

Integrating Biosystematic Data into Conservation Planning: Perspectives from Southern Africa's Succulent Karoo

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Abstract.—In this paper we explore the role that biosystematists can play in conservation planning. Conservation planning concerns the location and design of reserves that both represent the biodiversity of a region and enable the persistence of that biodiversity by maintaining key ecological and evolutionary processes. For conservation planning to be effective, quantitative targets are needed for the spatial components of a region that reflect evolutionary processes. Using examples from southern Africa's Succulent Karoo, we demonstrate how spatially explicit data on morphological variation within taxa provide essential information for conservation planning in that such variation represents an important surrogate for the spatial component of lineage diversification. We also provide an example of how the spatial components of evolutionary processes can be identified and targeted for conservation action. Key to this understanding are the recognition and description of taxonomic units at all spatial scales. Without the recognition of subspecific variation, it is difficult to formulate evolutionary hypotheses, let alone set quantitative targets for the conservation of this variation. Given the escalating threats to biodiversity, and the importance of planning for persistence by incorporating ecological and evolutionary processes into conservation plans, it is essential that systematists develop hypotheses on the spatial surrogates for these processes for a wide range of lineages. The important questions for systematists to be asking are (1) how is variation distributed in the landscape, and (2) how did it come about? Conservation planners too need to highlight these spatial components for conservation action. [Cape Floral Kingdom; conservation planning; evolutionary processes; morphological variation; phylogeography; spatial surrogates; Succulent Karoo; systematics; taxonomy.]

Conservation planning is a branch of conservation biology that seeks to identify spatially explicit options for the preservation of biodiversity (Pressey et al., 1993; Williams et al., 1996). It involves making decisions about the use of a parcel of land based on the biological, environmental, and anthropogenic attributes of that parcel and its neighbors. Alternative systems of conservation areas are, in essence, hypotheses about effective ways of promoting the persistence of biodiversity. Invariably, these options are constrained by several factors, such as the existing reserve system (Pressey, 1994), the extent and configuration of transformed habitat (Lombard et al., 1997), and forms of land use that are financially more viable (at least in the short term) than conservation (Ferrier et al., 2000).

To be most effective, conservation planning should be systematic. Systematic approaches share the following features: They are data-driven; target-directed; efficient; transparent and repeatable; and flexible (Cowling et al., 1999; Pressey, 1999; Margules

and Pressey, 2000). The data used in making these decisions must be spatially explicit. Biological features (e.g., species, subspecies, "evolutionary significant units," "management units," habitats, landscape units) and their patterns of occurrence (e.g., range sizes, extent of suitable habitat, migration patterns) need to be identified in precise terms if they are to be targeted for conservation action. Equally important is the requirement to identify salient natural processes (e.g., dispersal distances or catastrophic events) and the spatial components of the landscape with which they are associated (e.g., within a valley, between a wetland and adjacent meadow, or up a mountain side). These are key components of evolutionary processes.

Although a systematic planning approach based only on the distribution of biological features in a landscape may efficiently identify a set of conservation priorities, that approach has a major limitation. The outcome reflects the options for achieving targets for pattern only. Reserve systems designed to retain only biodiversity pattern will not

ensure long-term conservation because they fail to explicitly consider the ecological and evolutionary processes that maintain and generate biodiversity (Frankel and Soule, 1981; Hunter et al., 1988; Moritz, 1994; Balmford et al., 1998; Cowling et al., 1999). Specifically, if the persistence of evolutionary processes is to be promoted, biosystematic and evolutionary data must be integrated into conservation planning (Erwin, 1991; Vane-Wright et al., 1991; Moritz, 1994, 1995; Faith, 1996; Thompson, 1996; Cowling et al., 1999; Crandall et al., 2000).

Adequate protection of natural processes, including ongoing diversification of lineages, requires three considerations in conservation planning, all analogous to those for biodiversity pattern:

- Identification of processes that must be addressed. What processes, biotic or abiotic, most influence the diversification within lineages? Examples include maintenance of natural disturbance regimes, movements of animals, and competitive interactions.
- Identification of the spatial surrogates for processes. What are the spatial and temporal scales over which these key processes operate (e.g., between individuals, between lakes, between mountain peaks)?
- Setting quantitative targets for the spatial surrogates of processes that should be given protection in a regional conservation plan. How much area is required to ensure that a particular process is allowed to operate, fluctuate, and change without unnatural impedance or truncation such that the process will still be allowed to influence the evolutionary trajectory of a taxon? Such questions might deal with the minimum size of protected areas in particular environments, the length of the edaphic interface, and amount of habitat required for pollinator breeding, among others.

Biosystematic and evolutionary biologists seldom consider the implications of their research for conservation planning. Not only do these implications warrant more attention, but also they need to be conceptualized spatially if they are to be useful in planning,

which is inevitably a spatial process. Presenting a hypothesis about the diversification of a lineage in terms of who is related to whom is not sufficient; what is more important is how this diversification occurred. What attributes of the taxa concerned, and of the biotic and natural environment, facilitated this diversification (i.e., key ecological or evolutionary processes) and how are these elements distributed in the landscape? If examining these questions were done routinely, it would contribute greatly to the conservation of biodiversity. Achieving this goal really requires the integration of systematic, autecological, and community ecological studies.

Here we explore some of the contributions that biosystematists can make to conservation through identifying the spatial components of evolutionary patterns and processes. We use examples from the winter-rainfall Succulent Karoo biome of the Capé Floral Region of South Africa (Rutherford, 1997) (Fig. 1) to illustrate these contributions.

IDENTIFYING SPATIAL COMPONENTS OF EVOLUTIONARY PATTERNS AND PROCESSES

Numerous pleas in the literature call 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 natural processes (Pickett and Thompson, 1978; Frankel and Soule, 1981; Hunter et al., 1988; Erwin, 1991; Moritz, 1994; Thompson, 1996; Cowling et al., 1999). Regarding evolutionary processes, investigators have debated as to whether priority should be given to areas supporting ancestral taxa with evolutionary potential (Williams et al., 1991; Linder, 1995) or those areas representing evolutionary fronts of currently speciating taxa (Erwin, 1991; Brooks et al., 1992; Fjeldsa, 1994; Moritz, 1995). Recently, Moritz and coworkers 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 (Moritz and Faith, 1998). However, except for some preliminary work by Cowling and Pressey (2001), no studies have attempted to identify the spatial components of a wide spectrum of evolutionary processes or to set

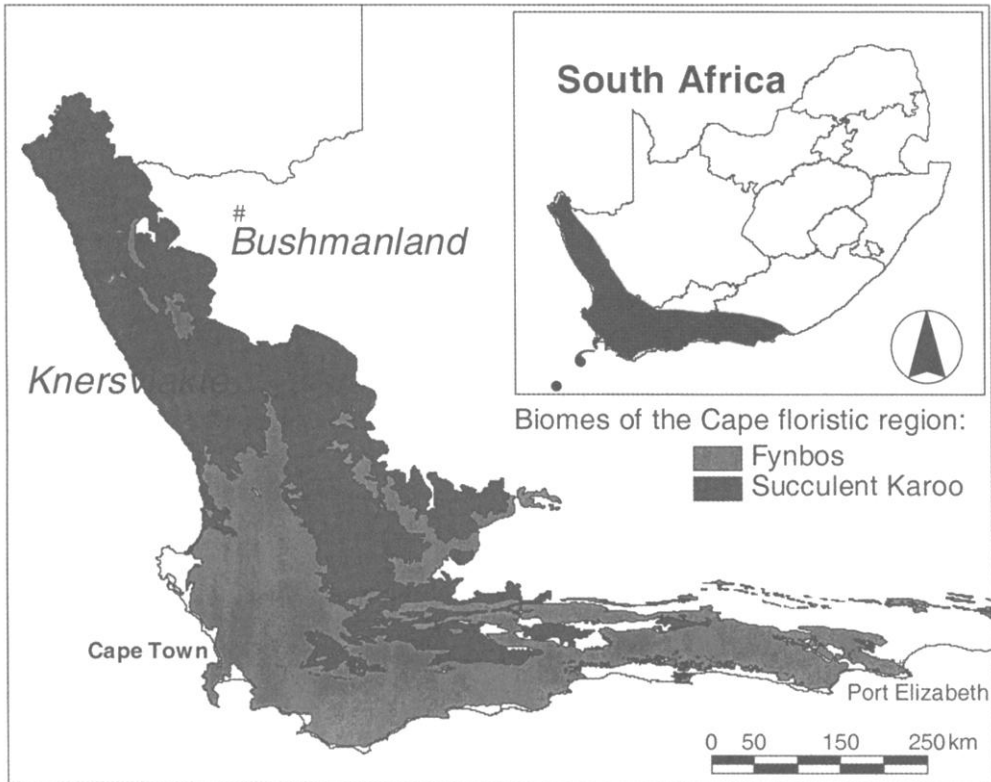


FIGURE 1. Location of the winter-rainfall Succulent Karoo biome of southern Africa, showing the locations of the geographical regions discussed in this paper.

explicit targets for the protection of evolutionary processes in particular regions.

Despite the need to incorporate evolutionary processes into conservation planning exercises, few have explicitly mentioned what these processes are (Crandall et al., 2000). From a conservation perspective, we can conceptualize evolutionary processes as those that determine the spatial distribution of genetic variation and, most importantly, adaptive variation among populations (Crandall et al., 2000)—for example, gene flow, natural selection, nonrandom mating, genetic drift, and hybridization.

In plants, gene flow includes pollination (pollen movement distances, pollinator interactions, and so forth) and seed dispersal (seed movement distance, seed establishment, and other factors). From a conservation planning perspective, gene flow is important to consider because it is a spatial process and influences the effects of selection and drift directly. A continuum of gene flow levels exists, ranging from panmixia (complete mixing) on the one hand to com-

plete isolation on the other (Crandall et al., 2000).

Evolutionary significant units (ESUs), as defined by Moritz (1994), constitute one extreme in the continuum (complete isolation through historical vicariance), but are they really the most important units to consider in the context of the development and persistence of biodiversity? Divergence, particularly through genetic drift, is perhaps more likely in more isolated populations, although evidence (primarily from laboratory studies) suggests that speciation through drift in allopatric populations is, at best, a very slow process (Rice and Hostert, 1993). On the other hand, a substantial body of accumulating evidence suggests that adaptive divergence and even speciation (the evolution of reproductive isolation) often happens as a result of strong, multifarious divergent selection with or without gene flow (Rice and Hostert, 1993; Schluter, 1996; Losos et al., 1998).

Genetic data have perhaps been overemphasized in the identification of process, primarily as a result of the emphasis placed

on ESUs, defined as reciprocally monophyletic groups of populations (Moritz, 1994) as units of conservation (Bininda-Emonds et al., 2000; Crandall et al., 2000). For conservation purposes, the spatial components of processes that cause contemporary divergence between populations should also be emphasized, not just the product of this process (i.e., the ESU) (Erwin, 1991; Moritz, 1998; Crandall et al., 2000). In particular, genetic variation, which is expressed phenotypically and thus has potential adaptive significance or is at least exposed to present and future selective regimes, should be considered. The importance of historical patterns (ESUs) is that they represent sets of populations evolving on potentially independent trajectories (Moritz, 1994). Genetic data are probably most relevant here in terms of understanding the spatial scale of gene flow, patterns of colonization, and degree of divergence between taxa (e.g., intraspecific population genetics, phylogeography). That information is relevant, for example, when setting targets for the number, configuration, and combination of taxa to conserve (i.e., evolutionary pattern targets).

In setting targets for evolutionary processes, the spatial component of selection, the primary process causing population divergence relevant to population persistence, is what is important. This component is probably most easily estimated through spatially explicit analyses of patterns of functionally important morphological or autecological differentiation and their underlying environmental gradients. Spatially autocorrelated variations in plant morphological, physiological, reproductive, or dispersal traits are all indicative of differential selection in response to environmental gradients within the range of a given taxon. This information is relevant for determining the spatial components for the underlying driving variables of this divergence. Of course, it is not feasible to collect genetic level data for all lineages, and morphological and autecological data are more easily obtained and equally relevant. Perhaps more important from a planning perspective is that the spatial components of evolutionary processes need to be easily recognized. How far does one have to move in geographical space before recognizing observable change in a driving variable (e.g., valleys either side of

a mountain range; across juxtaposed soil types, the presence of a different pollinator)? Surrogacy is of great relevance for we will never have all the data for all lineages.

Phylogenetic studies have an important place in conservation planning, especially in the identification of pattern (Erwin, 1991; Vane-Wright et al., 1991; Moritz, 1995). In addition, phylogenies are useful for gaining insight into important processes, particularly the mode of speciation, primarily through comparative phylogenetic methods (Felsenstein, 1985; Barraclough and Vogler, 2000). Studies of this nature are limited in southern Africa. Phylogenetically independent contrasts have been used by Linder and Vlok (1991), Linder (1995), and Goldblatt and Manning (1996) to show that genetic divergence between sister species occurs through edaphic selection. However, an explicit consideration of the spatial components of their studies, in particular, the spatial scale of geographic isolation and edaphic gradients, is required for this work to contribute significantly to conservation planning in the region. Furthermore, because the spatial scale of evolutionary process is likely to vary between taxonomic groups, one must compare as many unrelated taxa as possible to understand the relevant spatial components of process (Moritz and Faith, 1998). Thus, if systematic and evolutionary studies provide spatially explicit data, they could cumulatively contribute to the body of information required to adequately consider process goals and targets in planning exercises.

From a planning, rather than taxonomic, perspective, any abiotic or biotic pattern or process that can markedly influence evolutionary processes needs to be considered. Environmental gradients that represent major selective forces should be a principal focus of conservation planning. Examples for plant diversification include edaphic interfaces, climatic gradients, and riverine corridors that allow movement and diversification (Cowling and Pressey, 2001). Above all, these components need to be identified, mapped, and targeted if they are to be considered in conservation plans. In the example that follows, we demonstrate how an evolutionary framework can be incorporated in a regional conservation plan.

SPATIAL COMPONENTS OF EVOLUTION IN CONSERVATION PLANNING

Evolutionary processes were explicitly incorporated into developing a systematic reserve plan in the Knersvlakte (Fig. 1), a region within the Succulent Karoo biome covering ~10,000 km² and receiving <140 mm of rainfall annually. With 129 known endemic plant species (Hilton-Taylor, 1994a), the Knersvlakte has been recognized as a priority region for plant conservation in the biome (Hilton-Taylor, 1994b; Cowling and Hilton-Taylor, 1998; Lombard et al., 1999). It is renowned for its rich flora of minute succulents associated with quartz-pebble lag-gravel fields (Schmiedel and Jürgens, 1999). Other hard rock substrata such as quartzite and limestone also support a biologically interesting and distinct flora (Desmet et al., 1999) (Fig. 2).

The objective of this study was to identify priority areas for the establishment of a national park in the region. Strong emphasis was placed on conservation of the patterns of biodiversity as well as the ecological and evolutionary processes associated with the region's quartz field habitats. These habitats are unique within the Succulent Karoo biome and support the greatest number of endemic plant species, mainly dwarf succulents (<30 cm tall) and geophytes (Schmiedel and Jürgens, 1999).

Selecting areas for conservation action followed an explicit protocol for reserve design consisting of a series of six steps (Table 1) to identify and implement a reserve system designed for the persistence of biodiversity pattern and process (Cowling et al., 1999; Pressey and Cowling, 2001). The second step (Table 1) is where the bulk of the



FIGURE 2. A typical Knersvlakte landscape, showing quartz patches dominated by small to very small shrubs and dwarf succulents. (Insert) A closer view of a quartz patch with a typical dwarf succulent, *Argyroderma delactii* (Mesembryanthemaceae), nestled amongst quartz pebbles. Photos: P. G. Desmet.

TABLE 1. Six steps in the reserve design protocol for achieving retention and persistence (from Cowling et al., 1999).

Steps	Action
Step 1	Identify types, patterns, and rates of threatening processes
Step 2	Identify natural features to be protected—elements of biodiversity pattern (e.g., species, habitats) as well as spatial components of the region that serve as surrogates for ecological and evolutionary processes
Step 3	Set targets for representation of spatial components and design of conservation areas
Step 4	Lay out options for achieving the representation and design targets
Step 5	Select potential conservation areas to achieve representation and design targets
Step 6	Implement conservation actions <ul style="list-style-type: none"> • Set priorities for scheduling conservation action on the basis of irreplaceability and vulnerability • Allocate forms of conservation management • Fine-tune boundaries of conservation areas

biological data were integrated, in identifying what spatial components (surrogates for pattern and process) need to be protected in the expanded conservation system (e.g., endemic taxa, unique habitats, abiotic gradients).

Despite the unique diversity of this region, plant distribution data such as phytosociological surveys, vegetation maps, or herbarium records did not exist in South Africa. Instead of species data, the planning process used spatial information on the diversity and density of “key” plant habitats. These habitats (quartz-pebble lag-gravel fields or quartz patches and quartzite and limestone rock, which are particularly distinctive floristically) were identified through consensus of expert opinion and analysis of available herbarium information. A rapid survey of succulent plant species in the planning domain showed that diversity is centered on the intersection of the Sout River and the N7 National Highway (Fig. 3), with northern and southern centers branching off from this center. This pattern in species diversity correlates with the density and distribution of key habitats. The central area has the largest aerial extent, diversity, and juxtaposition of key plant habitats. Key habitats in the northern and southern centers show less fine-scale patterning and greater uniformity in species composition between patches of similar habitats (lower gamma diversity). Key habitats in these areas are also less abundant and more diffuse, the habitat patches being more isolated in the landscape and generally only one type of key habitat occurring in the general vegetation matrix. By contrast, in the central region one commonly finds two or three closely juxtaposed key habitats within the same vegetation matrix.

With any planning exercise, the variety of ecological and evolutionary processes that need to be considered is large (e.g., Cowling et al., 1999). Several of these were identified as applicable to the Knersvlakte, but from a practical standpoint, to explicitly consider every process within a systematic planning approach is almost impossible. Planners have to judge which processes (a) impact most on the persistence of biodiversity and (b) are most in need of conservation action, that is, are most vulnerable (Step 1, Table 1). In the Knersvlakte, of key importance was the identification of the spatial extent of the evolutionary “playing field” in the region, the area responsible for the observed swarm of morpho-taxa that characterize the landscape.

From observations on turnover patterns in taxa, morphological variation within taxa across the landscape, seed dispersal, and pollinator ecology (Hartmann, 1973; Desmet et al., 1998), we concluded that morphological variation was nested within minor drainage basins within the study area (Fig. 3). That is, our primary evolutionary hypothesis was that endemic taxa are most often restricted to a single or several adjacent drainage basins (high gamma diversity) and that greatest morphological variation within taxa is observed between drainage basins. Thus, each drainage basin could be regarded as a discrete and distinct evolutionary unit. The mechanisms driving the isolation of taxa between basins are a combination of plant and pollinator biological processes as well as hydrogeomorphological processes (Hartmann, 1973; Desmet et al., 1998) (Table 2). Thus, drainage basins act as a spatial surrogate for the environmental, plant demographic, and autecological patterns and processes

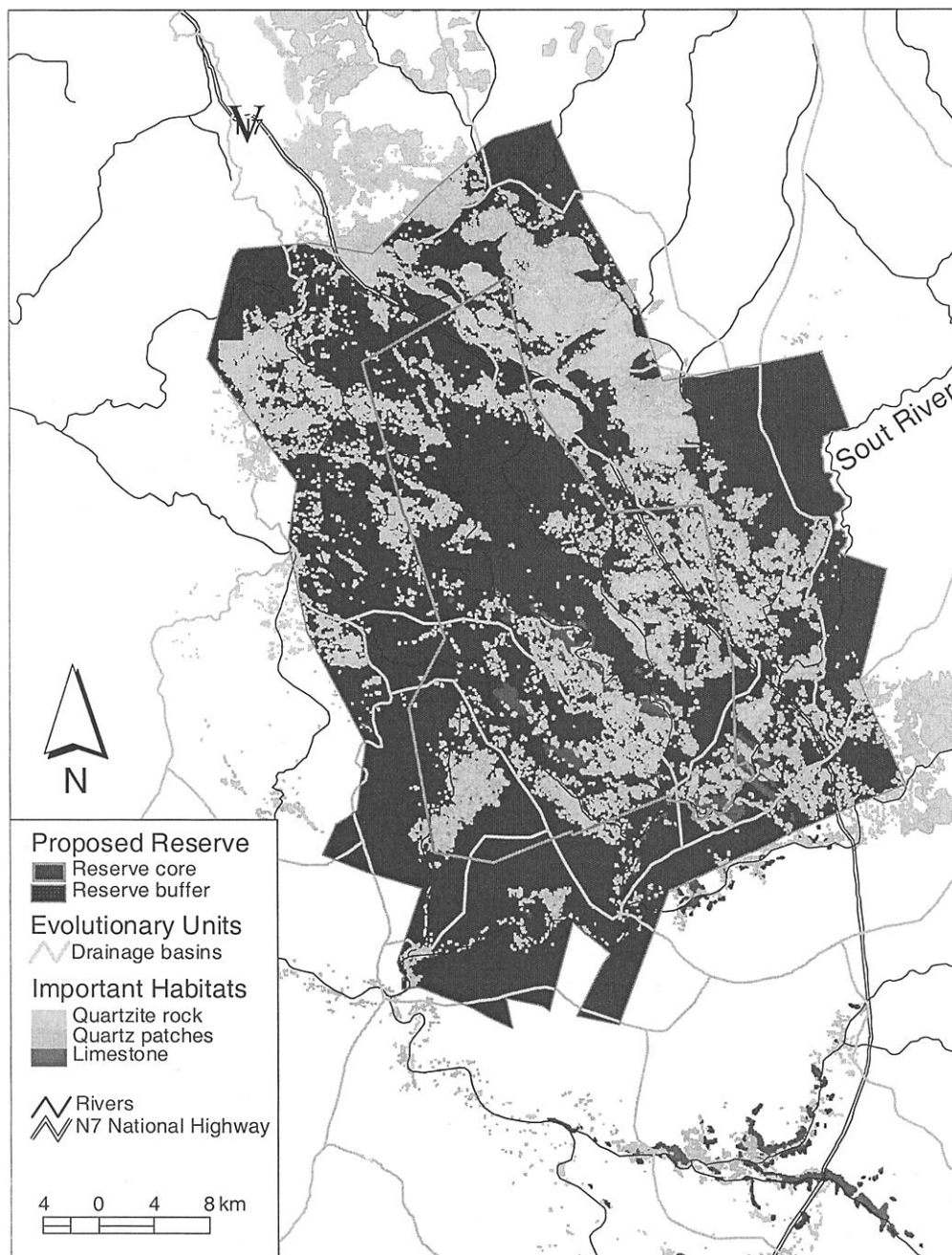


FIGURE 3. Distribution of important plant habitats in the Knersvlakte region in relation to minor drainage basins, rivers, and significant human infrastructure.

responsible for the observed diversification in the region.

This model stresses connectivity of the basins. Patches of the habitat that represent the most edaphically extreme selective regime in the landscape (saline quartz

patches) and that support the greatest number of range-restricted endemic plants are consistently associated with bottom slopes (Schmiedel and Jürgens, 1999). This habitat is distributed as "islands" in the landscape along drainage lines. Thus, to ensure

TABLE 2. Key patterns and processes considered in developing a spatial context for the conservation of evolutionary patterns and processes in the Knersvlakte.

Biological processes (short term, <1 year)	
1.	Short distance water-assisted seed dispersal, generally down slope.
2.	Short distance movement by solitary bees (Anthophoridae) and bee-fly (Nemestrinidae, Bombyliidae) pollinators.
3.	Extreme plant habitat specificity of endemic plants.
Hydrogeomorphological (medium term, 10–100 years)	
1.	Connectivity and development of quartz lag-gravel patches along drainage lines and with progressive headward erosion of river catchments.
2.	Catenal position of quartz patch types with saline quartz patches always associated with the bottom slope position.

maintenance of gene flow between patches of this habitat, the basins must stay linked by way of river valley corridors. Furthermore, whereas point diversity is moderate to high within a drainage basin, compositional turnover between adjacent habitats is exceptional (high beta diversity), indicating that levels of speciation are high across habitat boundaries associated with catenas and changes in underlying geology (Desmet et al., 1998; Schmiedel and Jürgens, 1999). Therefore, the inclusion of areas with a diversity of juxtaposed plant habitats is also important.

For the reserve design process, these evolutionary hypotheses, inferred from patterns of morphological variation, were used to derive a set of explicitly quantitative targets and qualitative rules for area selection. Quantitative targets were also set for the representation of key habitats. We also used adjacency and connectivity rules to ensure the inclusion of at least three drainage basins connected by way of drainage corridors. Rather than selecting areas distributed across the entire planning domain (i.e., best representation of habitats or pattern targets), we restricted the reserve outcome to the central area of the Knersvlakte, which has the greatest density and diversity of habitats as well as the most adjacent drainage basins.

Within our systematic planning context, application of these hypotheses, no matter how tenuous, does not necessarily pose a problem because the assumptions are explicit and testable and can be modified when more detailed data become available. The process of testing the evolutionary hypotheses is underway, involving the development of a phylogeography of the genus *Argyrodema* (Mesembryanthemaceae; 11 taxa), which is endemic to the Knersvlakte

and shows large taxic variation along habitat and geographical gradients (Hartmann, 1973; Desmet et al., 1998; Schmiedel and Jürgens, 1999).

Incorporation of evolutionary hypotheses into conservation planning is limiting in several respects. Although phylogenetic analyses may reveal selection processes that resulted in the current morphological patterns, those processes may no longer be the dominant selective forces currently in operation or likely to operate in the future. Planners must be able to make predictions as to how plants may respond to changes in these gradients. Only when we know what happened in the past can we attempt to make predictions about the future. In addition, lack of congruence in phylogenetic and taxonomic circumscriptions derived for the same taxa from different data sets (morphometric vs. allozymes vs. flavonoids, for example) imposes uncertainties about true relationships and can lead to the generation of alternative evolutionary hypotheses. Finally, there is often lack of congruence between two or more phylogenetic groups occupying the same biome. The spatial relationships and scales within one plant genus may or may not correspond to those in a vertebrate or fungal group or another plant group. Evolutionary processes of different types and spatial scales may be driving selection in different groups. This requires that at a regional scale, conservation plans must include criteria for a range of organisms (Fjeldsa, 1994; Lombard, 1995). Different parts of a regional reserve network will focus on conserving processes relevant to different groups of organisms. In some systems, however, key selective processes, such as fire, influence a wide spectrum of lineages. Identifying processes having such a general or widespread effect would be a useful exercise.

Adding spatial targets for evolutionary processes to the reserve design process changes the necessary configuration of selected areas. A reserve selection algorithm (Pressey et al., 1993) that achieves only targets for pattern representation (e.g., different habitats) focuses on areas containing large areal extents of targeted habitats, areas that are spread throughout the planning domain. Adding evolutionary process targets (e.g., adjacent drainage basins with a high diversity of habitats connected by way of river corridors) substantially alters the set of areas selected.

Without explicit targets for evolutionary processes, systematic conservation planning approaches cannot effectively incorporate persistence into reserve scenarios. Although this example is based on assumptions regarding the importance and spatial extent of habitat types and the spatial surrogates of evolutionary processes, it nonetheless fulfills an important requirement of successful conservation planning by being systematic and explicit. Given that reserves networks are generally implemented gradually (Pressey et al., 1996; Cowling et al., 1999), alterations in a regional conservation plan because of improved data or modified hypotheses can be incorporated at a later date.

In this example, delaying the development of the regional conservation plan until better data became available would seriously compromise the conservation goals. Recent developments in the mining industry in the region have placed many key habitats under threat. A South African government decision on mining policy, granting all holders of mineral rights a two-year period in which to commence mining before losing their mining rights under a "use it or lose it" policy, has prompted many holders to apply for mining permits. Mining in the region focuses on key habitats within the core area of the identified reserve such as limestone outcrops or diamond deposits in paleoriver terraces under saline quartz patches.

Targeting of these habitats by miners has already destroyed an important proportion of these habitats within the core area, thereby compromising targets for connectivity. After the development of this reserve plan, the provincial government has received 10 mining applications covering 30% of the core area of the proposed reserve. Without the

plan, regional conservation and planning authorities would not have been aware of the importance of these areas. This example also highlights the importance of being able to assess the development of threats to biodiversity, particularly threats to the continuation of evolutionary processes, and to develop conservation plans and actions in anticipation of these threats.

VARIATION AT ALL TAXONOMIC SCALES, AREA SELECTION, AND EVOLUTIONARY HYPOTHESES

Conservation planning requires a currency with which to objectively determine the conservation importance of areas and to assess the "cost," in terms of lost conservation opportunities or biodiversity, of alternative reserve outcomes (Vane-Wright et al., 1991; Williams et al., 1991; Franklin, 1993; Moritz, 1994, 1995; Humphries et al., 1995). The literature contains much debate as to the best way of defining biological entities for conservation planning (e.g., Vane-Wright et al., 1991; Franklin, 1993; Humphries et al., 1995; Noss, 1996; Prendergast et al., 1999). In practice, any well-defined biodiversity entity can be used. In this section we illustrate the effects of changing the definition of the biodiversity surrogates—in this case, species—on conservation planning outcomes. We also provide another example of how information about infraspecific variation can be used to formulate testable hypotheses that provide spatially explicit data on evolutionary processes.

Species are commonly the target feature of conservation action. They are a practical surrogate with which to set targets for capturing biological variation because they are generally well-defined according to an internationally recognized set of principles and because most point biological data are collected at this scale. When setting targets for evolutionary processes, the spatial components of selection, reflecting the primary processes causing population divergence relevant to population persistence, are important. These components are probably most easily estimated through spatially explicit analyses of patterns of functionally important morphological differentiation and underlying environmental gradients. In essence, defined taxa can act

as convenient surrogates for evolutionary processes, but this depends greatly on the level of understanding of taxon genetic, morphological, and autecological details implicit in the taxic definition. At the one extreme, systematists choose to lump variation into easily defined superspecies. At the other extreme, some systematists identify a proliferation of subspecific "morphotaxa" in an effort to capture the obvious morphological variation observed. This is especially relevant in a species-rich region like the Succulent Karoo in succulent genera such as *Conophytum* (Mesembryanthemaceae) (Hammer, 1993) and *Haworthia* (Asphodelaceae) (Bayer, 1999).

Although the superspecies approach is taxonomically robust, in a practical conservation context it results in the loss of biodiversity. For example, a revision of the genus *Cephalophyllum* (Mesembryanthemaceae) included *C. anemoniflora* (L. Bol.) Schwant., a creeping leaf-succulent endemic to the shores of False Bay in Cape Town, in the more widespread taxon *Jordaaniella dubia* (Haw.) H.E.K. Hartmann (Hartmann, 1984). This action effectively removed the South African Red Data Book status the taxon had enjoyed. Without any formal threatened status, there were no legislative means of protecting the taxon, which has subsequently gone extinct in the wild. Although flower color (salmon pink instead of the golden yellow in *J. dubia*) and differences in leaf size and shape are hardly grounds for specific rank in the Mesembryanthemaceae, this "ecotype" is distinct within the *J. dubia* complex and perhaps is indicative of a distinct evolutionary history or adaptation to a unique local environment. Without some form of taxonomic recognition, biodiversity hidden within such super-species concepts will not be explicitly considered by conservation planning exercises or legislators. Given the threats facing biodiversity, taxonomic work that does not explicitly recognize observable subspecific variation within taxa can lead to loss of biodiversity (Sangster, 2000).

When setting quantitative targets for taxonomic features in a conservation planning process (such as, "the reserve network must contain at least three known populations of species A"), taxonomic decisions can alter planning outcomes. Consider an example from the inselberg region of northern Bushmanland (Fig. 1). The Bushmanland land-

scape is characterized by open, sand-covered plains dotted with quartzite inselbergs as much as several kilometers in diameter and 200 m above the plains. In the southwest part of the study area, the mountains are continuous with the central Namaqualand uplands and fall within the predominantly winter-rainfall or Succulent Karoo biome. The plains to the east receive exclusively summer rainfall and the flora is typical of the Nama Karoo biome (Jürgens, 1991). The geology and topography of the inselbergs on this plain create climates that are moderated by aspect and by occasional orographic precipitation associated with passing winter fronts. The vegetation of these inselbergs is typical of the Succulent Karoo and thus constitute islands of winter-rainfall vegetation within a generally summer rainfall vegetation matrix (Desmet, 2000).

An earlier study looking at the importance of inselbergs in the region (Desmet, 2000) ranked inselbergs on the basis of, among other variables, the occurrence of succulent plant species. This dataset is useful for illustrating some of the attributes of taxonomic datasets. Each of 33 inselbergs was reassessed by using data on the occurrence of the genus *Conophytum* (Mesembryanthemaceae). Three classifications of the same taxa were used, based on different levels of taxonomic delimitation (Table 3). This genus is useful for such analyses because it is generally restricted to the hard substrata associated with inselbergs, it is well-known taxonomically (Hammer, 1993), and, as a result of its popularity in cultivation, intraspecific variation is well documented. The observed taxa were reclassified according to species; subspecies and varieties; and recognized forms or undescribed subspecific taxa (Table 3). With this dataset, the program C-Plan (Pressey, 1998; Ferrier et al., 2000) was used to calculate the irreplaceability of each inselberg with three sets of conservation targets, respectively reflecting the three levels of taxonomic distinction.

Irreplaceability is a measure assigned to an area (in this example, an inselberg) that reflects its importance in the context of the planning domain (e.g., the inselberg region of northern Bushmanland) for achieving a set of regional conservation targets—in this example, at least one occurrence of each taxon. Irreplaceability can be defined in two ways (Pressey et al., 1994): the likelihood of

TABLE 3. Levels of classification of species in the genus *Conophytum* occurring on 33 inselbergs and surrounding sites in northern Bushmanland. Nomenclature according to Hammer (1993).

Species	Subsp./Var.	Form
<i>C. achabense</i>		
<i>C. angelicae</i>	<i>angelicae</i>	dwarf large
<i>C. bilobum</i>	<i>bilobum</i>	
<i>C. blandum</i>		
<i>C. burgeri</i>		
<i>C. calculus</i>	<i>vanzyltii</i>	
<i>C. depressum</i>		
<i>C. ectypum</i>	<i>ectypum</i> <i>ignavum</i> <i>flavum</i>	
<i>C. flavum</i>		
<i>C. friedrichiae</i>		
<i>C. fulleri</i>		dwarf large diploid polyploid
<i>C. limpidum</i>		
<i>C. lithopsoides</i>	<i>kennedyi</i> <i>koubergens</i> <i>lithopsoides</i>	
<i>C. lydiae</i>		
<i>C. marginatum</i>	<i>karamoepense</i> <i>marginatum</i> <i>maughanii</i>	arm955 karamoepense marginatum
<i>C. maughanii</i>		
<i>C. mirabile</i>		
<i>C. pageae</i>		
<i>C. pellucidum</i>	<i>neohallii</i> <i>pellucidum</i>	
<i>C. praesectum</i>		
<i>C. ratum</i>		
<i>C. roodiae</i>		regular small grey
<i>C. smorenskaduense</i>	<i>herrmarium</i>	
<i>C. stevens-jonesianum</i>		
<i>C. wettsteinii</i>	<i>wettsteinii</i>	

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 (i.e., achieves all the conservation targets) is reduced if that area is lost or made unavailable for conservation. Areas of high irreplaceability have a high likelihood of being needed to achieve the conservation targets for the planning region. Few or no alternatives are available and the risk is risk that one or more of the targets will be compromised if processes such as clearing, mining, or grazing degrade these areas. Areas with low irreplaceability have more options, giving planners more flexibility in designing systems of protected areas, and more replacements are available if the areas are degraded (Pressey et al., 1994). Figure 4 summarizes the change in

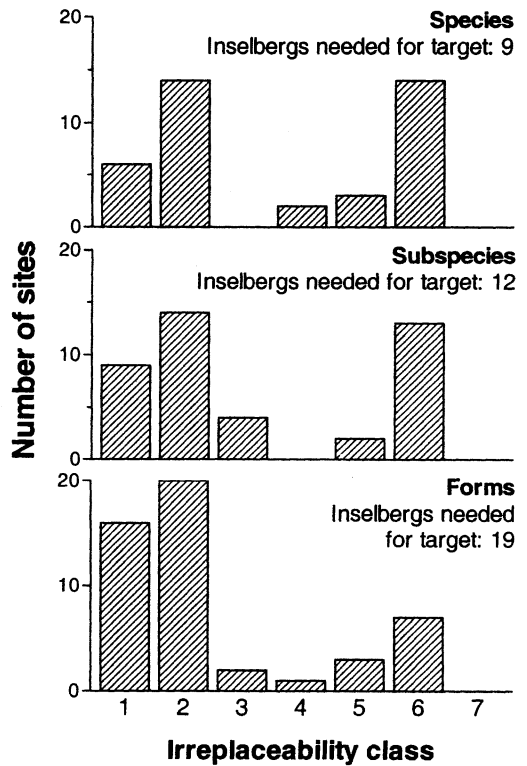


FIGURE 4. Comparison of the frequency distribution of irreplaceability of inselbergs according to the three different levels of taxic classification presented in Table 3. Irreplaceability classes 1 and 0 contain only values of 1.0 or 0, respectively. Classes 2–6 are equal-width subdivisions of intermediate values.

irreplaceability values (a continuous variable ranging from 0 to 1) of inselbergs with each taxic scenario. With increasing refinement in the taxic data, the number of inselbergs with irreplaceability values of 1.0 increases. A related outcome is an increase in the number of inselbergs required to achieve the target of representing each taxon at least once in the reserve scenario. These results reflect morphological and taxonomic turnover between inselbergs. As might be expected with an “island” flora, variation is nested on or around inselbergs and is greatest between inselbergs. Within a species complex, different forms replace each other on different inselbergs.

Generally there is never more than one species from a subgenus on any inselberg. In only two cases do sister species cooccur and in both cases they are restricted to opposite ends of the two largest inselbergs. The same holds true for subspecies/variety and form rank. At the largest and most

species-rich site, which forms the eastern boundary of the Namaqualand mainland, nine species in seven subgenera are present. In both cases, the sister taxa occur in distinct habitats. Although the "morpho-taxa" (forms) recognized in this analysis may not constitute legitimate species, the observable variation is informative of underlying evolutionary processes. Diversification occurs regionally along a macroclimatic gradient associated with the east–west summer–winter rainfall gradient; at the landscape scale through allopatric processes associated with the island nature of suitable habitats; and locally across habitat boundaries. It is imperative that this information not be lost in systematic studies. Not only is this variation a valid part of biodiversity pattern, but also it can throw light on the evolutionary processes involved. This classification provides the basis for the formulation of evolutionary hypotheses that can be tested through more rigorous sampling and analysis focused on specific evolutionary questions. Using morphological or genetic data to develop a phylogeny is the first step towards this understanding. The results of systematic studies need to be interpreted in an evolutionary context. In addition to a phylogeny, models need to be generated that attempt to explain the probable evolution of the observed biological variation. Above all, these models need to be projected on the physical landscape. Key questions are include, What is the variation and how did it come about?; Who or what was involved in creating/facilitating/driving this variation?; and, Where did it happen? Answers to questions such as what are the dominant environmental variables across which speciation/species turnover is occurring; where are hybrid zones located; and where are potential barriers/vectors for gene flow located, can easily be incorporated into conservation planning exercises. However, answers to these questions will differ for different lineages. What is required is the close integration of systematic, autecological, and community ecological information into developing an understanding of the processes responsible for the patterns of diversity we observe in the landscape. Good systematic studies underpin successful conservation planning, and systematists need to be aware of the important role they play in this regard. Accordingly, systematic studies

need to be mindful of the real-world implications of taxonomic decisions, and results need to be interpreted in a spatially and evolutionary explicit context.

CONCLUSIONS

For conservation planning to be effective, persistence goals need to be incorporated into the planning process. To achieve this, targets for evolutionary patterns (variation) and processes (diversification) must be identified and achieved—which requires planners to have spatially explicit data. Unfortunately, such data are mostly lacking. Systematists need to be aware of the importance of collecting data and performing analyses that are spatially explicit or have spatially explicit outcomes.

We have identified two major issues that systematists need to consider for their data to be relevant for conservation planning:

- The identification and publication of units of selection at all taxic scales; and
- The formulation of spatially explicit hypotheses, however tentative, on the evolution of units that make up a classification.

Both of these issues are central to identification of targets for the conservation of evolutionary processes. Whereas the first-mentioned issue does not pose major problems (systematists routinely document variation within taxa), the second represents a considerable challenge. However, without spatially explicit data on evolutionary processes, planners will not be able to set effective conservation targets and thereby cannot ensure the persistence of biodiversity. In the face of ever-increasing threats to biodiversity and the reality that comprehensive phylogeographic studies cannot be performed on more than a fraction of lineages, it is essential that systematics develop hypotheses on the spatial components of evolutionary processes, no matter how sparse the data. Furthermore, conservation planners need to recognize the importance of evolution in identifying reserve networks.

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