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MEDITERRANEAN-TYPE ECOSYSTEMS

From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich mediterranean-climate desert of southern Africa

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Abstract. Conservation planning has hitherto concentrated largely on the representation of biodiversity patterns within a system of conservation areas. Only recently has there been an emphasis on retaining segments of the optimal conservation area by defining implementation priorities in terms of the irreplaceability of areas and their vulnerability to threatening processes. The conservation of ecological and evolutionary processes that sustain and generate biodiversity, a requirement for a system of conservation areas that promotes biodiversity persistence, has received very little attention. By designing conservation systems in order to represent spatial features as surrogates for ecological and evolutionary processes, and by scheduling the implementation of areas in order to minimise the impacts of threats on these processes, it is theoretically possible to achieve a conservation system that combines retention and persistence. Here we discuss the requirements for establishing a sustainable (retention + persistence) conservation system in southern Africa's Succulent Karoo, a mediterranean-climate desert that is very rich in plant species. Firstly, we discuss planning issues salient to both representation and design, and indicate the location, size and role in conservation of the spatial components (surrogates for processes) necessary for a system of conservation areas in the Succulent Karoo intended for retention + persistence. Next we lay out the requirements for a conservation system in the region and summarise some existing work on representation and retention of plant species. We then present a protocol for decision-making and apply it by designing a hypothetical system of conservation areas. Finally, we compare representation of Red Data Book plant species in a system identified for pattern retention with our similar-sized system designed for retention + persistence. The latter conserves 37% fewer species, indicating that design for persistence incurs a cost in terms of representation. This cost is offset by developing a conservation system that is likely to persist in the face of global change, and that will sustain processes responsible for the maintenance and genesis of biodiversity.

Key words. Biodiversity conservation, climate change, conservation of pattern and process, persistence, representation, reserve design.

INTRODUCTION

In recent years considerable progress has been made in developing practical protocols for designing representative reserve systems (see Csuti *et al.*, 1997; Pressey, Possingham & Day, 1997 for reviews). Traditionally, reserves have been established in an ad hoc manner, often on economically marginal land and usually to conserve one or few charismatic species (Pressey, 1994; Rebelo, 1997). These non-strategic and usually politically expedient decisions have resulted in biased reserve systems that actually increase the costs of establishing representative ones (Pressey & Tully, 1994). Moreover, they fail to protect ecosystems, habitats and species most in need of protection (Rebelo, 1992; Aiken, 1994; Davis & Stoms, 1996). In an attempt to provide a more explicit and rational basis for area

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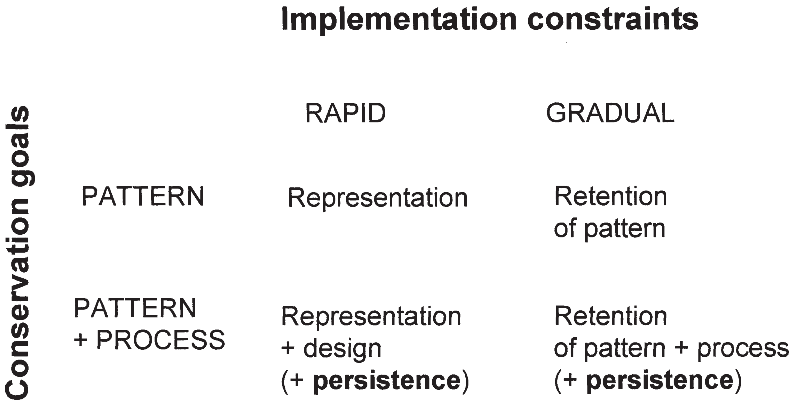

Fig. 1. Four strategies for conservation planning as framed by conservation goals (pattern *v.* pattern + process) and implementation constraints (rapid *v.* gradual). Note that the only path from retention to retention + persistence is by adding design to representation.

selection, scoring systems were introduced in the 1970s (see Margules & Usher, 1981), but these did not identify representative reserve systems in an efficient and effective manner (Pressey, 1997).

The 1980s saw the emergence of the 'minimum set' approach to conservation planning—the identification of whole systems of complementary areas which collectively achieve some overall conservation goal (e.g. Kirkpatrick, 1983; Margules, Nicholls & Pressey, 1988; Rebelo & Siegfried, 1992; Pressey *et al.*, 1993). The most common minimum set analyses are iterative or stepwise algorithms that apply a sequence of rules to find the most appropriate areas for selection at any stage, then recalculate the potential contribution of all unselected areas based on the features already represented, and reapply the rules. The approach has many advantages (Pressey, 1997; Pressey *et al.*, 1997). These include: the requirement for explicit representation goals; the achievement of these goals with the minimum resources (high efficiency); and, in some cases, an ability to select a large number of alternative reserve systems providing different scenarios of cost, land availability and other factors (high flexibility).

From representation to retention

Goal-directed or minimum-set algorithms generally identify a notional set of reserves to achieve a goal such as the representation of X% of the total area of each vegetation type in a region or X localities of each threatened species (Fig. 1). If the whole reserve system can be implemented with the stroke of a pen (perhaps if the planning context is entirely public land or if there are abundant resources for nature conservation), then ongoing loss or degradation of habitat will not compromise the achievement of the representation goal. A much more common planning situation, however, is for a the implementation of a notional reserve system to take years or decades, during which time the agents of biodiversity loss continue to operate. In such situations, strategies for maximizing representation on paper must be complemented or replaced by those that maximize 'retention' in the face of ongoing loss or degradation of habitat (Fig. 1). Maximizing the retention of the natural features of interest is defined here as minimizing the extent to which the original representation goals are compromised by habitat loss while the system of conservation areas is developing.

A crucial consideration in maximizing retention is the assignment of priorities for protection in the face of real-world constraints (Pressey *et al.*, 1996). The concepts of irreplaceability (Pressey, Johnson & Wilson, 1994) and vulnerability (Pressey *et al.*, 1996) were developed to explicitly define conservation value and priority for representative areas. In its simplest form, irreplaceability is a measure of the likelihood that an area will be needed to achieve a conservation goal; vulnerability is a measure of the imminence or likelihood of the biodiversity in an area being lost to current or impending threatening processes. Thus, irreplaceability is a measure of conservation value whereas conservation priority is the value of an area combined with some assessment of the urgency with which it should be conserved (Pressey, 1997). Areas of high irreplaceability and high vulnerability are highest priorities for conservation action, especially when the rate of implementation of the reserve system is likely to be slow (Pressey & Taffs, subm.). Focusing conservation resources on such areas will maximize the extent to which representation goals will be achieved on the ground. Retention goals are implicit in a number of conservation planning studies (e.g. Myers, 1988; Dinerstein & Wikramanayake, 1993; Lombard *et al.*, 1997; Rebelo, 1997) and have been explicitly incorporated into assessments of habitat protection in New South Wales (Pressey *et al.*, 1996; Pressey & Taffs, subm.).

From retention to persistence

Retention goals have generally been formulated in the context of threats to biodiversity such as land clearance (e.g. Dinerstein & Wikramanayake, 1993; Pressey *et al.*, 1996), urbanization (Rebelo, 1997) and encroachment by squatters (Peres & Terborgh, 1995). The ultimate goal of conservation planning is to enable biodiversity to persist not only despite such direct threats but also in the face of less obvious human-induced disturbances (e.g. altered fire regimes, changed forest structure, increased sedimentation) as well as longer-term ecological and evolutionary processes. This is not to deny the importance of habitat loss for the immediate persistence of biodiversity, but long-term persistence goals also need to be considered in designing and implementing reserve systems. We define design in this paper as the size, shape, connectivity, orientation and juxtaposition of conservation areas intended to address issues such as viable populations, minimization of edge effects, maintenance of disturbance regimes and movement patterns, continuation of evolutionary processes, and resilience to climate change. We contrast design, which concerns the maintenance of natural processes, with representation—the complementary goal concerned mainly with sampling the pattern of biodiversity (Fig. 1). The exception is when representation leads to the conservation of processes incidentally or deliberately through attempts to focus on entities such as broad vegetation types or landscapes that incorporate ecological interactions and physical flows and cycles (e.g. Noss, 1987).

Achieving both retention and persistence in situations where the full implementation of a system of conservation areas is likely to be slow and accompanied by ongoing loss of habitat requires consideration of the following. (a) Representation and design in the identification of candidate conservation areas; and (b) sound decisions about the progressive implementation of conservation action so that land use and other threats have minimal impact on the desired outcome. We also suggest that the only path from retention to retention + persistence is by adding design to representation (Fig. 1) before identifying priorities for implementation. In the implementation phase of a reserve system designed for retention + persistence, the importance of threatening processes in compromising the achievement of both representation and design goals will need to be considered and balanced.

This paper describes the rationale for developing a sustainable system of conservation areas for the Succulent Karoo, a species-rich desert region in southern Africa. After a brief description of the study area, we describe patterns and processes salient to conservation planning in the region. These are framed as conservation planning issues and depicted as spatial components for a conservation system. Since implementation of the system will be gradual—owing to land tenure and financial constraints—we include an explicit protocol for decision-making which we apply by designing a system of conservation areas for retention + persistence. Finally, we compare representation of Red Data Book plant species in a system identified by Lombard *et al.* (in press) for retention of pattern, with a similar-sized system designed for retention + persistence.

STUDY AREA

Biological and ecological features

The Succulent Karoo is a predominantly winter-rainfall desert region that occupies 112,000 km^2 on the arid fringes of the South Africa's Cape Floristic Region (Bond & Goldblatt, 1984) (Fig. 2). It includes 4849 species of vascular plants (40% endemic) (Hilton-Taylor, 1996) and is home to the richest succulent flora in the world (van Jaarsveld, 1987). It is also a centre of diversity for reptiles and many different groups of invertebrates (Vernon, in press). The recent and explosive diversification in the Mesembryanthemaceae, the largest succulent plant family in the region, has been described as an event unrivaled among flowering plants (Ihlenfeldt, 1994). Aspects of the biogeography and ecology of the Succulent Karoo are summarized in Jürgens (1991), Hilton-Taylor (1996), Milton *et al.* (1997), Cowling & Hilton-Taylor (in press) and Cowling, Esler & Rundel (in press). Below we describe

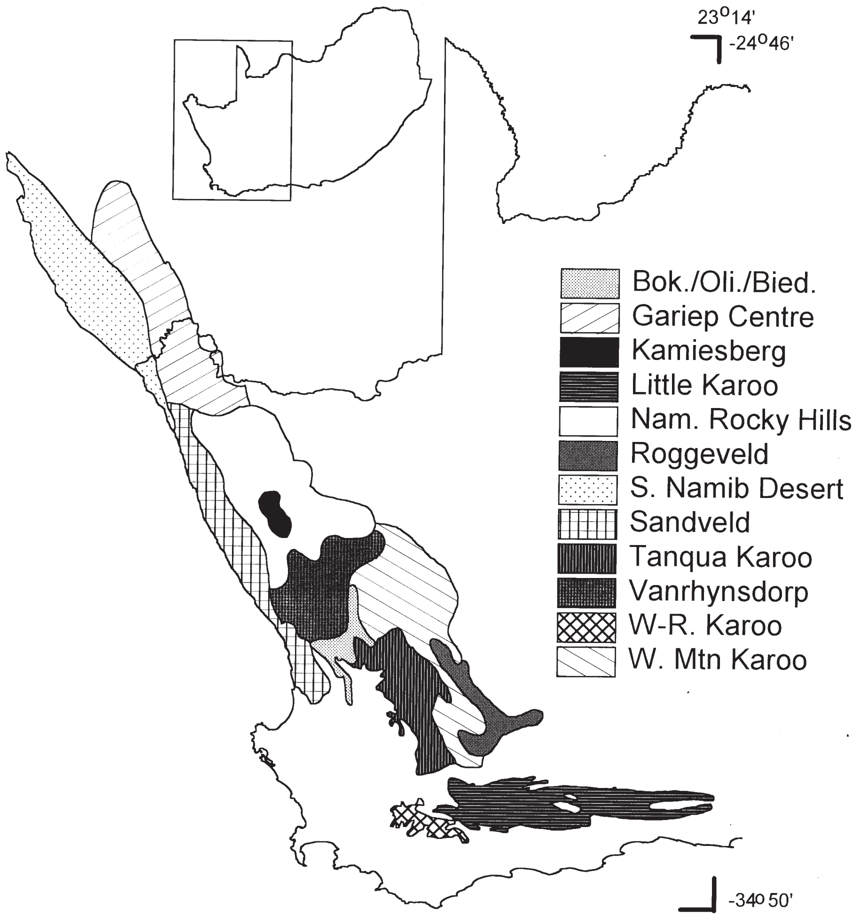

Fig. 2. Map of the Succulent Karoo showing the delimitation of bioregions according to Hilton-Taylor (1994, 1996). Bok./Oli./Bied. = Bokkeveld/Olifants/Biedouw, Nam. = Namaqualand, S. = Southern, W-R. = Worcester-Robertson, W. = Western.

only those biological features that are salient to conservation planning for the region.

1. As a consequence of an unusual composition and high endemism, the flora of the Succulent Karoo is unique (Cowling & Hilton-Taylor, in press). The region includes 1940 endemic plant species and sixty-seven endemic genera (Hilton-Taylor, 1996).
2. Local and regional plant richness is very high. Thus, on average seventy species are recorded in a tenth-hectare plot (in one plot, the tally was 113!) (Cowling *et al.*, 1989). Larger areas support about four times the number of species than comparable winter-rainfall deserts elsewhere in the world (Cowling *et al.*, 1998). In the mountainous desert of the Gariep Centre (Fig. 2), 331 species have been recorded in 1.3 km^2 in an area where annual rainfall is less than 70 mm (von Willert *et al.*, 1992).
3. This high regional richness is the result of high compositional change of species-rich communities along environmental and geographical gradients, i.e. high beta and gamma diversity, respectively (Cowling *et al.*, 1989; Cowling & Hilton-Taylor, in press). Many species are extreme habitat (mainly edaphic) specialists of limited range size (Cowling & Hilton-Taylor, in press). Point endemism is most pronounced among succulents (especially Mesembryanthemaceae) and bulbous lineages, and is concentrated on hard substrata, especially quartzites, shale ridges and quartz

lag-gravel plains (Desmet & Cowling, in press a; Schmiedel & Jürgens, in press). The area is home to 851 Red Data Book species (Hilton-Taylor, 1996).
4. Unlike other deserts, the dominant perennial component in Succulent Karoo communities comprises relatively short-lived (5–15 years) leaf succulent shrubs (Gotzmann, Jürgens & Cowling, in press) which are incapable of sprouting after prolonged droughts or heavy grazing. The age structure of these succulents is uneven: plants die and are replaced continuously, often resulting in significant compositional change over decades-long periods (Gotzmann *et al*., in press). Furthermore, the majority of succulent and bulb lineages are insect-pollinated obligate out-crossers with limited dispersal distances.

Conservation and threats

About 2.1% or 2352 km^2 of the Succulent Karoo is conserved in six statutory reserves (Hilton-Taylor, 1994). The largest of these is the 162,445 ha Richtersveld National Park, a reserve established on the basis of a contract between South African National Parks and the community who occupy this communally-owned land. Larger reserves (>10,000 ha) are represented in only four of the Succulent Karoo's twelve bioregions (Fig. 3) and conserve only 80 (9%) of its 851 Red Data Book plant species (Lombard *et al*., in press). Thus, the reserve system for the Succulent Karoo is grossly inadequate for conserving the region's biodiversity.

More than 90% of the Succulent Karoo is used as natural grazing (Hilton-Taylor, 1994), a form of land use that is theoretically not incompatible with the maintenance of biodiversity and ecosystem processes. Thus about 100,000 km^2 remains in a natural or semi-natural state. However, much of the remaining natural habitat is vulnerable to a wide range of immediate threats. These, in order of their overall importance, are as follows.

1. The expansion of communally-owned land and the associated overgrazing and desertification (Hilton-Taylor, 1994; Todd & Hoffman, in press).
2. Overgrazing of commercial (privately-owned) rangelands.
3. Agriculture, especially in the valleys of perennial rivers.
4. Mining for diamonds, heavy minerals, gypsum, limestone, marble, monazite, kaolin, ilmenite and titanium in the Sandveld, Southern Namib Desert, Vanrhynsdorp Centre and Richtersveld bioregions (Hilton-Taylor, 1994; Desmet, 1996).
5. Illegal collection of succulents and bulbs.

PATTERNS AND PROCESSES TO BE CONSIDERED IN CONSERVATION PLANNING IN THE SUCCULENT KAROO

We anticipate that the achievement of conservation goals in the Succulent Karoo will rely heavily on off-reserve management approaches in addition to strict reservation. In this and the subsequent section, we therefore use the term 'conservation areas' to refer to both reserves and areas covered by off-reserve protection. Here we discuss some patterns and processes salient to locating and designing a system of conservation areas that will promote retention + persistence (Fig.1).

Planning issues for representation + design (the precursors of retention + persistence—Fig. 1) are discussed, by way of examples, in the text below. Table 1 lists the spatial components of a conservation system in the region intended for retention + persistence. The geographical locations of some spatial components are shown in Fig. 4.

Representation issues

Sampling of species

Here the aim is to set conservation targets for species in terms of numbers of localities or areas of actual or predicted distribution or core habitat. Targets should ideally reflect relative need for protection in terms of the species' natural rarity and vulnerability to threatening processes.

With regard to species, the approach in the Succulent Karoo (Lombard *et al*., in press) has been to focus on the region's extraordinarily rich Red Data Book (RDB) flora, comprising 851 species and subspecies, most of which are rare and highly range restricted (Hilton-Taylor, 1996). This approach has three advantages. Firstly, components of the RDB classification embody threatening processes; hence, the use of these species promotes pattern retention in conservation planning. Secondly, since this subset of the flora reflects the upper range of the region's high compositional turnover along environmental and geographical gradients, a

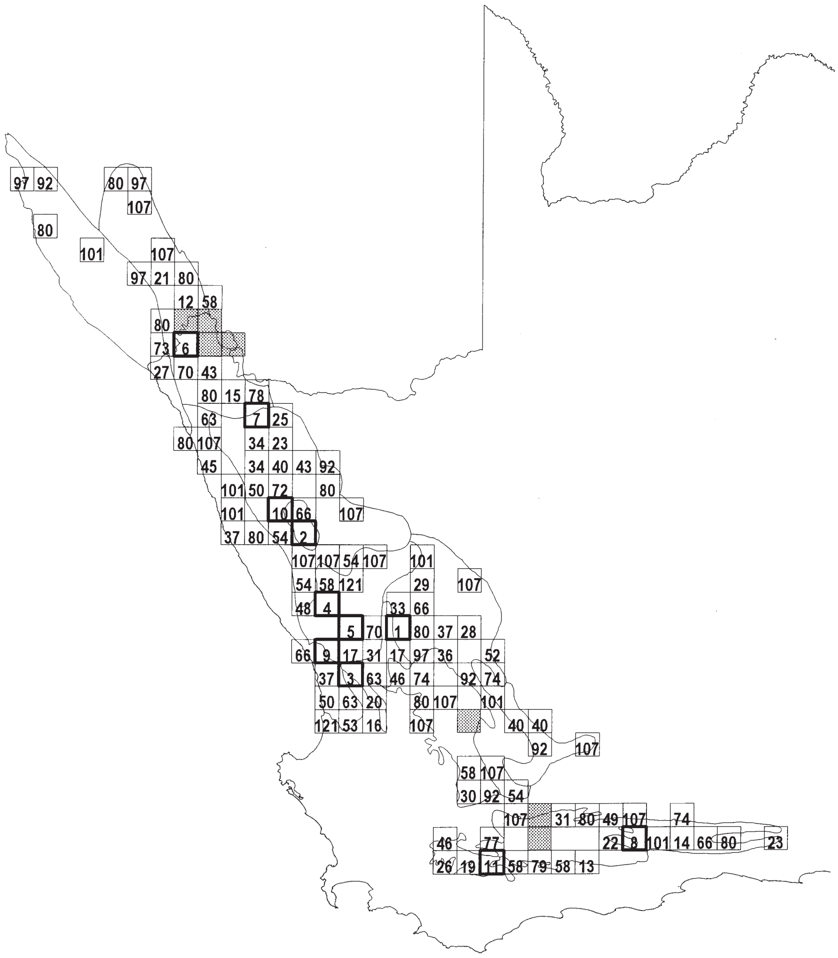

Fig. 3. The real-world scenario for a reserve configuration identified by Lombard *et al.* (in press) for retention of Red Data Book species in the Succulent Karoo. Numbers are the sequence in which quarter degree squares (QDS) were selected, on the basis of RDB species representation (see text for details). The top eleven QDS, mooted as core conservation areas, have bold borders. The existing conserved QDS are shaded.

conservation system based on representation of RDB species is likely to capture a great deal of floristic diversity generally (Lombard *et al.*, in press). Thirdly, the RDB database comprises 1972 distribution records captured at the quarter degree scale ($QDS = 15' \times 15'$), and is considered to be reasonably reliable as a presence-absence database (C. Hilton-Taylor, pers. comm.). However, there are no species data at the level of individual farms, which ultimately will be the units of land acquisition and management for the conservation system. Conversion from QDS- to farm-scale will need to be done in the implementation phase of the system that is outlined later in this paper.

Sampling of land classes as surrogates for species

Since RDB species are under-represented in certain habitats, especially those characteristic of the Sandveld, Tanqua Karoo and Roggeveld bioregions (Desmet & Cowling, in press a; Lombard *et al.*, in press), land classes—as surrogates for species—will also need to be sampled to achieve representation of biodiversity (see

Table 1. Spatial components as surrogates of ecological and evolutionary processes that should be represented in a system of conservation areas in the Succulent Karoo intended for retention + persistence (Fig. 1).

Spatial components	Size (ha)	Role in conservation
Small conservation areas	<1000	Protection of viable populations of locally endemic plant species and plant-insect interactions; maintenance of small-scale disturbance regimes
Large conservation areas	>100,000	Protection of viable populations of large mammals including gemsbok, leopard and black rhinoceros and nomadic birds; maintenance of faunal metapopulations associated with small-scale disturbance patches
Entire sand movement corridors	10,000–50,000	Maintenance of inland movement of sands and gradients of soil development important for soil-specific plant assemblages and promoting diversification of plant species.
Whole river catchments draining from the uplands to the coast	15,000–40,000	Protection of riverine and wash habitats that: have distinctive species assemblages; provide stepping stones of hard substrata for movement, and associated diversification, of plant species between the uplands and the coast; contain nesting sites for ecologically important hymenopteran pollinators; and provide dry-season refugia for larger ungulates.
Juxtaposed edaphically different habitats	1000–5000	Maintenance of ecological (edaphic) diversification of poorly-dispersed lineages
Whole minor drainage basins associated with quartz fields	1000–10,000	Maintenance of presumed evolutionary fronts, distinct between basins, consisting of different nested clades of derived taxa
Areas spanning the gradient from uplands to coastal lowlands and interior basins	50,000–1,000,000	Maintenance of seasonal migration of springbok and other ungulates and the associated disturbance regimes
Large and steep climatic gradients	5000–3,000,000	Facilitation of shifts in species' distribution in response to climate change

also Kirkpatrick & Brown, 1994; Faith & Walker, 1996). As in the case of species, targets that reflect conservation needs must be set for land classes in terms of occurrences or (preferably) extent within the selection units for the conservation system.

Sampling of environmental and geographical variation within land classes as surrogates for unmapped biological variation

In many instances RDB species data at the QDS scale will not distinguish the floristic heterogeneity within land classes in response to subtle environmental gradients. Therefore, these land classes must be subdivided and representation targets must be set for the subdivided ranges. For example, vegetation on quartz fields shows considerable variation within apparently homogeneous drainage basins of 1000–10,000 ha (P. G. Desmet & A. E. Ellis, unpubl. data). The same is probably true of quartz-slope habitats and other hard substrata throughout the Succulent Karoo (Desmet & Cowling, in press a; Schmiedel & Jürgens, in press), whereas softer surfaces are more internally homogeneous.

Representation and design issues

Sampling of spatial components as surrogates for ecosystem processes

The maintenance of processes that sustain ecosystem structure and functioning is essential for achieving persistence goals for systems of conservation areas (Pickett & Thompson, 1978; Baker, 1992; Noss, 1996; Bond, 1994). Therefore, targets must be set for the representation of landscapes, other appropriate land classes, or particular geographic features that will ensure the maintenance of these ecosystem processes. Below we describe some of the processes that must be accommodated for in a conservation system in the Succulent Karoo that is designed for persistence.

The movement of marine sediments in the Sandveld region (Fig. 4) is a large-scale (10–50,000 ha) (Table 1), dynamic process that drives ecosystem functioning and

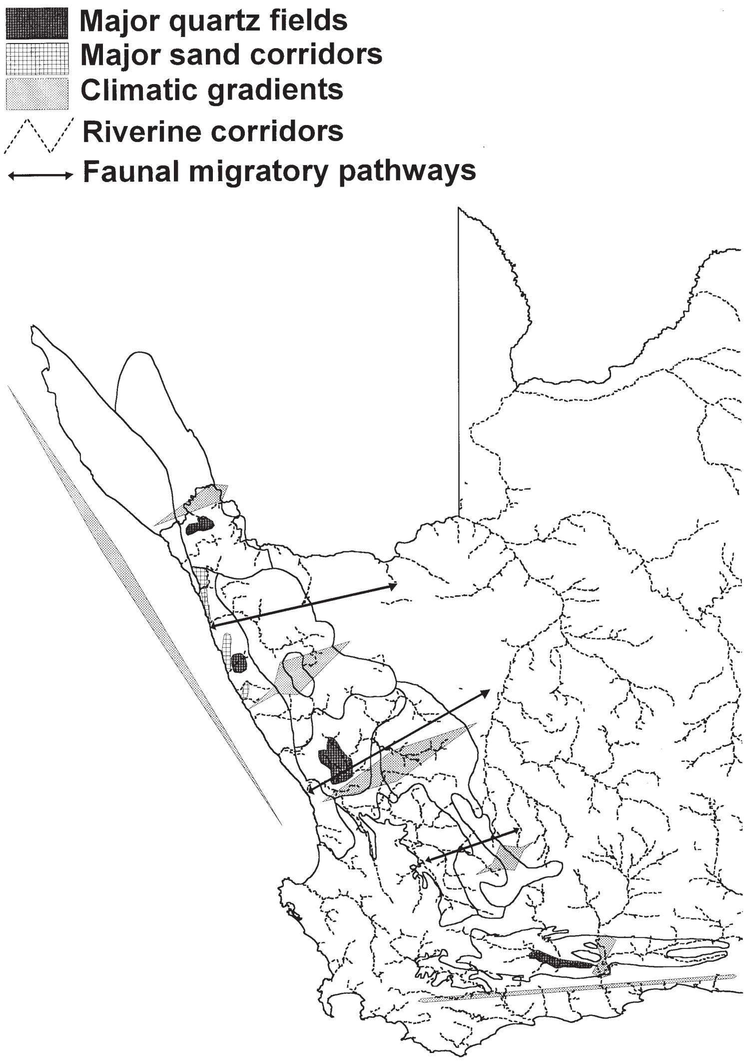

Fig. 4. Location of spatial components in the Succulent Karoo required for representation in a system of conservation areas designed for retention + persistence (see Fig. 1). Thickness of lines indicating climatic gradients is proportional to the steepness of the gradient. In some cases (e.g. sand movement corridors, riverine corridors), spatial configuration is pre-defined by the features themselves; others (e.g. faunal migratory pathways, climatic gradients for migration or adjustment to climate change) do not have predefined boundaries.

determines biodiversity patterns (Desmet, 1996). The north-moving Benguela Current carries a large sediment load, some of which is deposited in protected embayments. During times of lower sea level, these sediments are exposed and blown inland, under the influence of the strong, southerly summer wind-regime. The result is a complex sequence of sediments, ranging from young, calcareous sands, to older, reddish sands underlain by a calcrete or siliceous hardpan. Each sediment type, corresponding to a different age of deposition, supports a different assemblage of plants (Desmet, 1996; P. G. Desmet & R. M. Cowling, unpubl. data). Truncation of this dynamic habitat complex by inappropriate placement of infrastructure, especially near the coastal margin, would irreversibly disrupt this process of landscape and ecosystem evolution.

The riverine and wash ecosystems of the Succulent Karoo (Fig. 4) support structurally and functionally heterogeneous assemblages (Milton *et al*., 1997). These are probably associated with a wide variety of important ecological processes operating over different spatial scales (and see below in relation to interspecific interactions, regular faunal movements, and evolutionary processes). While most of the perennial riverine ecosystems in the Succulent Karoo have been transformed by agriculture (Hilton-Taylor, 1994), it is still possible to include a limited number of seasonal rivers in future conservation areas. Ideally, this would involve the conservation of their entire catchments (15–40,000 ha) to minimize the impacts of present or future land uses on flow regimes and water quality.

There are, of course, many other important ecosystem processes that we have not considered here. Unfortunately, no ecosystem-level research has been conducted in the Succulent Karoo. However, by ensuring that large (*c*. 100,000 ha) conservation areas (Table 1) span substantial environmental gradients (Noss, 1996), it should be possible to accommodate other processes not specifically targeted in conservation planning.

Sampling of spatial components features as surrogates for evolutionary processes

Conservation areas should be designed to sustain lineages and processes that generate diversity. This is easier said than done. Well-resolved phylogenies are essential to inform planning aimed at maintaining evolutionary processes. Unfortunately, cladograms are not available for the vast majority of Succulent Karoo lineages, nor are they likely to be so in the foreseeable future. Furthermore, very little is known about diversification in the Succulent Karoo. While biotic factors, specifically pollinator-plant interactions have clearly played a role in the diversification of certain lineages, habitat specialization appears to be an overarching process (Hammer, 1992; Ihlenfeldt, 1994; Goldblatt & Manning, 1996; Desmet, Ellis & Cowling, 1998; Cowling & Hilton-Taylor, in press; Desmet & Cowling, in press a).

Owing to the apparent prevalence among Succulent Karoo plant lineages of edaphic (ecological) diversification, conservation planning should set targets for inclusion in the conservation system of juxtaposed, edaphically differentiated land classes. This would facilitate continuous colonization of non-core habitat, thereby providing opportunities for diversification after population isolation. Because of the fine-scale heterogeneity that is associated with these processes (Cowling & Hilton-Taylor, in press), relatively small areas (1000 ha) would be required to sustain them (Table 1).

Rapid diversification among some Succulent Karoo plant lineages—the Mesembryanthemaceae in particular (Ihlenfeldt, 1994; Desmet *et al*., 1998)—is a contemporary phenomenon. Conservation planning needs to target habitats and lineages that are associated with these evolutionary processes. Controversy exists as to whether priority should be given to areas supporting ancestral taxa with evolutionary potential (Linder, 1995) or those representing evolutionary fronts of currently speciating taxa (Erwin, 1991; Brooks, Mayden & McLennan, 1992; Moritz, 1995). On the quartz fields of the Vanrhynsdorp Centre (Fig. 4), the proposed mode of diversification within certain lineages of Mesembryanthemaceae is the evolution, via disruptive selection, of progressively dwarf forms in response to gradients of increasing edaphic aridity (Ihlenfeldt, 1994). In the genus *Argyroderma*, which comprises eleven species all endemic to these quartz fields (Hartmann, 1978), the parapatric derivatives coexist sympatrically with the ancestral 'metaspecies' (*sensu* Linder, 1995), *Argyroderma fissum* (Ihlenfeldt, 1994). Furthermore, different clades of derived taxa are nested within drainage basins (Desmet *et al*., 1998). Thus, each of these drainage basins, ranging in size from 1000 to 10,000 ha, may comprise a distinct evolutionary front, including both the ancestral and younger species. If conservation areas that promote persistence are to be established in this part of the region, then the goal should be to include a few entire and adjacent drainage basins. Such a system will preserve the potential for habitat-related diversification within a drainage basin, as well as geographical diversification associated with occasional gene flow between adjacent basins. Similar processes are associated with other quartz-field areas in the Succulent Karoo (Schmiedel & Jürgens, in press).

Diversification may also be associated with bedrock outcrops exposed along drainage lines in the sandy Sandveld bioregion (Fig. 4). These hard surfaces provide stepping-stones for the dwarf-succulent lithophillous flora to migrate between the granitic uplands and the rocky coastline, where some local endemics are found (P. G. Desmet & R. M. Cowling, unpubl. data). Diversification is also likely to be related to patterns of development of marine sediments in the Sandveld (see above). Large conservation areas

(10,000–40,000 ha) will be necessary to contain and protect these evolutionary processes (Table 1).

Design issues

Extent and quality of habitat to maintain viable populations

Here the objective is to set targets for the extent, shape, configuration and connectivity of habitat for selected species. Targets might be set separately for core, suitable and marginal habitat or weighted to promote the conservation of core habitat. In the absence of good information on habitat relationships, location within distributional range might indicate core habitat.

Very few studies have been carried out on minimum viable populations of plant species, and all of these have focused on the demography of threatened plants (e.g. Menges, 1990; Burgman & Lamont, 1992; Bradstock *et al*., 1996). Nothing is known about minimum viable populations of Succulent Karoo species. Many species, including most Red Data Book taxa, are habitat specialists occupying very limited ranges (Cowling & Hilton-Taylor, in press). However, owing to small stature, local population sizes may be quite considerable (Desmet *et al*., 1998; Desmet & Cowling, in press a). The relative importance of deterministic (i.e. external) as opposed to stochastic factors in increasing vulnerability to extinction is not known. Most Succulent Karoo species are vulnerable to small population effects (i.e. stochastic factors—Caughley, 1994), since they are short-lived, non-sprouters with continuous recruitment (Gotzmann *et al*., in press), and are obligate outcrossers with limited pollen and gene dispersal (Ihlenfeldt, 1994; Cowling & Hilton-Taylor, in press).

It is possible that naturally rare species, which comprise the majority of the Succulent Karoo's RDB species (Hilton-Taylor, 1994), have reproductive traits which enable them to cope with small population sizes (Lawton, 1993; Kunin, 1997). We suggest, albeit tentatively, that deterministic factors may pose a greater threat than stochastic factors in causing the extinction of rare plants in the Succulent Karoo (see, for example, Midgley *et al*., 1997). Therefore, we suggest that small conservation areas (<1000 ha) are adequate to conserve populations of locally endemic plant species (Table 1).

The minimum viable populations of higher trophic organisms such as gemsbok, leopard and black rhinoceros, all of which used to inhabit most Succulent Karoo landscapes (Skead, 1980), also need to be considered. The impact of these larger mammals, especially the herbivores, is likely to of great importance for the maintenance of plant community structure and function (Owen-Smith & Danckwerts, 1997). Small population studies (Caughley, 1994) are relevant to the amount and quality of habitat required to maintain populations of larger mammals. In fynbos ecosystems, which are more productive than those of the Succulent Karoo, conservation areas in excess of 100,000 ha are required to preserve viable populations of top predators (Rebelo, 1992). (Table 1). Similarly, large conservation areas, in the order of 100,000 ha, are required to conserve populations of the rich nomadic bird fauna that periodically penetrates into the Succulent Karoo from the adjacent, summer-rainfall Bushmanland Plateau (Dean, 1995). Both these and the larger mammalian herbivores require for their long-term persistence large areas of grass-covered (*Stipagrostis* spp.) sandplain that is found along the inland margin of the Sandveld bioregion. This habitat is also sought after by communal and commercial ranchers.

Maintenance of interspecific interactions

The conservation of interspecific interactions that drive ecological and coevolutionary processes is central to the notion of a system of conservation areas that promotes persistence (Bond, 1994; Thompson, 1996). These interactions include pollinator and dispersal mutualisms, plant-herbivore interactions, and predator-prey systems. Targets must be set to address the relevant representation and design issues so that interactions are maintained.

Very little is known about these sorts of interactions in the Succulent Karoo. Pollination systems appear to be dominated by generalists in terms of fauna and flora (Struck, 1994). However, recent research suggests that diversification of some lineages has been promoted by pollinator-flower coevolution, e.g. Iridaceae and Geraniaceae with long-tongued flies (Nemestrinidae) (Goldblatt, Manning & Bernhardt, 1995; Manning & Goldblatt, 1996), and Iridaceae, Liliaceae (*sensu lato*) and Orchidaceae with monkey beetles (Scarabaeidae: Hoplinii) (Picker & Midgley, 1996). These pollinators have played an important role in shaping flower morphology. Unfortunately, despite the importance for conservation planning, very little is known about the habitat requirements of insect pollinators in the Succulent Karoo.

Succulent Karoo plants exhibit numerous physical and chemical adaptations to herbivory by invertebrates, reptiles and mammals (van Jaarsveld, 1987; Milton, 1991, 1992). Of particular interest is the coevolutionary relationship between molerats (Bathyergidae) and the storage organs of the region's rich geophyte flora (Lovegrove & Jarvis, 1986). Anecdotal evidence suggests that tortoises, which consume the dry capsules of Mesembryanthemaceae (Milton *et al*., 1997), may disperse their seeds for considerable distances, thereby playing a crucial role in the metapopulation dynamics of this otherwise poorly dispersed group. The local extinction of the larger herbivore fauna over much of the Succulent Karoo has truncated many coevolutionary processes; their reintroduction to conservation areas is essential for the continuation of these relationships.

Many plant-insect interactions may operate over a very small scale (tens of meters) and could be sustained in small conservation areas (<1000 ha) (Table 1). In some cases, specific habitats will be needed within conservation areas. For example, the exposed walls of drainage lines provide nesting sites for ecologically important hymenopteran pollinators (Gess, 1981; Gess & Gess, 1989). Interactions between plants and larger herbivores (e.g. migratory movement of springbok, see below) may require large expanses (>500,000 ha) of intact habitat for their maintenance (Table 1).

Maintenance of regular faunal movements

The seasonal movements of larger mammals are an example of a large-scale process that once influenced ecosystem function in the region (Owen-Smith & Danckwerts, 1997). Perhaps the most spectacular of these migrations was that of the springbok. Prior to the rinderpest epidemic of 1896, large herds of these antelope moved in autumn from the summer-rainfall plains of Bushmanland and the Upper Karoo, into the Sandveld, and Tanqua Karoo bioregions, respectively (Skinner, 1993) (Fig. 4). Historical records from Namaqualand suggest that these treks amounted to springbok 'in their millions'. We can only speculate as to the impacts of large concentrations of ungulates on Succulent Karoo ecosystems (see below). Although it may be impossible re-establish these large-scale migratory cells—up to 1,000,000 ha in extent (Skinner, 1993)—within a system of conservation areas, it is certainly possible to encourage them on a smaller scale. Thus, a conservation area spanning the gradient from the uplands of the Namaqualand Rocky Hills (summer grazing) to the coastal (Sandveld) lowlands (winter grazing), encompassing areas of some 50,000 ha, would probably enable some limited seasonal migration (Hoffman *et al*., in press).

At a more local scale, riverine habitats are important in providing shelter and forage for larger ungulates during the dry season (Dean & Milton, in press). Multiple samples of these habitats are therefore probably necessary as drought refugia in a system of conservation areas for the Succulent Karoo.

Maintenance of irregular or 'nomadic' faunal movements

Faunal nomadism, in which movements are irregular and where destinations may differ from year to year, is considered to be an adaptation to resources that are patchy in space and time. Hence, nomadism is more prevalent in the summer-rainfall Nama Karoo where rainfall is both patchy and unreliable (Dean, 1997), than in the Succulent Karoo where rainfall is spatially and temporally more predictable (Desmet & Cowling, in press b). Nonetheless, components of the large nomadic bird fauna principally larks, sandgrouse, canaries, buntings, bustards, sunbirds, and some raptors of the Bushmanland Plateau (Dean, 1995, 1997), frequently move to the grass-covered plains of the Sandveld bioregion to breed, especially during times of prolonged drought in the interior (Dean, 1995). These birds probably play an important but hitherto unstudied role in plant population and ecosystem processes (W. R. J. Dean, pers. comm.). Large (>100,000 ha) areas (Table 1) of good quality grassy habitat are required to sustain populations of nomadic birds. Alternatively, multiple conservation areas can be located so that one or more always contain some suitable habitat.

Maintenance of disturbance regimes

Design for the accommodation of disturbance regimes within conservation areas is crucial for the long-term maintenance of diversity (Pickett & Thompson, 1978; Baker, 1992). This can be achieved in different ways. (a) Setting targets for the size of conservation areas to be larger than the largest patch created by the relevant disturbance regime(s); (b) locating individual conservation areas so that they will collectively contain all the important successional stages created by the disturbance regime(s); and (c) designing management activities in one or more conservation areas to maintain important successional stages.

Very little is known about natural disturbance regimes and biodiversity maintenance in the Succulent Karoo. Various burrowing animals, including molerats, porcupines and suricates, create small-scale disturbances that impact on plant community structure (Dean & Milton, in press). Another small-scale disturbance process is associated with *heuweltjies* or mima-like mounds that occur over much of the Succulent Karoo. These are low, circular features, some 10–15 m in diameter, distributed across the landscape in a regular pattern (Lovegrove & Siegfried, 1989). The mounds are zoogenic, initially created by termites (*Microhodotermes viator*) and often colonized by a wide variety of burrowing animals (Milton & Dean, 1990). As a result, nutrient-enriched subsoil is brought to the surface creating a substratum physically and chemically very different from the intervening matrix. Thus, *heuweltjies* support a flora that is markedly different in appearance and composition to that of the surrounding vegetation (Midgley & Musil, 1990), and apparently play an important role in plant successional processes (Yeaton & Esler, 1990). Although appropriately designed small to medium-sized (1000–5000 ha) conservation areas in the Succulent Karoo are likely to include a large number of heuweltjies and other small-scale disturbance patches, larger reserves are probably required to maintain metapopulations of fauna associated with these sites e.g. aardvarks.

Rare, catastrophic drought is a large-scale disturbance in the Succulent Karoo, the impacts of which have been poorly documented. Von Willert *et al*. (1992) report that an unusually severe drought in the Richtersveld in the late 1970s resulted in the death of most perennial shrub individuals especially leaf-succulents. However, by the late 1980s, the vegetation had recovered completely in terms of plant density and cover, but not composition (Gotzmann *et al*., in press). There is no predictive understanding of the interaction between drought and grazing intensity by domestic livestock, and hence, the areal requirement for effective conservation.

The grazing and trampling impacts of migratory herds of springbok represent a large-scale (Table 1) disturbance regime that probably had a profound impact on community structure and ecosystem processes in the Succulent Karoo (Skinner, 1993; Owen-Smith & Danckwerts, 1997). The re-establishment of seasonal migratory movements for springbok and other larger ungulates within conservation areas—as discussed above—will ensure the maintenance of this disturbance regime.

Resilience to climate change

Systems of conservation areas that promote persistence must maximize the ability of species to move in response to climate change as well as sustaining evolutionary processes that will lead to future diversification in response to altered climates (Graham, 1988; Holdgate, 1994; Halpin, 1997). Should it be possible to conserve large intact landscapes and associated evolutionary fronts (see above), there is no reason why the rapid diversification and fine-scale habitat partitioning of the Succulent Karoo flora will cease (indeed, this may accelerate) in response to climate change.The requirement to facilitate shifts in distribution has important implications for both the location and design of conservation areas, depending on the management and condition of the matrix surrounding the conservation system (McNeely, 1994; Lombard 1996; Chapin *et al*., 1998). Design for climate change in any region needs information on the magnitude and direction of change of climatic variables such as mean rainfall, rainfall seasonality and mean temperature. Just as importantly, it requires effective planning responses relative to climatic gradients and the interaction of climate with other environmental variables determining species' ranges.

The Succulent Karoo encompasses a wide range of climatic gradients, both steep and shallow, that encompass a large range in terms of areal extent (Desmet & Cowling, in press b) (Fig. 4). Exceptionally large and steep gradients, with high biological change per unit distance, are associated with the escarpment zone inland of the Atlantic coastline. Here rainfall increases very rapidly from the warm, arid (<150 $mm.yr^{-1}$) lowlands to the cool and relatively moist (*c*. 400 $mm.yr^{-1}$) uplands along altitudinal gradients of 300–800 m that span distances of 3–15 km (Jürgens *et al*., 1997). In the Richtersveld, there is also a rapid transition from winter rainfall Succulent Karoo conditions on seaward slopes, to summer rainfall Nama Karoo environments on the inland slopes of the same mountain complex, possibly the most pronounced and steep boundary between two biomes anywhere in the world (Jürgens, 1991). There are also similarly large and steep climatic gradients in the inselberg country of the Little Karoo. A much shallower gradient, associated principally with declining rainfall (*c*. 200–25 $mmyr^{-1}$), and increasing fog incidence and wind regime, occurs along the 650 km of coastline between the southern margin of the Sandveld bioregion and the northern boundary of the Southern Namib Desert in Namibia (Jürgens *et al.*, 1997). The gradient of decreasing rainfall seasonality, from the Worcester-Robertson Karoo bioregion to the eastern border of the Little Karoo, spanning a distance of some 375 km, is similarly shallow (Milton *et al.*, 1997).

According to predictions of Global Change Models (Hadley Centre—HadCM2; Climate Systems Model—National Centre for Atmospheric Research), the current scenario for climate change in the Succulent Karoo is for a 1.5–2.5°C increase in mean annual temperature and a decline of 3–15% in the percentage of winter rain produced by the westerly frontal systems. The decrease in annual rainfall may be as high as 25%. Thus, the anticipated climate change is likely to have substantial impacts on the biota of the strongly winter-rainfall, western part of the region (Namaqualand), which is finely adapted to the contemporary mild, winter-rainfall climate (Cowling *et al.*, in press). Given that many Succulent Karoo plant species, especially the local endemics, are poorly dispersed, relatively short-lived, and extreme habitat specialists (Desmet & Cowling, in press a; Schmiedel & Jürgens, in press), climate change is likely to result in widespread extinctions. Conservation areas must be designed to minimize these impacts.

Factors other than climate (e.g. soil type, microhabitat, competition, disturbance regimes, extreme events) play an important role in determining the present distributions of species (e.g. Yeaton & Esler, 1990; Milton *et al.* 1997; Desmet & Cowling, in press a), so shifts in ranges will not necessarily parallel shifts in climatic envelopes (Bond & Richardson, 1990; Woodward & Diament, 1991; Pacala & Deutschman, 1995; Schneider & Root, 1996). Moreover, areas of rock, soil or terrain unsuitable for some species could prevent adjustment of species' ranges even within conservation areas (Peters & Darling, 1985). Furthermore, the rate of change could be so rapid that some species will not keep pace with the movement of their climatic envelope (Dobson, Jolly & Rubenstein, 1989), particularly as many plant species in the Succulent Karoo are poor dispersers.

Given the lack of knowledge of the factors, both physical and biological, that determine the contemporary distributions of the Succulent Karoo biota, as well as the uncertainty regarding the magnitude and direction of climate change, it is an extremely difficult task to design a reserve system that will be resilient to climate change. Clearly, there is a requirement to locate, configure and connect conservation areas relative to climatic gradients, perhaps favouring the larger, steeper gradients (more change per unit distance) to accommodate for the low dispersal distances prevalent in the flora. Given the high level of local endemism in the flora, it will be impossible to cater for range adjustments of all species in conservation areas. Therefore, it will be necessary to ensure that key parts of the unconserved matrix remain suitable for range adjustments. Finally, consideration should be given to locating conservation areas for selected species in areas that are now climatically marginal or unsuitable but which are likely to become suitable.

DESIGNING AND IMPLEMENTING A SYSTEM OF CONSERVATION AREAS FOR BOTH RETENTION AND PERSISTENCE

In this section we lay out the requirements for a conservation system designed for retention + persistence. Firstly, we summarize and assess work by Lombard *et al.* (in press) on a system for pattern (plant species) retention. Then we present a generic protocol for making decisions about priority conservation areas intended to promote retention + persistence. Next, by following the steps in this protocol, we design a hypothetical system of conservation areas for the Succulent Karoo—in addition to the existing reserve system—to promote persistence by capturing both pattern and process. Finally, we compare the effectiveness for RDB species conservation of a system identified only for pattern retention (Lombard *et al.*, in press) with the similar-sized hypothetical one that incorporates retention + persistence.

Previous work on representation and retention in the region

Using data on Red Data Book plant species in quarter degree squares, Lombard *et al.* (in press) identified a notional reserve system for the Succulent Karoo that addresses both representation and retention for targets of at least one occurrence of each species in the conservation system. Owing to the high turnover of RDB species along environmental and geographical gradients, they found that 127 (58%) of the region's 220 QDS were required to fulfil the goal of conserving each species at least once. The top 5% of QDS (eleven squares) identified by the reserve selection algorithm contained 440 RDB species (53% of the total) in about

8% of the region (Fig. 3). They incorporated retention goals by estimating for each selected QDS a measure of irreplaceability (quantified as the number of single cell endemics per QDS), and a measure of vulnerability (quantified as the combined score for RDB species' endangerment where extinct species are scored highest and non-threatened species are scored lowest). They then used the sum of irreplaceability and vulnerability scores to derive a new set of priorities based on the goal of retention (minimizing the extent to which representation of each species at least once would be pre-empted by the loss of species). These eleven priority QDS's (Fig. 3) conserve 375 RDB species (44% of total), including sixty species threatened with extinction. Notably, the most effective sequence of QDS conservation intended to achieve retention is somewhat different from that which achieves the highest efficiency of representation.

A protocol for combining representation with design and scheduling in conservation decisions (retention + persistence)

If conservation planning in the Succulent Karoo is to maximize both retention and persistence, a more comprehensive approach is needed than that illustrated by Lombard *et al.* (in press). Retention, as a strategy for implementing conservation areas on the ground, must be replaced by retention + persistence (Fig. 1). This requires the selection of candidate conservation areas to address both representation and design (Table 1, Fig. 5) and for the sequence of implementation of new conservation areas to minimize the extent to which both representation and design targets are compromised by ongoing loss and degradation of habitat. We outline a planning protocol here (Table 2) for achieving retention + persistence. It assumes that landholders and other interest groups will be involved in the design stage of the conservation system. If they are not, then any idealized conservation design is likely to fail because of unforeseen problems in implementation, including lack of understanding and acceptance by people whose co-operation is essential.

The first step is to identify types, patterns and rates of threatening processes. In the Succulent Karoo, this amounts to identifying cadastral units (i.e. farms and blocks of state land, communal land and land owned by mining companies) as well as particular habitats and natural processes, and then assessing their vulnerability to threats such as grazing, agriculture, mining and climate change. Furthermore, the time-frame over which these threats will operate must be estimated.

The second step, already discussed in the previous section of this paper, involves identification of the spatial components that need to be protected in the expanded conservation system. Some of these will be elements of biodiversity pattern. Others will serve as surrogates for the ecological and evolutionary processes that should be protected in a reserve system intended for retention + persistence.

In the third step, quantitative targets must be set for the representation of these spatial components, taking into account the need of each component for protection from threatening processes. This presents a serious challenge to conservation planners. For example, how many and which quartz-field drainage basins are required to maintain diversification of Mesembryanthemaceae lineages? Which climatic gradients and associated juxtaposed landscapes are most likely to facilitate migration of poorly-dispersed organisms in response to climate change?

The fourth step requires that the options for achieving representation + design targets (Fig. 1)—the ultimate but elusive goal for conservation planning—are laid out. A way of mapping the spatial options for achieving a set of conservation targets is to calculate and map the irreplaceability of each part of the landscape (Pressey *et al*., 1995). A map of irreplaceability, with values allocated to all parts of the landscape, is therefore a map of the options for achieving a set of targets. Areas that are totally irreplaceable are non-negotiable parts of an expanded conservation system, regardless of what form of conservation management is applied (see Step 6). Other areas are replaceable and negotiable to varying extents.

Step 5 is to locate and design potential conservation areas for representation + design. The overall aim of this step is to identify conservation areas that will collectively achieve all the targets for pattern and process. The system of proposed conservation areas might be much larger than the area considered feasible, but sound decisions about the relative importance and urgency of protection for specific parts of the landscape (Step 6) can only be made when the full requirements of all targets have been laid out. Candidate areas will be chosen that contribute to as many targets as possible.

Step 6 is the actual implementation of conservation action—a very complex part of the planning process. It involves three interdependent lines of work, which are likely to proceed in parallel, not sequentially. These

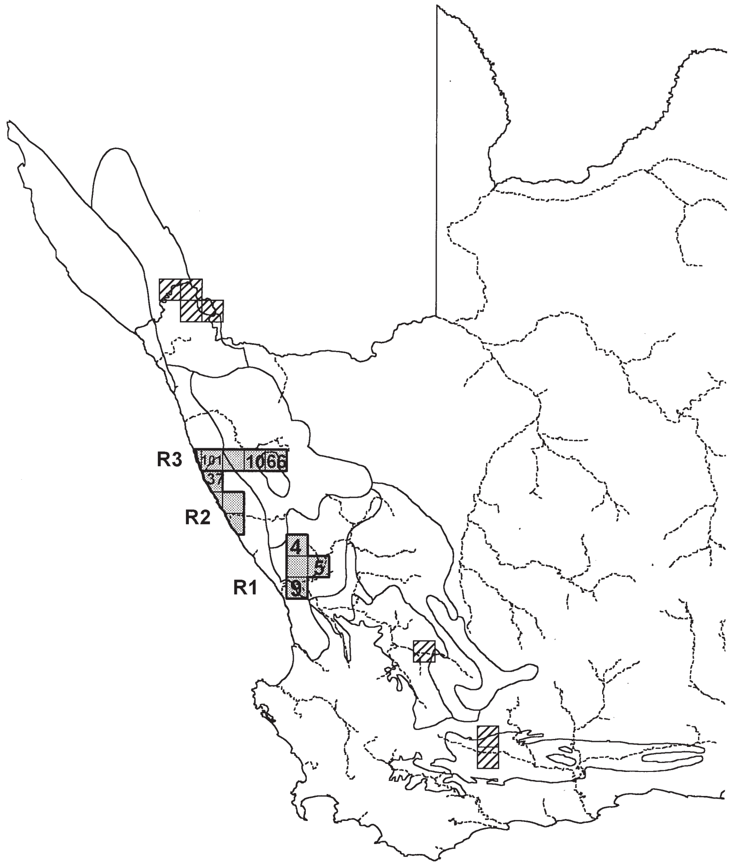

Fig. 5. A hypothetical reserve system (R1, 2 and 3—see text) in the Succulent Karoo that has been designed to achieve retention of pattern (RDB species representation) and process (representation of spatial components (Table 1)). Numbers within quarter degree squares (QDS) are the sequence in which QDS were selected by Lombard *et al.* (in press) on the basis of both RDB species representation. The QDS included in the existing reserve system are shaded.

Table 2. Steps in the protocol for achieving retention + persistence

Step 1	Identify types, patterns and rates of threatening processes
Step 2	Identify natural features to be protected (these will be elements of biodiversity pattern, e.g. species, habitats, as well as spatial components of the region that act as surrogates for ecological and evolutionary processes (see Table 1 for examples)
Step 3	Set targets for representation and design
Step 4	Lay out options for achieving representation + design targets
Step 5	Locate and design potential conservation areas to achieve representation + design targets
Step 6	Implement conservation actions in priority order

are: (1) scheduling conservation action (reservation or other) for specific parts of the region; (2) deciding on the balance between strict reservation and off-reserve management; (3) fine-tuning of conservation recommendations by selective inspection of areas on the ground and reassessment of data.

Scheduling requires that the recommended timing of conservation action should minimise the extent to which conservation targets are compromised before conservation management is applied (Pressey, 1997; Lombard *et al*., in press). This requires information on both threat (the likelihood or imminence of adverse impacts—from Step 1) and irreplaceability (the consequences of loss or degradation of habitat—from Steps 4 and 5). When conservation goals deal with both pattern and process, as is the case here, there are no established ways of comparing the risks of alternative approaches to implementation. For example, how should the outright loss of five RDB species or a 20% loss of the target for a land type be compared to the effect of a new mine covering 100 ha of a sand corridor, or the narrowing of a migratory pathway for ungulates?

The issue of which form of protective management should be applied to particular parts of the landscape is complex. Decisions about the form of management to be applied to specific areas will depend on: (1) the need to use off-reserve management as a fall-back when resources for strict reservation are limited or when reservation priorities are unavailable for acquisition; (2) the distribution of threatening processes that do not warrant protection by reservation; (3) which parts of the unreserved matrix most require management to maintain the integrity and connectivity of reserves.

All these decisions will be taken in the context of the variety of off-reserve management tools currently or potentially available.

Examples of candidate conservation areas for both pattern and process

In an imaginary pristine landscape, with no threats looming and unlimited resources for conservation, it should be possible to design for representation + persistence. Such a system would conserve biodiversity maximally and persistently. The real world, fraught with escalating threats and shrinking budgets, demands difficult decisions and many compromises regarding the identification and implementation of conservation areas. For example, what are the costs, in terms of biodiversity representation, of adding persistence goals to a conservation system identified for retention?

We address this question here by proposing a hypothetical system of conservation areas for the Succulent Karoo—in addition to the existing reserve system—designed to capture both pattern and process. We do this by following the steps in the protocol outlined in the previous section. In order to compare the effectiveness of RDB species conservation for a system incorporating retention goals only (Lombard *et al*., in press) with one incorporating retention + persistence, the design incorporates the same number of QDS (i.e. eleven) as Lombard *et al*'s. (in press) system.

The design is mindful of the principal threatening processes operating in the Succulent Karoo, namely overgrazing on both communal and commercial rangelands, transformation of riverine habitats by agriculture, diamond and heavy mineral mining on the Sandveld coastline, and diamond and limestone mining in the Vanrhynsdorp Centre. No areas under communal ownership have been included in the system, since these are generally unavailable for strict reservation. In addition, areas severely impacted by diamond mining have been excluded as candidates for conservation. We have retained Lombard *et al.'s* (in press) representation target of conserving at least one population of each RDB species. Representation targets for the spatial components listed in Table 1 are as follows:

- at least one large (>100,000 ha) conservation area with habitat suitable for viable populations of larger mammals and nomadic birds;
- at least one entire sand movement corridor;
- at least one untransformed whole river (source to coast) catchment;
- juxtaposed edaphically differentiated habitats within several bioregions;
- two or more adjacent minor drainage basins within at least one quartz field region;
- at least one area capable of supporting a seasonal migration of larger ungulates;
- all areas should encompass climatic gradients that are as large and steep as is possible.

Clearly, this is a hypothetical exercise that is not intended to be pre-emptive. Comprehensive planning will require a more detailed assessment of threatening processes (step 1 of the protocol) and a more explicit depiction of spatial components (cf. Fig. 4). Planning will also require a more objective assessment of options (step 4) and a more spatially explicit location and design of candidate areas (step 5). Since this is a hypothetical system, we comment very generally on priorities for implementation (step 6).

The proposed system involves the establishment three additional reserves in the Succulent Karoo (Fig. 5). The first reserve (R1) comprises an area of about 265,000 ha that extends from the southern part of Sandveld bioregion, across the Vanrhynsdorp Centre, to the southern reaches of the Namaqualand Rocky Hills. This is a large reserve that includes habitat suitable for some larger mammal and migratory bird species; encompasses a great diversity of juxtaposed edaphically differentiated habitats; includes several minor drainage basins within the most diverse quartz-field area in the Succulent Karoo; and includes a moderately large and steep climatic gradient (lowlands to medium-altitude granitic uplands). Owing to its large size, the reserve will accommodate all smaller-scale disturbance regimes previously discussed. The proposed reserve also scores highly in terms of representation and retention goals: it includes three high-scoring QDS (4, 5 and 9) identified by Lombard *et al*. (in press), and seventy RDB species of which thirteen are vulnerable to extinction i.e. they are classified as rare, vulnerable, endangered or extinct (Lombard *et al*., in press).

The second reserve (R2)—a coastal park entirely confined to the Sandveld bioregion—covers about 175,000 ha and is contiguous on its northern boundary with R3 (see below) (Fig. 4). This is a large reserve that includes habitat suitable for many large mammal and migratory bird species; encompasses an entire sand corridor and associated diversity of edaphic habitats; and comprises a section of the south-north climatic gradient in the Sandveld. Owing to its large size, the reserve will accommodate all smaller-scale disturbance regimes previously discussed. The reserve includes one QDS (37) identified in the system of Lombard *et al*. (in press) system, and twenty RDB species, three of which are threatened.

The third reserve (R3), which comprises about 282,000 ha, extends from the relatively moist uplands of the Kamiesberg Centre, via the Namaqualand Rocky Hills, to the Sandveld and the Atlantic coastline (Fig. 4). This reserve fulfils almost all of the representation targets for the spatial components identified in Table 1. It is a large reserve that includes suitable habitat for all larger mammal and migratory bird species; conserves a river catchment from source to coast; includes a great variety of juxtaposed edaphically differentiated habitats within three bioregions; includes an entire quartz field region; is capable of supporting seasonal migration of larger ungulates between extensive upland and lowland regions; and encompasses extremely large and steep climatic gradients, from the arid lowlands to some of the coolest and wettest regions of the Succulent Karoo. The proposed reserve includes three QDSs (10, 66 and 101) identified in Lombard *et al*'s. (in press) system, and fifty-five RDB species, six of which are threatened.

Thus, overall, the hypothetical reserve system more than fulfils the reservation targets for spatial components that will maintain patterns and processes. There are potentially many alternative designs that will achieve representation more efficiently—this must be the subject of further research. However, existing land use practices will severely constrain flexibility. Thus, the selected area of Sandveld in R2 comprises the only part of the coastal margin and only sand corridor that are not impacted by open cast diamond and heavy mineral mining. Additionally, the river catchment in R3 is the last-remaining one outside of communal lands that has not been transformed in places by agriculture.

It will also be necessary to examine the existing reserve system (Fig. 3) in terms of its contribution to representation targets for persistence. The Richtersveld National Park encompasses a great diversity of edaphic habitats and includes some of the largest and steepest climatic gradients in the Succulent Karoo (von Willert *et al*., 1992). Although this large park is capable of supporting populations of larger mammals and their migratory movements, this target is compromised by the inclusion within the park boundary of domestic livestock (Hendricks, 1998). The Anysberg Nature Reserve in the Little Karoo spans a large and steep climatic gradient that extends into the adjacent Nama Karoo and Fynbos biomes, and also includes some quartz field habitat.

As mentioned above, priorities for implementation in terms of reservation of spatial components must be dictated by irreplaceability and threatening processes. For example, the quartz fields of the Vanrhynsdorp Centre (R1) are home to some seventy endemic plant species and support plant evolutionary patterns and processes of global significance (Schmiedel & Jürgens, in press; Desmet *et al*., 1998); their biodiversity is irreplaceable. However, these quartz-field habitats are threatened by diamond mining and the adjacent endemic-rich limestone outcrops by quarrying. Similarly, the Sandveld reserve (R2) includes is the only part of the Succulent Karoo coast that has not been mined; there are proposals for large-scale heavy mineral mining as well as small-scale diamond mining that will impact the sand corridor and other habitats. The grasslands of the coastal hinterland within R3, habitat essential for sustaining populations of larger herbivores and migratory birds, are being claimed by communal ranchers. Without timeous intervention in these areas, opportunities for a conservation system designed for persistence will be compromised severely.

How does the system proposed by Lombard *et al.* (in press) compare with the hypothetical system in terms of RDB species conservation? The eleven QDS selected by Lombard *et al*. (in press) (Fig. 3) included 375 RDB species, sixty of which are threatened. In the hypothetical system, also comprising eleven QDS, only 139 RDB species are included, twenty-one of which are threatened. Therefore, in this case, designing for persistence incurs substantial costs in terms of species representation. However, these costs are offset by the considerable gains of designing a system for long-term persistence of biodiversity. The conservation of additional RDB species will have to involve off-reserve management or the establishment of small (<1000 ha) flora reserves (Table 1) managed by landowners or local authorities.

CONCLUDING DISCUSSION

There are limited resources for the expansion of the formal reserve system in the Succulent Karoo, and difficult choices must be made in establishing an expanded system. We have discussed the requirements and provided a protocol for developing a system that will enable biodiversity to persist into the next millenium. Rather than maximize conservation of contemporary biodiversity patterns, this system will conserve ecological and evolutionary processes essential for sustaining biodiversity. Priorities for implementation must be dictated by considering and balancing irreplaceability and vulnerabilty to threatening processes, of pattern and process—a nontrivial exercise. The ultimate goal is a conservation system of reserves and off-reserve management practices that provides for retention + persistence.

Planning for retention + persistence is fraught with uncertainty—it exposes our ignorance of key conservation issues, especially the the identity and role of processes in maintaining biodiversity patterns. These gaps could form the basis of a focused research programme, spanning different levels of integration. Unfortunately, the time and resources necessary to undertake the requisite research are not available. There is also very little we can borrow from research in other arid lands owing to the unique characteristics of Succulent Karoo biota and ecosystems (Cowling *et al*., 1999).

It is probably realistic to accept that more than 90% of the Succulent Karoo will remain unreserved. Thus, the management of this matrix will be essential for the preservation of much of the region's biodiversity and the maintenance of processes that sustain and generate it. Of relevance here is the establishment of biosphere reserves; the encouragement of biodiversity-friendly forms of land use, such as plant-based ecotourism and some forms of game farming; and the introduction of economic incentives to encourage these alternative forms of land use. Without the involvement of human communities, the implementation and maintenance of both on- and off-reserve conservation initiatives will not be viable. In every sense, humans are key players for the persistence of biodiversity in the Succulent Karoo. Given its status as the only arid-land biodiversity hotspot (Myers & Mittermeier, in press), this is a serious responsibility.

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