
Designing Large-Scale Conservation Corridors for Pattern and Process

MATHIEU ROUGET,^{*} RICHARD M. COWLING,[†] AMANDA T. LOMBARD,[†]
ANDREW T. KNIGHT,[†] AND GRAHAM I.H. KERLEY[‡]

^{*}Kirstenbosch Research Centre, South African National Biodiversity Institute, Claremont 7735, South Africa and Botany Department, University of Cape Town, Rondebosch 7701, South Africa, email rouget@sanbi.org

[†]Department of Botany and Terrestrial Ecology Research Unit, Nelson Mandela Metropolitan University, P.O. Box 77000, Port Elizabeth 6031, South Africa

[‡]Terrestrial Ecology Research Unit and Department of Zoology, Nelson Mandela Metropolitan University, P.O. Box 77000, Port Elizabeth 6031, South Africa

Abstract: *A major challenge for conservation assessments is to identify priority areas that incorporate biological patterns and processes. Because large-scale processes are mostly oriented along environmental gradients, we propose to accommodate them by designing regional-scale corridors to capture these gradients. Based on systematic conservation planning principles such as representation and persistence, we identified large tracts of untransformed land (i.e., conservation corridors) for conservation that would achieve biodiversity targets for pattern and process in the Subtropical Thicket Biome of South Africa. We combined least-cost path analysis with a target-driven algorithm to identify the best option for capturing key environmental gradients while considering biodiversity targets and conservation opportunities and constraints. We identified seven conservation corridors on the basis of subtropical thicket representation, habitat transformation and degradation, wildlife suitability, irreplaceability of vegetation types, protected area networks, and future land-use pressures. These conservation corridors covered 21.1% of the planning region (ranging from 600 to 5200 km²) and successfully achieved targets for biological processes and to a lesser extent for vegetation types. The corridors we identified are intended to promote the persistence of ecological processes (gradients and fixed processes) and fulfill half of the biodiversity pattern target. We compared the conservation corridors with a simplified corridor design consisting of a fixed-width buffer along major rivers. Conservation corridors outperformed river buffers in seven out of eight criteria. Our corridor design can provide a tool for quantifying trade-offs between various criteria (biodiversity pattern and process, implementation constraints and opportunities). A land-use management model was developed to facilitate implementation of conservation actions within these corridors.*

Key Words: biological processes, conservation implementation, conservation planning, landscape connectivity, landscape linkages

Diseño de Corredores de Conservación de Gran Escala para Patrones y Procesos

Resumen: *La identificación de áreas prioritarias que incorporen patrones y procesos biológicos es uno de los mayores retos de las evaluaciones de acciones de conservación. Debido a que la mayoría de los procesos a gran escala están orientado a lo largos de gradientes ambientales, proponemos acomodarlos mediante el diseño de el diseño de corredores de escala regional para capturar esos gradientes. Con base en principios de planificación de conservación sistemáticos, tales como la representación y la persistencia, identificamos grandes extensiones de terrenos no transformados (i.e., corredores de conservación) para conservar patrones y procesos en el Bioma de Matorral Subtropical de África del Sur. Combinamos el análisis de la trayectoria de menor costo con un algoritmo dirigido a un objetivo para identificar la mejor opción para capturar gradientes*

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ambientales clave al mismo tiempo que se toman en cuenta objetivos de biodiversidad y oportunidades y restricciones de conservación. Identificamos siete corredores de conservación a partir de la representación del matorral subtropical, la transformación y degradación del hábitat, aptitud de la vida silvestre, no reemplazo de tipos de vegetación, redes de áreas protegidas y presiones de uso de suelo futuras. Estos corredores de conservación abarcaron 21.1% de la región de planificación (entre 600 y 5200 km²) y alcanzaron objetivos para procesos biológicos con éxito y, en menor grado, para tipos de vegetación. Los corredores que identificamos tienen la intención de promover la persistencia de los procesos ecológicos (gradientes y proceso fijos) y cumplir con la mitad del patrón de biodiversidad. Comparamos los corredores de conservación con un diseño simple de corredor consistente en una franja de ancho fijo a lo largo de los ríos principales. Los corredores de conservación fueron mejores que los corredores ribereños en siete de ocho criterios. Nuestro diseño de corredores puede aportar una herramienta para la cuantificación de compensaciones entre diversos criterios (patrón y proceso de biodiversidad, constricciones y oportunidades de implementación). Desarrollamos un modelo de gestión de uso de suelo para facilitar la implementación de medidas de conservación dentro de estos corredores.

Palabras Clave: conectividad del paisaje, implementación de medidas de conservación, procesos biológicos, planificación de conservación, vínculos entre paisajes

Introduction

A major challenge for conservation assessments is to identify priority areas that incorporate biological and environmental patterns (species and land classes) and processes (e.g., migration). Incorporating processes into assessments invariably requires large tracts of the planning region (e.g., Noss et al. 2002; Cowling et al. 2003a) and is best approached at a landscape scale (e.g., Balmford et al. 1998; Terborgh & Soulé 1999; Noss 2003). Several approaches to incorporate processes have been suggested (Pressey et al. 2003), including incorporating spatial connectivity in target-driven algorithms (Possingham et al. 2000), targeting species persistence (Williams & Araujo 2000), accommodating processes associated with focal species, especially large mammals (Carroll et al. 2001; Kerley et al. 2003), and identifying spatial components of processes (Rouget et al. 2003). A problem with these approaches is that they do not always consider the achievement of large (landscape)-scale processes and pattern targets simultaneously (but see Noss et al. 2002; Cowling et al. 2003a). Generally, and usually implicitly, a trade-off between representation (sampling biodiversity pattern) and persistence (ensuring ecological functioning) ensues. In these cases, persistence is invariably relegated behind representation as a conservation goal (Carroll et al. 2001; Muruthi 2004).

Many large-scale processes such as biota movement (Laurance & Laurance 1999), geographic speciation (Cowling & Pressey 2001; Moritz 2002), or response to climate change (Midgley et al. 2003) are aligned along environmental gradients. All contain an element of direction and spatial linearity. These processes are therefore best accommodated by designing large-scale corridors (or landscape linkages) that capture the environmental gradients and facilitate biota movement and dispersal in relation to a range of spatial and temporal scales.

Corridors are most frequently conceptualized as areas of natural habitat that are contiguous or isolated (i.e., linkages or stepping stones) and enable particular plant and animal species dispersal and migration processes essential for their persistence in a landscape (Bennett 2003; Groves 2003). Significant controversy surrounds the design and efficacy of these features (Hobbs 1992; Simberloff et al. 1992; Dobson et al. 1999; Bennett 2003). Here we conceptualize corridors as regional-scale features that comprise extensive tracts of largely untransformed habitat aligned along major environmental gradients. The major role of these corridors is to ensure that regional-scale processes are integrated into the conservation assessment. These corridors should also achieve targets for pattern and process features and consider the opportunities and constraints for their implementation. Our concept is firmly rooted in the principles and practices of systematic conservation assessment where the overall goal is to achieve the representation and persistence of biodiversity (Cowling et al. 1999; Margules & Pressey 2000). Similar initiatives have and are being conducted by international nongovernmental organizations (e.g., Conservation International 2000; Dinerstein et al. 2000; Sanderson et al. 2002a; Muruthi 2004). These initiatives differ from our approach, however, in that they are not target-driven, systematic assessments.

We designed large-scale conservation corridors in the Subtropical Thicket Biome of South Africa as part of the Subtropical Thicket Ecosystem Planning (STEP) project (Knight et al. 2003b). Ours is the only account that we are aware of that describes the design of extensive conservation corridors based on the principles of systematic conservation planning while simultaneously being mindful of implementation issues. Our discussion of the outcomes emphasizes the problems associated with design based on multiple criteria and the opportunities and challenges for implementing conservation action.

Methods

Planning Context

The planning region for our study was centered on the Subtropical Thicket Biome (Low & Rebelo 1996); it covers 105,454 km² and straddles the Western and Eastern Cape Provinces of South Africa (Fig. 1). It was subdivided into six primary water catchments and a coastal region (hereafter referred to as catchments) (Fig. 1), encompassing the eight biogeographic subdivisions of the thicket biome (Vlok et al. 2003). Sixteen percent of the planning region has been transformed to agriculture, urbanization, afforestation, and alien invasive plants, and 12% has been severely degraded by overgrazing, leaving 72% of the habitat intact. Eight percent of the planning region is highly threatened by development pressures (urbanization, agriculture, or afforestation) that are likely to affect biodiversity negatively over the next 20 years (Cowling et al. 2003b). Almost half the region faces minimal land-use pressures over this time period. Areas of particular concern are mainly along the coastal belt. The semiarid interior of the planning region faces low-impact land-use pressures.

Subtropical thicket is composed of dense, spiny, and usually succulent thicket up to 3 m tall, which may occur in solid stands or as a mosaic of thicket clumps with other

vegetation types (Vlok et al. 2003). Subtropical thicket has high plant species richness and endemism, most endemics being succulents and geophytes, and is associated with two globally recognized centers of succulent plant endemism: the Little Karoo Center of the Succulent Karoo in the west and Albany Center in the east (van Wyk & Smith 2001). The Subtropical Thicket Biome is contained in the southwestern sector of the Maputaland-Pondoland-Albany hotspot recognized by Conservation International (Steenkamp et al. 2005).

The fauna of the Subtropical Thicket Biome, although diverse, does not demonstrate the level of endemism of the flora. Mammal diversity is relatively high, with 48 species of large and medium-sized mammals. Unfortunately, many of these species have been extirpated, and all have undergone extensive reductions in their distribution. An important feature of the mammal fauna is the presence of two megaherbivores (African elephant [*Loxodonta Africana*] and black rhinoceros [*Diceros bicornis*]), which are recognized as keystone species in structuring subtropical thicket plant communities (Kerley et al. 2002). The avifauna is diverse, with 421 species of birds recorded within the planning region (no endemics). Ten "important bird areas" occur within the planning domain (Barnes 1998). The reptile fauna includes five tortoise species and relatively high endemism (13 species) among the lizards and snakes (Branch 1998). The amphibian

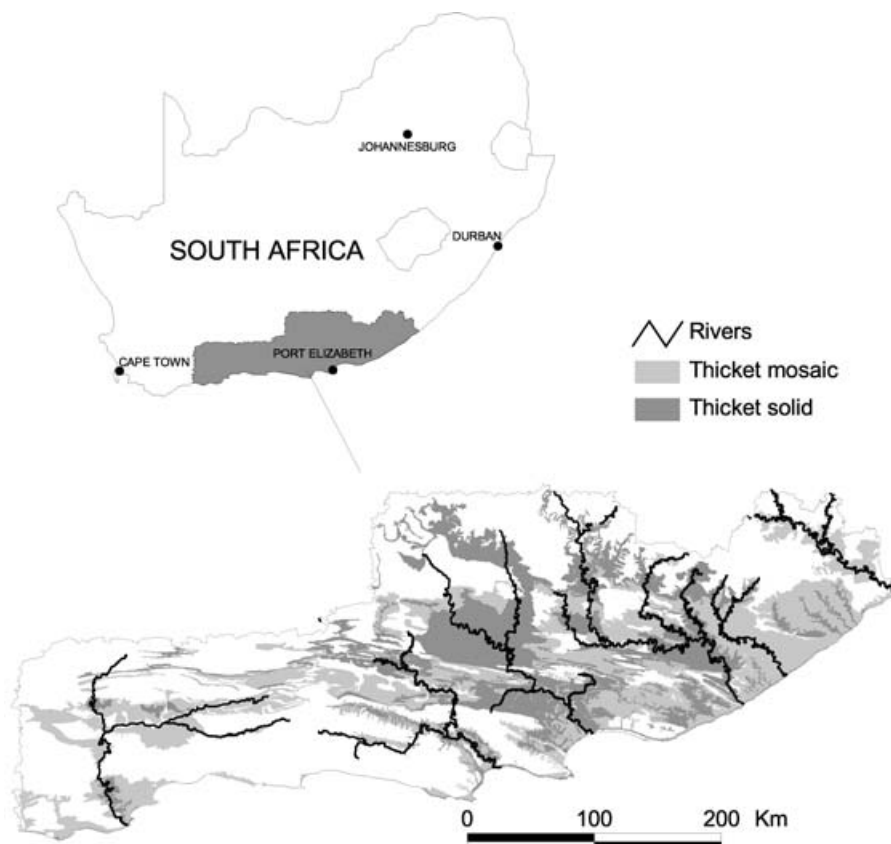


Figure 1. The location of the Subtropical Thicket Biome and the Subtropical Thicket Ecosystem Planning (STEP) planning domain. Subtropical thicket vegetation is classified as "solid" or "mosaic" (see text). Major rivers are indicated.

fauna includes at least five endemic species (Passmore & Carruthers 1995). Although the invertebrate diversity and endemism is probably high, little is known about this group.

The STEP project was a 4-year initiative (July 2000–June 2004) funded by the Global Environment Facility. The overall aims of STEP were to conduct a conservation assessment to identify priority areas that would ensure that the long-term conservation of the subtropical thicket biota and that the assessment outcomes were implemented through the policies and practices of public and private-sector agencies responsible for land-use planning and management of natural resources in the region (Cowling et al. 2003b; Knight et al. 2003a; Pierce 2003).

The need for such a conservation assessment resulted from (1) the high diversity and endemism of the subtropical thicket biota; (2) an existing biased protected area system; (3) an escalation in land-use pressures that threaten biodiversity in this area; (4) diminishing capacity of institutions responsible for land management; (5) a general lack of awareness of the importance, economic and otherwise, of subtropical thicket biodiversity; (6) opportunities associated with a shift to biodiversity-based rural economies, especially game farming and ecotourism; (7) current conservation initiatives (e.g., Greater Addo Elephant National Park); and (8) rapidly unfolding opportunities to mainstream the outcomes of this assessment into land-use legislation and policy.

Cowling et al. (2003b) provide a detailed description of the conservation assessment, including biodiversity features, biodiversity targets, land-use opportunities, and constraints. Here we provide a brief summary of the assessment.

The STEP conservation assessment, undertaken at the 1:100,000 scale, used as biodiversity features 169 vegetation types (of which 112 are thicket types), three wetland types, and five spatial surrogates (hereafter components) of ecological and evolutionary processes (Table 1). Models were used to determine the potential distribution and community-adjusted abundance of 48 species of large and medium-sized mammals (Boshoff et al. 2001). Here we used habitat suitability for the African elephant, a focal species in the subtropical thicket biome (Kerley et

al. 2002), to enhance corridor design. We used a simple spreadsheet model to estimate the potential elephant density based on forage availability within the mammal habitats, partitioned within the herbivorous guilds, and the metabolic requirements of the mammals (see Boshoff et al. [2001] for more details). We rescaled elephant density from 0 to 100 to quantify habitat suitability for elephants.

We set conservation targets for all the biodiversity features we used in this study (Table 1). Vegetation-type targets, expressed as a percentage of the type's area before transformation, were set based on species-area data derived from phytosociological relevés (Desmet & Cowling 2004) and ranged from 10% to 26%. Targets for wetland and forest types were set at 100%, as required by South African legislation. Overall, vegetation-type targets are higher in the western part of the planning region and lower in the east, although for subtropical-thicket types, targets peak in the central parts. These target patterns reflect patterns of species rarity among vegetation types (Desmet & Cowling 2004): Local endemism is highest in the fynbos and succulent karoo vegetation in the west (Pressey et al. 2003) and lowest in grassland and savanna vegetation in the east, whereas in subtropical thicket, local endemism peaks in the central part of the planning region (Vlok et al. 2003).

C-Plan (New South Wales National Parks and Wildlife Services, Armidale, available from <http://www.ozemail.com.au/~cplan>), a conservation assessment software, was linked to ArcView (ESRI, Redlands, California) and used to calculate irreplaceability pattern (Ferrier et al. 2000) based on the biodiversity features and targets mentioned above. Irreplaceability measures the likelihood of selecting planning units for achieving representation targets. Irreplaceability values range from 0 (not needed) to 1 (irreplaceable, essential for achieving the set of targets) (Pressey et al. 1994). The units of selection for the assessment—the planning units—were based on cadastral data and included statutory protected areas.

Planning for Persistence

A key component of the STEP conservation assessment was planning for the persistence of biodiversity (Cowling

Table 1. Biodiversity features considered in the STEP conservation assessment to ensure biodiversity representation and persistence.

<i>Feature*</i>	<i>Description</i>	<i>Target</i>	<i>Additional references</i>
Habitat types	169 vegetation and 3 wetland types mapped at 1:100,000	10–26% of original (pretransformation) area	Desmet & Cowling 2004
Wildlife suitability	habitat suitability for focal species (elephant)	1000 individuals in planning region	Boshoff et al. 2001; Kerley et al. 2003
Spatially fixed processes	biome interfaces, riverine corridors, and sand movement corridors	100% of extant area	Rouget et al. 2003
Spatially flexible processes	upland-lowland and macroclimatic gradients	at least one in each biogeographic region	

*Cowling et al. (2003b) provides details of each biodiversity feature.

et al. 1999; Rouget et al. 2003). Spatially fixed processes were mapped and included in the irreplaceability analysis (see below), whereas spatially flexible processes (i.e., gradients) were captured by designing corridors. The most extensive ecological and evolutionary processes in the Subtropical Thicket Biome are aligned along several major biological gradients. These are largely nested within distinct biogeographic regions associated with the major (north-south aligned) river drainage systems of the planning region (Gouritz, Gamtoos, Sundays, Fish, Buffalo, and Kei rivers) but also are aligned along east-west trending climatic gradients (e.g., along the Great Escarpment, a major topographic feature running east and west in the northeastern part of the planning region) and the coastal dune systems (Vlok et al. 2003). Our overall aim in designing corridors was to represent these biological gradients (north-south upland-lowland and east-west macroclimatic gradients) within each biogeographically distinct water catchment. Corridor design, therefore, focused primarily on ensuring biodiversity persistence (i.e., the long-term maintenance of ecological and evolutionary processes), on which the conservation assessment is founded.

We translated the persistence goal into four key functions that the corridors must fulfill (in priority order): (1) maintain ecological processes (gradients) in subtropical thicket vegetation to enable movement of biota over ecological and evolutionary time scales; (2) ensure habitat retention and connectivity; (3) maximize wildlife habitat suitability; and (4) represent biodiversity pattern (to integrate biodiversity persistence and representation).

We used cost-distance analysis in a geographic information system (GIS) to design corridors. Cost-distance functions in ArcInfo (version 7.2, ESRI, Redlands, California) provide a spatially explicit framework that incorporates these criteria for identifying the least costly (or the most efficient) route to connect a landscape. Corridors were derived in three stages: stage 1, primarily driven by biological process considerations, identified the core area of the corridor (referred to as "conservation paths"); stage 2 expanded the core area to improve representation of habitats and the persistence of processes; and stage 3 further expanded corridors into areas of high irreplaceability value for biodiversity pattern (see below). We named conservation corridors and paths after their associated river catchments.

Identification of Conservation Paths (Stage 1)

Conservation paths aim to capture the processes associated with upland-lowland and climatic gradients operating at a macroscale. Although these macro-scale gradients could occur in various parts of the region, the functionality of such gradients relies on several ecological and human factors. Based on the first three key functions mentioned above, we hypothesized that maximum functionality would be achieved when gradients, in decreasing

order of importance, (1) run through subtropical thicket vegetation types, (2) are not in transformed habitats (urban areas excluded from the analysis), (3) run through habitats highly suitable for wildlife, (4) encompass other process components (i.e., riverine corridors, biome interfaces, sand movement corridors), (5) link protected areas, and (6) are not in areas likely to be transformed in future.

We developed criteria to quantify the functionality of these gradients. These relate to (1) the presence of subtropical thicket vegetation and its condition, (2) the occurrence of process components, (3) the degree of suitability of wildlife habitat (with suitability of elephant habitat as a surrogate), (4) the location of protected areas, and (5) future land-use pressures (Table 2). Criteria relating to 4 and 5 illustrate how we incorporated implementation issues into the location of the paths. Table 2 indicates the relative importance of each criterion and the respective cost incurred. Given the cost values assigned, criteria of higher rank override lower rank criteria (i.e., intact habitat was always more suitable than transformed or degraded habitat irrespective of wildlife habitat suitability). The relative cost of each criterion reflects the priority order of the key functions mentioned above.

We developed a cost surface (referred to as a map of landscape suitability) that reflects the options for achieving upland-lowland and macroclimatic gradients by combining all these criteria. The cost surface was first derived at a 25-m resolution by adding all criteria (with their respective cost) and was then aggregated to 1000 m based on the mean cost value (Fig. 2). Thus low-cost areas represent the nearly optimal location for such ecological process components (gradients). In our case, protected areas of pristine subtropical thicket, which were also highly suitable for wildlife, were considered the best areas to achieve these gradients, whereas highly transformed habitat that was not subtropical thicket was considered least suitable.

We constrained the 1-km-wide conservation paths within single primary water catchments by anchoring them to major river mouths and ending them at the northern margin of subtropical thicket. River mouths were selected because of key ecological processes associated with their estuaries and wetlands (Heydorn & Tinley 1980). Based on the landscape suitability surface, least-cost surface analysis identified the best option to link start and end points. Urban areas, including rural settlements, were excluded (i.e., the paths could not traverse urban areas). This procedure selected conservation paths with the highest landscape suitability for the considered criteria.

Expanding Conservation Paths toward Corridors (Stage 2)

The 1-km-wide conservation paths represent a nearly optimal location and the bare minimum extent for conserving processes along upland-lowland and macroclimatic

Table 2. Criteria used to derive conservation paths in relation to the functionality of macroclimatic and upland-lowland gradients that the conservation paths aim to achieve.

<i>Criteria</i>	<i>Objective</i>	<i>Value</i>	<i>Change in cost</i>
Thicket biome	favor thicket biome	subtropical thicket vegetation	0
		nonthicket vegetation	+5000
Habitat transformation	avoid transformed areas	natural (untransformed)	0
		transformed	+4800
Habitat degradation	avoid degraded areas (including invaded areas)	intact	0
		moderately degraded	+1800
		severely degraded	+3200
Elephant suitability ^a (categorical)	favor suitable habitat for wildlife	high	0
		medium	+300
		low	+600
		not suitable	+900
Process component	include spatially fixed processes	process	0
		no process	+150
Protected areas	link protected areas	statutory protected areas ^b	0
		nonstatutory protected areas	+20
		outside protected areas	+80
Land-use pressures	avoid areas likely to be transformed	0 (no threat)	0
		1 (low threat)	+15
		2 (medium threat)	+30
		3 (high threat)	+45
Elephant suitability (continuous)	favor suitable habitat for wildlife	from 0 (high) to 14 (low)	0–14

^aElephant suitability was first included as a categorical variable to ensure that highly suitable areas receive a lower cost than any area of medium suitability, irrespective of the values for the criteria below. The last criterion helps refine elephant suitability by assigning a range of values within each category.

^bStatutory protected areas, which are underpinned by strong legislation and owned and run by national, provincial, or local authority agencies. Nonstatutory protected areas, underpinned by weak or nonexistent conservation legislation, comprise public or private land managed for conservation and other land uses. See Cowling et al. (2003b) for details.

gradients. We expanded these paths to (1) buffer the conservation path, (2) include fixed process surrogates, (3) achieve targets for vegetation types, (4) select areas highly suitable for wildlife (with the African elephant as a surrogate species), and (5) incorporate existing protected areas. The expansion was adjusted to avoid areas threatened by future land-use pressures. In doing this, we identified large conservation corridors of contiguous, extant habitat that achieved conservation targets for process and pattern and considered implementation opportunities and constraints.

We identified criteria—similar to those for the conservation paths—to expand these paths into functional corridors. A new cost surface was required to consider areas of high irreplaceability for pattern targets (biodiversity pattern was not used to identify the conservation paths). This second cost surface was controlled by the extent of untransformed thicket, irreplaceability values for achieving vegetation type targets, wildlife habitat suitability (based on areas suitable for elephant), distribution of protected areas, and future land-use pressures. Figure 3a illustrates how we assigned a cost value to each criterion. Although

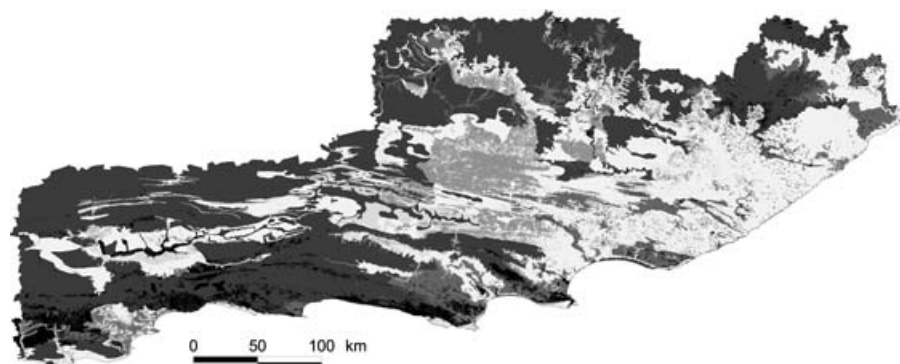
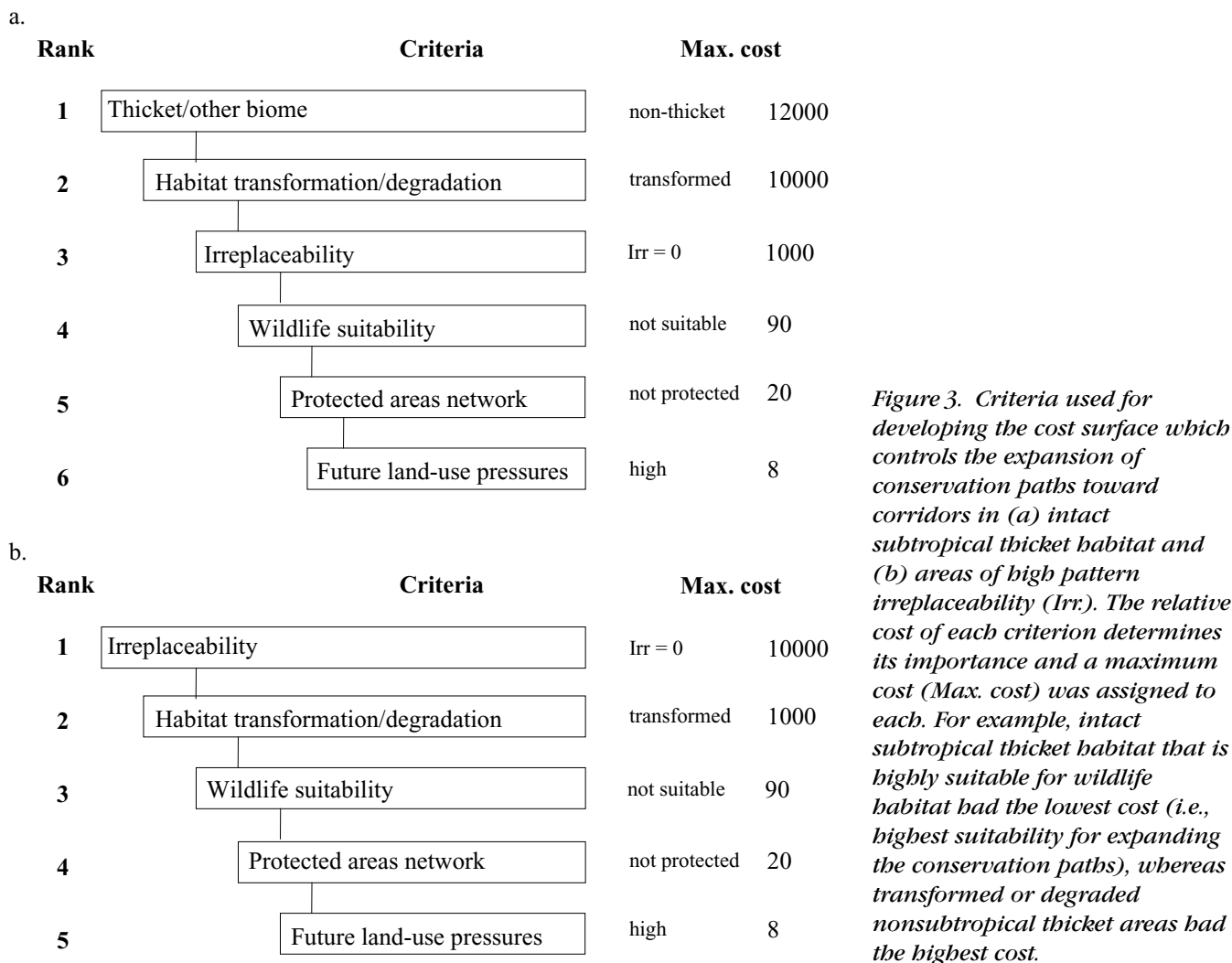


Figure 2. Landscape suitability surface showing the options for achieving upland-lowland and macroclimatic gradients based on the cost surface (see Table 2 for the list of criteria used). The shading relates to the landscape suitability (light shading means more suitable). Options for achieving the paths were greatest in the eastern part of the planning domain, where large tracts of untransformed subtropical thicket still occur.



we put a high cost on habitat transformation and degradation to avoid transformed areas, preliminary analyses showed that maintaining large ratios of relative cost of each criterion had a greater influence on corridor design than small variations of the cost assigned to each criterion.

Using least-cost analysis, we identified the extent to which the conservation paths could be expanded based on the second cost surface (Fig. 3a). The expansion was controlled by calculating the incremental cost extending at a right angle from the conservation paths; the expansion was stopped when the cost of corridors reached 0.25% of the total cost (overall cost of all the 1-km² cells in the planning domain). This cutoff was arbitrarily set to control the maximum width of the conservation corridor. The actual width of the corridors varied according to the landscape suitability. The paths were most easily expanded in untransformed thicket vegetation of high irreplaceability. In hostile areas (i.e., transformed nonsubtropical thicket) the extent of the corridor was restricted to the 1-km-wide conservation path. We then adjusted the boundaries to planning units, with the exception of the

Dune corridor, where the planning unit size was much larger than the width of available untransformed dune subtropical thicket vegetation, which is often confined to a very narrow strip immediately inland of the coast.

Expanding the Corridors into High Irreplaceability Areas (Stage 3)

Finally, we explored the extent to which corridors could be expanded to capture areas of high-irreplaceability for biodiversity. Irreplaceability values were recalculated in C-Plan for planning units, starting from the current configuration of corridors (from stage 2). We considered the contribution of corridors to targets for biodiversity features (Table 1), assuming that each of the corridors was afforded conservation management relatively consistent with that of protected areas. Spatially flexible processes were excluded because the corridors achieved them. The identified planning units were important for achieving remaining biodiversity targets. A new cost surface was required to update the irreplaceability pattern.

This third cost surface was controlled by irreplaceability values for achieving biodiversity targets, extent of untransformed areas (we no longer differentiated between subtropical thicket and nonsubtropical thicket vegetation types), wildlife habitat suitability (with African elephant suitability as a surrogate), distribution of protected areas, and future land-use pressures. Figure 3b illustrates how we assigned cost to each criterion. The lowest cost was allocated to intact habitat of high irreplaceability.

As in stage 2, we identified the extent to which the conservation paths could be expanded based on this new cost surface (Fig. 3b). The expansion stopped when the cost of corridors reached 0.25% of the total cost of the planning domain. The boundaries of the corridors were then adjusted to planning units except for the Dune corridor, where the size of the planning units was much larger than an appropriately sized corridor (see above).

Assessing Corridor Effectiveness

To test the adequacy of our approach, we compared the corridors identified here with a simple corridor designed to follow the courses of the major rivers (Fig. 1) and the dune coast. Such corridors, albeit simply designed, would nonetheless ensure biodiversity persistence by capturing the major east-west and north-south gradients. A similar design was used in the conservation assessment for the Cape Floristic Region (Cowling et al. 2003a). Our simple corridor design consisted of river buffers. We buffered the major rivers with a fixed width, which was adjusted to match the same area as the STEP corridors (2,225,000 ha). We compared both sets of corridors in relation to the criteria mentioned above: extent of natural area, thicket representation, elephant suitability, achievement of pattern targets (vegetation types), achievement of process targets, avoidance of land-use pressures (i.e., implementation constraints), and linkages to protected areas (implementation opportunities).

Results

Conservation Paths and Corridors

The identified paths represented the shortest and most suitable routes to achieve upland-lowland and macroclimatic gradients that pass through the major biogeographic subdivisions of the planning region (Fig. 4a). The Gouritz-Little Karoo and Gamtoos-Groot paths captured north-south upland-lowland gradients and east-west macroclimatic gradients. They were primarily constrained by subtropical thicket vegetation and habitat transformation at the mouth of the Gouritz and the Gamtoos rivers. The Sundays-Camdeboo and the Fish-Kowie paths captured north-south upland-lowland gradients and east-west macroclimatic gradients along the Great Escarp-

ment. The Sundays-Camdeboo path was constrained by habitat degradation in the middle Sundays River valley. The Gqunube-Amatole path avoided rural settlements. The location of the Kei path was not seriously affected by habitat transformation. Finally, the Dune path, running along the entire coast, was interrupted by urban development throughout and alien plant infestation in the west.

Figure 4b shows the location of the seven corridors in the planning domain. Together they comprise 25% of the planning region. Other than the Gouritz-Little Karoo and Gamtoos-Groot corridors, which are surrounded by much nonsubtropical thicket vegetation, all encompassed >80% subtropical thicket vegetation (Appendix). Thicket condition was >80% intact in all but the Sundays-Camdeboo, Fish-Kowie, and Gqunube-Amatole corridors, where much habitat has been transformed by overgrazing by domestic livestock. Other forms of transformation were <10% in all corridors. Overall, the corridors were effective in incorporating the existing protected areas (Appendix). Statutory protected areas covered between 0% (Kei) and 27% (Sundays-Camdeboo) of the corridor area and nonstatutory protected areas between 1.8% (Kei) and 15.6% (Fish-Kowie). Only the Dune corridor encompassed a high proportion of high-threat area, largely owing to pressures from urbanization.

Corridor Assessment

Of the 169 vegetation and three wetland types in the planning domain, the corridors and existing statutory protected areas together achieved targets for 84 (48.8%) types. Another 30 vegetation types had >50% of their targets achieved in the corridors. The corridors, in combination with statutory protected areas, were reasonably effective in incorporating the spatially fixed process components. They incorporated some 56% of the extant area of both biome interfaces and riverine corridors and 86% of sand movement corridors.

Together with the statutory protected areas, the conservation corridors occupied almost a quarter of the planning domain. When comparing the effectiveness of these conservation corridors in achieving the design criteria, the conservation corridors outperformed the river buffers for seven of eight criteria (Table 3). They were better at capturing intact area, subtropical thicket habitat, elephant suitability, macroscale gradients, fixed processes, and protected areas and at minimizing threats. River buffers were slightly better at capturing biodiversity targets (50.9 vs. 48% target achieved).

Discussion

Our aim here was not to provide a comprehensive assessment of various planning approaches. Rather, we sought to highlight the key differences of corridors in relation

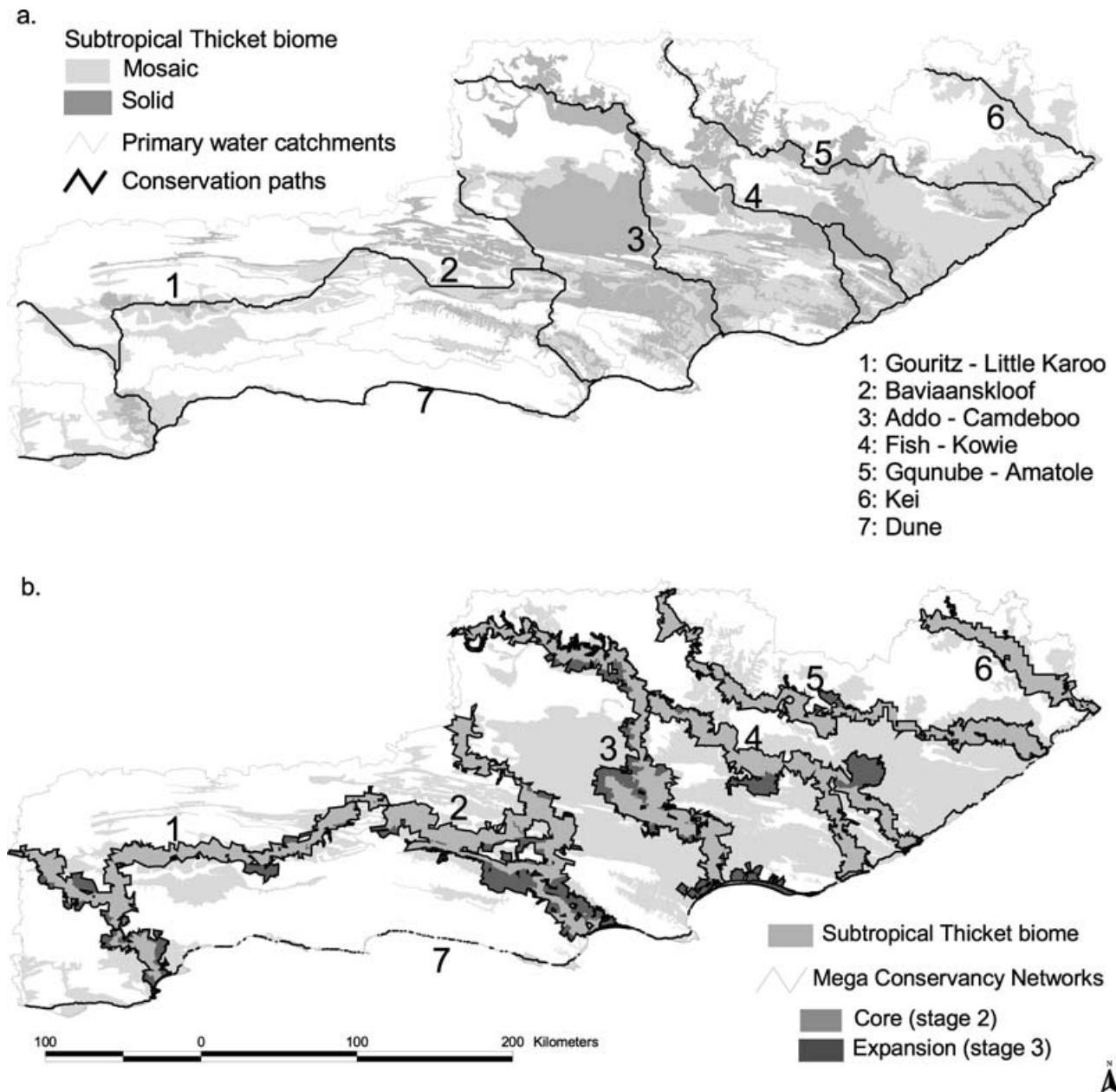


Figure 4. Identification of (a) conservation paths and (b) corridors for achieving upland-lowland and macroclimatic gradients. Each conservation path represents the most suitable route for capturing upland-lowland and macroclimatic gradients within each water catchment and along the dune coast. Corridors integrate biodiversity pattern and processes and avoid land-use pressures.

to other widely used approaches. Many researchers have used expert judgment to identify regional-scale corridors (e.g., Conservation International 2000; Dinerstein et al. 2000; Muruthi 2004). The drawback of this approach is that the achievement of pattern targets is often not considered. The same criticism may be leveled at approaches that rely entirely on identifying conservation areas that fulfill the requirements of focal species alone (Carroll et al. 2001; Sanderson et al. 2002b). An advantage of our approach is that we have combined elements of the sys-

tematic (target-driven) approach with the focal species (African elephant) requirement and accommodated, as far as possible, implementation opportunities and constraints. Expert knowledge was also used to identify the process components, as was the case for the conservation plan for the Cape Floristic Region (Cowling et al. 2003a), and to identify the cost assigned to each criterion used in the corridor design. The net result is a transparent and defensible system of corridors that ensures biodiversity persistence through large-scale processes, maximizes target

Table 3. Adequacy of STEP corridors and river buffers in terms of capturing intact habitat, subtropical thicket habitat, elephant suitability, processes, target achievement for vegetation types, inclusion of protected areas, and inclusion of areas subject to low land-use pressures.

	<i>Statutory protected areas</i>	<i>River buffers</i>	<i>STEP corridors</i>
Area (% of planning region)	7.3	21.1	21.1
Intact natural area (% of area)	95.8	83.3	85.3
Thicket biome (% of natural areas)	26.7	73.1	85
Elephant suitability (average value)	21.6	47.8	52.1
Gradients (%)	7.1	49.0	100.0
Fixed processes (%)	15.4	49.4	60.0
Pattern target achieved (%)*	13.6	50.9	48.0
Statutory protected areas (%)	100.0	27.5	47.7
Nonstatutory protected areas (%)	0.0	19.6	22.1
Low threat (%)	100.0	76.0	78.5

*The percentage of biodiversity features achieved includes the contribution of statutory reserves plus areas of corridors/buffers outside statutory reserves.

achievement for spatially fixed processes and pattern features, and accommodates implementation opportunities.

Corridor Effectiveness

Achieving biodiversity pattern and process targets simultaneously is a challenging task few conservation assessments have attained (Noss et al. 2002; Cowling et al. 2003a). Our approach aimed to capture key biological processes (aligned along major environmental gradients) while representing as much biodiversity pattern as possible and facilitating implementation. The seven conservation corridors we identified capture all key environmental gradients, include a significant amount of other (spatially fixed) process components, and achieve targets for 48% of the pattern (vegetation type) features. Although conservation corridors did not perform better than simple river buffers in achieving vegetation type targets, they were more effective in achieving process targets (the primary objective of these corridors). Focusing on capturing key biological processes in the Subtropical Thicket Biome greatly enhances the prospects for ensuring biodiversity persistence (Cowling et al. 1999; Rouget et al. 2003). Furthermore, conservation corridors integrate well with existing conservation areas because they include almost 50% of the statutory protected areas. Conservation corridors were slightly more successful than the river buffers in avoiding future land-use pressures; this was the criterion with the lowest cost, however, and in many cases (especially along the dune coast) areas of high land-use pressure could not be avoided.

Other conservation instruments have been proposed in the planning region to ensure the retention of biodiversity features not included in the corridors. For example, guidelines have been developed that will enable local government, which is legally bound to incorporate biodiversity issues into their planning processes, to limit development in endangered habitats (defined as vegetation types for which the amount of remaining extent habitat is less than or marginally greater than the biodiversity target), in spatially fixed process components that are unreserved, and in the corridors themselves (Pierce 2003; Pierce et al. 2005). Therefore, when implemented, conservation corridors, together with this other conservation instrument, will ensure adequate conservation in the planning region of biodiversity targets for process and pattern. The implementation of both of these conservation instruments to date has been very encouraging (Pierce et al. 2005).

Corridor Design

Our approach for designing corridors is based on systematic conservation planning principles (Margules & Pressey 2000) that differ from previous corridor studies which rely mainly on expert judgment (Conservation International 2000; Dinerstein et al. 2000; Muruthi 2004). We set quantitative targets for biodiversity pattern and used the concept of irreplaceability to identify areas that are representative of the planning region's vegetation types. Irreplaceability, however, was not the only criterion we used. It was integrated with other criteria related to implementation opportunities (incorporating existing protected areas) and constraints (avoiding areas vulnerable to future land use pressures). By combining these criteria we managed to achieve simultaneously several potentially conflicting conservation goals. Although our approach is largely quantitative, expert knowledge played a crucial role in the identification of and cost assigned to each criterion used in the design. The approach is sufficiently general to be applied to other areas. The final configuration of the conservation corridors, however, depends mostly on the relative cost of each criterion. This design can provide a tool for quantifying trade-offs between various criteria (biodiversity pattern and process, implementation constraints and opportunities). Further sensitivity analysis (e.g., on the relative cost assigned to each criterion) would be required to fully understand these trade-offs. Future research should focus on the interplay between expert judgment and exploratory analyses in which criteria are interchanged and costs are varied in determining the most biological meaningful criteria and cost values.

We acknowledge that various existing conservation planning tools could partly address the issues covered here. Using conventional conservation planning approaches, based on target-driven algorithms embedded in C-Plan or Marxan, it is possible to set targets for pattern and

process and to ensure spatial connectivity (Possingham *et al.* 2000). These approaches, however, cannot design corridors *per se*. Ours differs from these in that we consciously aligned our notional conservation system along environmental gradients and incorporated a wide array of design criteria in addition to connectivity. The focus was on explicit recognition of macroscale ecological processes and their appropriate design rather than connectivity of component sites to ensure larger reserves.

Designing corridors might not be appropriate in all planning regions. Given the large area of untransformed habitat still remaining in the planning region (72% of the planning domain), designing regional-scale corridors, which capture major environmental gradients across large distances, was still feasible. This might not be possible in other areas where transformation is more extensive. Under certain conditions increasing connectivity can even be harmful for biodiversity (Dobson *et al.* 1999). Planning approaches must be justified by the planning goal and the biological requirements of the area.

Planning for Implementation

Implementing conservation action requires more than just a systematic conservation assessment. An assessment must be coupled with stakeholder involvement and an implementation strategy (Knight *et al.* 2006). Our assessment was supported by a 4-year public participation process (Boshoff & Wilson 2004). An implementation strategy was also developed cooperatively with stakeholders (Knight *et al.* 2003). The entire process was integrated through an explicit conservation planning framework (Knight & Cowling 2003a). The conservation assessment is but one essential facet to solving the challenge of conserving and managing the Subtropical Thicket Biome.

The corridor design process outlined in our assessment was complemented, in practice, with the development of a model of ecologically sustainable land management called the Megaconservancy Network concept (Knight *et al.* 2003b). This model, developed with stakeholder input, was designed specifically for optimizing the socioecological conditions of the Subtropical Thicket Biome that provide opportunities for implementing conservation action. These opportunities include, for example, the rapid expansion of indigenous game ranching and indigenous game-based ecotourism and the high number of agricultural conservancies (private land-management agreements).

Each conservation corridor design represents a distinct megaconservancy network, each comprising a contiguous patchwork of properties of various tenures and land uses (e.g., privately owned land for stock farming, communal grazing land, ecotourism, and protected areas) that maximizes landscape heterogeneity (Forman 1995; Fabricius *et al.* 2003). It is proposed that properties (planning units) be managed in a coordinated, cooperative,

and integrated way. A megaconservancy network is a mechanism (a network of people) for aligning visions for landscape futures (Brunckhorst 2000) and cooperatively managing capital flows (e.g., natural, financial, social) to better ensure the simultaneous achievement of agricultural production, water use, and nature conservation goals (Hobbs & Saunders 1991). For example, several landowners may establish a conservancy across diverse landscapes to maximize the benefits provided for their individual ecotourism ventures. Participants in a megaconservancy network are committed to halting the loss of indigenous biodiversity and improving their own livelihoods. The approach is one of conservation through stewardship rather than establishment of strict reserves. The motto for megaconservancy networks is "Keeping people on the land in living landscapes."

Considerable progress has been made with fine-scale planning for implementing and achieving conservation action in three of the megaconservancy networks, namely Gouritz-Little Karoo, Baviaanskloof-Groot, and Sundays Camdeboo. Work has also begun in the Fish-Kowie Megaconservancy Network. Research at this scale requires a much better understanding of implementation opportunities and constraints, especially regarding issues such as landowner aspirations, institutional arrangements, capital and resource flows, and socioecological resilience (Brunckhorst 1998), than was required for this regional-scale study. Nonetheless, the approach adopted for this assessment, which was mindful of implementation issues, contributed greatly to the rapid implementation of conservation actions currently being undertaken in the planning region (Pierce *et al.* 2005).

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Appendix . Characteristics of conservation corridors in terms of the criteria used for deriving the landscape suitability surface.

	<i>Gouritz-Little Karoo</i>	<i>Gamtoos-Groot</i>	<i>Sundays-Camdeboo</i>	<i>Fish-Kowie</i>	<i>Gqunube-Amatole</i>	<i>Kei</i>	<i>Dune</i>	<i>PR^a</i>
Area (km ²)	3939	5227	4960	3686	3039	1433	606	105,454
Stages 1–2 (%) ^b	79	72	68	79	95	100	100	na
Biome								
thicket (%)	66	66	80	90	78	79	98	45
Habitat degradation								
intact (%)	86	82	50	65	67	95	96	72
degraded (%)	5	15	48	31	27	1	4	24
Wildlife suitability ^c								
mean value	26	32	66	78	66	77	82	41
Irreplaceability ^d								
mean value	0.21	0.24	0.38	0.12	0.09	0.02	0.23	0.09
Protected areas								
statutory (%)	11	20	27	14	10	0	10	7
nonstatutory (%)	11	6	15	16	22	2	15	12
Land-use pressures								
low to none (%)	83	92	89	78	65	67	44	77

^aEntire planning region, including corridors; na, not applicable.

^bPercentages are expressed in relation to the total area of each corridor.

^cElephant wildlife suitability ranges from 0 to 100 (most suitable).

^dValues range from 0 to 1 (1, irreplaceable, essential for achieving biodiversity target).