Rapid plant diversification: Planning for an evolutionary future

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Systematic conservation planning is a branch of conservation biology that seeks to identify spatially explicit options for the preservation of biodiversity. Alternative systems of conservation areas are predictions about effective ways of promoting the persistence of biodiversity; therefore, they should consider not only biodiversity pattern but also the ecological and evolutionary processes that maintain and generate species. Most research and application, however, has focused on pattern representation only. This paper outlines the development of a conservation system designed to preserve biodiversity pattern and process in the context of a rapidly changing environment. The study area is the Cape Floristic Region (CFR), a biodiversity hotspot of global significance, located in southwestern Africa. This region has experienced rapid (post-Pliocene) ecological diversification of many plant lineages; there are numerous genera with large clusters of closely related species (flocks) that have subdivided habitats at a very fine scale. The challenge is to design conservation systems that will preserve both the pattern of large numbers of species and various natural processes, including the potential for lineage turnover. We outline an approach for designing a system of conservation areas to incorporate the spatial components of the evolutionary processes that maintain and generate biodiversity in the CFR. We discuss the difficulty of assessing the requirements for pattern versus process representation in the face of ongoing threats to biodiversity, the difficulty of testing the predictions of alternative conservation systems, and the widespread need in conservation planning to incorporate and set targets for the spatial components (or surrogates) of processes.

There are numerous pleas in the literature for integrated systems of conservation areas that will maintain disturbance regimes, migratory corridors, habitat diversity, landscape connectivity, evolutionary templates, and other spatial features necessary for the maintenance of evolutionary processes (1–4). There has been some debate as to whether priority should be given to areas supporting ancestral taxa with evolutionary potential (5, 6) or those representing evolutionary fronts of currently speciating taxa (7–10). Recently, Moritz and coworkers (11) have used comparative phylogeography to identify areas that encompass both the adaptive and historical components of genetic diversity of vertebrates in the rainforests of northeastern Australia. However, there have been no studies that attempt to identify the spatial components of a wide spectrum of evolutionary processes or to set explicit targets for their protection in particular regions.

If we are to plan for an evolutionary future, then evolutionary processes—those that maintain genetic diversity and promote diversification—must be explicitly considered, and represented, in the conservation plan (1, 11, 12). This is not a trivial issue. There are very few places in the world, in particular in its endemic-rich and threatened regions (13), where evolutionary processes and their spatial components are understood well enough to be included in conservation planning. Over the past few decades, considerable insights have been gained regarding evolutionary processes in the Cape Floristic Region (CFR) of South Africa, especially for plants. Because the available data are representative of most plant lineages in the region, they provide a good basis for conservation planning.

In this paper, we provide a brief overview of evolutionary processes in the CFR, a species-rich region that is recognized as a global priority for conservation action (13). We focus in particular on rapid diversification of plant lineages. We then review briefly some recent developments in systematic conservation planning and the need to extend these ideas to apply not only to biodiversity pattern, but also to ecological and evolutionary processes. Because conservation planning is a spatially explicit exercise, even processes must be protected by their spatial components or surrogates. Accordingly, we describe a framework for planning for an evolutionary future in the CFR, identifying seven types of spatial components of evolutionary processes, setting explicit conservation targets for each, and outlining the development of a conservation plan to achieve these targets. We conclude by discussing the difficulty of testing predictions about biodiversity persistence deduced from alternative conservation plans, the contributions of the approach presented here, and its potential for widespread application.

Rapid Diversification in the CFR

Rapid diversification, often associated with key innovations and leading to flocks of species that show fine-scale habitat discrimination, has been reported for some plant lineages (26–28), especially on islands (29, 30), for Andean birds (9), and for fish, most notably the cichlids of the African Rift Lakes (19). Without a doubt, the distinctive evolutionary feature of the CFR is the recent and massive diversification of many plant lineages (20, 21). The region includes some 9,000 plant species in 90,000 km^2, 69% of which are endemic (21)—one of the highest concentrations of endemic plant species in the world (13). This diversity is concentrated in relatively few lineages that have radiated spectacularly. Thus, 13 genera (of a total of 988) each comprise more than 100 species, and together these account for 25% of all species in the flora (21). Similarly, of the region's 173 families, 12 each comprise more than 200 species and, in combination, include 64% of the CFR's flora.

Although the evidence is patchy, it seems certain that this massive diversification has occurred relatively recently, mostly after climatic deterioration in the late Pliocene when seasonal (Mediterranean-type) climates developed and recurrent fire became an important ecological factor (22, 23). That many lineages are in the midst of massive diversification events is suggested by the restriction of localized endemics to very young sediments (20), the large clusters of closely related species resulting in poor phylogenetic resolution in clades (24, 25), and

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a very recent (post-Pleistocene) appearance in the pollen record of species-rich taxa, notably the Mesembryanthemaceae (26).

Diversification-prone lineages in the CFR are not a random assemblage either biologically or ecologically. Generally, component species among woody groups are low, fire-killed (i.e., nonsprouting) shrubs with poorly dispersed seeds, small and weakly persistent seed banks, and insect-pollinated flowers (21, 27, 28). These traits, especially fire sensitivity, which could be regarded as a key innovation (in the sense of ref. 29; see also refs. 22 and 27), have favored increased diversification rates. Thus, fire-induced plant mortality increases generation turnover, thereby providing potential for more rapid evolution than sprouters (compare refs. 27 and 30). Small and weakly persistent seed banks, in combination with fire sensitivity, result in nonoverlapping generations, thereby increasing the probability of the manifestation of genetic novelties associated with each generation, as well as increasing the probability of population fragmentation via fire-induced local extinction (22, 27). Finally, restricted gene flow, a consequence of short-distance seed dispersal and insect pollination, promotes isolation and hence diversification of populations in different habitats (31, 32).

A simple microgeographic speciation model applies (28): subpopulations of common species, presumably with considerable genetic diversity, are isolated geographically by fire-induced local extinction or climate change, on the periphery of the parent population in a different habitat. This process can occur very rapidly (even after a single fire) and, owing to limited gene flow, over small spatial scales. In these isolated populations, a combination of chance fixation of new genes and strong selection in a different habitat results in rapid speciation. Predictably, the overwhelming majority of range-restricted, terminal taxa are habitat, principally edaphic, specialists (20, 27, 33, 35), implying a strong ecological component to the diversification processes (21, 31, 34).

Adaptation to pollinators has also played a major role in the diversification of the CFR's flora (35). This is especially true of the region's large geophyte flora (*ca.* 1,500 species) where specialist pollinators have driven speciation in several groups (e.g., refs. 36–38). Strong selection for specialist pollinators is presumably a consequence of the scarcity of pollinators and widespread pollen limitation in the infertile and fire-prone CFR landscapes (39). However, ecological factors, especially soil type, may nonetheless play an overriding role in speciation amongst geophytes, as in the irid genus *Lapeirousia* (33).

Diversification of the CFR biota has also occurred in relation to meso- and macroscale ecological gradients, also operating over larger temporal scales than those described above. These larger processes are the consequence of geographic isolation driven by oscillating climate change during the Pleistocene (21, 40). There is some evidence for ecological diversification of both plant and invertebrate lineages in relation to the high environmental diversity associated with lowland–upland gradients (6, 34, 41). Riverine systems that breach montane migration barriers, thereby linking dry interior basins with mesic coastal forelands, are important for migration and exchange between these biotas: subsequent isolation of populations may also play a role in speciation (42). Plants and invertebrates have also diversified across the macroclimatic gradients evident in the CFR (41, 43). There may also be as yet undisclosed levels of within-species genetic variation between geographically isolated parts of the CFR.

Further rapid climate change is likely to cause the extinction of many of the range-restricted and habitat-specialist members of the actively speciating flocks in the CFR (44–47). However, by changing habitat characteristics and promoting population isolation, climate change may also enhance turnover of actively diversifying lineages. Another widespread influence is ongoing transformation of habitats to intensive uses. The challenge for conservation planning is, therefore, to create conditions that enable evolutionary processes to continue in a rapidly changing world (48).

Systematic Conservation Planning

Conservation planning is a branch of conservation biology that seeks to identify spatially explicit options for the preservation of biodiversity (49, 50). Alternative systems of conservation areas are, in essence, hypotheses about effective ways of promoting the persistence of biodiversity. It is vital, therefore, that planning considers not only the representation of populations, species, and other components of biodiversity pattern, but also—as we argue below—the processes that underpin these patterns. In order for these processes to be represented in a conservation plan, they must be explicitly identified by their spatial components [e.g., a particular physiographical gradient across which lineages have diversified (9, 12)].

Invariably, the conservation options arising from a plan are constrained by a number of factors, such as the existing reserve system (51), the extent and configuration of transformed habitat (52), and forms of land use that are financially more viable (at least in the short term) than conservation (53). To be effective, conservation planning should be systematic. Systematic approaches share the following features: they are data-driven; target-directed; efficient; explicit, transparent, and repeatable; and flexible (12, 54).

A map of irreplaceability, such as the one shown in Fig. 1, is an outcome of a systematic approach that presents options for planning new protected areas (55). Essentially, irreplaceability is a measure assigned to an area that reflects its importance, in the context of the planning domain (e.g., the CFR), for achieving a set of regional conservation targets (e.g., a specified extent of each habitat type). Irreplaceability can be defined in two ways (57): the likelihood of an area being required to achieve the set of conservation targets for the region; and the extent to which the options for achieving a system of conservation areas that is representative (achieves all of the conservation targets) is reduced if that area is lost or made unavailable.

In areas of high irreplaceability, all or most extant habitat is required to achieve targets; in areas of low irreplaceability, there is greater flexibility in the array of available areas required to meet regional conservation targets (55). In the case of the CFR (Fig. 1), the broad pattern of irreplaceability is largely driven by agricultural transformation. Areas comprising habitat types that have been almost entirely transformed—mainly renosterveld and allied shrublands of the coastal lowlands (58)—have maximum irreplaceability. All extant occurrences of these habitats are required to fulfill the conservation target, and options for protected area establishment, or some form of conservation action, are severely constrained. In contrast, sites that include habitats associated with remote and infertile mountain landscapes, which are in a largely pristine state and where most protected areas are located (59), have low irreplaceability: here there are numerous options to meet the outstanding conservation targets.

Although the analysis in Fig. 1 provides a solid base for systematic conservation planning, it has a major limitation. The outcome reflects the options for achieving targets for pattern only. The representation of biodiversity pattern (species, habitats, etc.) is only one component of an effective conservation plan; an explicit consideration of the evolutionary processes that will maintain biodiversity in the long term is also required (11, 12), especially in a world that is increasingly threatened by habitat loss and climate change (44, 45).

Planning for Ecological and Evolutionary Processes

The past 20 years have seen the development of systematic conservation protocols that identify whole sets of complementary areas that collectively achieve some overall conservation goal—the "minimum set" approach (49, 60). In this strategy, the

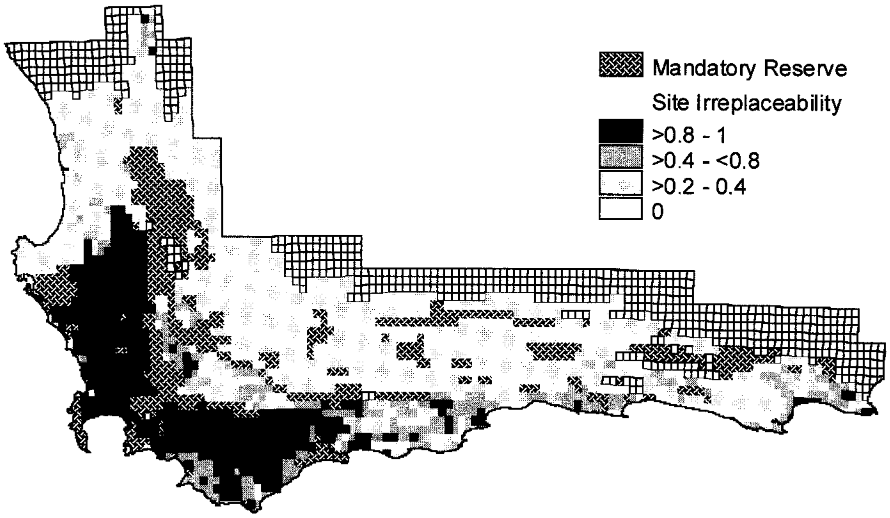

Fig. 1. A map of site irreplaceability for the CFR. Areas (planning units comprising 1/16° cells) where existing reserves cover >50% of the area are regarded as mandatory reserves. Totally irreplaceable units include areas of habitat that are essential to meet reservation targets, whereas units where irreplaceability is zero comprise habitat for which reservation targets have been achieved. The analysis, driven by explicit reservation targets for 88 Broad Habitat Units (BHUs), and mapped at 1:250,000 (56), was undertaken by using C-PLAN, a decision support system linked to a geographic information system (53).

conservation goal consists of quantitative targets for each species (e.g., at least one occurrence) or each habitat (e.g., at least 10% of its total area). The aim is to represent the required amount of each species or habitat in as small an area as possible. Usually, rapid implementation of the reserve system is assumed implicitly, so there is no basis for deciding how to schedule conservation action among the selected areas in relation to prevailing threats.

A more realistic scenario, however, is for implementation of the 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. A crucial consideration in maximizing retention is the assignment of priorities based on the irreplaceability of a site and its vulnerability to biodiversity loss as a result of current or impending threatening processes (61). In this scenario, areas with high irreplaceability and high vulnerability are the highest priorities for conservation action. The objective of the approach is to minimize the extent to which representation targets are compromised by ongoing loss of habitat and species. The same rationale underlies some approaches to identifying conservation areas globally (13).

A further step is needed, however, for conservation planning to truly address the long-term persistence of biodiversity. The implementation of reserve systems that are designed to retain only biodiversity pattern will not ensure long-term conservation. This is because these systems do not explicitly consider the ecological and evolutionary processes that maintain and generate biodiversity (1, 3, 11, 12, 62). The ultimate goal of conservation planning should be the design of systems that enable biodiversity to persist in the face of natural and human-induced change. Design is defined here 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.

Given that the implementation of reserve systems is almost always gradual, and accompanied by ongoing loss of habitat, the conservation of both pattern and process will require two things: consideration of representation and design in the identification of potential conservation areas; and sound decisions about the progressive implementation of conservation action so that land use and other threats have minimal impact on the desired outcome.

In the implementation phase of a reserve system designed for retention and persistence, the importance of threatening processes in compromising the achievement of both pattern and process goals will need to be considered and balanced (12). This strategy should achieve greater long-term benefits for biodiversity than strategies based only on the representation of pattern.

Planning for an Evolutionary Future in the CFR

Because conservation planning is a spatial exercise, an essential requirement of planning for the maintenance of natural processes is the identification of the spatial components of those processes—examples are habitat gradients or geographical barriers that are associated with lineage turnover. To our knowledge, no studies have integrated these spatial requirements into a conservation plan. This we are attempting to do in a current exercise for the CFR.

On the basis of our present understanding of diversification processes in the CFR, we identified seven spatial components to be protected to promote ongoing evolution and set targets for each (Table 1). These targets can be used to produce a map of irreplaceability for evolutionary processes but, in the overall conservation plan, are combined with requirements for representing biodiversity pattern and the continuation of various ecological processes. The next step was to design a system of conservation areas by selecting from areas that contain one or more of the spatial components in Table 1. The options associated with the selection of areas were constrained by several factors, including a pragmatic requirement to incorporate the existing reserve system; the avoidance of excessively transformed areas; and the need to select, where possible, areas also with high irreplaceability for targets for biodiversity pattern. In many instances, especially in lowland regions, habitats are so extensively transformed that it is no longer possible to achieve process targets—the evolutionary future of the CFR has already been severely compromised.

Fig. 2 shows the sequential assembly of the conservation system designed to achieve evolutionary process targets in the CFR. The rule applied for the design sequence was to initially attempt to achieve targets for which there were limited options

Table 1. Spatial components of evolutionary processes in the CFR

Spatial component	Method of identification	Target	Key evolutionary process conserved
Juxtaposed edaphically different habitats	Identify planning units with particular combinations of Broad Habitat Units (56) that reflect strong edaphic contrasts (limestone and adjacent acidic substrata) known to be associated with plant diversification processes. Exclude ''unsuitable'' planning units based on fragmentation of native vegetation and lack of contiguity with other units.	At least one example of each specified combination of Broad Habitat Units in each major climatic zone.	Ecological diversification of plant lineages in relation to fine-scale edaphic gradients (20).
Entire sand movement corridors	Identify planning units containing the three specific dune pioneer habitats. Exclude any corridors (sediment-sources) with limited conservation potential of surrounding land (particularly in the sediment-sink or downwind zones). Assume stands of dense alien plants make corridors irrecoverable.	At least one entire corridor of each type.	Ecological diversification of plant lineages in relation to fine-scale edaphic gradients (20).
Whole riverine corridors	Identify major rivers that link inland basins with coastal plains. Identify untransformed corridors or parts of corridors.	All of any intact, or the untransformed parts of each of the major corridors (five river systems; ten river corridors).	Migration and exchange between inland and coastal biotas (42).
Gradients from uplands to coastal lowlands and interior basins	Identify planning units on the following interfaces of upland and lowland: Coastal range/coastal plain Coastal range/interior basin Inland range/interior basin Inland range/Karoo basin which would allow the construction of corridors between these landscapes.	At least one example of each gradient within each of the major climate zones (9). Gradients width must encompass at least one untransformed planning unit and maximize climatic heterogeneity.	Ecological diversification of plant and animal lineages in relation to steep environmental gradients (6, 34, 41).
Macro-scale climatic gradients	Complement gradients between lowlands and uplands (meso scale) with macro-scale connectivity in two main directions: North–south in the western CFR along both the coastal forelands and inland mountains; East–west in the southern and eastern CFR along coastal forelands, coastal mountains, interior basins, and interior mountains.	Unbroken transects along all of the geographical gradients.	Geographical diversification of plant and animal lineages in relation to macroclimatic gradients (56, 58).
Mega wilderness areas	Identify contiguous planning units that encompass ca 500,000 ha of untransformed habitat, transcend biome boundaries (63), and include all or part of a riverine corridor.	One in the northwestern, one in the southern, and one in the southeastern CFR.	Maintenance of all evolutionary processes, including predator–prey processes involving top predators (59).
Transitions between major Broad Habitat Unit categories (56) and biome boundaries.	Where possible, expand conservation areas to encompass these transitions.	As many transitions as possible.	Exchange between phylogenetically distinct biotas.

The components need to be identified geographically and given quantitative targets for conservation planning. The term ''planning units'' refers to areas used in our current planning exercise as the preliminary building blocks of an expanded system of conservation areas. They are 1/16° grid cells each covering about 4,000 ha. About 2,510 planning units cover the whole CFR.

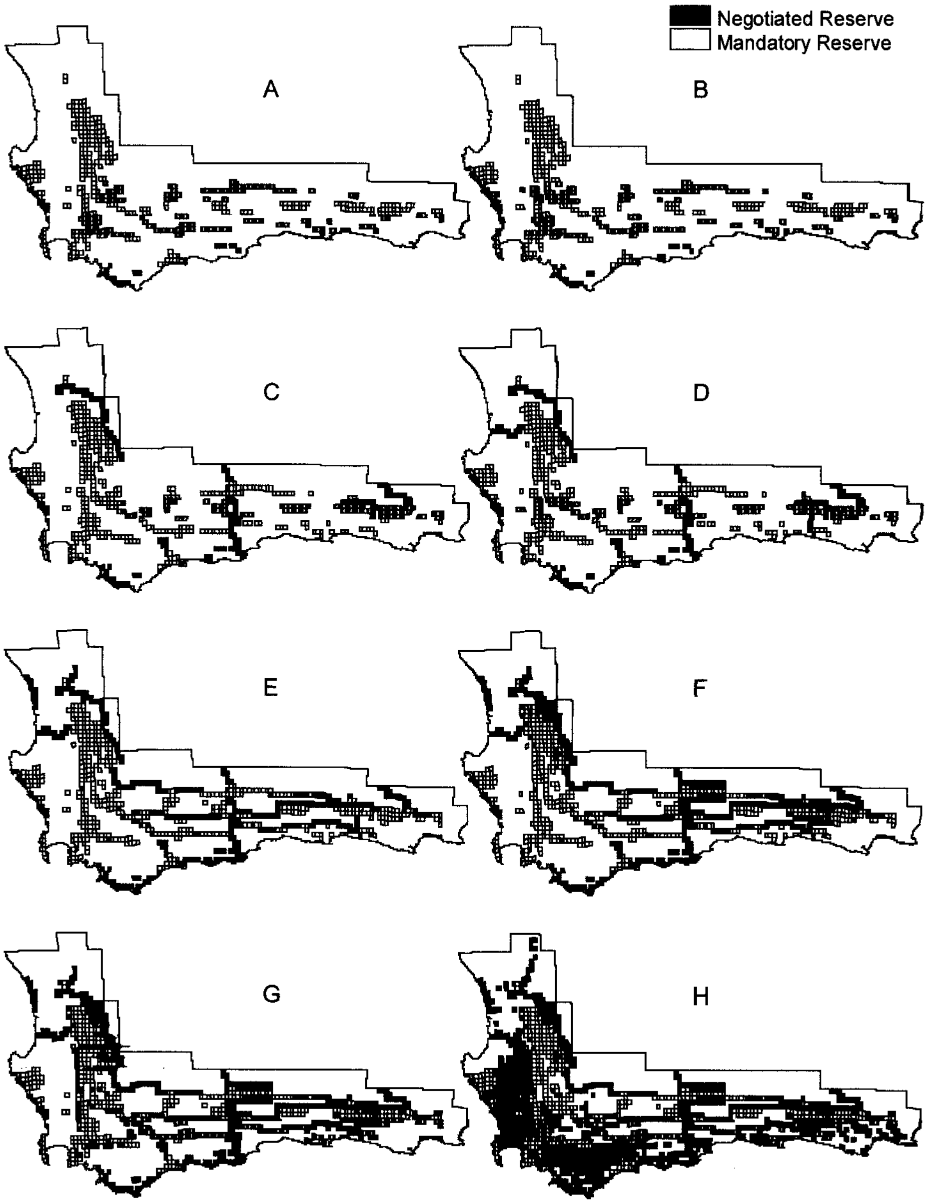

Fig. 2. Stages in the design of a system of conservation areas for the CFR that will achieve targets for biodiversity pattern and ecological and evolutionary processes. (*A*) juxtaposed edaphically different habitats; (*B*) entire sand movement corridors; (*C*) whole riverine corridors; (*D*) upland–lowland gradients; (*E*) macroclimatic gradients; (*F*) mega wilderness areas; (*G*) major biological transitions not identified in stages *A–F*; and (*H*) an additional minimum set of areas required to achieve all pattern targets. The minimum set was identified by using a reserve selection algorithm driven by irreplaceability (53).

(e.g., unique combinations of edaphic substrata), proceeding to targets offering greater flexibility in terms of spatial location. Particular attention was given to achieving more than one target within any one notional reserve. Nonetheless, the overall system depicted in Fig. 2 is one of several options for conserving processes and is accordingly presented as an example of the approach that we have used. Areas contributing to process targets were selected in the C-PLAN software system (53) as negotiated reserves, whereas the existing reserve system is depicted as mandatory reserves. The mandatory reserves, however, do not contribute substantially to achieving process targets. Of the total area selected to achieve the targets, only 41% was contributed by the existing reserve system, and the area contribution of this system to each of the seven spatial components ranged from 0–48%. Thus, in addition to being another example of an ad hoc reserve system that is inadequate in terms of pattern representation (ref. 59; see also ref. 51), extant CFR reserves are not located in a manner that will sustain evolutionary processes.

The components identified in Table 1 comprise the spatial requirements of evolutionary processes at many spatial scales. The planning units themselves, each comprising about 4,000 ha, are sufficiently large to sustain regular, whole-patch fires (64), a disturbance essential for the maintenance of key evolutionary processes (22), to maintain plant and insect biodiversity (65–67), and to maintain plant–insect pollinator relations (67, 68). However, larger areas of juxtaposed habitat encompassing the spatial components of evolutionary processes that operate over meso- and macroscale ecological gradients, are required to ensure the long-term persistence of biodiversity in the CFR. Accordingly, we hypothesize that the system identified in Fig. 2 will ensure ongoing diversification in the CFR by conserving the spatial components of key evolutionary processes. The maintenance of juxtaposed habitats over different spatial scales should impart a measure of resilience to impending climate change (44), which is predicted to have a substantial effect on the flora and vegetation of the CFR (69).

A key issue in conservation planning is the scheduling of conservation action on the ground, requiring choices in both space and time (61). In principle, irreplaceability and vulnerability to threatening processes should guide priorities for implementation: action should minimize the extent to which conservation targets are compromised before conservation management is applied (61). However, when conservation targets deal with the representation of both pattern and process, as is the case for this study, there are no established ways of comparing the relative risks of alternative approaches to implementation. For example, how should the outright loss of an extensively transformed and fragmented habitat be compared with the loss of a section of climatic gradient, comprising adequately conserved habitat but essential for sustaining evolutionary processes? Resolving these conflicts is a major challenge for conservation planning (12), and is the subject of ongoing research. A key contribution is the establishment of irreplaceability maps for the achievement of process targets.

Discussion and Conclusions

The system of conservation areas identified in Fig. 2 represents a set of hypotheses about the maintenance biodiversity and ongoing diversification in the CFR. The major prediction is that this system will maintain more biodiversity in the long term than alternative systems based on pattern representation only (12). It is not feasible, ethically or practically, to test this prediction: the scale and nature of the problem rule out experiments. We can, however, monitor and, where possible, adjust the design as results and more data become available; although, given the rapid escalation of all components of global change, time is not on our side (9, 11).

The contributions of the conservation planning approach that we have used for the CFR are the spatial identification of evolutionary drivers and the setting of explicit targets for these spatial components. Furthermore, in the larger project described partially here, these considerations are being integrated more thoroughly than shown in this indicative and preliminary account. The larger study will also have to face difficult tradeoffs between the representation of pattern and process, as well as between requirements for biodiversity conservation and other socioeconomic considerations. There are no easy answers for resolving these conflicts, nor can they be ignored.

Finally, the concepts and analytical techniques used in this study are of general applicability. The big challenge for all regions is to identify the spatial components of evolutionary processes and set targets for these. Biodiversity is being lost everywhere at an alarming rate. The current focus on pattern representation in conservation planning will only temporarily slow the rate of extinction. It is vitally important to plan for evolutionary futures everywhere.

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