# Identifying spatial components of ecological and evolutionary processes for regional conservation planning in the Cape Floristic Region, South Africa

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**Abstract.** Conservation seeks ultimately to protect and maintain biodiversity indefinitely. Most biodiversity features targeted in past conservation planning have been largely aspects of ecological and biogeographical pattern rather than process. However, the persistence of biodiversity can only be ensured through consideration of the ecological and evolutionary processes that underpin biodiversity, as well as its present spatial pattern. This paper identifies spatial surrogates of ecological and evolutionary processes for regional conservation planning in one of the world's biodiversity hotspots, the Cape Floristic Region. We identified six types of spatial components (namely edaphic interfaces, upland–lowland interfaces, sand movement corridors, riverine corridors, upland–lowland gradients and macroclimatic gradients) as surrogates for key processes such as ecological and geographical diversification, and species migration. Spatial components were identified in a GIS using published data and expert knowledge. Options for achieving targets for process components have been seriously compromised by

habitat transformation. Between 30 and 75% of the original extent of the spatial components currently remain functional. Options for achieving upland–lowland and macroclimatic gradients are very limited in the lowlands where most of the habitat has been transformed by agriculture. We recommend that future studies place their research on ecological and evolutionary processes in a spatially explicit framework. Areas maintaining adaptive diversification (e.g. environmental gradients, ecotones) or containing historically isolated populations should be identified and protected. The spatial dimensions of ecological processes such as drought and fire refugia also need to be determined and such insights incorporated in conservation planning. Finally, connectivity within these areas should be ensured to maintain species migration and gene flow.

**Key words.** Biodiversity hotspot, biodiversity, conservation, fynbos, karoo, plant and animal diversification, species persistence.

## INTRODUCTION

Conservation planning aims to ensure the representation and the persistence of biodiversity indefinitely (Terborgh & Soulé, 1999; Margules &

Pressey, 2000; Moritz, 2002). The goal of biodiversity representation has been expressed in many different ways from protecting species occurrences to conserving entire ecosystems (e.g. Franklin, 1993; Noss & Cooperrider, 1994; Rebelo, 1997). The goal of biodiversity persistence requires the consideration not only of biodiversity patterns,

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but also of the processes that maintain, sustain and generate this biodiversity (Balmford *et al.*, 1998; Cowling *et al.*, 1999a; Margules & Pressey, 2000). Ensuring that protected areas represent all biodiversity features to some extent will not necessarily guarantee their persistence. Ecological and evolutionary processes should be directly incorporated into conservation planning by identifying the spatial requirements of these processes (Balmford *et al.*, 1998).

The most common and long-standing approach to addressing processes in conservation planning has been to consider generic design criteria such as the size, shape and connectivity of conservation areas (Shafer, 1990; Noss *et al.*, 1997). These criteria relate partly to the effective population sizes of species in conservation areas, and therefore to demographic, genetic and evolutionary processes important in the persistence of those species and their adaptation to changing environments (Caughley & Gunn, 1996). Variations on this theme include targeting species where persistence is more likely (Williams & Araújo, 2002). Size and connectivity can also be important in facilitating adjustments of species' distributions to climate change (Noss, 2001), and size can influence the persistence of natural disturbance regimes (Pickett & Thompson, 1978; Bond & van Wilgen, 1996). A second, related, approach to addressing processes in conservation planning is to parameterise design criteria with information on the specific requirements of selected species, often referred to as 'focal species' (Lambeck, 1997; Carroll *et al.*, 2001). Parameters for design then include estimates of minimum viable populations, densities of individuals, habitat suitability, ability to move between conservation areas through different matrix conditions, and response to human disturbance and infrastructure, all informed by natural history observations as well as population viability analysis and metapopulation modelling (Hanski & Ovaskainen, 2000; Noss *et al.*, 2002). Information on focal species is necessary to refine the generic recommendations from reserve design, such as 'bigger is better' and 'more connected is better'.

The persistence of other biodiversity processes also requires more than generic design criteria. Although it is generally true that more natural processes will continue in larger conservation areas (Cowling *et al.*, 1999a; Pressey *et al.*, 2003), the persistence of other processes will hinge on conservation of their particular spatial components (Cowling *et al.*, 1999a, 2003; Cowling & Pressey, 2001; Desmet *et al.*, 2002; Moritz, 2002). We define spatial components here as the physical features of a region with which particular ecological and evolutionary processes are associated. These can be identified in many ways. They might include drought refugia (Morton *et al.*, 1995), climatic refugia (Noss, 2001), ecotones (Smith *et al.*, 1997) and unusual geologies associated with endemic species (Coleman & Kruckeberg, 1999). In the Cape Floristic Region (CFR), we have associated distinctive processes with surface geology and soils, climate, topography, drainage systems, and the configuration of remaining native vegetation. These features could be missed or only partly incorporated into conservation plans unless they are specifically identified and targeted (Cowling & Pressey, 2001; Moritz, 2002; Cowling *et al.*, 2003). The spatial components of processes have rarely been considered in conservation planning. Although the literature on ecological and evolutionary processes is huge, very little is relevant to conservation planning because most of the studies have failed to identify the spatial dimensions of these processes. Since conservation planning is about making spatial choices, much information on biodiversity processes is of limited use to planners.

The formulation of a strategic conservation plan for the CFR has required the derivation of spatially explicit surrogates for ecological and evolutionary processes (Cowling & Pressey, 2001; Cowling *et al.*, 2003). The CFR has long been recognised as a global priority for conservation action. The region is one of the world's biodiversity hotspots (Myers *et al.*, 2000), and is home to over 9000 plant species, 70% of them endemic (Goldblatt & Manning, 2000). The biodiversity of the CFR originated from a wide array of ecological and evolutionary processes operating over spatial scales of a few to hundreds of thousands of hectares (Cowling, 1992; Goldblatt, 1997; Cowling & Pressey, 2001; Cowling & Lombard, 2002; Linder, 2003). Here, we focus on those processes that operate predominantly at medium and large spatial scales (> 50 ha), and specifically, processes that are likely to be inadequately protected in a conservation plan based on

generic design criteria or focal species. Our aim is to identify the spatial components of key processes that maintain and generate biodiversity in the CFR so that they can be incorporated into regional conservation planning. The rationale for identifying these components is provided by Pressey *et al*. (2003) and Cowling *et al*. (2003).

## METHODS

Cowling *et al*. (1999b) identified ecological and evolutionary processes that operate at medium and large scales (50–50 000 ha) that enable the diversification of plant lineages, the migration of fauna and flora, and resilience to climate change in the CFR (see also Cowling & Pressey, 2001; Pressey *et al*., 2003). In this study, we identified the spatial components of some of these processes that are associated with: juxtaposed edaphically different habitats, entire sand movement corridors, riverine corridors, upland–lowland interfaces, gradients from uplands to coastal lowlands and interior basins, and macroclimatic gradients that encompass major climatic transitions (see Table 1). These spatial components have been integrated into a conservation plan for the CFR, which also considered the representation of land classes and plant and vertebrate species' records (Cowling *et al*., 2003).

We identified the spatial components of large-scale ecological processes in a Geographic Information System. The processes components can be divided into two groups: 'spatially fixed' and 'spatially flexible' (see Table 1). Spatially fixed components capture processes that are associated with clearly defined, physical features of the region. There are no spatial choices for accommodating them. An example in the CFR is plant diversification along edaphic interfaces. The spatial component (the interface) consists of a strip just a few metres wide where contrasting parent materials abut and where plant speciation is known to occur (Goldblatt, 1982). Spatially flexible components capture ecological and evolutionary processes that can persist in various spatial configurations. For example, migration of biota occurs along upland–lowland gradients in the CFR (Kruger, 1977) but the precise migration route is not spatially well defined. In such cases, several spatial options probably exist.

Below, we present the primary data sets from which the spatial components of processes were derived. We then describe the role and the spatial dimension of each process component.

### Study area

The study area represents the planning domain of the conservation plan for the CFR (Cowling *et al*., 2003). It consists primarily of the CFR, as delimited by Cowling & Heijnis (2001), an area of 87 892 km$^2$ in the south-western corner of South Africa. The domain also extends approximately 60 km beyond the boundaries of the CFR to accommodate processes that transcend the biophysical boundaries between the CFR and adjacent biomes (Nama–Karoo, Succulent Karoo, Thicket; Cowling *et al*., 1997). Approximately 30% of the CFR (mostly in the lowlands) has been transformed by cultivation, urbanization and invasion by alien trees (Rouget *et al*., 2003; see also Reyers *et al*., 2001).

### Primary GIS layers used for defining the spatial dimensions of process components

*Biodiversity pattern*
Cowling & Heijnis (2001) developed a system of land classes to act as broad-scale biodiversity surrogates for the CFR. Because biodiversity patterns in the CFR are largely driven by climate, geology and topography (Cowling, 1992), they identified broad habitat units (BHUs) on the basis of unique combinations of these three factors as well as expert knowledge. The 102 BHUs they identified in the planning domain (Fig. 1) can be grouped according to parent material, topography, and major biogeographic zones. Nine BHUs are characterized by acidic, and five by alkaline substrata; 63 BHUs are in the lowlands and 39 in the uplands, and BHUs can be grouped into seven biogeographic zones based on those presented in Goldblatt & Manning (2000). The BHU classification represents a reasonable surrogate for vegetation types and plant species diversity (Cowling & Heijnis, 2001). Lombard *et al*. (2003) also found that BHUs mirror diversity patterns in the Proteaceae, an important plant group in the CFR that has similar biogeographical patterns to most Cape clades (Linder, 2003).

**Table 1** The characteristics of spatial components of large-scale ecological and evolutionary processes in the Cape Floristic Region (CFR). Details on the reasons for identifying these processes, and their role in conservation are given in Pressey *et al.* (2003). BHU = Broad Habitat Unit (Cowling & Heijnis, 2001)

| Spatial component | Process | Method of identification | Primary GIS layers |
|---|---|---|---|
| *Spatially fixed* | | | |
| Edaphic interfaces | Ecological diversification of plant lineages | 500 m buffer of untransformed habitat along juxtaposed BHUs on acidic and alkaline substrata | BHUs Habitat transformation |
| Sand movement corridors | Inland movement of marine sands and associated soil development | Functional corridor comprising intact source and sink areas | BHUs Habitat transformation |
| Riverine corridors | Migration and exchange between inland and coastal biotas | 250 m buffer of untransformed habitat along riverine systems linking coastal and inland subregions | Perennial rivers in the CFR Habitat transformation |
| Upland–lowland interfaces | Ecological diversification of plant lineages | 500 m buffer of untransformed habitat between all lowland and upland BHUs | BHUs Habitat transformation |
| *Spatially flexible* | | | |
| Upland-lowland gradients | Ecological diversification of plant and animal lineages; migration of biota | 1 km-wide strip of untransformed habitat linking unique combinations of lowland and upland BHUs | Upland–lowland interfaces Habitat transformation |
| Macroclimatic gradients | Geographic diversification of plant and animal lineages; migration of biota | 1 km strip of untransformed habitat linking major biogeographic zones | BHUs Habitat transformation |
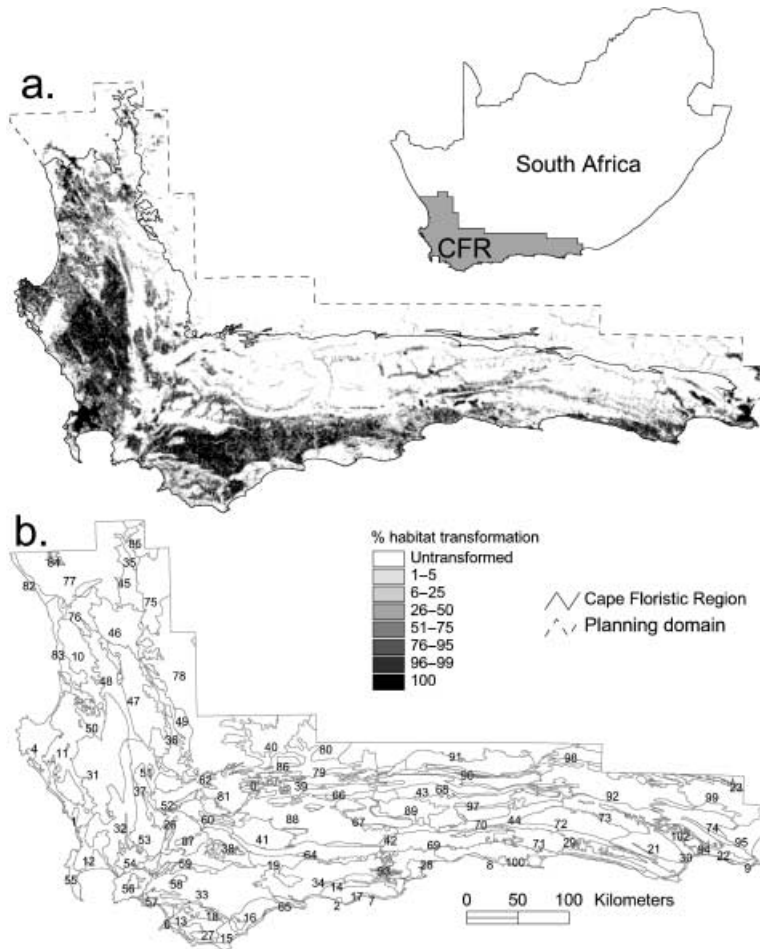
**Fig. 1** The Cape Floristic Region and the planning domain for systematic conservation planning (see text), showing (a) patterns of habitat transformation, and (b) Broad Habitat Units (Cowling & Heijnis, 2001) as surrogates for biodiversity patterns.

*Riverine systems in the CFR*

To identify riverine corridors, we used a GIS layer of perennial and nonperennial rivers (mapped at 1 : 250 000 scale) supplied by the Department of Water Affairs and Forestry.

*Habitat transformation*

Current (1996) habitat transformation was mapped using remote sensing at a scale of 1 : 250 000 (Lloyd *et al.*, 1999; Rouget *et al.*, 2003). We distinguished the following land use categories: agriculture, forestry, urbanisation, and areas invaded by alien plants (Rouget *et al.*,

2003). We used habitat transformation to identify three categories of habitat: extant, restorable, and lost. We categorised areas currently free of urbanisation, agriculture (including forestry), or invasion by high-density alien plants as extant and we considered them for retention to conserve biodiversity processes. Areas currently affected by agriculture or alien plants were classified as potentially restorable, to supplement the extant areas. Our assumption is that although biodiversity pattern has been irretrievably altered in such areas, processes could possibly still operate or be restored. Urban areas were disregarded for the

retention or restoration of biodiversity processes (i.e. such areas are considered to be lost for conservation purposes).

We used biodiversity pattern (i.e. BHUs), habitat transformation pattern and the distribution of rivers to derive the spatial configuration of process components. The rationale for the derivation of spatial dimensions is discussed below.

## Edaphic interfaces

### Role and definition
Edaphic interfaces represent specific juxtapositions of soil types, specifically combinations of acidic and alkaline parent materials, which drive ecological plant diversification (Rourke, 1972; Williams, 1972; Goldblatt, 1982; Linder & Ellis, 1990; Cowling & Holmes, 1992a; Linder & Mann, 1998; Bakker *et al.*, 1999; Reeves, 2001). We considered any untransformed section of interface larger than 50 ha as suitable for maintaining species diversification. Although this process can occur within a few meters of the interface, a 500-m buffer on each side of the interface allowed for inaccuracies in mapping BHUs and also provided interface sections of sufficient size to consider in conservation planning.

### Setting spatial dimensions
We used the boundaries between unique combinations of acidic and alkaline BHUs to identify edaphic interfaces. We first used a buffer of 500 m on either side of the boundary between acidic and alkaline BHUs to delineate 1-km-wide interfaces. We then subdivided these interfaces into sections of approximately 50 ha (500 m wide on either sides, and 500 m long) irrespective of land use. To identify extant sections, we determined the percentage of transformed habitat (i.e. urban, cultivated or invaded areas) for each section. We considered all untransformed (< 1% transformation) sections as extant (see Fig. 2). All transformed sections were deemed restorable, except for those with where urban areas covered more than 1% of the area. For each interface, we recorded the original length and area (prior to habitat transformation), and the length of extant and restorable sections.

## Entire sand movement corridors

### Role and definition
Sand movement corridors allow the movement of marine sand inland. In previous climatic phases, these sand movements produced gradients of soil development that promoted plant species diversification (McLachlan & Burns, 1992). Sand
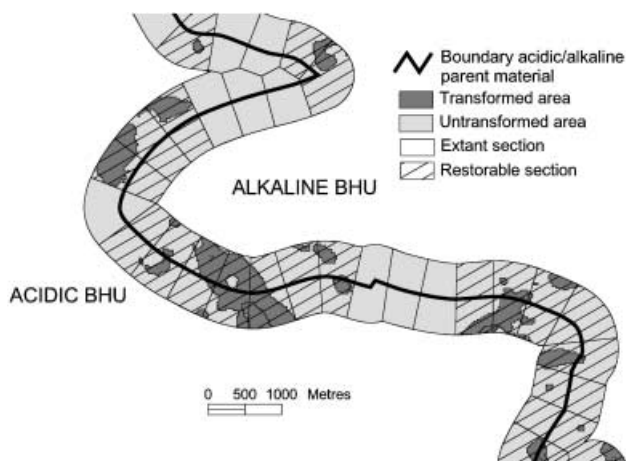


**Fig. 2** Identification of suitable sections of edaphic interfaces to sustain ecological processes. Edaphic interfaces occur between Broad Habitat Units characterized as 'acidic' and 'alkaline' (see text). Extant and restorable sections of the 500 m–buffered interfaces were determined based on habitat transformation pattern (see Methods).

movement corridors were defined on the basis of three BHUs (S, SE and SW Dune Pioneer). Although most of them are now inactive following stabilization by alien plants and infrastructure, they could be reactivated by removal of aliens and future climatic conditions. Three sections of each corridor are important for sand movement: the upwind section (source of sand), the core, and the downwind section (further migration of sand inland).

*Setting spatial dimensions*
Based on BHUs, we identified seven sand movement corridors in the CFR. We characterised upwind and downwind areas using a 500-m buffer on the source and downwind sections of each sand corridor. We calculated the proportion of each section currently transformed by urbanisation, agriculture, high-density alien plants, or traversed by a major road. We categorised sand movement corridors as functional, restorable, and lost according to the extent of habitat transformation. We considered a corridor to be functional if less than 50% of each section was transformed. In cases where more than 50% of any section was transformed but less than 50% of each section was affected by urbanisation, we considered the corridor to be nonfunctional but restorable. If more than 50% of one section was affected by urbanisation, we considered the corridor nonfunctional and nonrestorable.

## Whole riverine corridors

### Role and definition
We defined interbasin riverine corridors as those that breach the Cape Folded Mountain Belt, thereby linking interior basins to the coast and/or the Karoo basin to interior basins. Riverine corridors facilitate animal movement and plant dispersal by linking the three major topographic regions of the CFR: the coastal lowland, the coastal and interior mountains, and the interior basin and mountains (see Fig. 3). There is evidence that migration of plant species along riverine corridors has resulted in species diversification (Bayer, 1999). Riverine corridors also act as refugia from drought and fire and have provided refugia for mesic species during major climatic events in the past (Geldenhuys, 1997). We assumed that a buffer area of 250 m on either sides of the river would be sufficient for species dispersal, and we considered untransformed sections 500 m long (25 ha) to be minimal to serve as refuge areas for conservation planning.

### Setting spatial dimensions
We identified six interbasin riverine systems in the CFR. All tributary rivers up to second order were included, as were first-order tributaries if they were source streams for the riverine system or, if they joined two basins. We buffered all
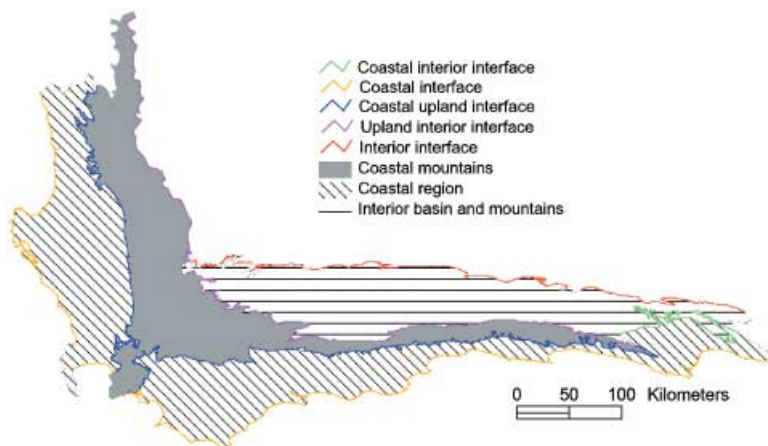


**Fig. 3** Major topographic regions in the Cape Floristic Region. Subdivisions are based on Broad Habitat Unit boundaries. Interfaces used to identify upland-lowland gradients are shown.

streams by 250 m on each side to identify 500 m wide riverine corridors and subdivided riverine corridors into sections of approximately 25 ha (250 m wide on both sides, and 500 m long). To identify extant sections, we measured the percentage of transformed habitat (i.e. urban, agriculture or high-density aliens) for each section. We considered all untransformed sections as extant (percentage of transformed area < 1%). All transformed sections were deemed restorable, except for those where urban areas covered more than 1% of the area. We calculated the total length of extant and restorable sections for each riverine corridor.

## Upland–lowland interfaces

### Role and definition

We defined upland–lowland interfaces as short gradients for diversification and range adjustment in response to climate change (Midgley *et al.*, 2002, 2003). Because of differences in elevation, climate, parent material and age of the surfaces between upland and lowland BHUs, these interfaces are associated with ecological diversification of plant (Goldblatt, 1979; Kurzweil *et al.*, 1991) and possibly animal lineages. The interfaces also facilitate seasonal movements between uplands and lowlands (Kruger, 1977). We assumed that a 1-km-wide buffer along the upland–lowland boundary would accommodate range adjustment and we considered each unique boundary between upland and lowland BHUs as a separate interface to reflect differences in species assemblages.

### Setting spatial dimensions

At each unique boundary between upland and lowland BHUs, we used a 500-m buffer along each side of the boundary to delineate the interface. We subdivided the buffered area into sections of approximately 50 ha (500 m wide on both sides, and 500 m long). To identify extant sections, we measured the percentage of transformed habitat (i.e. urban, agriculture, high-density aliens) for each section. We considered all untransformed sections as extant (percentage of transformed area < 1%). We considered all transformed sections as restorable, except for those with more than 1% urbanisation. For each interface, we recorded the original length and area

(prior to habitat transformation), as well as the length of extant and restorable sections.

## Upland-lowland gradients

### Role and definition

Upland–lowland gradients are important for seasonal movements of animals (Kruger, 1977; Fraser *et al.*, 1989), and local-scale adjustment of species distributions to climate change (Midgley *et al.*, 2002, 2003). Due to strong climatic and edaphic differences between the upland and lowland environments, they are also associated with ecological diversification of plant (Rourke, 1972; Cowling, 1983; Bruyns & Linder, 1991; Linder & Vlok, 1991; Manning & Linder, 1992; Linder, 1995; Linder & Mann, 1998; Bakker *et al.*, 1999; Reeves, 2001) and animal (Enrödy-Younga, 1988; Coe & Skinner, 1993) lineages. Gradients connect distant BHUs and cross larger parts of adjacent BHUs than upland–lowland interfaces. The role of gradients is, however, constrained by previous and future habitat transformation, especially in the lowlands.

Following Campbell (1983), we identified three types of gradients, namely:

(1) Coastal: from the coastal fringe to the coastward interface of the coastal mountains, except in the far east of the CFR where the coastal plain interfaces with the interior mountains.
(2) Coastal mountain: from the coastwards interface of the coastal mountains to the inland interface of the coastal mountains.
(3) Interior: from the inland interface of the interior mountains to the inland interface of the coastal mountains, except in the far east of the CFR where they extend to the coastwards interface of the interior mountains.

We assumed that a 1-km-wide gradient would act as suitable corridor for plant and animal migration. Because of intense habitat transformation in the lowlands, upland–lowland movement will be unlikely outside our delineated gradients for many species, particularly the less mobile and slower moving organisms.

### Setting spatial dimensions

We used least-cost path analysis in Arc/Info to identify suitable gradients. Least-cost path analysis seeks the shortest route (in terms of distance

and cost) to link nominated start and end points. In separate analyses we derived two sets of paths for each gradient type (coastal, coastal mountain, and interior) (Table 2). For example, in the case of coastal gradients, we identified paths that would link each BHU of the coastal interface (starting from the coastal fringe) anywhere to the coastal mountain interface. We then identified paths that would link each BHU combination of the coastal mountain interface anywhere to the coast (Fig. 3). All analyses used a grid resolution of 1 km. We used the percentage of habitat transformation within each 1-km cell as a cost factor. This means that it was (arbitrarily) 100 times more 'expensive' to cross a completely transformed cell than to cross a completely untransformed cell. Consequently, paths tended to avoid transformed areas. We specified that paths could not cross cells where urbanisation covered more than 5% of the cell area. There were sometimes several ways of linking two interfaces through untransformed habitat; in such cases the analysis selected gradients along the least expensive route (in terms of both distance and habitat transformation).

For each gradient identified, we calculated the total length and the percentage of transformation. We categorised gradients unaffected by agriculture or high density alien plants as extant and the others restorable (the scale of restoration being indicated by the degree of transformation).

## Macroclimatic gradients

### Role and definition

The aim was to locate macroclimatic gradients so as to traverse major biogeographic regions (see Fig. 4). In the uplands, such gradients are important for the geographic diversification of plant (Rourke, 1969, 1972; Reeves, 2001) and animal (Enrödy-Younga, 1988) lineages as a result of vicariance — in response to past climatic fluctuations — and dispersal events (Linder, 2003). Macroclimatic gradients are also important for species distribution adjustments resulting from climate change. Midgley *et al.* (2003) predicted that lowland Proteaceae species would adjust their distributions into montane habitats and migrate along existing climatic gradients. In the western part of the CFR, macroclimatic gradients are orientated north–south, whilst gradients in the eastern CFR are orientated east–west, following seasonal rainfall patterns. We considered two sets of gradients based on topography: one traversing lowland habitats (coastal and interior basin) and the other one traversing upland habitats (coastal and interior mountains). We assumed that a 1-km-wide gradient of untransformed habitat would maintain ecological processes associated with these gradients.

### Setting spatial dimensions

We used an approach for identifying macroclimatic gradients similar to that for upland–lowland
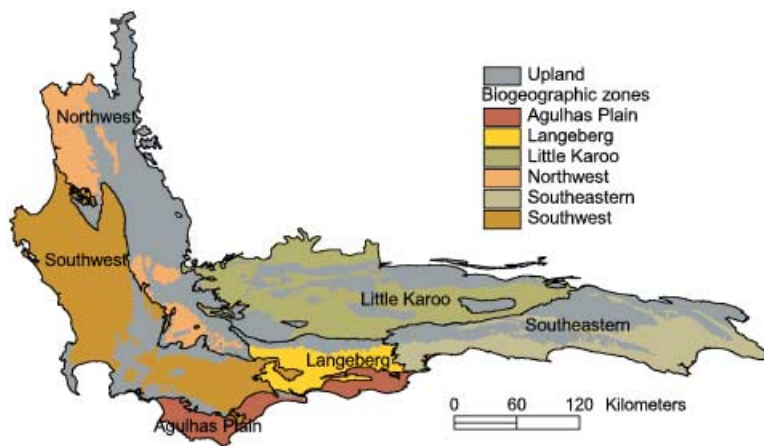


**Fig. 4** Biogeographic zones of the Cape Floristic Region based on Broad Habitat Units (see text). Macroclimatic gradients were identified to traverse each of these regions (see Methods).

**Table 2** Characteristics of least-cost paths used to identify upland–lowland gradients. These gradients link upland and lowland habitats through three major topographic regions: coastal, coastal mountains and interior (see Fig. 3). Gradients were constrained to traverse untransformed habitat as much as possible. The source indicates the starting point of the gradients and the destination, its ending point. Interfaces are shown in Fig. 3

| Gradient type | Source | Destination | Number |
|---|---|---|---|
| Coastal | Each BHU along the coastal fringe | Anywhere along the coastal upland interface | 14 |
| | Each unique BHU combination along the coastal upland interface | Anywhere along the coastal fringe | 15 |
| Coastal mountain | Each unique BHU combination along the coastal upland interface of the coastal mountain | Anywhere along the interior upland interface of the coastal mountain | 12 |
| | Each unique BHU combination along the interior upland interface of the coastal mountain | Anywhere along the coastal upland interface of the coastal mountain | 14 |
| Interior | Each unique BHU combination along the interior upland interface of the coastal mountain and along the coastal upland interface of the interior mountain | Anywhere along the interior interface | 15 |
| | Each BHU along the interior interface | Anywhere along the interior upland interface of the coastal mountain and along the coastal upland interface of the interior mountain | 15 |

gradients (above), i.e. we derived least-cost path analysis, at a grid resolution of 1 km, to identify the least expensive routes that crossed all biogeographic zones between nominated start and end points in both uplands and lowlands (Table 3). We stipulated that paths could not cross cells where urbanisation covers more than 5% of the cell area.

## RESULTS

### Spatially fixed components of processes

Before habitat transformation, plant diversification could be maintained along 600 km of edaphic interfaces (Fig. 5). Today, this process can only occur along 29% of the original interface length (Table 4). Habitat transformation has been so extensive in the lowlands that 50 ha fragments of untransformed habitat along some interfaces no longer exist. Intact interfaces currently exist between the following BHUs: Langebaan Fynbos/Thicket Mosaic and Blackheath Sand Plain Fynbos; Cape Flat Fynbos/Thicket Mosaic and Blackheath Sand Plain Fynbos; and Hagelkraal Limestone Fynbos and Elim Fynbos/Renosterveld Mosaic. Moreover, more than 50% of the first two interfaces have been lost following urbanization, which compromises any restoration effort.

Based on BHUs, we identified seven large sand masses in the CFR, referred to as sand movement corridors. These have generally been less impacted by habitat transformation than have other spatial components since 75% of the total area was still extant (Table 4). However, one corridor (Port Elizabeth) can no longer function due to urbanisation, and two others (Walker Bay and Cape St Francis) will require major restoration (mainly alien plant clearing).

Among all riverine systems of the CFR, only six allow migration between the interior basin and the coast. Less than 50% of the total length of these riverine systems is still extant and can maintain ecological processes associated with riverine corridors (Table 4). Habitat transformation has mostly affected riverine corridors in the coastal region, thus preventing migration to and from the coast (Fig. 6). None of the six riverine corridors can sustain migration of biota along their whole length since between 14 and 85% of

**Table 3** Characteristics of least-cost paths used to identify macroclimatic gradients. These gradients link each biogeographic zone through upland or lowland habitats (see Fig. 4). Gradients were constrained to traverse untransformed habitat as much as possible

| Gradient type | Source | Destination |
| --- | --- | --- |
| Upland E–W | Eastern boundary of coastal mountains in the South-eastern region | Western boundary of coastal mountains in the North-west region |
| Upland E–W | Eastern boundary of interior mountains in the South-eastern region | Western boundary of interior mountains in the North-west region |
| Upland N–S | Southern boundary of coastal mountains in the South-eastern region | Northern boundary of coastal mountains in the North-west region |
| Lowland E–W | Eastern boundary of coastal lowlands in the South-eastern region | Western boundary of coastal lowlands in the South-west region |
| Lowland E–W | Eastern boundary of coastal lowlands in the South-eastern region | Western boundary of coastal lowlands in the Agulhas region |
| Lowland E–W | Eastern boundary of coastal lowlands in the South-eastern region | Western boundary of interior basin in the Little Karoo region |
| Lowland N–S | Southern boundary of coastal lowlands in the South-eastern region | Northern boundary of coastal lowlands in the North-west region |
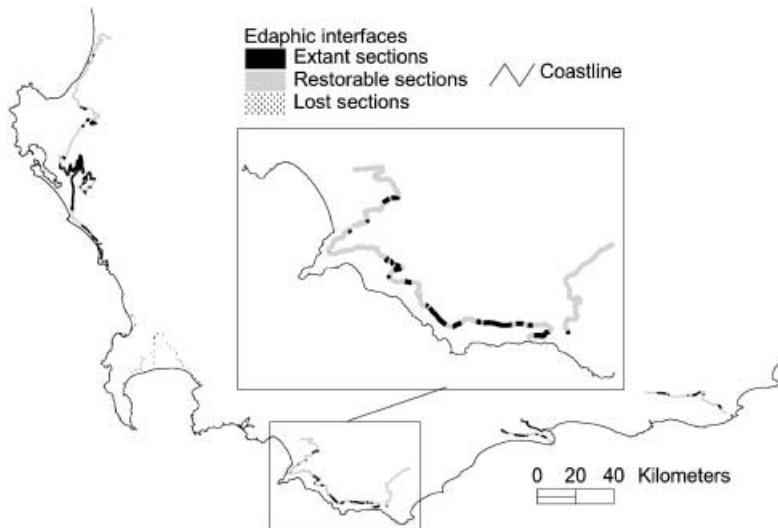


**Fig. 5** Extant and restorable edaphic interfaces in the Cape Floristic Region. Extant portions consist of 50 ha of untransformed habitat along boundaries between 'acidic' and 'alkaline' Broad Habitat Units. Sections currently transformed by agriculture or alien plant invasion are considered restorable, whereas urbanized sections are regarded as lost.

each corridor has been transformed and will need restoration. Without restoration, riverine corridors are reduced to acting as refugia — using extant habitat as stepping stones — while their migration role has been severely compromised (Fig. 6).

Upland–lowland interfaces covered a total distance of over 9000 km and comprise 143 unique combinations of lowland and upland habitats (Table 4). Over 50% of the total length cannot sustain ecological processes because of habitat transformation. Restoration needs to be considered,

**Table 4** Extent of habitat transformation for each spatial component. Extant sections are untransformed by agriculture, urbanisation and invasion by alien plants. Restorable sections are transformed by agriculture or invasion by alien plants. Sections currently urbanised are regarded as lost (of no value to biodiversity conservation)

| Spatial component | % extant | % restorable | % lost | Total |
|---|---|---|---|---|
| Edaphic interfaces (*n* = 8) | 29.56 | 61.75 | 8.69 | 604 km |
| Sand corridors (*n* = 7) | 75.71 | 19.20 | 5.09 | 20545 ha |
| Riverine corridors (*n* = 6) | 47.10 | 51.11 | 1.70 | 6740 km |
| Upland–lowland interfaces (*n* = 143) | 57.61 | 39.95 | 2.44 | 9046 km |
| Upland–lowland gradients | | | | |
| Coastal (*n* = 29) | 88.88 | 11.12 | — | 1270 km |
| Coastal mountain (*n* = 26) | 99.71 | 0.29 | — | 1169 km |
| Interior (*n* = 30) | 99.94 | 0.06 | — | 1116 km |
| Macroclimatic gradients | | | | |
| Lowland (*n* = 4) | 91.63 | 8.37 | — | 2147 km |
| Upland (*n* = 3) | 99.92 | 0.08 | — | 1445 km |
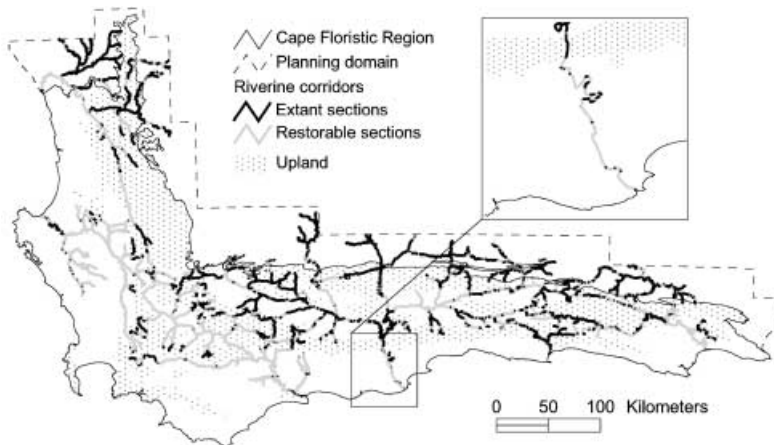


**Fig. 6** Extant and restorable riverine corridors in the Cape Floristic Region. Extant portions consist of 25 ha of untransformed habitat along the river. Sections currently transformed by agriculture or stands of invasive alien trees are considered restorable, whereas urbanized sections are regarded as lost.

especially along the coastal–upland interface, where transformation for agriculture has been most severe (Fig. 7).

## Spatially flexible components of processes

We identified 65 upland–lowland gradients in the CFR, which link coastal habitats to coastal mountains and to interior habitats (and vice versa) (see Fig. 8). Their routes were determined by the extent of habitat transformation (Fig. 1). The amount of restoration required varied according to the gradient location. In the coastal lowlands, 11% of the overall gradient length was transformed and thus needed restoration. In the interior basin and mountains, almost no restoration is required (Table 4). The same situation occurred in the coastal mountains where biota could potentially migrate along these upland–lowland gradients. In the coastal lowlands, only six gradients (out of 29 identified) traversed untransformed habitat over their entire length; all the others required restoration to a certain extent. Habitat transformation in the coastal
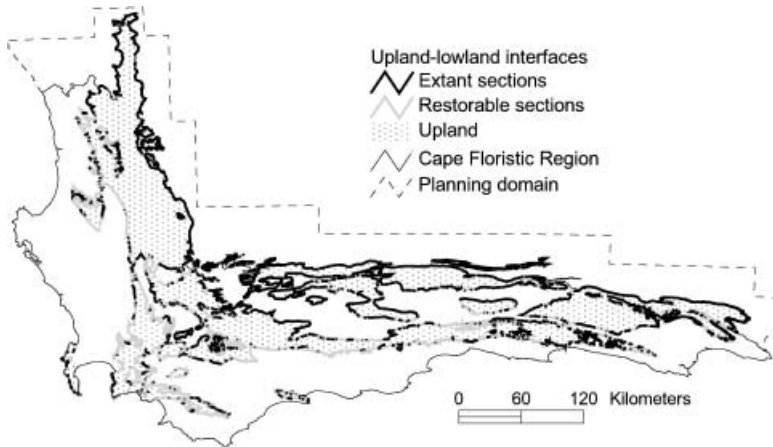
**Fig. 7** Upland–lowland interfaces in the Cape Floristic Region. Extant portions comprise 50 ha of untransformed habitat along the boundary between 'upland' and 'lowland' Broad Habitat Units. Sections currently transformed by agriculture or stands of invasive alien trees are considered restorable, whereas urbanized sections are regarded as lost.
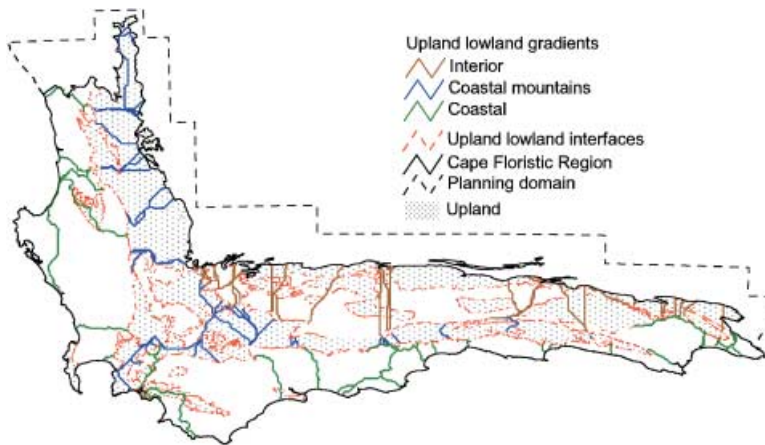


**Fig. 8** Upland–lowland gradients in the Cape Floristic Region. These link major topographic regions (see Fig. 3) and traverse untransformed habitat as much as possible.

lowlands has seriously constrained the trajectory of the gradients, and some gradients were forced to follow very sinuous routes to avoid transformed areas (Fig. 8). We identified seven macroclimatic gradients (Fig. 9) that link all the major biogeographic zones shown in Fig. 4. Gradients crossing upland habitats were less affected by habitat transformation than those running through lowland habitats. All upland gradients could act as migration routes since they were completely untransformed, whereas all lowland gradients required restoration to maintain migration processes (Table 4). Like the upland–lowland gradients, the trajectory of macroclimatic gradients was more sinuous in lowland than in upland habitats (Fig. 9).
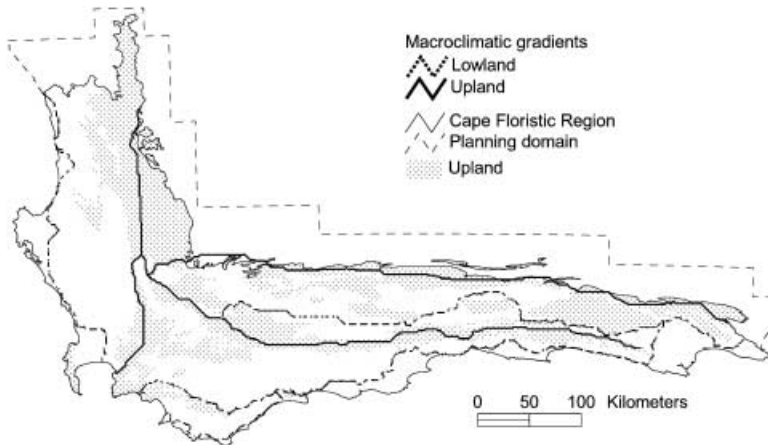
**Fig. 9** Macroclimatic gradients in the Cape Floristic Region. These gradients traverse each biogeographic zone through lowland or upland habitats. They traverse untransformed habitat as much as possible.

## DISCUSSION

### Conserving biodiversity patterns and processes in the CFR

No set of surrogates will encompass all processes of potential significance to biodiversity. We have, however, attempted to define the spatial dimensions of key ecological and evolutionary processes for use in systematic conservation planning in the CFR. We have identified processes required to maintain and generate diversity in all lineages across an entire ecoregion. We have assumed that processes driving evolution and diversification in the future will be similar to those of the past. We did not identify spatial dimensions for herbivore- and carnivore-related processes. These processes were, however, incorporated in the conservation plan for the CFR by targeting suitable areas for medium- and large-size mammals, which can maintain predator–prey relationships (Boshoff *et al.*, 2001; Cowling *et al.*, 2003; Kerley *et al.*, 2003). Some of the advantages of such an approach are that: (i) the spatial dimensions of both ecological and evolutionary processes are explicitly considered; (ii) the entire biota is considered; and (iii) resilience to climate change impacts is accommodated.

We acknowledge some shortcomings in our approach. The spatial dimensions of processes were defined at a broad scale and over a rela-

tively short time. Much more information is required to define their spatial dimensions at higher resolution. We did not explicitly consider fine-scale ecological processes because the maintenance of many processes that operate at the scale of landscapes, such as insect-mediated pollination, can be achieved by protecting and managing even fairly small parcels of land — albeit at considerable cost (Frazee *et al.*, 2003). Plant and invertebrate diversity seems to be maintained in habitat fragments as small as 5 ha provided they are subject to appropriate fire management and kept free of invasive plants (Bond *et al.*, 1988; Cowling & Bond, 1991; Kemper *et al.*, 1999; Donaldson *et al.*, 2003). Consequently, populations of specialised invertebrate pollinators that drive speciation in many plant lineages (e.g. Johnson, 1995; Goldblatt & Manning, 1999) can also be maintained — along with those of their host plants — in very small areas (see Steiner, 1998).

We acknowledge that the configuration of our spatial components might be too narrow in some cases to sustain ecological diversification or to allow species migration. As for upland–lowland and macroclimatic gradients, there are no guarantees that all these corridors, especially the sinuous upland–lowland gradients that wind around transformed land, will provide effective migratory routes for most lineages. The role of corridors in conservation has been widely debated

(Hobbs, 1992; Beier & Noss, 1998). No single configuration of corridors is likely to be suitable for all elements of the biota of a region (Laurance & Laurance, 1999). The identification of focal species likely to be most sensitive to fragmentation might help to configure these corridors (Lambeck, 1997; Bunn *et al.*, 2000). However, in all facets of the study we used a precautionary rule for setting the spatial dimensions of gradients. To allow for the greatest flexibility in plant or animal movement, we identified possible gradients for each habitat type of the upland–lowland interfaces. Therefore, each species occurring in this habitat type has the potential to move along these upland–lowland gradients. Although gradients mostly traverse untransformed habitat, plant species are unlikely to move across certain habitat transitions, since many species in the Cape flora are edaphic specialists. For example, the edaphic transition between mountain fynbos and karoo vegetation is much more abrupt than between mountain fynbos and renosterveld (Cowling & Holmes, 1992b). We did not consider such transitions in developing these gradients, and portions of gradients could well prove to be *cul-de-sacs*.

Finally, given the time scale over which some of these ecological and evolutionary processes operate, it is not practically feasible to monitor the efficiency of spatial components for maintaining and generating biodiversity. We are forced to rely on past evidence or modelling studies to determine the extent to which certain configurations of land can maintain key processes.

Despite the limitations mentioned above, there is an urgent need to incorporate the spatial components of processes into systematic conservation planning. This is the only way to target explicitly evolutionary and ecological processes. While the spatial components will differ between different biogeographic zones and for different lineages, it will not be possible to collect all of the data required to identify the spatial components in a really rigorous way. Conservation planning must proceed before results of all ongoing research are available. The only short-term solution, especially in data-poor areas, is to use the expert knowledge of population, community and landscape ecologists and evolutionary biologists, to make informed estimates of spatial dimensions.

The consideration of spatial components of processes changed the final configuration of the conservation plan for the CFR, adding to the total area of land identified for conservation (Cowling *et al.*, 2003). Many of the areas that we have identified as important for ensuring the maintenance of processes fall outside areas selected for conservation on the basis of existing biodiversity features. Conserving biodiversity processes undoubtedly adds to the cost of conservation, and there will always be tensions between protecting biodiversity features (generally easier to justify in a cash-strapped economy), and conserving biodiversity processes whose roles are sometimes poorly known and whose spatial dimensions cannot be defined with certainty (Margules & Pressey, 2000). In the conservation plan for the CFR, Cowling *et al.* (2003) attempted to strike this balance by ensuring that process components, which were introduced in the first stage of the planning process, also contributed to achieving targets for biodiversity features. The plan also identified as priorities small fragments of habitat essential for achieving pattern targets, as well as large tracts of intact landscape where a wide range of process targets could be achieved.

The identification of the spatial dimensions of ecological and evolutionary processes can provide guidelines for prioritising areas for restoration at the regional scale. For example, in the lowlands, habitat transformation has seriously compromised the role played by ecological and evolutionary processes in maintaining and generating biodiversity. Sixty percent of the length of edaphic interfaces as defined in this paper has been transformed by agriculture or dense stands of alien plants (Table 4). In some cases, restoration may be the only option for ensuring the continued functioning of these processes. Restoration will involve the clearing of aliens and the conversion of agricultural lands to some condition more conducive to natural functioning. A range of valid endpoints for restoration may be defined, and different levels of intervention will be required, depending on the process or aspect of functioning of particular concern (Holmes & Richardson, 1999). Clearing of alien vegetation has received considerable attention under the *Working for Water* programme (Van Wilgen *et al.*, 2001). However, very little is known about

the processes and the costs of restoring agricultural lands to a more natural condition. Several restoration efforts are underway in the CFR, but these are directed at restoring essential components of ecosystem functioning (such as watershed stability after fire) or conserving existing biodiversity (usually rare species). We argue that the identification of the spatial dimensions of ecological and ecological processes, as discussed in this paper, provides a sound basis for setting priorities for restoring damaged systems. Restoration efforts in areas thus identified will benefit existing biodiversity features, but will provide long-term insurance, ensuring that the biota has the best chance for survival in the face of global change.

## Incorporating ecological and evolutionary processes in conservation planning

Most conservation biologists advocate the need for protecting ecological and evolutionary processes, but the identification of their spatial dimensions is still in its infancy. The concept of the evolutionary significant unit (ESU) was developed to consider evolutionary processes in conservation (Ryder, 1986; Moritz, 1994). Because the ESU focuses on historical isolation rather than adaptive diversity, recent work has suggested that adaptive features maintaining the context of selection should rather be conserved (Crandall et al., 2000; Desmet et al., 2002). General rules which apply to many species, if not the whole ecosystem, should be sought. Moritz (2002) argues for a strategy that considers the underlying evolutionary and ecological processes for each species or system. This is not a trivial task. Conservation, systematics and evolutionary biologists must start thinking of, and developing appropriate spatial dimensions for these key processes.

We need to ensure that the processes that maintain adaptive diversity and evolutionary potential are conserved (Crandall et al., 2000; Cowling & Pressey, 2001; Moritz, 2002). With regard to conservation planning, adaptive diversity can be spatially preserved by identifying and targeting areas where species diversification occurs or has occurred. Potential candidates for diversification of plant and animal lineages might be ecotones or ecological discontinuities (e.g.

abrupt transition between acidic and alkaline parent material). In the CFR for example, we identified edaphic interfaces as the adaptive component of genetic diversity (*sensu* Moritz, 2002; p. 240) because ecological factors have played an overriding role in speciation among Cape plants (Goldblatt & Manning, 2000; Linder, 2003). There is evidence from elsewhere that ecotones might be a source of ecological diversification caused by divergent selection (Smith et al., 1997). Based on complementary, such ecotones might not emerge as a priority for conservation actions (Smith et al., 1997). When identifying spatial components for species diversification, it is also important to separate ecological from geographical diversification as well as the temporal scale at which they operate. In this study, edaphic interfaces captured ecological diversification at a microscale whilst upland–lowland gradients captured ecological diversification at a mesoscale, and macroclimatic gradients specifically addressed geographic diversification at a macro-scale.

To maintain evolutionary potential, the network of genetic connections and interactions between populations should be preserved. Conservation planners need to maximize species movement and migration within biogeographic units. This can be achieved by targeting specific migration routes such as riverine corridors linking interior and coastal basins in the CFR. Furthermore, due to ongoing habitat transformation, spatial connectivity in fragmented landscape has become a crucial component of population persistence (Smith & Hellmann, 2002; Brooker & Brooker, 2003). New reserve selection algorithms can now address spatial connectivity to some extent (Possingham et al., 2000; Briers, 2002). Protecting connectivity of habitats across environmental gradients is vital for allowing species to respond to rapid climate changes and this should be a priority in all regional-scale conservation planning (Kareiva et al., 1993; Midgley et al., 2003).

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