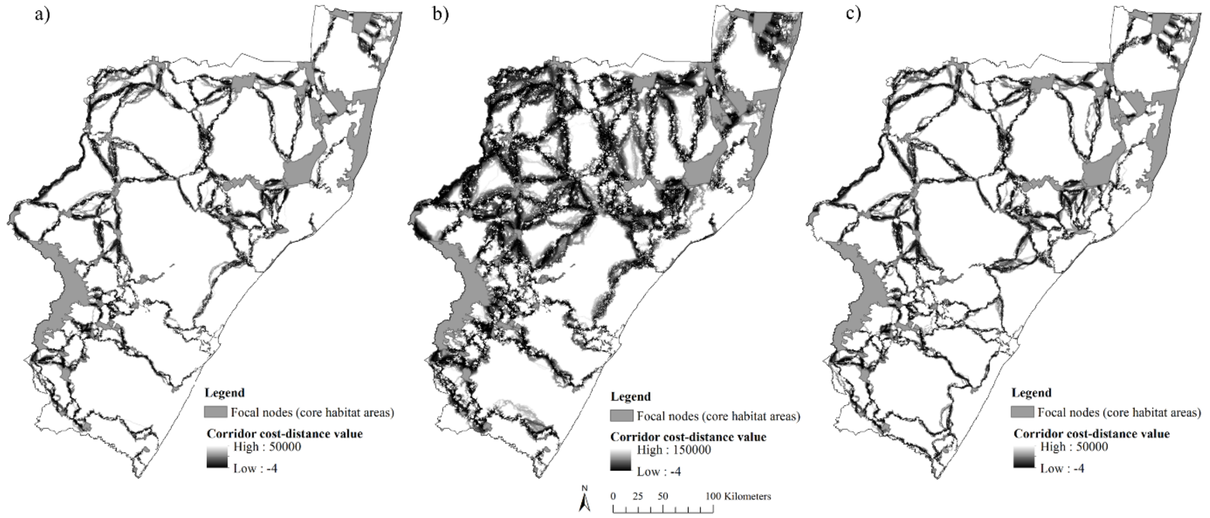


Figure 4 The various corridor outputs: a) corridor 1 (resistance layer 1), using primarily natural vegetation and a corridor cost distance width of 50 000; b) corridor 2 (resistance layer 1), using primarily natural vegetation and a corridor cost distance width of 150 000; c) corridor 3 (resistance layer 2), using relaxed resistance values and a corridor cost distance width of 50 000, in order to create essential corridors in the south-east of the province.

The statistics discussed below refer only to the first corridor map based on resistance layer 1 as it represents the most conservative conservation option and should be the minimum basis of corridors implemented. The corridor network encompasses all the vegetation types of KZN. The corridors consisted of 5.3% historical fields, indicating their importance for linking the landscape.

The irreplaceable areas of the province largely occur on the mid- and south-east coast of the province (Supplementary Information 4). This coincides with the critically endangered vegetation types (below their conservation target), which are highly transformed and fragmented. Thus it was difficult for corridors to be created in the irreplaceable 1 areas due to the high levels of transformation and fragmentation. The same proportion (3%) of irreplaceable 1 areas were represented in the corridors as occurred in the province. A greater proportion of irreplaceable class ‘002’ and ‘005’ values were represented in corridors than remaining natural in the province (12.7% versus 7.6%, and 10% versus 4.4% respectively), demonstrating the prioritisation of the spatial location of corridors in these areas.

Similarly, the areas of highest β-diversity occur on the eastern side of the province, especially in the north-eastern (Maputaland) region. The south-eastern coastal regions are highly transformed limiting the opportunity of corridor establishment but the iSimangaliso Wetland Park in the north-east, a World Heritage Site, along with the corridors and other protected areas assist in capturing areas of high β-diversity.

The predicted climatically stable areas common to both the HadCM2 and GFDL2.1 models are spread throughout the province. Approximately 22.8% of the province is predicted to have climatically stable areas across the 23 environmental domains, although only 16.2% remains natural vegetation. Protected areas contain slightly more climatically stable areas (31%). The corridors add another 6.8% of climatically stable areas, with 29% of the corridor area containing climatically stable areas.

The pinch point analysis indicates where the loss of a small area could disproportionately compromise connectivity (McRae 2012a), and is not necessarily restricted to narrow corridors (Supplementary Information 6). These areas need to be prioritised if the corridor network is to remain connected. The centrality analysis (Supplementary Information 7) investigated how important each focal node and linkage was for keeping the corridor network connected (McRae 2012b). The most important protected areas for maintaining landscape connectivity are shown in dark grey (Fig. 1). These reserves consist of a World Heritage site, provincial protected areas and privately owned stewardship sites, highlighting the contribution made by a range of protected area types and sizes.

A few protected areas were completely disconnected. Two of these are small protected areas in the large towns of Pietermaritzburg and Howick, whilst the third protected area lies in a highly productive agricultural landscape with high degrees of cultivation and timber plantations. Finer scale linkages will be required in the urban areas to link the protected areas, whilst restoration activities will be required in the agricultural landscape to link the protected area. Reserves on the far south-east of the province also exhibited low degrees of connectivity.

The protected areas in the metropolitan area of eThekwini (Durban), and other highly transformed areas, were not disconnected. This was a function of corridors being established along the national and major roads of the city. This was due to the resolution of the analysis (100 m), the vegetated road reserves adjacent to the major highways, not setting the roads to be absolute barriers, and the nature of major roads which tend to take the shortest path. These corridors can easily be removed using the software. However, the reserves within the metropolitan areas would become disconnected at the scale at which our corridors were developed. The opportunity exists to use the road reserves for plant connectivity restoration (Tikka et al 2000).

6.6 Discussion

We developed a system of corridors linking existing protected areas that were orientated along the major environmental gradients correlated with plant composition, and that where possible, included areas of high plant β-diversity, predicted climatically stable areas and areas important for threatened and endemic plant species and vegetation types. This approach provides a biological underpinning to the development of corridors and builds efficiency on where best to meet species specific targets, maximises species diversity and captures areas known to maintain ecological processes that promote genetic diversity.

The corridors were planned for thousands of plant species whose dispersal processes, especially long distance events, are mostly not known. The resistance values used may not apply equally to all plant species, and disjunctions, for instance in soil types, may preclude habitat specific species from utilising the corridors. The persistence of these species will require a targeted conservation effort. Further research is required on species specific dispersal processes and distances and the velocities at which species will be able to track changing environmental conditions, which will allow the corridors to be refined.

The method conserves both common and threatened or endemic species. Conserving common species is important as they have important ecological and functional roles in ecosystems, and in the face of global change, may be at risk of rapid decline (Lindenmayer et al 2011). In particular, species that have widespread environmental conditions are exposed to a broad range of environmental drivers.

The maps are coarse-grained and should not be used as an implementable linkage design, but should rather be used as a guide for linkage designs (Beier et al 2011). The focus or best practice should be to retain large, uninterrupted areas of pristine habitat (Williams et al 2005) which would facilitate landscape linkages, minimise edge effects and ensure adequate levels of habitat protection. It is more cost effective to take early action (Hannah et al 2007) and prevent habitat loss and degradation, than to try and restore linkages in disconnected landscapes. Where neighbouring regions have similar connectivity studies, for example the neighbouring province of Mpumalanga (Fourie et al 2015), efforts should be made to edge match the linkages to ensure biological connectivity across political governance boundaries.

The longer corridors should be prioritised for the establishment of new protected areas to shorten the distance between protected areas. Environmental impact assessments should direct appropriate conservation friendly development in the corridor areas. The discount areas outside of the corridor network could be used for finer-scale linkages, stepping stone areas or future protected areas. This is especially true of the critically endangered vegetation types and irreplaceable areas in highly transformed areas, as the highly fragmented areas did not support landscape scale corridor establishment. If corridors are to be established in these areas then there is no option but to include less optimal land cover classes. However, it is then essential that areas then be appropriately managed and restored to support plant species diversity.

Historical fields and old cultivated fields outside of the corridor network should be prioritised for future development rather than primary rangeland. Effective management of the corridors is essential, especially to prevent the spread of alien invasive species and to ensure that appropriate fire and grazing regimes are applied (Lawler 2009; Bazelet and Samways 2011). The possibility of using road reserves to link protected areas in built-up areas should be researched in this context, although this may be detrimental to animal species that disperse plant seeds, especially along the major highways. The spread of alien plants along road reserves may negate any benefits derived from increased connectivity unless adequately controlled.

Different protected areas made different contributions towards landscape connectivity, but this is known to be scale and species dependant (Maciejewski and Cummings 2016). Maciejewski and Cummings (2016) suggest that the ecological resilience of the protected area network is increased by having a range of protected area types and sizes. Our results indicate that landscape connectivity in KZN is indeed reliant on a variety of protected area types and sizes. Current government budgetary cuts for provincial conservation agencies is limiting formal protected area expansion hence other models of protected area expansion must be explored and relied upon.

6.6.1 How much is enough?

A lot of uncertainty surrounds the question of how wide corridors should be and how much of the landscape should be protected or managed for biodiversity conservation. This is dependent on the habitat specificity and dispersal ability of species (With and Crist 1995). Evidence in Swedish grasslands suggests that most species extinctions occur when the remaining area is below 10-30% (Cousins et al 2003). Species migration rates slow markedly below 25% habitat availability (Collingham and Huntley 2000). Flather and Bevis (2002) describe a persistence threshold of 30-50% of habitat amount, where after there is a rapid decline is the ability of landscapes to support viable populations. Noss et al (2012) suggest that the appropriate area should be what is biologically required to sustain species, populations and communities into the future, and suggest that 50% of a region be managed for conservation objectives. Importantly, habitat amount does not equate to habitat availability, since disconnected habitat patches may not be able to be used by dispersing species (Saura and Pascual-Hortal 2007). Ultimately, system size is fundamental to overall ecological resilience, with the probability of extinction less in larger areas (Cumming 2011).

Cowling et al (2003) suggest corridors at least 1 km wide. A rule of thumb proposed by Harris and Scheck (1991) suggests that for the movement of entire assemblages, with little known biology of the species, and that are expected to function over decades, the corridors should be kilometres wide.

Our first corridor output, along with the protected area network, conserves approximately 32% of the landscape, and the corridor widths are at least 1 km wide, with the exception of the identified pinch points. Our second corridor output, along with the protected area network, conserves approximately 50% of the available landscape and has wider corridors, and is suggested as the appropriate size to support viable populations of species into the future based on the persistence threshold (Flather and Bevis 2002) and the recommendations of Noss et al (2012). However, the south-eastern section of the province is lacking adequate connectivity and additional protected areas and linkages are required in the midlands, and should thus be prioritised for further conservation action.

6.6.2 Implementation

The corridors have been developed with a purely ecological focus (ecological resilience). If they are to succeed, they will need to be implemented following the full socioecological considerations of resilience thinking, considering institutional interventions, economics, and social impacts (Carpenter et al 2001). There will need to be political buy-in, maintained into the future (Cumming et al 2013), and cross-sectoral awareness amongst policy-makers, as well as sympathetic management from land owners across different land tenure systems (Midgley et al 2003). Perverse incentives to further transform the landscape need to be removed. Habitat and corridor targets will need to be formally adopted and mechanisms and funding to facilitate protected area expansion, strengthened. Indeed, to meet the significant challenges of global change will require transformations in resource use, social organisation and settlement (Nelson et al 2007), as well as behavioural, technological and institutional change (Dellas and Pattberg 2013). However, the rapid rate of anthropogenic transformation occurring in the province (Jewitt et al 2015b) may out-pace bureaucratic implementation timelines resulting in the implementation of corridors lagging behind development.

6.7 Conclusions

Early debate related to corridor efficacy (Simberloff et al 1992) has waned in recognition of the importance of landscape connectivity (Worboys et al 2015). The coarse-filter approach adopted here will not benefit all species all the time and despite good connectivity it is likely that some species will not be able to migrate (Groves et al 2012) or may fail to keep pace with the projected changes (Pearson and Dawson 2005). These species will require targeted conservation efforts such as translocation.

However, this framework is suggested as a way to conserve most floristic diversity into the future. Our method of providing a biological underpinning to the development of corridors and the use of appropriate target amounts of habitat preservation will maximise floristic persistence potential in the face of global change. This approach is recommended for use in other global landscape connectivity initiatives where biological data is available, in order to maintain floristic diversity. The approach may be customised to fit available data and may be complemented by the use of abiotic surrogate variables where they are known to be correlated to diversity. The spatial prioritisation of the corridors, the identification of critical linkages and protected areas to maintain landscape connectivity and the identification of vulnerable areas within the corridors guides conservation planning and action. Our framework adds to the growing body of research related to connectivity science, especially for plant communities.

This province still has the opportunity to maintain meaningful connections in the majority of the landscape. Priority should be given to preventing further habitat loss and maintaining landscape connectivity so as to maximise the potential of species to persist in the face of rapid global change. A threat analysis at the points of greatest vulnerability should be undertaken and appropriate management action taken. A lack of implementation of landscape connectivity will lead to further habitat loss and fragmentation, resulting in significant risk to plant diversity.

6.8 Acknowledgements

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Chapter 6

Appendix 12 Supplementary Information 1: Identification of the historical cultivated fields of KwaZulu-Natal

Prior to the 1960s, agricultural expansion was pronounced due to agricultural subsidies and minimum selling prices. This encouraged cultivation on marginal lands, but the fields were abandoned after the subsidies were withdrawn (Biggs and Scholes 2002). These historical fields, which have returned to secondary vegetation, are often difficult to detect on the imagery used, and at the scale at which the land cover map was developed. The secondary vegetation is depauperate in terms of the original plant species complement, especially in terms of geophytic plants and specialised species such as terrestrial orchids, and thus should not be prioritised for biodiversity conservation planning. Hence a need existed to identify historical agricultural lands.

A project was undertaken to map agricultural fields from raster scanned topographic maps, circa the 1960s and 1970s (GeoTerraImage 2013). The majority of the map sheets used were dated between 1960 and 1970 (Fig. 1), although a few earlier and later dated map sheets had to be used to complete the provincial coverage. A total of 19.3% of the province was cultivated circa 1960/1970 (Fig. 2). An additional 664 893ha (7%) of the landscape was identified as historical fields, but which were mapped as natural vegetation on the 2011 land cover map. A new category called ‘Historical fields’ was added to the land cover map to account for this. This is in addition to the ‘old cultivated fields’ category already mapped on the land cover map. More recent abandoned agricultural fields are easier to detect on the satellite imagery used to develop the land-cover map, hence they are more likely to be included in the land-cover map category ‘old cultivated fields’.

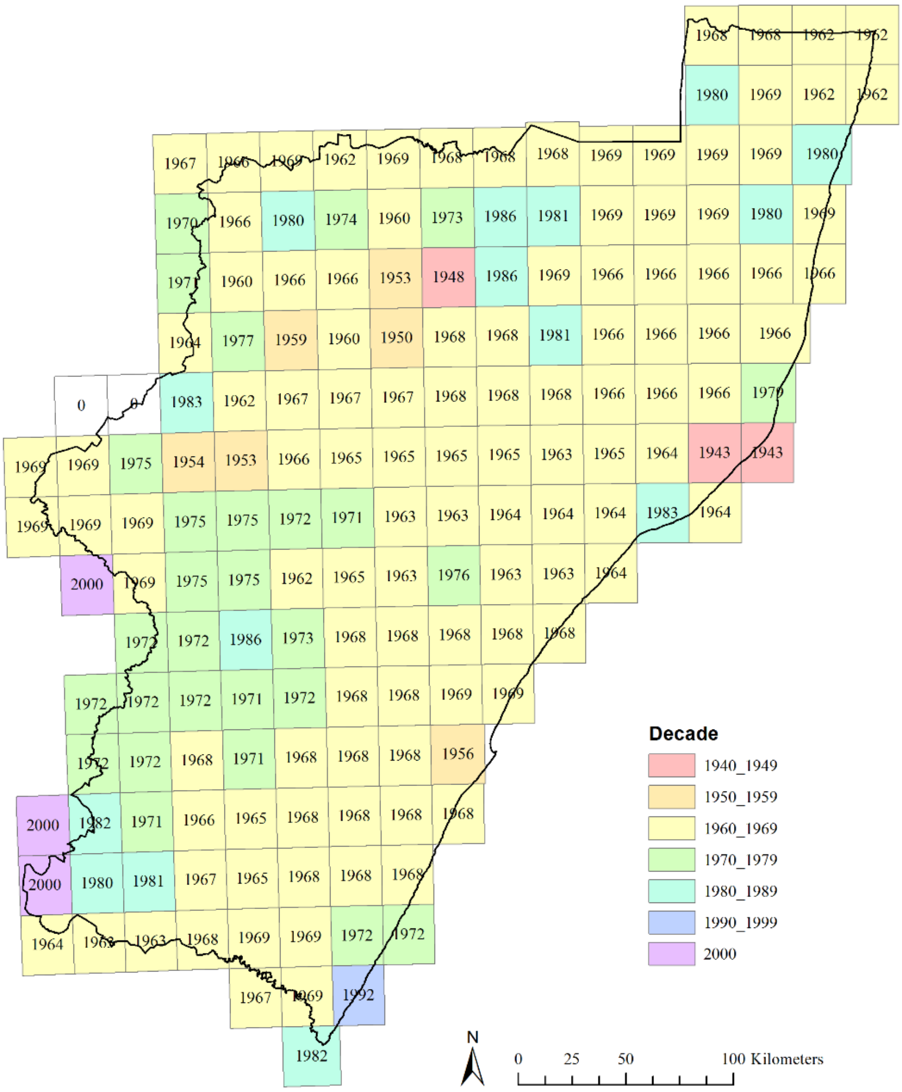

Fig. 1 Dates of the topographic maps used to determine the historical fields in KwaZulu-Natal (KZN)

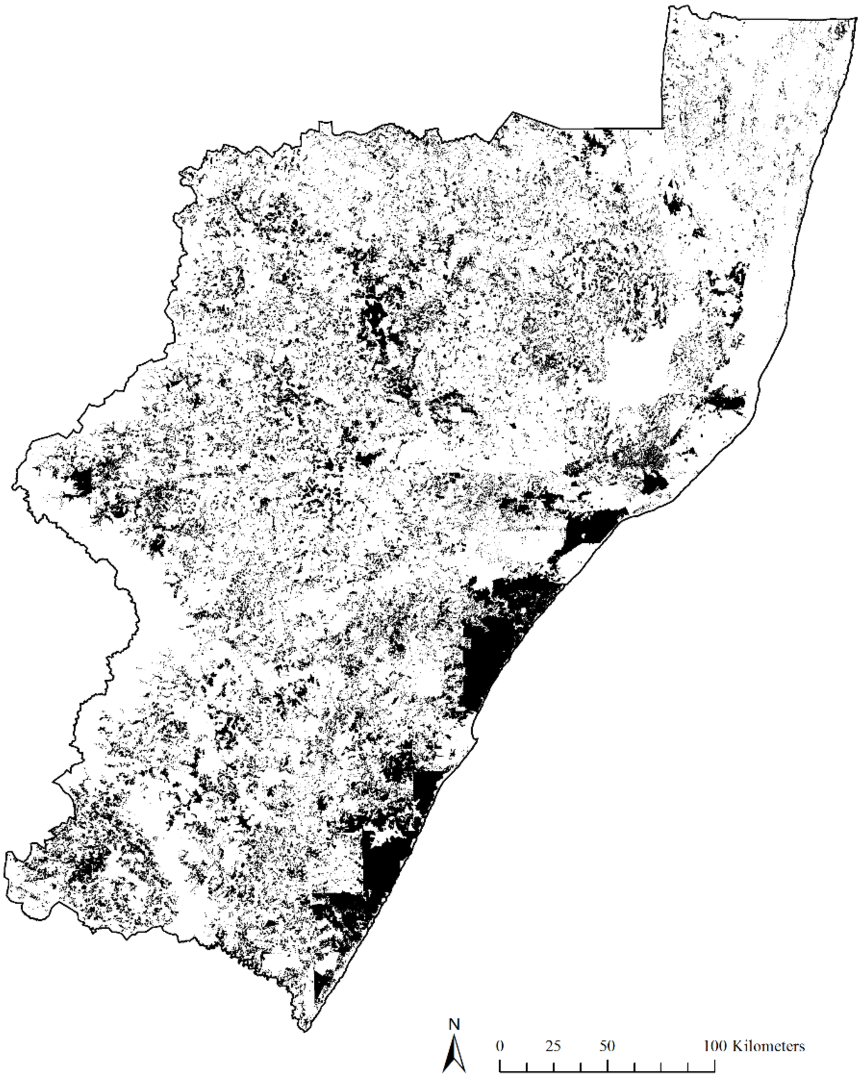

Fig. 2 Extent of historical agricultural fields (19.3%) in KwaZulu-Natal (KZN) circa 1960/1970. These may still be used as agricultural fields, or may have been abandoned or converted to another land use.

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Appendix 13 Supplementary Information 2: Beta diversity values for KwaZulu-Natal and their discount values

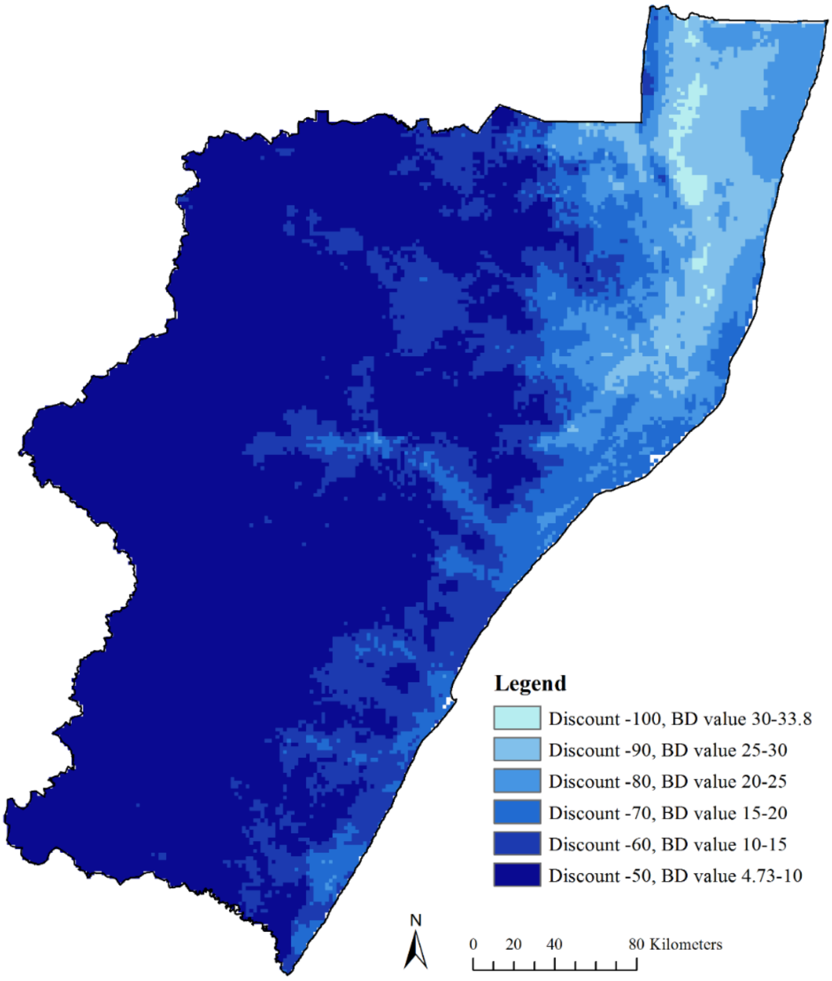

Fig. 3 Beta diversity values for KwaZulu-Natal (KZN) and their discount values (modified from Jewitt et al 2016).

Reference

Jewitt D, Goodman PS, O'Connor TG, Erasmus BFN, Witkowski ETF (2016) Mapping landscape beta diversity of plants across KwaZulu-Natal, South Africa, for aiding conservation planning. Biodivers Conserv 25:2641-2654

Appendix 14 Supplementary Information 3: List of vegetation types and plant species, and their targets used in the systematic conservation plan

Table 1. List of vegetation types, targets and conservation status used in the plant systematic conservation plan (adapted from Mucina and Rutherford (2006) who provide a detailed description of each vegetation type). Status and target amounts were determined by Jewitt (2014)

Key	Vegetation type	Target (ha)	Biome	Status
F1	Amersfoort Highveld Clay Grassland	3578	Grassland	Least Threatened
F2	Basotho Montane Shrubland	773	Grassland	Least Threatened
F3	Delagoa Lowveld	1666	Savanna	Critically Endangered
F4	Drakensberg Afroalpine Heathland	1730	Grassland	Least Threatened
F5	Drakensberg Foothill Moist Grassland	88417	Grassland	Least Threatened
F6	Drakensberg-Amathole Afromontane Fynbos	385	Grassland	Least Threatened
F7	Dry Coast Hinterland Grassland	69100	Grassland	Vulnerable
F8	East Griqualand Grassland	49471	Grassland	Vulnerable
F9	Eastern Free State Sandy Grassland	989	Grassland	Least Threatened
F10	Eastern Valley Bushveld	78438	Savanna	Least Threatened
F11	Granite Lowveld	695	Savanna	Endangered
F12	Income Sandy Grassland	100698	Grassland	Vulnerable
F13	Ithala Quartzite Sourveld	22146	Grassland	Least Threatened
F14	KaNgwane Montane Grassland	1984	Grassland	Endangered
F15	KwaZulu-Natal Coastal Belt Grassland	102876	Indian Ocean Coastal Belt	Critically Endangered
F16	KwaZulu-Natal Coastal Belt Thornveld	27980	Indian Ocean Coastal Belt	Vulnerable
F17	KwaZulu-Natal Highland Thornveld	115111	Savanna	Least Threatened
F18	KwaZulu-Natal Hinterland Thornveld	38135	Savanna	Least Threatened
F19	KwaZulu-Natal Sandstone Sourveld	44918	Grassland	Critically Endangered
F20	Lebombo Summit Sourveld	2823	Grassland	Endangered
F21	Lesotho Highland Basalt Grassland	306	Grassland	Least Threatened
F22	Low Escarpment Moist Grassland	30841	Grassland	Least Threatened

F23	Mabela Sandy Grassland	5321	Grassland	Endangered
F24	Makatini Clay Thicket	6141	Savanna	Least Threatened
F25	Maputaland Coastal Belt	55298	Indian Ocean Coastal Belt	Endangered
F26	Maputaland Pallid Sandy Bushveld	15357	Savanna	Least Threatened
F27	Maputaland Wooded Grassland	26981	Indian Ocean Coastal Belt	Endangered
F28	Midlands Mistbelt Grassland	125912	Grassland	Endangered
F29	Moist Coast Hinterland Grassland	109388	Grassland	Endangered
F30	Mooi River Highland Grassland	61395	Grassland	Vulnerable
F31	Muzi Palm Veld and Wooded Grassland	13232	Savanna	Least Threatened
F32	Northern Drakensberg Highland Grassland	19089	Grassland	Least Threatened
F33	Northern KwaZulu-Natal Moist Grassland	167261	Grassland	Vulnerable
F34	Northern Zululand Mistbelt Grassland	12166	Grassland	Vulnerable
F35	Northern Zululand Sourveld	89380	Savanna	Least Threatened
F36	Paulpietersburg Moist Grassland	68175	Grassland	Vulnerable
F37	Pondoland-Ugu Sandstone Coastal Sourveld	11289	Indian Ocean Coastal Belt	Critically Endangered
F38	Southern Drakensberg Highland Grassland	24248	Grassland	Least Threatened
F39	Southern KwaZulu-Natal Moist Grassland	53320	Grassland	Vulnerable
F40	Southern Lebombo Bushveld	27976	Savanna	Least Threatened
F41	Swaziland Sour Bushveld	9598	Savanna	Least Threatened
F42	Tembe Sandy Bushveld	21029	Savanna	Least Threatened
F43	Thukela Thornveld	53976	Savanna	Least Threatened
F44	Thukela Valley Bushveld	67121	Savanna	Least Threatened
F45	uKhahlamba Basalt Grassland	32443	Grassland	Least Threatened
F46	Wakkerstroom Montane Grassland	35554	Grassland	Least Threatened
F47	Western Maputaland Clay Bushveld	29013	Savanna	Vulnerable
F48	Western Maputaland Sandy Bushveld	2875	Savanna	Least Threatened
F49	Zululand Coastal Thornveld	12756	Savanna	Critically Endangered
F50	Zululand Lowveld	126524	Savanna	Vulnerable

Table 2. List of modelled plant species distributions, targets, plant families and their red list status used in the plant systematic conservation plan. The red list status was obtained from SANBI (2015)

Key	Scientific name	Target (ha)	Family	Red list status
F101	*Acalypha angustata* Sond.	2000	EUPHORBIACEAE	Least Concern
F102	*Acalypha entumenica* Prain	640	EUPHORBIACEAE	Endangered A2c
F103	*Alepidea amatymbica* Eckl. & Zeyh.	9	APIACEAE	Vulnerable A2d
F104	*Aloe saundersiae* (Reynolds) Reynolds	16	ASPHODELACEAE	Critically Endangered B1ab(ii,iii,iv,v)+2ab(ii,iii,iv,v)
F105	*Asclepias woodii* (Schltr.) Schltr.	640	APOCYNACEAE	Near Threatened B1ab(ii,iii)
F106	*Aspidoglossum xanthosphaerum* Hilliard	710	APOCYNACEAE	Vulnerable D2
F107	*Barleria greenii* M.Balkwill & K.Balkwill	320	ACANTHACEAE	Critically Endangered B1ab(ii,iii,iv,v)+2ab(ii,iii,iv,v)
F108	*Barleria natalensis* Lindau	6000	ACANTHACEAE	Extinct[3]
F109	*Brachystelma molaventi* Peckover & A.E.van Wyk	600	APOCYNACEAE	Vulnerable D2
F110	*Brachystelma ngomense* R.A.Dyer	600	APOCYNACEAE	Endangered B1ab(iii)+2ab(iii)
F111	*Brachystelma tenellum* R.A.Dyer	1200	APOCYNACEAE	Vulnerable D2
F148	*Brunia trigyna* (Schltr.) Class.-Bockh. & E.G.H.Oliv.	600	BRUNIACEAE	Critically Endangered B1ab(v)+2ab(v); C2a(i); D
F112	*Ceropegia rudatisii* Schltr.	2000	APOCYNACEAE	Critically Endangered (Possibly Extinct)
F113	*Dierama erectum* Hilliard	4000	IRIDACEAE	Endangered B1ab(ii,iii,iv,v)
F114	*Dierama reynoldsii* I.Verd.	8000	IRIDACEAE	Least Concern
F115	*Diospyros glandulifera* De Winter	6000	EBENACEAE	Least Concern
F116	*Drimia flagellaris* T.J.Edwards, D.Styles & N.R.Crouch	2000	HYACINTHACEAE	Rare
F117	*Encephalartos caffer* (Thunb.) Lehm.	300	ZAMIACEAE	Near Threatened A2
F118	*Encephalartos friderici-guilielmi* Lehm.	4000	ZAMIACEAE	Near Threatened A2d
F119	*Encephalartos ghellinckii* Lem.	8000	ZAMIACEAE	Vulnerable C1
F120	*Encephalartos laevifolius* Stapf & Burtt Davy	600	ZAMIACEAE	Critically Endangered A2acde
F121	*Erica revoluta* (Bolus) L.E.Davidson	62	ERICACEAE	Least Concern
F122	*Eucomis autumnalis* (Mill.) Chitt.	272	HYACINTHACEAE	Not Evaluated
F123	*Eugenia simii* Dummer[1]	551	MYRTACEAE	Vulnerable B1ab(iii,v)
F124	*Eugenia simii* Dummer[2]	249	MYRTACEAE	Vulnerable B1ab(iii,v)

F125	*Geranium natalense* Hilliard & B.L.Burtt [1]	572	GERANIACEAE	Vulnerable B1ab(i,ii,iii,iv,v)
F126	*Geranium natalense* Hilliard & B.L.Burtt[2]	4000	GERANIACEAE	Vulnerable B1ab(i,ii,iii,iv,v)
F127	*Gerbera aurantiaca* Sch.Bip.	572	ASTERACEAE	Endangered A2ac
F128	*Gerrardanthus tomentosus* Hook.f.	800	CUCURBITACEAE	Vulnerable D1+2
F129	*Helichrysum ingomense* Hilliard[1]	427	ASTERACEAE	Endangered B1ab(iii)
F130	*Helichrysum ingomense* Hilliard[2]	5773	ASTERACEAE	Endangered B1ab(iii)
F131	*Helichrysum woodii* N.E.Br.	16	ASTERACEAE	Rare
F132	*Hesperantha woodii* Baker	8000	IRIDACEAE	Least Concern
F133	*Holothrix majubensis* C.& R.H.Archer	300	ORCHIDACEAE	Rare
F134	*Huernia hystrix* (Hook.f.) N.E.Br. subsp. *parvula* (L.C.Leach) Bruyns	1200	APOCYNACEAE	Least Concern
F135	*Kniphofia albescens* Codd	4000	ASPHODELACEAE	Least Concern
F136	*Kniphofia albomontana* Baijnath	16000	ASPHODELACEAE	Least Concern
F137	*Kniphofia brachystachya* (Zahlbr.) Codd	6000	ASPHODELACEAE	Least Concern
F138	*Kniphofia breviflora* Baker	20000	ASPHODELACEAE	Least Concern
F139	*Kniphofia buchananii* Baker	16000	ASPHODELACEAE	Least Concern
F140	*Kniphofia galpinii* Baker	20000	ASPHODELACEAE	Least Concern
F141	*Kniphofia latifolia* Codd	800	ASPHODELACEAE	Endangered A2ace; B1ab(iii)+2ab(iii)
F142	*Kniphofia littoralis* Codd	4000	ASPHODELACEAE	Near Threatened B1ab(i,ii,iii,iv,v)
F143	*Leucadendron spissifolium* (Salisb. ex Knight) I.Williams subsp. *natalense* (Thode & Gilg) I.Williams	4000	PROTEACEAE	Near Threatened B2ab(i,ii,iii,iv,v)
F144	*Leucospermum gerrardii* Stapf	4000	PROTEACEAE	Near Threatened A2c
F145	*Leucospermum innovans* Rourke	500	PROTEACEAE	Endangered B1ab(ii,iii,v)+2ab(ii,iii,v)
F146	*Pachycarpus lebomboensis* D.M.N.Sm.	4000	APOCYNACEAE	Rare
F147	*Phylica natalensis* Pillans	1000	RHAMNACEAE	Vulnerable B1ab(iii)+2ab(iii)
F149	*Satyrium rhodanthum* Schltr.[1]	125	ORCHIDACEAE	Endangered B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)
F150	*Satyrium rhodanthum* Schltr.[2]	3875	ORCHIDACEAE	Endangered B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)
F151	*Schizoglossum singulare* Kupicha	600	APOCYNACEAE	Vulnerable D2
F152	*Senecio exuberans* R.A.Dyer[1]	29	ASTERACEAE	Endangered B1ab(ii,iii,iv)

F153	*Senecio exuberans* R.A.Dyer[2]	3971	ASTERACEAE	Endangered B1ab(ii,iii,iv)
F154	*Struthiola anomala* Hilliard	600	THYMELAEACEAE	Vulnerable D2
F155	*Vernonella africana* Sond.	6000	ASTERACEAE	Extinct[3]
F156	*Watsonia canaliculata* Goldblatt	1000	IRIDACEAE	Endangered B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)

[1] actual point data

[2] predicted surface

[3] based on known historical record

Table 3. List of plant species and their plant families (point data), targets and red list status used in the plant systematic conservation plan. The red list status was obtained from SANBI (2015)

Key	**Scientific name**	**Target (No. Planning units)**	**Family**	**Redlist status**
F201	*Acalypha angustata* Sond.	9	EUPHORBIACEAE	Least Concern
F202	*Acalypha entumenica* Prain	5	EUPHORBIACEAE	Endangered A2c
F229	*Afroaster ananthocladus* (Hilliard & B.L.Burtt) J.C.Manning & Goldblatt	9	ASTERACEAE	Least Concern
F231	*Afroaster confertifolius* (Hilliard & B.L.Burtt) J.C.Manning & Goldblatt	1	ASTERACEAE	Rare
F232	*Afroaster erucifolius* (Thell.) J.C.Manning & Goldblatt	1	ASTERACEAE	Least Concern
F230	*Afroaster hispida* (Thunb.) J.C.Manning & Goldblatt	24	ASTERACEAE	Least Concern
F234	*Afroaster lydenburgensis* (W.Lippert) J.C.Manning & Goldblatt	1	ASTERACEAE	Least Concern
F235	*Afroaster perfoliatus* (Oliv.) J.C.Manning & Goldblatt	4	ASTERACEAE	Least Concern
F236	*Afroaster pleiocephalus* (Harv.) J.C.Manning & Goldblatt	7	ASTERACEAE	Least Concern
F233	*Afroaster serrulatus* (Harv.) J.C.Manning & Goldblatt	4	ASTERACEAE	Least Concern
F401	*Afroligusticum wilmsianum* (H.Wolff) P.J.D.Winter	3	APIACEAE	Vulnerable B1ab(ii,iii,iv,v)
F203	*Alepidea amatymbica* Eckl. & Zeyh.	10	APIACEAE	Vulnerable A2d
F204	*Alepidea insculpta* Hilliard & B.L.Burtt	3	APIACEAE	Rare
F205	*Aloe dominella* Reynolds	3	ASPHODELACEAE	Near Threatened B1ab(ii,iii,v)
F206	*Aloe gerstneri* Reynolds	4	ASPHODELACEAE	Vulnerable B1ab(i,ii,iii,v)
F207	*Aloe inconspicua* Plowes	3	ASPHODELACEAE	Endangered B1ab(iii)+2ab(iii)
F208	*Aloe kniphofioides* Baker	2	ASPHODELACEAE	Vulnerable A2c
F209	*Aloe linearifolia* A.Berger	2	ASPHODELACEAE	Near Threatened A2c; B1ab(ii,iii,iv,v)
F210	*Aloe maculata* All.	13	ASPHODELACEAE	Least Concern
F211	*Aloe minima* Baker	11	ASPHODELACEAE	Least Concern
F212	*Aloe modesta* Reynolds	2	ASPHODELACEAE	Vulnerable B2ab(ii,iii,iv,v)
F213	*Aloe mudenensis* Reynolds	1	ASPHODELACEAE	Least Concern

F214	*Aloe prinslooi* I.Verd. & D.S.Hardy	1	ASPHODELACEAE	Near Threatened A2e
F215	*Aloe pruinosa* Reynolds	3	ASPHODELACEAE	Vulnerable B1ab(ii,iii,v)
F216	*Aloe saundersiae* (Reynolds) Reynolds	8	ASPHODELACEAE	Critically Endangered B1ab(ii,iii,iv,v)+2ab(ii,iii,iv,v)
F217	*Aloe vanbalenii* Pillans	3	ASPHODELACEAE	Least Concern
F218	*Anemone fanninii* Harv. ex Mast.	3	RANUNCULACEAE	Near Threatened A2d
F219	*Ansellia africana* Lindl.	8	ORCHIDACEAE	Declining
F220	*Anthospermum streyi* Puff	2	RUBIACEAE	Rare
F221	*Argyrolobium longifolium* (Meisn.) Walp.	3	FABACEAE	Vulnerable A2c
F222	*Argyrolobium marginatum* Bolus	2	FABACEAE	Least Concern
F223	*Asclepias bicuspis* N.E.Br.	5	APOCYNACEAE	Critically Endangered C2a(i)
F224	*Asclepias gordon-grayae* Nicholas	6	APOCYNACEAE	Endangered B1ab(iii)
F225	*Asclepias oreophila* Nicholas	8	APOCYNACEAE	Rare
F226	*Asclepias woodii* (Schltr.) Schltr.	2	APOCYNACEAE	Near Threatened B1ab(ii,iii)
F227	*Aspalathus abbottii* C.H.Stirt. & Muasya	3	FABACEAE	Vulnerable D2
F228	*Aspidoglossum demissum* Kupicha	4	APOCYNACEAE	Vulnerable D2
F237	*Athanasia grandiceps* Hilliard & B.L.Burtt	3	ASTERACEAE	Rare
F238	*Barleria greenii* M.Balkwill & K.Balkwill	6	ACANTHACEAE	Critically Endangered B1ab(ii,iii,iv,v)+2ab(ii,iii,iv,v)
F239	*Barleria natalensis* Lindau	1	ACANTHACEAE	Extinct[3]
F240	*Berkheya draco* Roessler	4	ASTERACEAE	Rare
F241	*Berkheya leucaugeta* Hilliard	3	ASTERACEAE	Rare
F242	*Berkheya pannosa* Hilliard	5	ASTERACEAE	Rare
F243	*Boophone disticha* (L.f.) Herb.	3	AMARYLLIDACEAE	Declining
F244	*Bowiea volubilis* Harv. ex Hook.f. subsp. *volubilis*	10	HYACINTHACEAE	Vulnerable A2ad
F450	*Brachystelma christianeae* Peckover	1	APOCYNACEAE	Vulnerable D2
F245	*Brachystelma franksiae* N.E.Br. subsp. *franksiae*	8	APOCYNACEAE	Vulnerable B1ab(iii,iv,v)
F246	*Brachystelma modestum* R.A.Dyer	2	APOCYNACEAE	Near Threatened B1ab(iii,v)
F247	*Brachystelma molaventi* Peckover & A.E.van Wyk	4	APOCYNACEAE	Vulnerable D2
F248	*Brachystelma natalense* (Schltr.) N.E.Br.	2	APOCYNACEAE	Critically Endangered B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v); C2a(ii)

F249	*Brachystelma ngomense* R.A.Dyer	5	APOCYNACEAE	Endangered B1ab(iii)+2ab(iii)
F250	*Brachystelma perditum* R.A.Dyer	1	APOCYNACEAE	Rare
F251	*Brachystelma petraeum* R.A.Dyer	4	APOCYNACEAE	Vulnerable D2
F252	*Brachystelma pulchellum* (Harv.) Schltr.	6	APOCYNACEAE	Near Threatened B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)
F253	*Brachystelma remotum* R.A.Dyer	2	APOCYNACEAE	Rare
F254	*Brachystelma tenellum* R.A.Dyer	3	APOCYNACEAE	Vulnerable D2
F255	*Brachystelma tenue* R.A.Dyer	1	APOCYNACEAE	Endangered A2ac; B1ab(i,ii,iii)+2ab(i,ii,iii)
F412	*Brunia trigyna* (Schltr.) Class.-Bockh. & E.G.H.Oliv.	4	BRUNIACEAE	Critically Endangered B1ab(v)+2ab(v); C2a(i); D
F256	*Brunsvigia undulata* F.M.Leight.	3	AMARYLLIDACEAE	Rare
F257	*Bulbine inflata* Oberm.	3	ASPHODELACEAE	Least Concern
F258	*Callilepis leptophylla* Harv.	2	ASTERACEAE	Declining
F259	*Calpurnia woodii* Schinz	4	FABACEAE	Vulnerable D2
F260	*Cassipourea mossambicensis* (Brehmer) Alston	2	RHIZOPHORACEAE	Least Concern
F261	*Cephalaria galpiniana* Szabó subsp. *galpiniana*	2	DIPSACACEAE	Vulnerable D2
F262	*Ceropegia cimiciodora* Oberm.	1	APOCYNACEAE	Vulnerable B2ab(ii,iii,v)
F263	*Ceropegia rudatisii* Schltr.	2	APOCYNACEAE	Critically Endangered (Possibly Extinct)
F264	*Ceropegia scabriflora* N.E.Br.	1	APOCYNACEAE	Data Deficient - Insufficient Information
F269	*Crassula obovata* Haw. var. *dregeana* (Harv.) Toelken	1	CRASSULACEAE	Vulnerable D2
F270	*Craterostigma wilmsii* Engl. ex Diels	2	SCROPHULARIACEAE	Least Concern
F271	*Crinum acaule* Baker	12	AMARYLLIDACEAE	Near Threatened B1ab(ii,iii,iv,v)
F272	*Crocosmia pearsei* Oberm.	2	IRIDACEAE	Rare
F273	*Crotalaria dura* J.M.Wood & M.S.Evans subsp. *dura*	1	FABACEAE	Near Threatened B1ab(iii)
F266	*Cyclosorus gueinzianum* (Mett.) J.P.Roux	1	THELYPTERIDACEAE	Least Concern
F274	*Cyrtanthus epiphyticus* J.M.Wood	5	AMARYLLIDACEAE	Least Concern
F275	*Cyrtanthus erubescens* Killick	2	AMARYLLIDACEAE	Rare
F276	*Cyrtanthus falcatus* R.A.Dyer	2	AMARYLLIDACEAE	Rare
F277	*Cyrtanthus nutans* R.A.Dyer	3	AMARYLLIDACEAE	Vulnerable B1ab(iii)
F278	*Cyrtanthus obliquus* (L.f.) Aiton	8	AMARYLLIDACEAE	Declining

F279	*Delosperma gracile* L.Bolus	1	AIZOACEAE	Least Concern
F280	*Dianthus mooiensis* F.N.Williams subsp. *kirkii* (Burtt Davy) S.S.Hooper	5	CARYOPHYLLACEAE	Not Evaluated
F281	*Diascia tugelensis* Hilliard & B.L.Burtt	1	SCROPHULARIACEAE	Rare
F282	*Dierama ambiguum* Hilliard	2	IRIDACEAE	Endangered A4c; B1ab(iii)
F283	*Dierama dubium* N.E.Br.	5	IRIDACEAE	Vulnerable B1ab(ii,iii,v)
F284	*Dierama erectum* Hilliard	7	IRIDACEAE	Endangered B1ab(ii,iii,iv,v)
F285	*Dierama luteoalbidum* I.Verd.	11	IRIDACEAE	Vulnerable B1ab(iii)
F286	*Dierama nixonianum* Hilliard	10	IRIDACEAE	Vulnerable B2ab(ii,iii,iv)
F287	*Dierama pallidum* Hilliard	4	IRIDACEAE	Vulnerable B1ab(ii,iii,iv,v)+2ab(ii,iii,iv,v)
F288	*Dierama pumilum* N.E.Br.	1	IRIDACEAE	Vulnerable B1ab(iii)
F289	*Dierama reynoldsii* I.Verd.	10	IRIDACEAE	Least Concern
F290	*Dierama sertum* Hilliard	4	IRIDACEAE	Near Threatened B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)
F291	*Dierama tysonii* N.E.Br.	4	IRIDACEAE	Vulnerable B1ab(ii,iii,iv,v)
F292	*Dioscorea brownii* Schinz	6	DIOSCOREACEAE	Endangered B1ab(iii,v)+2ab(iii,v); C2a(i)
F293	*Dioscorea sylvatica* Eckl.	7	DIOSCOREACEAE	Vulnerable A2cd
F294	*Diospyros glandulifera* De Winter	13	EBENACEAE	Least Concern
F295	*Disa oreophila* Bolus subsp. *erecta* H.P.Linder	3	ORCHIDACEAE	Rare
F296	*Disa sanguinea* Sond.	3	ORCHIDACEAE	Rare
F297	*Disa sankeyi* Rolfe	5	ORCHIDACEAE	Rare
F298	*Disa scullyi* Bolus	7	ORCHIDACEAE	Endangered A2c; C2a(i)
F299	*Disa tysonii* Bolus	3	ORCHIDACEAE	Rare
F300	*Disa zuluensis* Rolfe	1	ORCHIDACEAE	Endangered B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)
F301	*Disperis johnstonii* Rchb.f. ex Rolfe	1	ORCHIDACEAE	Near Threatened* D2
F302	*Disperis woodii* Bolus	4	ORCHIDACEAE	Declining
F303	*Dracosciadium italae* Hilliard & B.L.Burtt	5	APIACEAE	Vulnerable B1ab(i,ii,iii)
F304	*Dracosciadium saniculifolium* Hilliard & B.L.Burtt	1	APIACEAE	Rare
F305	*Elaeodendron transvaalense* (Burtt Davy) R.H.Archer	1	CELASTRACEAE	Near Threatened A4ad
F306	*Elaphoglossum drakensbergense* Schelpe	2	DRYOPTERIDACEAE	Least Concern

F307	*Encephalartos aemulans* Vorster	9	ZAMIACEAE	Critically Endangered B1ab(v)+2ab(v); C2a(ii)
F308	*Encephalartos caffer* (Thunb.) Lehm.	5	ZAMIACEAE	Near Threatened A2
F309	*Encephalartos cerinus* Lavranos & D.L.Goode	7	ZAMIACEAE	Critically Endangered A2acd; B1ab(i,ii,iv,v)+2ab(i,ii,iv,v); C2a(ii)
F310	*Encephalartos ferox* G.Bertol.	35	ZAMIACEAE	Near Threatened A4d
F311	*Encephalartos friderici-guilielmi* Lehm.	9	ZAMIACEAE	Near Threatened A2d
F312	*Encephalartos ghellinckii* Lem.	21	ZAMIACEAE	Vulnerable C1
F313	*Encephalartos lebomboensis* I.Verd.	12	ZAMIACEAE	Endangered A2acd; B1ab(ii,iii,iv,v)+2ab(ii,iii,iv,v)
F314	*Encephalartos msinganus* Vorster	18	ZAMIACEAE	Critically Endangered B1ab(iii,v)+2ab(iii,v); C1+2a(ii)
F315	*Encephalartos natalensis* R.A.Dyer & I.Verd.	135	ZAMIACEAE	Near Threatened A2ad
F316	*Encephalartos ngoyanus* I.Verd.	13	ZAMIACEAE	Vulnerable A4acd; C1
F317	*Encephalartos senticosus* Vorster	33	ZAMIACEAE	Vulnerable A2ace; C1
F318	*Erica albospicata* Hilliard & B.L.Burtt	7	ERICACEAE	Rare
F319	*Erica anomala* Hilliard & B.L.Burtt	5	ERICACEAE	Rare
F320	*Erica aspalathifolia* Bolus var. *aspalathifolia*	4	ERICACEAE	Declining
F321	*Erica cooperi* Bolus var. *cooperi*	1	ERICACEAE	Rare
F322	*Erica ebracteata* Bolus	9	ERICACEAE	Rare
F323	*Erica flanaganii* Bolus	1	ERICACEAE	Least Concern
F324	*Erica revoluta* (Bolus) L.E.Davidson	2	ERICACEAE	Least Concern
F325	*Eriosema latifolium* (Benth. ex Harv.) C.H.Stirt.	1	FABACEAE	Vulnerable D2
F326	*Eriosema populifolium* Benth. ex Harv. subsp. *populifolium*	2	FABACEAE	Endangered A2c; B1ab(ii,iii,iv)
F327	*Eriosema umtamvunense* C.H.Stirt.	8	FABACEAE	Endangered A2c
F328	*Eriosemopsis subanisophylla* Robyns	13	RUBIACEAE	Vulnerable A2c; B1ab(iii)+2ab(iii)
F329	*Eriospermum mackenii* (Hook.f.) Baker subsp. *mackenii*	6	RUSCACEAE	Not Evaluated
F330	*Eucomis autumnalis* (Mill.) Chitt.	20	HYACINTHACEAE	Declining
F331	*Eucomis bicolor* Baker	14	HYACINTHACEAE	Near Threatened A2d
F332	*Eucomis montana* Compton	2	HYACINTHACEAE	Declining
F333	*Eugenia simii* Dummer	8	MYRTACEAE	Vulnerable B1ab(iii,v)
F334	*Eulophia macowanii* Rolfe	2	ORCHIDACEAE	Least Concern

F335	*Eulophia speciosa* (R.Br. ex Lindl.) Bolus	29	ORCHIDACEAE	Declining
F336	*Euphorbia bupleurifolia* Jacq.	2	EUPHORBIACEAE	Declining
F337	*Euphorbia flanaganii* N.E.Br.	4	EUPHORBIACEAE	Vulnerable A2cd+4cd
F338	*Geranium drakensbergensis* Hilliard & B.L.Burtt	6	GERANIACEAE	Rare
F339	*Geranium natalense* Hilliard & B.L.Burtt	2	GERANIACEAE	Vulnerable B1ab(i,ii,iii,iv,v)
F340	*Gerbera aurantiaca* Sch.Bip.	48	ASTERACEAE	Endangered A2ac
F341	*Gerrardanthus tomentosus* Hook.f.	2	CUCURBITACEAE	Vulnerable D1+2
F342	*Gladiolus oppositiflorus* Herb	1	IRIDACEAE	Least Concern
F343	*Gladiolus symonsii* F.Bolus	11	IRIDACEAE	Rare
F344	*Gnaphalium griquense* Hilliard & B.L.Burtt	3	ASTERACEAE	Rare
F345	*Haemanthus deformis* Hook.f.	2	AMARYLLIDACEAE	Vulnerable B1ab(v)
F346	*Helichrysum album* N.E.Br.	8	ASTERACEAE	Rare
F347	*Helichrysum citricephalum* Hilliard & B.L.Burtt	1	ASTERACEAE	Critically Endangered B1ab(i,ii,iii,iv,v)
F348	*Helichrysum drakensbergense* Killick	10	ASTERACEAE	Rare
F349	*Helichrysum ingomense* Hilliard	2	ASTERACEAE	Endangered B1ab(iii)
F350	*Helichrysum longinquum* Hilliard	5	ASTERACEAE	Rare
F351	*Helichrysum nimbicola* Hilliard	1	ASTERACEAE	Rare
F352	*Helichrysum pagophilum* M.D.Hend.	2	ASTERACEAE	Rare
F353	*Helichrysum pannosum* DC.	5	ASTERACEAE	Endangered A2c
F354	*Helichrysum tenax* M.D.Hend. var. *pallidum* Hilliard & B.L.Burtt	6	ASTERACEAE	Rare
F355	*Helichrysum woodii* N.E.Br.	10	ASTERACEAE	Rare
F356	*Hesperantha ingeliensis* Hilliard & B.L.Burtt	2	IRIDACEAE	Rare
F357	*Hesperantha pubinervia* Hilliard & B.L.Burtt	1	IRIDACEAE	Rare
F358	*Hesperantha woodii* Baker	3	IRIDACEAE	Least Concern
F359	*Holothrix majubensis* C.& R.H.Archer	2	ORCHIDACEAE	Rare
F360	*Huernia hystrix* (Hook.f.) N.E.Br. subsp. *parvula* (L.C.Leach) Bruyns	5	APOCYNACEAE	Least Concern
F361	*Huttonaea oreophila* Schltr.	5	ORCHIDACEAE	Rare
F362	*Huttonaea woodii* Schltr.	1	ORCHIDACEAE	Vulnerable D2

F363	*Hypoxis hemerocallidea* Fisch., C.A.Mey. & Avé-Lall.	5	HYPOXIDACEAE	Declining
F364	*Inulanthera montana* (J.M.Wood) Källersjö	1	ASTERACEAE	Rare
F265	*Itea rhamnoides* (Harv.) Kubitzki	5	ESCALLONIACEAE	Least Concern
F365	*Jamesbrittenia silenoides* (Hilliard) Hilliard	1	SCROPHULARIACEAE	Least Concern
F366	*Killickia compacta* (Killick) Bräuchler, Heubl & Doroszenko	1	LAMIACEAE	Rare
F367	*Killickia grandiflora* (Killick) Bräuchler, Heubl & Doroszenko	1	LAMIACEAE	Rare
F368	*Kniphofia albescens* Codd	4	ASPHODELACEAE	Least Concern
F369	*Kniphofia albomontana* Baijnath	3	ASPHODELACEAE	Least Concern
F370	*Kniphofia brachystachya* (Zahlbr.) Codd	7	ASPHODELACEAE	Least Concern
F371	*Kniphofia breviflora* Baker	8	ASPHODELACEAE	Least Concern
F372	*Kniphofia buchananii* Baker	17	ASPHODELACEAE	Least Concern
F373	*Kniphofia coddiana* Cufod.	5	ASPHODELACEAE	Near Threatened B1ab(iii)
F374	*Kniphofia evansii* Baker	5	ASPHODELACEAE	Rare
F375	*Kniphofia galpinii* Baker	4	ASPHODELACEAE	Least Concern
F376	*Kniphofia ichopensis* Schinz var. *aciformis* Codd	3	ASPHODELACEAE	Data Deficient - Insufficient Information
F377	*Kniphofia latifolia* Codd	15	ASPHODELACEAE	Endangered A2ace; B1ab(iii)+2ab(iii)
F378	*Kniphofia littoralis* Codd	10	ASPHODELACEAE	Near Threatened B1ab(i,ii,iii,iv,v)
F379	*Kniphofia pauciflora* Baker	2	ASPHODELACEAE	Critically Endangered D
F380	*Kniphofia triangularis* Kunth subsp. *obtusiloba* (A.Berger) Codd	2	ASPHODELACEAE	Rare
F381	*Leucospermum gerrardii* Stapf	6	PROTEACEAE	Near Threatened A2c
F382	*Leucospermum innovans* Rourke	1	PROTEACEAE	Endangered B1ab(ii,iii,v)+2ab(ii,iii,v)
F383	*Lotononis amajubica* (Burtt Davy) B.-E.van Wyk	5	FABACEAE	Rare
F384	*Lotononis bachmanniana* Dummer	1	FABACEAE	Near Threatened A4c; B1ab(iii)+2ab(iii)
F385	*Macowania conferta* (Benth.) E.Phillips	5	ASTERACEAE	Vulnerable D2
F386	*Macowania deflexa* Hilliard & B.L.Burtt	2	ASTERACEAE	Rare
F387	*Macowania hamata* Hilliard & B.L.Burtt	3	ASTERACEAE	Rare
F388	*Melanospermum italae* Hilliard	2	SCROPHULARIACEAE	Vulnerable B1ab(iii)
F389	*Merwilla plumbea* (Lindl.) Speta	5	HYACINTHACEAE	Near Threatened A2bd

F430	*Merwilla plumbea* (Lindl.) Speta	30	HYACINTHACEAE	Near Threatened A2bd
F390	*Microcoelia obovata* Summerh.	2	ORCHIDACEAE	Data Deficient - Insufficient Information
F391	*Monsonia natalensis* R.Knuth	2	GERANIACEAE	Least Concern
F392	*Moraea graminicola* Oberm. subsp. *graminicola*	3	IRIDACEAE	Near Threatened A2c; B1ab(iii)
F393	*Moraea hiemalis* Goldblatt	3	IRIDACEAE	Vulnerable B1ab(i,ii,iii,iv,v)
F394	*Moraea unibracteata* Goldblatt	3	IRIDACEAE	Vulnerable B1ab(ii,iii,iv,v)
F395	*Nerine bowdenii* Watson	1	AMARYLLIDACEAE	Rare
F396	*Nesaea wardii* Immelman	2	LYTHRACEAE	Vulnerable D2
F397	*Ophrestia oblongifolia* (E.Mey.) H.M.L.Forbes var. *velutinosa* H.M.L.Forbes	3	FABACEAE	Least Concern
F398	*Osteospermum attenuatum* Hilliard & B.L.Burtt	2	ASTERACEAE	Rare
F267	*Osteospermum moniliferum* L. subsp. *moniliferum*	1	ASTERACEAE	Least Concern
F399	*Pachycarpus lebomboensis* D.M.N.Sm.	2	APOCYNACEAE	Rare
F400	*Pachycarpus rostratus* N.E.Br.	1	APOCYNACEAE	Critically Endangered (Possibly Extinct)
F402	*Phylica natalensis* Pillans	3	RHAMNACEAE	Vulnerable B1ab(iii)+2ab(iii)
F403	*Phymaspermum villosum* (Hilliard) Källersjö	2	ASTERACEAE	Rare
F404	*Polygala praticola* Chodat	5	POLYGALACEAE	Data Deficient - Insufficient Information
F405	*Polystachya zuluensis* L.Bolus	1	ORCHIDACEAE	Data Deficient - Insufficient Information
F406	*Protea comptonii* Beard	8	PROTEACEAE	Near Threatened A2c
F407	*Protea dracomontana* Beard	11	PROTEACEAE	Least Concern
F408	*Protea nubigena* Rourke	1	PROTEACEAE	Critically Endangered B1ab(v)+2ab(v); D
F409	*Pseudoscolopia polyantha* Gilg	9	SALICACEAE	Near Threatened B1ab(iii,v)
F410	*Psoralea abbottii* C.H.Stirt.	4	FABACEAE	Vulnerable B1ab(i,ii,iii,iv,v)
F268	*Pterygodium nigrescens* (Sond.) Schltr.	8	ORCHIDACEAE	Least Concern
F411	*Raphionacme lucens* Venter & R.L.Verh.	9	APOCYNACEAE	Near Threatened D2
F413	*Restio zuluensis* H.P.Linder	12	RESTIONACEAE	Vulnerable B1ab(iii)+2ab(iii)
F414	*Rhodohypoxis incompta* Hilliard & B.L.Burtt	5	HYPOXIDACEAE	Rare
F417	*Riocreuxia woodii* N.E.Br.	1	APOCYNACEAE	Critically Endangered (Possibly Extinct)
F418	*Salpinctium natalense* (C.B.Clarke) T.J.Edwards	3	ACANTHACEAE	Rare

F419	*Sandersonia aurantiaca* Hook.	15	OLCHICACEAE	Declining
F420	*Satyrium microrrhynchum* Schltr.	6	ORCHIDACEAE	Rare
F421	*Satyrium rhodanthum* Schltr.	13	ORCHIDACEAE	Endangered B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)
F422	*Schizochilus bulbinella* (Rchb.f.) Bolus	5	ORCHIDACEAE	Rare
F423	*Schizochilus gerrardii* (Rchb.f.) Bolus	10	ORCHIDACEAE	Endangered B1ab(iii)+2ab(iii)
F424	*Schizoglossum bidens* E.Mey. subsp. *hirtum* Kupicha	1	APOCYNACEAE	Data Deficient - Insufficient Information
F425	*Schizoglossum elingue* N.E.Br. subsp. *purpureum* Kupicha	1	APOCYNACEAE	Rare
F426	*Schizoglossum ingomense* N.E.Br.	2	APOCYNACEAE	Threatened
F427	*Schizoglossum montanum* R.A.Dyer	2	APOCYNACEAE	Rare
F428	*Schizoglossum peglerae* N.E.Br.	1	APOCYNACEAE	Endangered B1ab(ii,iii,v)+2ab(ii,iii,v)
F429	*Schizoglossum quadridens* N.E.Br.	1	APOCYNACEAE	Data Deficient - Insufficient Information
F415	*Searsia grandidens* (Harv. ex Engl.) Moffett	3	ANACARDIACEAE	Least Concern
F416	*Searsia rudatisii* (Engl.) Moffett	5	ANACARDIACEAE	Endangered A2ac
F431	*Selago longiflora* Rolfe	4	SCROPHULARIACEAE	Endangered B1ab(i,ii,iii,iv,v)
F432	*Selago monticola* J.M.Wood & M.S.Evans	8	SCROPHULARIACEAE	Least Concern
F433	*Senecio dregeanus* DC.	13	ASTERACEAE	Vulnerable B1ab(iii)+2ab(iii)
F434	*Senecio erubescens* Aiton var. *incisus* DC.	1	ASTERACEAE	Threatened (Raimondo et al., 2009)
F435	*Senecio exuberans* R.A.Dyer	1	ASTERACEAE	Endangered B1ab(ii,iii,iv)
F436	*Senecio mauricei* Hilliard & B.L.Burtt	6	ASTERACEAE	Rare
F437	*Senecio mbuluzensis* Compton	1	ASTERACEAE	Least Concern
F438	*Senecio ngoyanus* Hilliard	6	ASTERACEAE	Vulnerable B1ab(i,ii,iii,iv,v)
F439	*Senecio saniensis* Hilliard & B.L.Burtt	3	ASTERACEAE	Rare
F440	*Senecio umgeniensis* Thell.	7	ASTERACEAE	Threatened?
F441	*Senecio villifructus* Hilliard	3	ASTERACEAE	Endangered B1ab(iii)+2ab(iii)
F442	*Sisyranthus fanniniae* N.E.Br.	4	APOCYNACEAE	Vulnerable B1ab(iii)+2ab(iii)
F443	*Stachys comosa* Codd	4	LAMIACEAE	Threatened
F444	*Stachys rudatisii* Skan	3	LAMIACEAE	Least Concern
F445	*Stangeria eriopus* (Kunze) Baill.	29	ZAMIACEAE	Vulnerable A2acd+4cd

F446	*Stenoglottis longifolia* Hook.f.	3	ORCHIDACEAE	Least Concern
F447	*Struthiola anomala* Hilliard	2	THYMELAEACEAE	Vulnerable D2
F448	*Syncolostemon latidens* (N.E.Br.) Codd	5	LAMIACEAE	Vulnerable B1ab(ii,iii,iv,v)+2ab(ii,iii,iv,v)
F449	*Syncolostemon ramulosus* E.Mey. ex Benth.	3	LAMIACEAE	Vulnerable D2
F451	*Tephrosia bachmannii* Harms	1	FABACEAE	Vulnerable A2c
F452	*Tephrosia pondoensis* (Codd) Schrire	2	FABACEAE	Endangered B1ab(iii,v); C2a(i)
F453	*Thesium jeanae* Brenan	1	SANTALACEAE	Rare
F454	*Thunbergia venosa* C.B.Clarke	5	ACANTHACEAE	Rare
F455	*Turraea pulchella* (Harms) T.D.Penn.	3	MELIACEAE	Vulnerable A2c; B1ab(ii,iii,iv,v)
F456	*Turraea streyi* F.White & Styles	2	MELIACEAE	Critically Endangered (Possibly Extinct)
F457	*Vanilla roscheri* Rchb.f.	6	ORCHIDACEAE	Near Threatened D2
F458	*Vitellariopsis dispar* (N.E.Br.) Aubrév.	4	SAPOTACEAE	Rare
F459	*Wahlenbergia pinnata* Compton	1	CAMPANULACEAE	Near Threatened D2
F460	*Warburgia salutaris* (G.Bertol.) Chiov.	30	CANELLACEAE	Endangered A2acd
F461	*Watsonia bachmannii* L.Bolus	4	IRIDACEAE	Vulnerable B1ab(iii,v)+2ab(iii,v)
F462	*Watsonia canaliculata* Goldblatt	10	IRIDACEAE	Endangered B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)
F463	*Watsonia confusa* Goldblatt	5	IRIDACEAE	Least Concern
F464	*Watsonia inclinata* Goldblatt	6	IRIDACEAE	Vulnerable D2
F465	*Watsonia latifolia* N.E.Br. ex Oberm.	9	IRIDACEAE	Least Concern
F466	*Watsonia mtamvunae* Goldblatt	4	IRIDACEAE	Vulnerable D2
F467	*Woodia verruculosa* Schltr.	7	APOCYNACEAE	Vulnerable D2
F468	*Xerophyta longicaulis* Hilliard	1	VELLOZIACEAE	Rare
F469	*Zeuxine africana* Rchb.f.	1	ORCHIDACEAE	Endangered D

[3] based on known historical record

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Appendix 15 Supplementary Information 4: The final C-Plan map, showing planning units that are 100% transformed, and irreplaceable areas

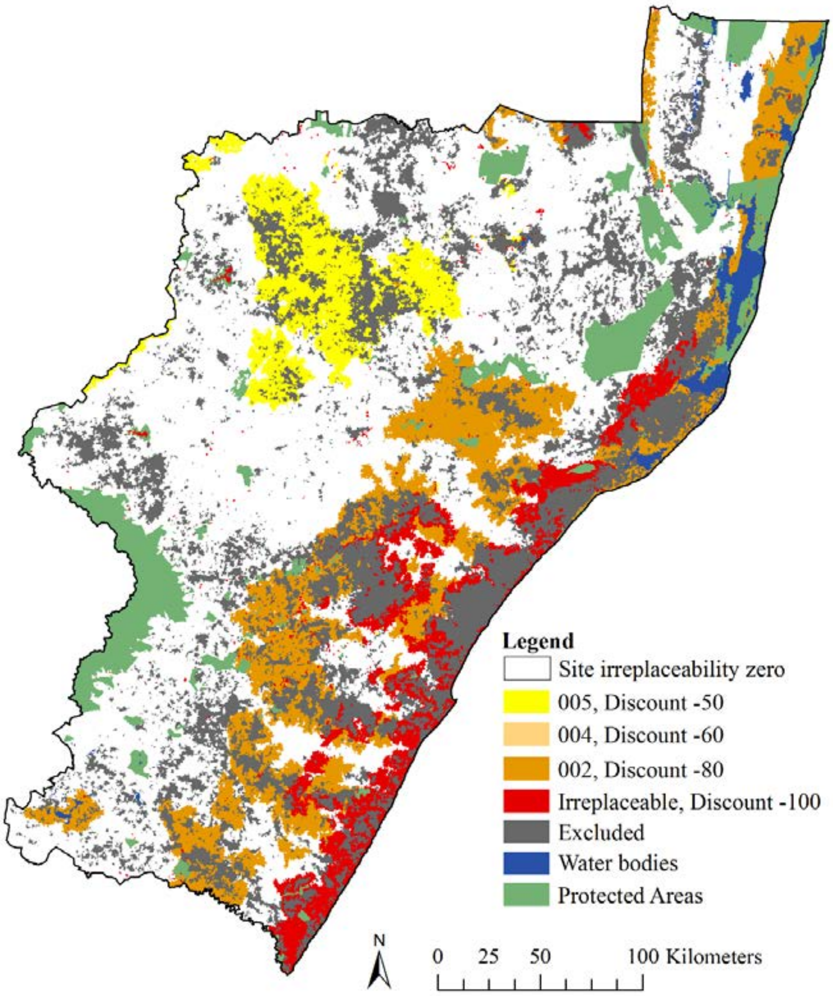

Fig. 4 The final floristic C-Plan map, showing planning units that are 100% transformed, and irreplaceable areas

Appendix 16 Supplementary Information 5: Climate stability map, based on the areas common to the HadCM2 and GFDL 2.1 climate models (Magnitude of change = 0)

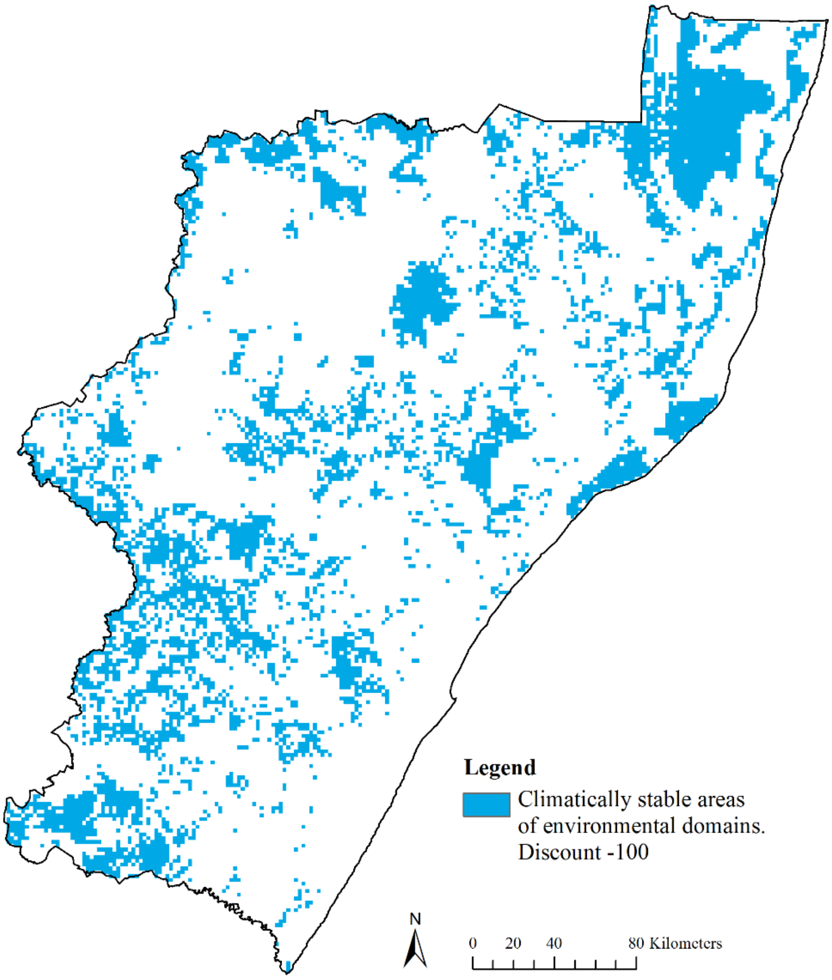

Fig. 5 Climate stability map, based on the areas common to the HadCM2 and GFDL 2.1 climate models (magnitude of change = 0) (modified from Jewitt et al 2015a)

References

Jewitt D, Erasmus BFN, Goodman PS, O’Connor TG, Hargrove WW, Maddalena DM, Witkowski ETF (2015a) Climate-induced change of environmentally defined floristic domains: a conservation based vulnerability framework. Appl Geogr 63:33-42

Appendix 17 Supplementary Information 6: Pinchpoints along the first corridor map, shown in red

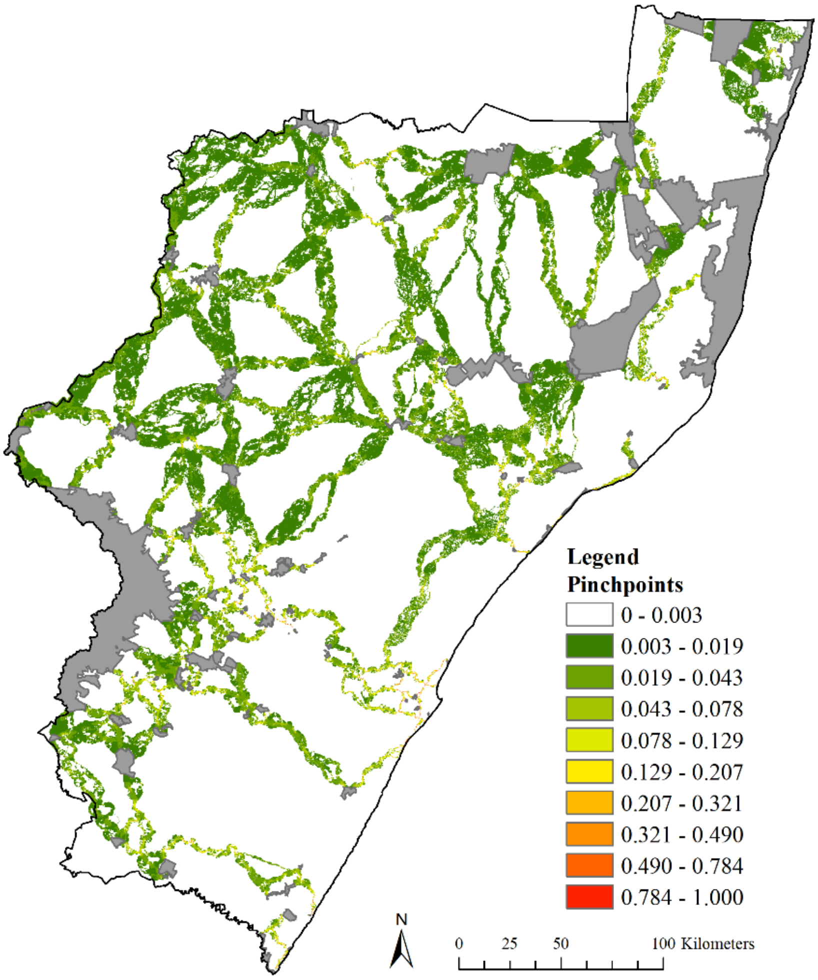

Fig. 6 Pinchpoints along the first corridor map, shown in red

Appendix 18 Supplementary Information 7: Centrality analysis showing critical protected areas and linkages required to maintain landscape connectivity

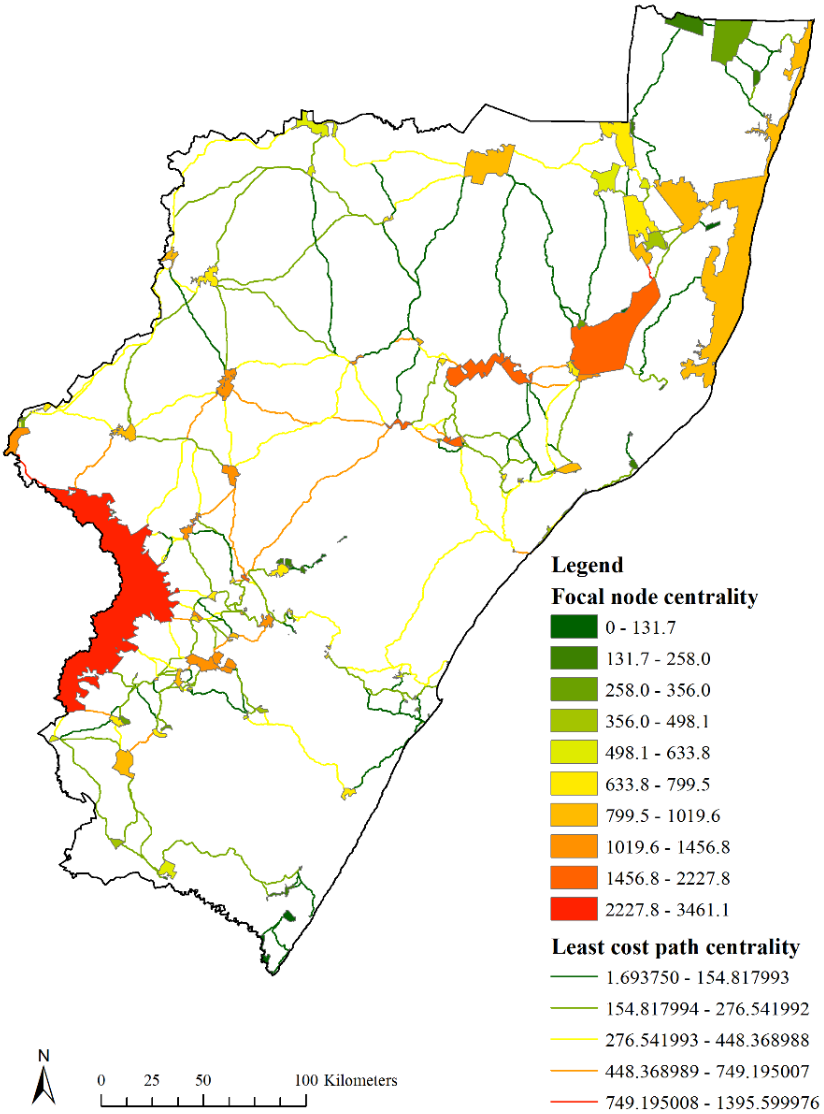

Fig 7. Centrality analysis showing critical protected areas and linkages required to maintain landscape connectivity. Higher values (red) indicate more important protected areas or linkages

CHAPTER 7

7. Discussion and Conclusions

This thesis investigated the important drivers structuring floristic community composition, pattern and turnover in grassland and savanna systems in KZN. The two major threats to the persistence of floristic communities, land cover change and climate change, were investigated with the aim of facilitating conservation planning to impart maximum resilience to enable the persistence of floristic diversity into the future.

The landscape approach adopted here aims to conserve the dynamic, multiscale ecological processes that create and maintain diversity and is ideal for regional conservation planning. The study focuses on the dominant matrix grassland and savanna species which underpin ecosystem structure and functioning and provide essential ecosystem services. A suite of products were developed which may be used to inform conservation planning and direct appropriate conservation action in the face of anthropogenically induced global change. The products complement traditional systematic conservation plans that focus on rare, threatened or endemic species. This chapter presents the main findings and implications of this research, and where appropriate, identifies priorities for further work.

7.1 The environmental variables structuring floristic composition and turnover

The environmental correlates of plant composition and turnover were quantified with the aim of facilitating conservation planning and to understand how these patterns may change in future. The identification of environmental gradients and areas of high species turnover, and their incorporation into conservation plans protects the supporting evolutionary and ecological processes that generate and maintain diversity (Fairbanks and Benn, 2000; Cowling et al., 2003; Rouget et al., 2003, 2006). The incorporation of climatic gradients into conservation plans may promote species range adjustments in response to climate change (Pressey, 2007).

The major gradient correlated to floristic composition in the province was temperature, specifically mean annual temperature, followed by soil fertility properties and precipitation variables (Jewitt et al., 2015a). This is in keeping with accepted understanding that vegetation distribution is determined by climate at regional scales (Lavorel, 1999) and soil type at landscape scales (Pearson and Dawson, 2003).

The temperature gradient was dominant which was not surprising given the strong altitudinal, and to a lesser degree, latitudinal gradients in the province. It was interesting however that mean annual temperature was the best predictor rather than minimum or maximum temperature variables. This is attributed to the lag effect associated with changes in plant species composition in response to altered temperature variables and the adaptation of species to current temperature ranges. This correlation may not hold in future given the prediction of an increase in heat waves, which in association with increased rainfall variability such as longer dry spells (IPCC, 2013), may rapidly drive species composition changes. Because temperature is well correlated to altitude, altitude may be used as a surrogate variable in this region. In order to ensure the best adaptation capacity to climate change, future protected areas and landscape linkages should incorporate a large altitudinal or temperature gradient.

Soil base status and cation exchange capacity, as indicators of soil fertility, were important correlates of floristic composition and turnover (Jewitt et al., 2015a; Jewitt et al., 2016). This was driven primarily by the distinctive dystrophic sandy soils of the Maputaland region. The geology of the province is aligned approximately in a north-south direction resulting in a similar soil type pattern which conflicts with the strong east-west altitudinal or temperature gradient. For instance, Maputaland species with specific soil requirements will not easily be able to track suitable climatic conditions in a westerly direction along the temperature gradient because of this soil disjunction. Species may be able to track suitable climates in a southerly direction along the coast but outside of protected areas these areas are some of the most highly transformed areas in the province (Jewitt et al., 2015b). Targeted conservation actions and monitoring of species with specific soil requirements are therefore essential.

The precipitation gradient was weak, primarily due to the complex precipitation pattern in the province related to the varied topography, orographic and oceanic influences (Jewitt et al., 2015a). Rainfall events in winter were significant for recharging soil water reserves and similarly rainfall events in the hottest summer months were important for ensuring plant water availability. Rainfall impacts are expected to vary locally and in association with temperature and soil gradients, making it more difficult to plan for and incorporate this gradient.

The environmental variables associated with spatial pattern were similar to those driving beta diversity. However, an important finding was that turnover was not uniform or linear along environmental gradients (Jewitt et al., 2016). Beta diversity was highest on dystrophic soils and in warm, drier summer regions. Understanding the nuance of turnover along the gradients facilitates the opportunity to maximise species representation in conservation plans (Ferrier,

2002) or in new protected areas. High turnover areas are where species would be susceptible to climate change (McKnight et al., 2007). Turnover rates along environmental gradients therefore indicate the sensitivity of systems to climate change (Fitzpatrick et al., 2013). The high beta diversity areas broadly corresponded to biome transition areas between grasslands, savannas and the Indian Ocean coastal belt and the KZN parts of the Maputaland-Pondoland-Albany biodiversity hotspot. Cowling et al. (1997) investigated regions of high species richness in South Africa and found areas along the subtropical east coast and eastern escarpment to be species rich. This was attributed to environmental heterogeneity and high total productivity of the region resulting in a complex mosaic of forest, grassland and savanna communities. Similarly Thuiller et al. (2006) revealed topographic heterogeneity to be the best explanatory variable of plant species richness.

7.2 Climate change implications

The changes to environmental domains posed by climate change over a medium term planning horizon were spatially predicted and appropriate conservation responses developed.

All six climate change models predict an increase in mean annual temperature (Engelbrecht et al., 2009). Applied to KZN, the region may expect temperature increases ranging between 1.5-2.1°C in mean annual temperature by 2050 (Jewitt et al., 2015c). The importance of frost duration as a predictor in the CART analysis (Jewitt et al., 2015a) is significant because frost limits the distribution of tropical savanna species (Smit 1990; Bredenkamp et al., 2002). A warming environment with a reduction in the number of frost days is likely to enable frost-sensitive savanna species to invade cooler grassland areas (Jewitt et al., 2015a). The environmental domain models (Jewitt et al., 2015c) also indicated that conditions suiting savanna species would increase at the expense of grassland systems. This evidence suggests a strong environmental pressure driving the expansion of conditions suited to savanna systems. There has already been a strong signal of bush encroachment (increase in woody plant density) in the country (O’Connor et al., 2014). This will be exacerbated by increasing atmospheric CO_2 levels which allow some savanna tree seedlings to rapidly recharge root starch reserves thereby escaping the fire trap (Kgope et al., 2010) and altered herbivory regimes, such as the removal of mega-herbivores (e.g. elephants) from the system which helps to moderate bush encroachment (O’Connor et al., 2014). Rapidly increasing CO_2 levels may lead to a decoupling of floristic pattern with climatic variables. Indeed anthropogenic changes are recasting biogeographic patterns (Frishkoff et al., 2016).

This raises important questions for the maintenance of grassland systems in KZN, and the prevention of savanna systems becoming thicket systems. A slight increase in woodiness in the grassland systems may initially be beneficial to the grassland species by affording a cooling effect from shade. These benefits will only accrue however provided that the competitive balance between grass and tree species is not significantly altered, that light does not become limiting for grassland species and that nitrogen fixing woody species do not significantly alter soil conditions especially in nutrient poor systems. Appropriate fire and herbivory regimes are essential to maintain the grass sward (O'Connor et al., 2014; Scott-Shaw and Morris, 2015). These are management levers that are effected at a land parcel scale. Land management can strongly impact biodiversity and can cause significant habitat modifications. It is therefore essential that relevant fire and herbivory research, specifically considering climate change impacts, is conducted and communicated and that land-owners have access to knowledgeable extension officers to guide veld (rangeland) management practices. Mechanical or chemical clearing of woody species is an option but it is costly to do so. From a policy perspective it may become necessary to change policies applicable to static systems, to ones that consider the dynamic nature of systems and account for the predicted direction of change in the system. For instance, EKZNW limits the introduction of faunal species outside of their historical ranges. Given that systems have already experienced bush encroachment and that this is predicted to continue, it is important to introduce browsers to exert browsing pressure on the woody component. Similarly it will be necessary to alter grazer to browser stocking ratios.

Kruger and Nxumalo (2016) investigated surface temperature trends in South Africa from 1931-2015. Four weather stations were based in KwaZulu-Natal with long-term temperature records (from 1931 and 1947 to 2015). They showed that mean annual temperature increased approximately 0.33 ºC at Emerald Dale, 0.96-1.66 ºC at Cedara, 1.66 ºC at Mt Edgecomb and 1.34 ºC at St Lucia, demonstrating an already strong warming signal in the province. The number of days per year with high minimum temperature have increased whilst the number of days per year with low minimum temperatures have declined. Similarly the number of days with high maximum temperatures have increased and the number of days with low maximum temperatures have declined. Along the eastern half of the country there were significant decreases in cold spell duration. Increases in warm spell durations were greatest in the northern and western interior. Extreme events became more extreme with time. Accelerated warming trends occurred from the 1960’s onwards. Seasonal trends existed which differed between regions, with summer and autumn temperatures displaying the strongest warming. These changes are likely to be exacerbated with increasing temperature trends.

Climate change predictions related to precipitation amount do not concur (Engelbrecht et al., 2009), with five downscaled models predicting a drying situation and one suggesting a slight increase in mean annual precipitation. This uncertainty occurs because greenhouse gas forcing is more indirect for rainfall than temperature (Fauchereau et al., 2003). The models for KZN predict a maximum decrease in mean annual precipitation of 91mm per annum and at best a slight increase of 28mm per annum (Jewitt et al., 2015c). However, the conformal-cubic atmospheric model (CCAM) is problematic in that it overestimates rainfall estimates east of the escarpment (Engelbrecht et al., 2009), hence it is likely that a drying scenario will exist for the province. In South Africa and KZN there has been an increase in extreme rainfall events but overall precipitation trends are not conclusive (Mason et al., 1999; Fauchereau et al., 2003; Kruger, 2006). However, Kruger (2006) reported a decrease in annual precipitation for Western KZN. Rainfall variability and drought conditions have increased since the 1960s in keeping with climate change predictions. The precipitation gradient in KZN is complex however and variables influencing plant water availability rather than precipitation amount *per se* will likely become more important in future.

Climate change impacts were modelled until 2050 (Jewitt et al., 2015c). During this period no environmental domains vanished and no novel ecosystems emerged. However it is likely that diminishing domains will disappear in the long-term and a novel suite of ecosystems emerge. A longer-term analysis should be conducted to identify disappearing domains and emerging novel ecosystems. Species occurring in these locations would be at considerable risk. Targeted species and land use monitoring should occur in these areas. Data used in this analysis were largely collected from the 1980’s onwards. It is possible that novel ecosystems already exist in the landscape – for instance the expansion of *Acacia* species (now *Senegalia* or *Vachellia* species) into grasslands from the 1900’s (O’Connor et al., 2014).

It is also evident that environmental domains within the existing PAs are set to change considerably. It is essential that species are able to track changing environmental conditions through the surrounding landscape matrix and for this to occur, sufficient natural habitat must remain in the landscape. If species become stranded within a PA and are unable to adapt to the new conditions within the PA, they are likely to become locally extinct within the PA. In this context PAs cannot be considered safe havens for biodiversity into the future. The dynamic nature of species and communities must be brought into conservation planning.

The scale used for the climate change study was coarse (0.5º) but represented the best available data at the time of the analysis. The mismatch in scale between future predictions and the current climatic variables means that important areas for biodiversity are underestimated. Future analyses conducted with finer-scaled data and the new Representative Concentration Pathways would be helpful to identify micro-refugia and refine the models.

7.3 Habitat loss

Habitat loss is currently the greatest immediate threat to biodiversity (Vitousek, 1994; MEA, 2005; Jetz et al., 2007; Titeaux et al., 2016). Indeed significant amounts (46.4%) of natural habitat have already been lost in KZN and the rates of recent habitat loss are high (1.2% per annum from 1994-2011) (Jewitt et al., 2015b). This loss of habitat has resulted in a loss of biodiversity and led to species population declines (O'Connor and Kuyler, 2009). The loss of biodiversity leads to a loss of resilience, the loss of evolutionary potential and a loss of response and functional types (Cumming, 2011), all of which negatively affect the ability of species to respond to global threats. The primary drivers of habitat loss were agriculture and timber plantations (Jewitt et al., 2015b). Other land-use categories such as the built environment, dams and mines were also significant features of the landscape. The drivers and rates of change differed among land tenure types.

The degree and rate of habitat loss is a game-changer in climate change adaptation strategies for biodiversity. Indeed, climate change impacts may even be irrelevant for the short-term survival of many landscapes. Common climate change adaptation strategies include landscape connectivity and an increase in the protected area estate (Hannah et al., 2007; Lawler, 2009; Heller and Zavaleta, 2009; Ackerly et al., 2010; Beier and Brost, 2010). These strategies are dependent on having natural habitat available in the landscape. The high rates of habitat loss threaten the ability to implement these strategies. The opportunity costs of adding to the protected area network and maintaining landscape connectivity increase as land availability decreases. Ignoring the threat of land cover change, when investigating climate change impacts in future, adds to the uncertainty of the models (Titeaux et al., 2016). These two threats will undoubtedly interact with each other (Mantyka-Pringle et al., 2015). Frishkoff et al. (2016) demonstrated that climate and land-use change impacted similar species, hence it is likely to homogenise biodiversity more severely than initially anticipated.

The fact that agriculture is the most land-hungry anthropogenic land-use in the province points to where the most effort should be directed, and opportunity exists, to protect the natural landscape. The existing cultivation footprint should not be expanded. The abandoned agricultural fields offer opportunities for land rehabilitation and crop expansion, especially if indirect climate change effects such as changing crop types dictate an expansion in area. Advances in agricultural technology will allow for greater crop yields from the same area (van Asselen and Verburg, 2013). Primary natural rangeland is well-suited to extensive grazing and browsing systems, both by domestic and wildlife species, but it is essential that appropriate stocking rates are applied. These land-uses should be promoted. The stakeholders of the other drivers of land cover change similarly need to be engaged.

The amount of natural habitat remaining as indicated on the land cover maps is optimistic. The scale at which the land cover maps were developed has not allowed for the identification of alien invasive species. Species such as *Acacia dealbata*, *Acacia mearnsii*, *Eucalyptus* species, *Solanum mauritianum*, *Chromolaena odorata*, *Lantana camara*, *Melia azedarach*, amongst others, are abundant in KZN (van Wilgen et al., 2012). These are not distinguished from the bush category on land cover maps. Further, the historical cultivated fields that have been abandoned for a long period of time are not easy to distinguish from primary rangeland and are underestimated on the land cover maps. Edge-effects on fragmented habitat patches (Laurance et al., 2014) have not been taken into account. Hence the amount of primary natural rangeland remaining in the province is considerably less than reported. Efforts to correct these aspects are ongoing.

Recent studies have shown the enormous loss of wilderness areas globally - 3.3 million km^2 (9.6%) since the early 1990s (Watson et al., 2016) of which Africa experienced the second largest extent of habitat loss. Watson et al. (2016) also demonstrated that the gain in protection of wilderness areas was significantly slower than the rate of habitat loss. Agriculture has been shown to be a major driver of habitat loss and resulting carbon emissions elsewhere in Africa where 74% of savanna and forest systems have been transformed in Tanzania’s Eastern Arc Mountains (Willcock et al., 2016). Coetzer et al. (2010) demonstrated extensive land cover transformation (36%) on the Kruger to Canyons

Biosphere Reserve on the South African Central Lowveld. Habitat loss is known to pose the greatest threat to plant diversity (Corlett, 2016). Planetary boundaries are rapidly being exceeded (Steffen et al., 2015; Newbold et al., 2016). In light of this knowledge it is critical that natural habitat is secured now for human well-being and biodiversity conservation. It is far more cost effective to act now (Hannah et al., 2007; Lawton et al., 2010; Cook et al., 2014) and prevent habitat loss and degradation than to try and rehabilitate lands and linkages in future.

Future land-use scenarios were not investigated because of the large uncertainty associated with these models. Economic opportunities, institutional factors, markets and policies drive land cover and land-use change (Lambin et al., 2001) as well as socio-political drivers and these may change rapidly. The land cover change analysis (Jewitt et al., 2015b) provides insight as to the major drivers of change and these are likely to continue. Possible future drivers of land-use change include hydraulic fracturing, biofuels, energy farms and mining, amongst others. However, if the CBD target 5 of “By 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced” is achieved, then the necessity of modelling future land cover change to predict habitat loss is reduced. The likelihood of this target being achieved is however, extremely small. Every effort should be made towards reaching this target which would involve considerable awareness campaigns involving social media to drive the public-policy interface, extensive inter-governmental and cross-sectoral collaboration, policy and legislation changes, consideration of the drivers of change associated with land tenure type, big business and providing incentives to conserve land, amongst others. Extensive resources should be directed towards adding to and managing protected areas and maintaining linkages in the landscape. Future land-use changes should be constrained to the existing transformation footprint, including the historical agricultural fields.

Despite an existing suite of conservation tools and legislation, transformation of the landscape is continuing and PAs are becoming isolated islands in the landscape. Possible reasons for this, amongst others, include short-term planning horizons related to political tenure periods, and declining budgets that are directed towards essential social and educational needs but without understanding the long-term consequences and dependencies of humans on the landscape. Socio-political turmoil is driving capital and policy investment. Economic accounting lacks cradle-to-grave calculations resulting in incorrect valuations of anthropogenic land-uses compared to natural land-uses. Further, land cover change and climate change are slow, cumulative drivers of change that are not readily observed by the public, resulting in a lack of belief in the importance of these threats.

7.4 Maintaining floristic diversity into the future

Chapter 6 builds on the insights gained from the previous four chapters to develop a coarse-grained connectivity map between protected areas to maintain floristic diversity in the face of land cover and climate change in the province. An understanding of landscape patterns and processes allows for the best placement of corridors in the landscape. The spatial location of the corridors was prioritised based on high turnover areas, climate refugia and areas important for rare, threatened and endemic plant species. The corridors were aligned to the major climatic gradients driving floristic pattern. Allowing species to track changing environmental conditions along environmental gradients represents the most natural and cost-effective way for species to adapt to climate change.

For large parts of the province, the protected areas are well connected and this should be maintained. However in highly transformed regions such as the midlands and along the south coast, finer scale corridors including restored areas will need to be established. Effective management of rangeland within the corridors is essential, especially the prevention and clearing of alien invasive plant species and the application of appropriate fire and herbivory regimes.

Consideration was given to the target amount of natural habitat that should be included in the corridor network. The persistence threshold suggests that when below 50% of natural habitat remains in the landscape, there is a rapid decline in the ability of the landscape to support viable populations (Flather and Bevis, 2002). Investigations into host-plant interactions with butterfly species has shown a cascading effect on higher trophic levels before the host plants become locally extinct (Harvey et al., 2016). Thus insufficient habitat for plant species will have unintended consequences for species at higher trophic levels. Noss et al. (2012) recommend that 50% of an area is required to sustain species, populations and communities in the long term. Given the rapid rate of habitat loss and the knowledge of the amount of habitat required to sustain life on earth, it is recommended that 50% of primary rangeland in KZN be set aside and managed to sustain the biodiversity occurring there. It is essential that a formal adoption and implementation of this target takes place.

Plant movement may be limited by their colonization capacity (Van der Veken et al., 2007), hence plant species may fail to track changing climates (Ash et al., 2016) even if sufficient connectivity exists in the landscape. This will be exacerbated as climate change accelerates. However, even if species are unable to track changing climates on their own, provided there is sufficient natural habitat remaining, species may be translocated in response to changing environmental suitability.

Globally the implementation of corridors has proven difficult (Ayram et al., 2015). The existence of this suggested corridor network does not mean that it will be adopted and used. Implementation of corridors tends to be more successful for charismatic, large-bodied species (Brodie et al., 2016). Implementation challenges will vary with land tenure type. Connie Hedegaard, a keynote speaker at the recent EcoSummit conference in France (29 August – 1 September 2016) and former European Commissioner for Climate Action (2010-2014), expanded on the priorities required to enable the implementation of the sustainable development goals. Many of these are relevant in this context too:

- Knowledge, facts and science should be communicated in a digestible, translatable form, including new technologies. The findings must be part of decision making.
- Knowledge must be brought into play faster and at relevant scales.
- New ways of being ‘interdisciplinary’ are required.
- A profound economic transition is required.
- Human behaviour needs to be changed away from a consumptive culture to one focussed on quality rather than quantity.
- The State must take responsibility. Political buy-in must be maintained continuously.
- Planning needs to occur for the long-term.
- Digital information needs to be sped up.
- A positive vision around global threats is required – people need to see themselves as part of the solution.

South African conservation planners have had varied success with implementing regional conservation plans and corridors. Recommendations to enhance the adoption and implementation of conservation plans includes the effective incorporation of implementation issues at all stages of the planning process, the involvement of stakeholders especially at the municipal level and mainstreaming biodiversity concerns as an implementation mechanism (Cowling and Pressey, 2003). Conservation planning products need to be useful and user-friendly for decision-makers, consultants and government officials (Pierce et al., 2005). Incentive-based stewardship agreements have made considerable contribution towards the conservation of flora (Von Hase et al., 2010). The incentives need not be financially based but recognition for the stewardship role is essential (Pasquini et al., 2009). Lombard et al. (2010) recommend a consensus on the vision to be achieved among multiple stakeholders involving appropriate institutions and suggest establishing a learning organisation that practices adaptive co-management. Reyers et al. (2009) recommend a transdisciplinary approach to bridge the gap between science and action.

An assessment of the successfulness of the findings of this thesis will depend on whether the outputs are used in conservation planning initiatives, the targets adopted, plans implemented and projected impacts are found to be correct. This can only be assessed as time goes by. Climate change and land cover change impacts will be ongoing and these can be monitored and quantified to determine the business-as-usual impacts, or if the findings are implemented, to determine the reduction in impacts compared to the current situation. Further transformation of the landscape might result in irreversible breaking of the corridor connections. This would be a good indicator to monitor and also to determine how robust the network is and hence to identify safeguards to landscape connectivity.

7.5 Future research

In addition to the research requirements already raised, the following research topics would benefit biodiversity conservation in the face of global change.

The threats facing biodiversity in KZN are multi-faceted and not limited to land cover and climate change. The harvesting of medicinal plants from the wild may drive local population extirpations (Xego et al., 2016). Nitrogen deposition has been shown to change species composition across a wide range of ecosystem types (Bobbink et al., 2010) and drive species loss (Vitousek et al., 1997; De Schrijver et al., 2011) as do other pollutants such as phosphorus (Carpenter et al., 1998). Increasing atmospheric CO_2 concentrations is altering plant carbon uptake and plant water use efficiencies (Franks et al., 2013). It is not known if management levers such as altered fire regimes are sufficient to counter the effects of increased CO_2, especially where fire regimes are altered because of increasing fire barriers being constructed. Agriculture is leading to landscape simplification and increased insecticide (Meehan et al., 2011) and herbicide use. All of these threats, and many others, are significant in their own right but the cumulative combination of threats, along with climate change and habitat loss, is not known and should be researched further. The lack of integrated threat projections impedes the ability to develop comprehensive biodiversity impact scenarios and therefore appropriate policy and management responses. A threat assessment of the corridors, especially in the high beta diversity sections and corridor bottlenecks, that considers alien invasive species as well as the afore-mentioned threats, is essential.

Habitat fragmentation as a result of habitat loss is having major biological consequences (Saunders et al., 1991). Fragmentation research, edge-effects and extinction dynamics related to plant communities represent a major research gap. Similarly, landscape genetic studies and gene flow related to habitat fragmentation are essential (Manel et al., 2003). Further research is required on understanding cascading effects, secondary extinctions and time lag implications (Brodie et al., 2014). Ongoing monitoring of land cover change is required to measure habitat loss, identify new drivers of change and fragmentation impacts.

This research has focussed on plant diversity and community composition. It is not known to what extent this research may be used as a surrogate for faunal diversity and conservation. Fairbanks et al. (2001) investigated the environmental correlates for birds in Kwazulu-Natal and identified five bird communities in the region based on strong temperature and precipitation gradients. Species with larger body sizes have a greater land area requirement per individual animal, often requiring more than one vegetation type. Similarly migratory species often cover vast distances and multiple habitats. This alters the scale and processes which drive faunal composition and diversity. Should the patterns and processes driving floristic diversity, and the impacts of habitat loss and climate change not be the same for faunal species, these will need to be researched. Future research should evaluate how small reserves that are linked by narrow corridors will support these species, especially since these species contribute to essential ecosystem processes.

Empirical data related to the effect of scale on patterns and processes, land cover change and climate change is required. Multiscale analysis is required to provide further insight into landscape patterns and heterogeneity (Wu, 2004). Similarly, the mismatch between national, provincial and local research effort, policies, regulations and implementation needs to be rectified.

New projects monitoring vegetation switches e.g. species composition changes or biome changes, need to be established. Newer technologies and high resolution imagery are enabling such fine scale monitoring to be conducted.

Cross-boundary spatial planning is required. The corridor network suggested here should link-up with corridors developed in neighbouring provinces and countries.

7.6 Conclusion

This thesis explored two major global threats, land cover change and climate change, to grassland and savanna systems in KZN. The landscape approach facilitates conservation planning and the results may be used to inform the science-policy interface by recommending best principles, legislative requirements and mandates required to conserve floristic diversity into the future.

Biodiversity continues to decline despite increasing conservation efforts (Rands et al., 2010; Oliver, 2016; Titeaux et al., 2016) and the future is indeed uncertain. The rates of habitat loss and predicted climate change impacts in the province are moving us towards uncharted and dangerous territory for the region’s biodiversity. Adopting targets that are socially or politically acceptable will not stem biodiversity decline, hence bolder thinking and action is required (Noss et al., 2012). Without this there may well be a resurgence of dragons.

7.7 References

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