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Planning for the Maintenance of Floristic Diversity in the Face of Land Cover and Climate Change

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Abstract Habitat loss and climate change are primary drivers of global 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. 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. 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. 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. 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 Beta diversity · Climate refugia · Corridors · Ecological processes · Gradients · Protected areas

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Introduction

Global 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 are often hostile to 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).

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 2011) 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, the maintenance of natural disturbance regimes such as 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). A combination of geology, elevation and latitude was highly successful in explaining variation in species diversity in northeastern U.S. such that geophysical diversity was an effective surrogate of species diversity for the purpose of conservation planning in the face of climate change (Anderson and Ferree 2010). These surrogate variables were not found effective in KwaZulu-Natal (KZN), South Africa, in which mean annual temperature, soil base status and precipitation variables were most effective for explaining variation in floristic composition (Jewitt et al. 2015c). In KZN soil fertility proved a superior predictor than parent geology, so did mean annual temperature, with the advantage of expressing a direct effect on plant physiology (Pausas and Austin 2001), which was superior to the indirect surrogates of elevation and latitude (Jewitt et al. 2015c). Importantly for KZN, these major environmental gradients will remain not withstanding future climate change. Under the premises that regional corridors encompassing a broad range of environments will allow species to adjust their geographic distributions in response to climate change (Hunter et al. 1988) and that species will respond individually to climatic changes rather than as whole communities (Midgley et al. 2003), we propose a framework for developing landscape connectivity using environmental variables identified as key determinants of variation in floristic composition in the KZN landscape. This framework, which will contribute to maintaining floristic diversity into the future, uses important environmental gradients, areas of high beta (β) diversity, and predicted climate change impacts correlated to floristic composition, and threatened and endemic plant locations to inform the spatial location of landscape linkages between protected areas. The justification for the use of these elements is detailed below.

We focus on plant communities at the landscape level because plants underpin habitat structure and functioning, and thus represent an essential starting point for understanding climate change impacts, particularly as they may not be able to track 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.

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 magnitude and direction 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 environmental change (Fitzpatrick et al. 2013), as high β-diversity areas are where species ranges are susceptible 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).

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 maintain connectivity in order to mitigate these threats as well as develop and implement meaningful targets for natural habitat retention.

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.

Methods

Study Area

KZN (Fig. 1) is floristically diverse containing more than 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). The temperature gradient is particularly strong due to an altitudinal range of over 3000 m over a distance of 160 km from the warm Indian Ocean in the east, to the top of the Drakensberg escarpment in the west, 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 geology and soils range from geologically young sandy soils in Maputaland to base-rich basalt, dolerite, rhyolite, shales, mudstone and tillite, and base-poor sandstones and granites (Partridge 1997).

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.

Framework Overview

The approach adopted in this analysis is presented in Fig. 2. The first step involves developing a baseline resistance

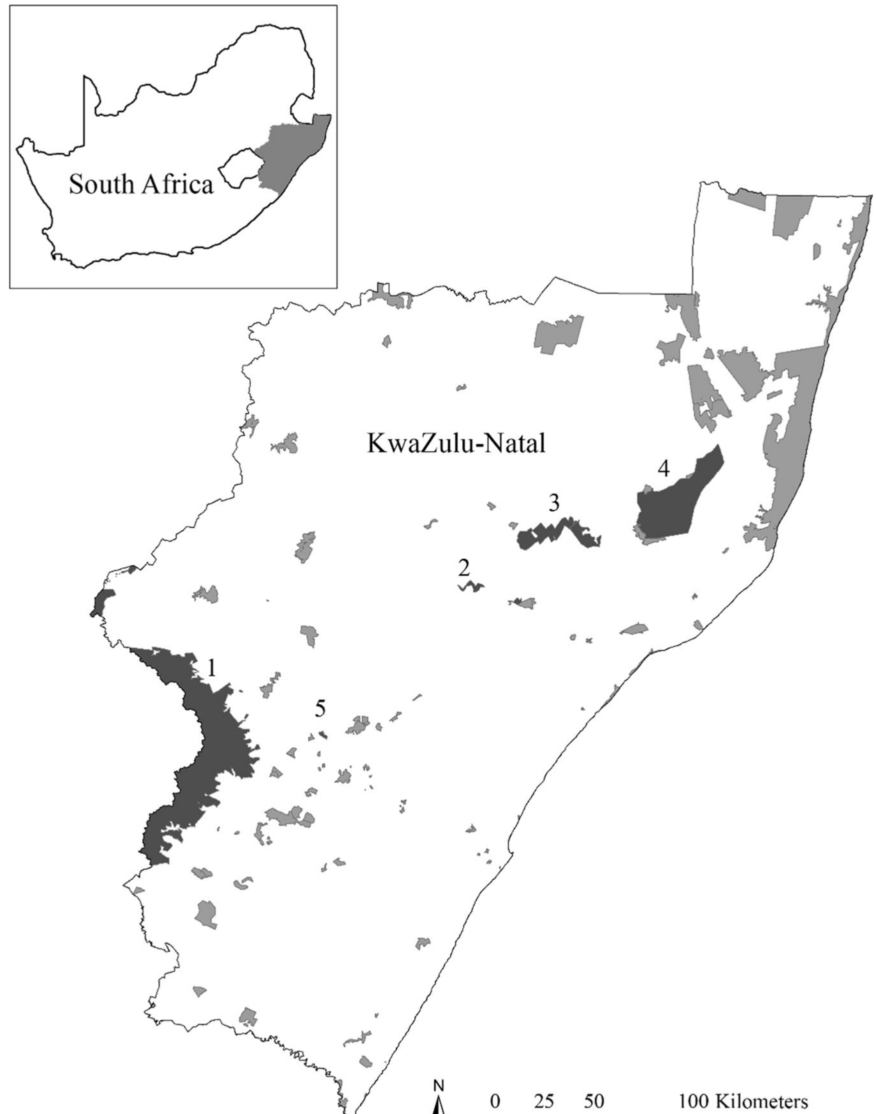

Fig. 1 Study area of KwaZulu-Natal (KZN), South Africa, with the protected areas or focal nodes shown in grey. The most important protected areas for maintaining landscape connectivity are shown in dark grey, where: (1) Maloti Drakensberg Park World Heritage Site; (2) Qudeni Forest Reserve; (3) eMakhosini-Opathe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

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.

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

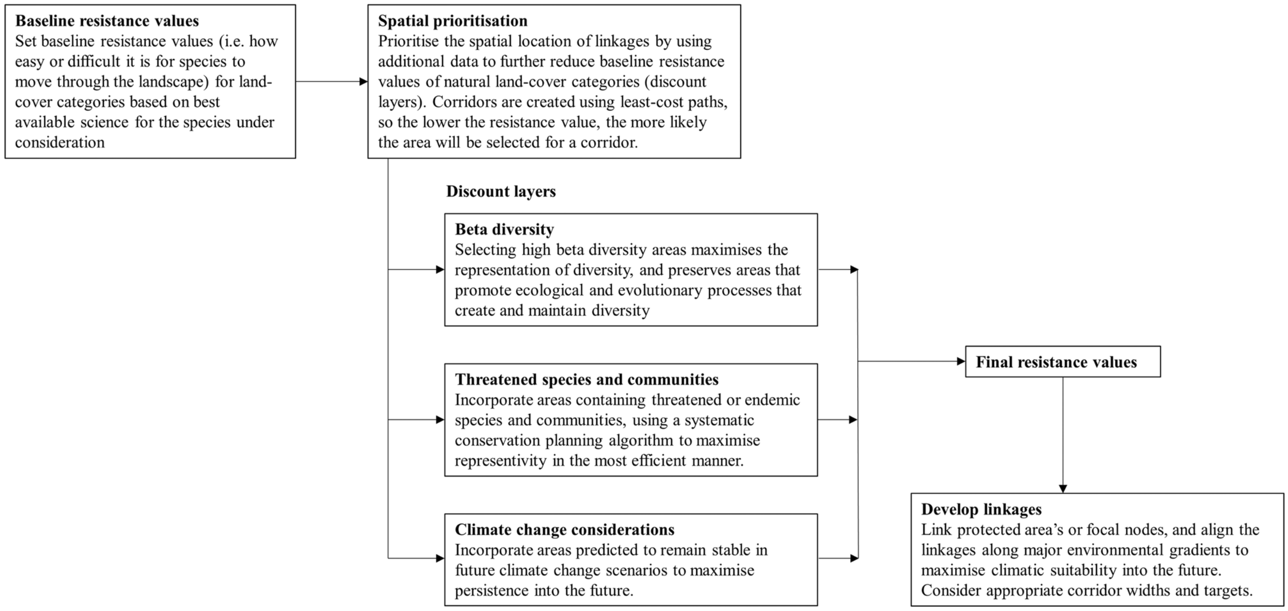

Fig. 2 Flow diagram detailing the development of the resistance values, discount layers and corridor development

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 community composition and diversity 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.

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 (i.e., the resistance values were lowered, making it more likely

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

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 (70–100 cc)	Yes	400	400
20	Bushland (<70 cc)	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

Table 1 continued

Code	Land cover category	Discountable	Resistance layer 1	Resistance layer 2
46	Rehabilitated mines—high vegetation		900	900
47	Rehabilitated mines—low vegetation		900	900
48	Historical fields		800	600

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

that these areas would be selected for corridors) 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 is detailed below.

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, 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 (i.e., mean

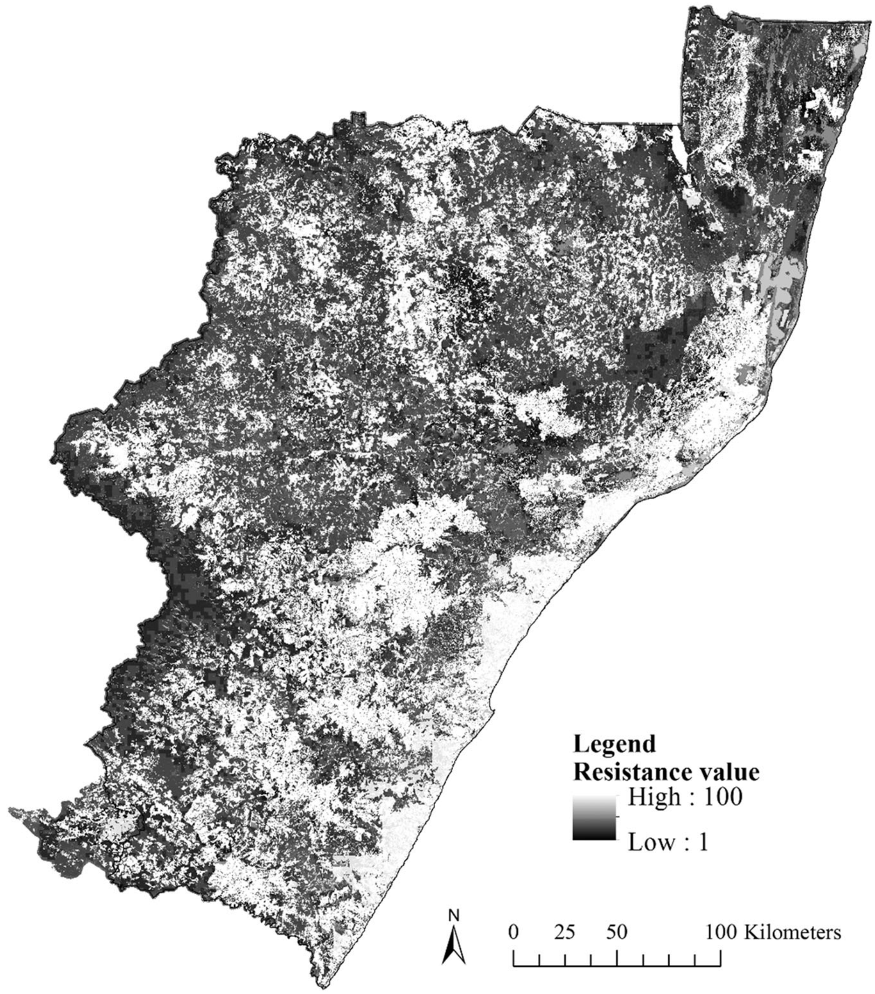

Fig. 3 Final resistance values (resistance layer 1), rescaled between 1–100, discounted for important plant areas, climatically stable areas and high β-diversity areas. Lower resistance values are shown in darker shades

annual temperature, mean annual precipitation and soil cation exchange capacity as an indicator of soil fertility). The combination of the three environmental variables (with the resulting environmental domains) represent the environmental stage upon which plant species will respond under changing climatic conditions. Twenty three unique environmental domains were identified for the province. The location of the environmental domains in future was explored using an ensemble of six downscaled conformal-cubic atmospheric models. Soil fertility was assumed to remain constant during the analysis period (until 2050), whilst future temperature and precipitation variables were modelled independently of each other. The two extremes of these models (HadCM2 and GFDL2.1) were used to identify the areas of the environmental domains that remained stable into the future. 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).

Analysis

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).

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.

Microclimate Analysis

We determined the degree of inclusion of microclimates within the corridors based on the method for determining the number of landforms in a neighbourhood (Anderson et al. 2014). A landform layer with ten landforms (EKZNW 2015) (Canyons or deeply incised streams; midslope drainages or shallow valleys; upland drainages or headwaters; U-shaped valleys; plains; open slopes; upper slopes or mesas; local ridges or hills in valleys; midslope ridges or small hills in plains; mountain tops or high ridges), derived from the 30 m Shuttle Radar Topography Mission digital elevation model (DEM), was used to determine the number of landforms around each 30 m cell. A focal variety analysis, using a 40 ha circular search area around each cell, was used to calculate the number of landforms occurring in a neighbourhood.

Results

The focal nodes conserve 9.08% of the terrestrial landscape. The area of the province considered permeable to plant dispersal is 69% (as per resistance layer 1). The first corridor output (Fig. 4a), 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% (Fig. 4b). 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. 4c).

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.

In order to follow the major temperature gradient in the province, the corridors were orientated in approximately north-south (latitudinal) and east-west (altitudinal) directions. The full range of both current and future temperature and precipitation gradients were incorporated in the corridor and protected area network, as were the full range of latitudinal and altitudinal gradients. Coastal latitudinal corridors could not be established due to the high level of transformation in these areas. The corridors captured the complexity of the rainfall gradient, ensuring that topographically related rain shadow and mistbelt areas were included from the coast to the mountains. Similarly, the full range of soil cation exchange capacity values were incorporated in the corridor and protected area network.

The irreplaceable areas of the province largely occur on the mid-coast 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

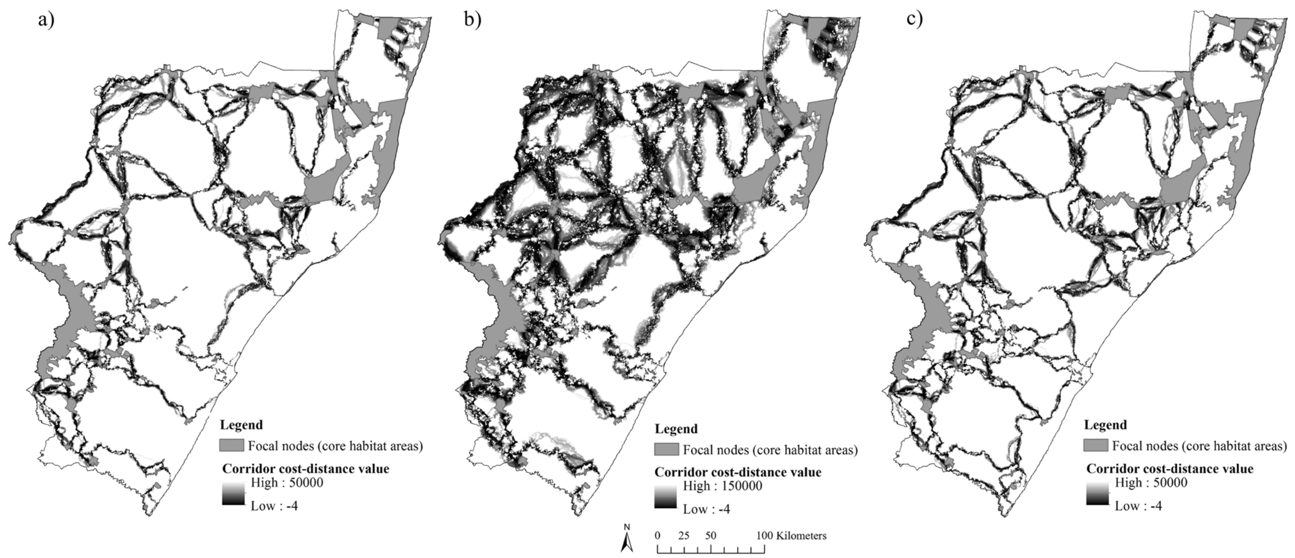

Fig. 4 The various corridor outputs: **a** corridor 1 (resistance layer 1), using primarily natural vegetation and a corridor cost distance width of 50,000; **b** corridor 2 (resistance layer 1), using primarily natural vegetation and a corridor cost distance width of 150,000; **c** corridor 3 (resistance 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

areas were represented in the corridors as occurred in the province. A greater proportion of irreplaceable ‘002’ and ‘005’ values were represented in corridors than remaining natural in the province (12.7% vs. 7.6%, and 10% vs. 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 microclimate analysis (Supplementary Information 6) based on the variety of landforms occurring within a 40 ha neighbourhood, revealed that the far north-eastern and north-western areas had fewer microclimates than the remainder of the province. The more varied the landscape, the more microclimates would exist, facilitating the persistence of species under changing climatic conditions (Anderson et al. 2014).

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 7). The centrality analysis (Supplementary Information 8) 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). The reserves important for maintaining landscape connectivity 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. 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.

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. The gradients, especially the temperature and soil fertility gradients, correlate to the geophysical landscape of the province. Hence these gradients will persist into the future providing a meaningful surrogate for plant species to respond to future climate change. Similarly, the topographically related precipitation patterns will persist despite changing precipitation amounts. 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 spatial prioritisation of the corridors is achieved by discounting the resistance values in the identified important areas of the province.

The corridors were planned for thousands of plant species whose dispersal processes, especially long distance events, are mostly not known. The values assigned to the resistance layer were based on quantified assessments of land use impacts on plant composition in the region and which also concurred with expert opinion-based assessments elsewhere in the world. 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. Animal dispersed species may be able to pass over inhospitable land-uses for plants to establish new populations in suitable habitat and will be less reliant on contiguous, least-cost paths between protected areas. 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.

Making the corridors as wide as possible ensured that varied topography and resulting landforms and aspect were included in the corridors, providing micro-refugial sites in which species could persist and disperse along with changing climates. The flatter areas of the province, with fewer landform varieties, do not offer as many micro-refugial sites. Species in these areas would be at greater risk from changing climates and should be monitored. The identified pinchpoint areas need to be prioritised for maintenance if the corridor network is to remain connected.

The disconnected protected areas require different management interventions dependent on their position within the landscape. 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 disconnected protected areas. The protected area connectivity in the metropolitan area was surprising but arose as a function of corridors being established along the national and major roads of the city which tend to take the shortest path. The connectivity was further enhanced due to the resolution of the analysis (100 m), the vegetated road reserves adjacent to the major highways and not setting the roads to be absolute barriers. 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 using our criteria. The opportunity exists to use the road reserves for plant connectivity restoration (Tikka et al. 2000). 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.

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 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 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).

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.

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 Bevers (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 Bevers 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.

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 socio-ecological 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.

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.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no competing interests.

Human of Animal Rights This article does not contain any studies with human participants or animals performed by any of the authors

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References

Ackerly DD, Loarie SR, Cornwell WK, Weiss SB, Hamilton H, Branciforte R, Kraft NJB (2010) The geography of climate change: implications for conservation biogeography. Divers Distrib 16:476–487

Anderson MG, Ferree CE (2010) Conserving the stage: Climate change and the geophysical underpinnings of species diversity. PLoS ONE 5 (7):e11554

Anderson MG, Clark M, Sheldon AO (2014) Estimating climate resilience for conservation across geophysical settings. Conserv Biol 28:959–970

Bazelet CS, Samways MJ (2011) Relative importance of management vs. design for implementation of large-scale ecological networks. Landscape Ecol 26:341–353

Beier P, Brost B (2010) The use of land facets to plan for climate change: conserving the arenas, not the actors. Conserv Biol 24:701–710

Beier P, Spencer W, Baldwin RF, McRae BH (2011) Toward best practices for developing regional connectivity maps. Conserv Biol 25:879–892

Bowers MA, Harris LC (1994) A large-scale metapopulation model of interspecific competition and environmental change. Ecol Model 72:251–273

Carpenter S, Walker B, Anderies JM, Abel N (2001) From metaphor to measurement: resilience of what to what? Ecosystems 4:765–781

CBD [Convention on Biological Diversity] (2011) Strategic plan for biodiversity 2011-2020 and the Aichi targets. Secretariat of the Convention on Biological Diversity, Montreal. Available from https://www.cbd.int/sp/targets. Accessed 29 April 2016

Collingham YC, Huntley B (2000) Impacts of habitat fragmentation and patch size upon migration rates. Ecol Appl 10:131–144

Cousins SAO, Lavorel S, Davies I (2003) Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden. Landscape Ecol 18:315–332

Cowling RM, Pressey RL, Rouget M, Lombard AT (2003) A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. Biol Conserv 112:191–216

Cumming GS (2011) Spatial resilience: integrating landscape ecology, resilience, and sustainability. Landscape Ecol 26:899–909

Cumming GS, Olsson P, Chapin III FS, Holling CS (2013) Resilience, experimentation, and scale mismatches in social-ecological landscapes. Landscape Ecol 28:1139–1150

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58

Dellas E, Pattberg P (2013) Assessing the political feasibility of global options to reduce biodiversity loss. Int J Biodivers Sci Ecosyst Serv Manage 9:347–363

Ezemvelo KZN Wildlife (2013) KwaZulu-Natal land cover 2011 v1 (clp_KZN_2011_LC_v1_grid_w31.zip). [GIS coverage]. Pietermaritzburg: Biodiversity Research and Assessment, Ezemvelo KZN Wildlife

Ezemvelo KZN Wildlife (2015) KZN Landform (Derived from modified 30m SRTM DEM). (landform_30mSRTMDEM_w31.zip. [GIS coverage]. Pietermaritzburg: Biodiversity Conservation Planning Division, Ezemvelo KZN Wildlife

Ezemvelo KZN Wildlife and GeoTerraImage (2013) 2011 KZN province land-cover mapping (from SPOT5 satellite imagery circa 2011): Data users report and metadata (version 1d). Pietermaritzburg: Ezemvelo KZN Wildlife, unpublished report

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Ferrier S (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? Syst Biol 51:331–363

Fitzpatrick MC, Sanders NJ, Normand S, Svenning J-C, Ferrier S, Gove AD, Dunn RR (2013) Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. P R Soc B 280:20131201. doi:10.1098/rspb.2013.1201

Flather CH, Bevers M (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. Am Nat 159:40–56

Fourie L, Rouget M, Lötter M (2015) Landscape connectivity of the grassland biome in Mpumalanga, South Africa. Austral Ecol 40:67–76

Freedman AH, Buermann W, Mitchard ETA, DeFries RS, Smith TB (2010) Human impacts flatten rainforest-savanna gradient and reduce adaptive diversity in a rainforest bird. PloS ONE 5(9): e13088. doi:10.1371/journal.pone.0013088

Groves CR, Game ET, Anderson MG, Cross M, Enquist C, Ferdaña Z, Girvetz E, Gondor A, Hall KR, Higgins J, Marshall R, Popper K, Schill S, Shafer SL (2012) Incorporating climate change into systematic conservation planning. Biodivers Conserv 21:1651–1671

Hannah L, Midgley G, Andelman S, Araújo M, Hughes G, Martinez-Meyer E, Pearson R, Williams P (2007) Protected area needs in a changing climate. Front Ecol Environ 5:131–138

Harris LD, Scheck J (1991) From implications to applications: the dispersal corridor principle applied to the conservation of biological diversity. In: Saunders DA, Hobbs RJ (eds) Nature Conservation 2: the role of corridors. Surrey Beatty & Sons, Sydney, NSW, pp 189–220

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol Conserv 142:14–32

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Hunter ML, Jacobson GL, Webb T (1988) Paleoecology and the coarse-filter approach to maintaining biological diversity. Conserv Biol 2:375–385

Jewitt D (2014) KZN vegetation types: targets, statistics and conservation status (December 2014). Unpublished report, Biodiversity Research and Assessment, Ezemvelo KZN Wildlife, Pietermaritzburg

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

Jewitt D, Goodman PS, Erasmus BFN, O'Connor TG, Witkowski ETF (2015b) Systematic land-cover change in KwaZulu-Natal, South Africa: Implications for biodiversity. S Afr J Sci 111(9/10):9. doi:10.17159/sajs.2015/20150019. 2015Art. #2015-0019pages

Jewitt D, Goodman PS, O'Connor TG, Witkowski ETF (2015c) Floristic composition in relation to environmental gradients across KwaZulu-Natal, South Africa. Austral Ecol 40:287–299

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

Jones-Farrand DT, Fearer TM, Thogmartin WE, Thompson III FR, Nelson MD, Tirpak JM (2011) Comparison of statistical and theoretical habitat models for conservation planning: the benefit of ensemble prediction. Ecol Appl 21:2269–2282

Joppa LN, O'Connor B, Visconti P, Smith C, Geldmann J, Hoffmann M, Watson JEM, Butchart SHM, Virah-Sawmy M, Halpern BS, Ahmed SE, Balmford A, Sutherland WJ, Harfoot M, Hilton-Taylor C, Foden W, Di Minin E, Pagad S, Genovesi P, Hutton J, Burgess ND (2016) Filling in biodiversity threat gaps. Science 352:416–418. doi:10.1126/science.aaf3565

Kark S, van Rensburg BJ (2006) Ecotones: marginal or central areas of transition? Isr J Ecol Evol 52:29–53

Koen EL, Garroway CJ, Wilson PJ, Bowman J (2010) The effect of map boundary on estimates of landscape resistance to animal movement. PLoS ONE 5(7):e11785. doi:10.1371/journal.pone.0011785

Laliberté E, Wells JA, DeClerck F, Metcalfe DJ, Catterall CP, Queiroz C, Aubin I, Bonser SP, Ding Y, Fraterrigo JM, McNamara S, Morgan JW, Sánchez Merlos D, Vesk PA, Mayfield MM (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecol Lett 13:76–86

Lawler JJ (2009) Climate change adaptation strategies for resource management and conservation planning. Ann NY Acad Sci 1162:79–98

Lindenmayer DB, Wood JT, McBurney L, MacGregor C, Youngentob K, Banks SC (2011) How to make a common species rare: a case against conservation complacency. Biol Conserv 144:1663–1672

Maciejewski K, Cumming GS (2016) Multi-scale network analysis shows scale-dependency of significance of individual protected areas for connectivity. Landscape Ecol 31:761–774

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR

McKnight MW, White PS, McDonald RI, Lamoreux JF, Sechrest W, Ridgely RS, Stuart SN (2007) Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. PLoS Biol 5(10):e272. doi:10.1371/journal.pbio.0050272

McRae BH (2012a) Pinchpoint Mapper Connectivity Analysis Software. The Nature Conservancy, Seattle, WA, Available at: http://www.circuitscape.org/linkagemapper

McRae BH (2012b) Centrality Mapper Connectivity Analysis Software. The Nature Conservancy, Seatlle, WA, Available at: http://www.circuitscape.org/linkagemapper

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89(10):2712–2724

McRae BH, Kavanagh DM (2011) Linkage Mapper Connectivity Analysis Software. The Nature Conservancy, Seattle, WA, Available at: http://www.circuitscape.org/linkagemapper

McRae BH, Shah VB, Mohapatra TK (2013) Circuitscape 4 User Guide. The Nature Conservancy. Available at: http://www.circuitscape.org

Midgley GF, Hannah L, Millar D, Thuiller W, Booth A (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. Biol Conserv 112:87–97

Monzón J, Moyer-Horner L, Palamar MB (2011) Climate change and species range dynamics in protected areas. BioScience 61:752–761

Nelson DR, Adger WN, Brown K (2007) Adaptation to environmental change: contributions of a resilience framework. Annu Rev Environ Resour 32:395–419

Noss RF, Dobson AP, Baldwin R, Beier P, Davis CR, Dellasala DA, Francis J, Locke H, Nowak K, Lopez R, Reining C, Trombulak SC, Tabor G (2012) Bolder thinking for conservation. Conserv Biol 26:1–4. doi:10.1111/j.1523-1739.2011.01738.x

Nuñez TA, Lawler JJ, McRae BH, Pierce DJ, Krosby MB, Kavanagh DM, Singleton PH, Tewksbury JJ (2013) Connectivity planning to address climate change. Conserv Biol 27:407–416

O'Connor TG (2005) Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the southern Drakensberg, South Africa. J Appl Ecol 42:975–988

O'Connor TG, Kuyler P (2009) Impact of land use on the biodiversity integrity of the moist sub-biome of the grassland biome, South Africa. J Environ Manage 90:384–395

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Partridge TC (1997) Evolution of landscapes. In: Cowling RM, Richardson DM, Pierce SM (eds) Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp 5–20

Pausas JG, Austin MP (2001) Patterns of plant species richness in relation to different environments: an appraisal. J Veg Sci 12:153–166

Pearson RG, Dawson TP (2005) Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biol Conserv 123:389–401

Pressey R, Watts ME, Barrett TW, Ridges ML (2008) The C-Plan conservation planning system: origins, applications, and possible futures. In: Moilanen A, Wilson KA, Possingham HP (eds) Spatial Conservation Prioritization: Quantitative methods and computational tools. Oxford University Press, Oxford, pp 211–234

Pressey RL (2004) Conservation planning and biodiversity: assembling the best data for the job. Conserv Biol 18:1677–1681

Pressey RL, Watts M, Ridges M, Barrett T (2005) C-Plan conservation planning software. User Manual. NSW Department of Environment and Conservation

Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landscape Urban Plan 83(2–3):91–103

Schaffers AP, Raemakers IP, Sýkora KV, ter Braak CJF (2008) Arthropod assemblages are best predicted by plant species composition. Ecology 89:782–794

Scholes RJ, Biggs R (2005) A biodiversity intactness index. Nature 434:45–49

Scott-Shaw CR (1999) Rare and threatened plants of KwaZulu-Natal and Neighbouring regions. KwaZulu-Natal Nature Conservation Service, Pietermaritzburg

Simberloff D, Farr JA, Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? Conserv Biol 6:493–504

South African National Biodiversity Institute (SANBI) (2015) Red list of South African plants version 2015.1. http://redlist.sanbi.org Accessed 14 Jan 2016

Statistics South Africa (2015) Mid-year population estimates 2015. Statistical release P0302. Pretoria: Statistics South Africa. Available from www.statssa.gov.za

Tikka PM, Koski PS, Kivelä RA, Kuitunen MT (2000) Can grassland plant communities be preserved on road and railway verges? Appl Veg Sci 3:25–32

Williams P, Hannah L, Andelman S, Midgley G, Araújo M, Hughes G, Manne L, Martinez-Meyer E, Pearson R (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. Conserv Biol 19:1063–1074. doi:10.1111/j.1523-1739.2005.00080.x

With KA, Crist TO (1995) Critical thresholds in species' responses to landscape structure. Ecology 76:2446–2459

Worboys GL, Ament R, Day JC, Locke H, McClure M, Tabor G, Woodley S (2015) Consultation draft, Guidelines for Connectivity Conservation: Part One, Definition: Connectivity Conservation Area, IUCN, 28 Rue Mauverney, Gland, Switzerland

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landscape Ecol 27:777–797