Patterns and evolution of plant diversity in the Cape Floristic Region

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The Cape Floristic Region (CFR) is a species-rich mediterranean-climate area with almost 9000 species packed in only 90,000 km^2, a remarkable 69% of the species being endemic. Most of the endemics however belong to relatively few lineages and generic-level diversity is moderate. The vast majority of these speciose groups typically grow in the dominant vegetation type (fynbos), comprising mainly low, non-sprouting (post-fire) shrubs with limited dispersal. However, resprouting geophytes are also very diverse, representing 17% of the total flora. While these patterns have long been recognized, gaps remain in the understanding of altitudinal and geographic gradients in species richness. Thus, at the regional scale – the focus of this paper – the west is much richer than the east, and in the west, montane regions are more diverse than the lowlands. Topographic diversity can be invoked to explain the altitudinal gradient, but no single explanation is sufficient to explain the west-east geographical gradient. Here, we put forward three types of explanations that are likely to be responsible for this gradient. (a) Differences in the contemporary environment: of chief importance are rainfall seasonality and reliability (precipitation being much more seasonal and reliable in the west). (b) Local diversity and turnover patterns: local diversity is invariant along the gradient but both beta and gamma diversity are higher in the west. (c) Differences in speciation and extinction histories: the west is likely to have had higher speciation and lower extinction rates, the former as a result of predictable seasonal rainfall (acting in conjunction with fire), and the latter owing to long-term climatic stability. In this context, the seasonal and more reliable climate in the west can also be linked to the higher geophyte diversity observed there. Recent molecular phylogenetic studies of a limited number of taxa largely suggest a mid-Miocene-Pliocene radiation age with a strong ecological component. However, in some groups, there is evidence of earlier (Oligocene) radiation events, involving geographic speciation. An even earlier diversification is reflected in the thicket and forest flora of the Cape, seldom referred to, yet comprising both ancient and speciose groups.

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Introduction

There is a long history of research on plant diversity in South Africa's Cape Floristic Region (Goldblatt & Manning 2002). Owing to relatively intensive collecting and exploration since the late 1700s (Gunn & Codd 1981), it was possible, by the mid 1900s, for Weimarck (1941) and Levyns (1952) to describe coarse patterns of richness and endemism that have endured to this day. Analytical approaches were introduced in the 1970s, first by Kruger and Taylor's (1979) pioneering work on species-area relations, followed by attempts to model local-scale (alpha) richness (Bond 1983; Cowling 1983a), and then assessments of compositional turnover along habitat and geographical gradients (beta and gamma diversity, respectively) (Cody 1986; Cowling 1990). Subsequently, most research has concentrated on explaining patterns of regional richness in relation to geographical and topographical gradients (Linder 1991; Cowling *et al.* 1992, 1997a; Cowling & Lombard 2002). Research on the evolutionary aspects of diversity has emphasized models that focus on phylogenetic, biological and ecological correlates of diversification, especially key biological traits (*e.g.* sexual reproduction, pollinator specificity) that promote diversification (*e.g.* McDonald *et al.* 1995; Johnson 1996; Ojeda 1998; Wisheu *et al.* 2000), as well as the role of ecological diversification via habitat specialization (Linder & Vlok 1991; Cowling & Holmes 1992). The evolutionary perspective has been greatly strengthened by the recent appearance of phylogenies that provide molecular clock estimates of diversification patterns (Bakker *et al.* 1999; Reeves 2001; Goldblatt *et al.* 2002; Caujapé-Castells *et al.* 2002; Linder 2003).

It is not possible to review the outcomes of all of this research in a short paper such as this. Instead we focus on patterns of regional scale richness (*i.e.* inventory data from areas between one and several thousands km^2 in size), and seek to explain the evolution of these patterns in terms of ecological, biological and historical (past environments) phenomena. We conclude that patterns of regional scale diversity are likely to be largely the result of contemporary and Pleistocene climatic stability on elevating speciation rates and depressing extinction rates.

Background

In this section we provide some background on the physiography and floristics of the CFR in order to place the diversity patterns in an appropriate ecological, biogeographic and historical context. Readers are referred to the following reviews for additional information: vegetation ecology (Cowling *et al.* 1997b), diversity patterns (Cowling *et al.* 1997a), floristics (Goldblatt & Manning 2002), and evolution (Linder 2003).

We follow Cowling *et al.* (1992) and Cowling and Lombard (2002) in dividing the CFR into two geographical (western and eastern) and two topographical (lowland and montane) subregions (Fig. 1). As we describe below, these categories are associated with distinct climates and topographies, respectively, although edaphic factors vary continuously along the west-east gradient (Campbell 1983).

Landscapes and soils

The landscapes are dominated by the Cape Folded Belt, comprising a series of parallel ranges of quartzitic sandstone (south-north trending in the west and west-east trending in the south) of moderate altitude (1000-2000m) but steep relief (Deacon *et al.* 1992). These areas we define as montane (Fig. 1). The coastal plain and intermontane basins – mostly situated at altitudes <300m – are underlain by softer sediments (principally shales), although the coastal margin is almost everywhere man-
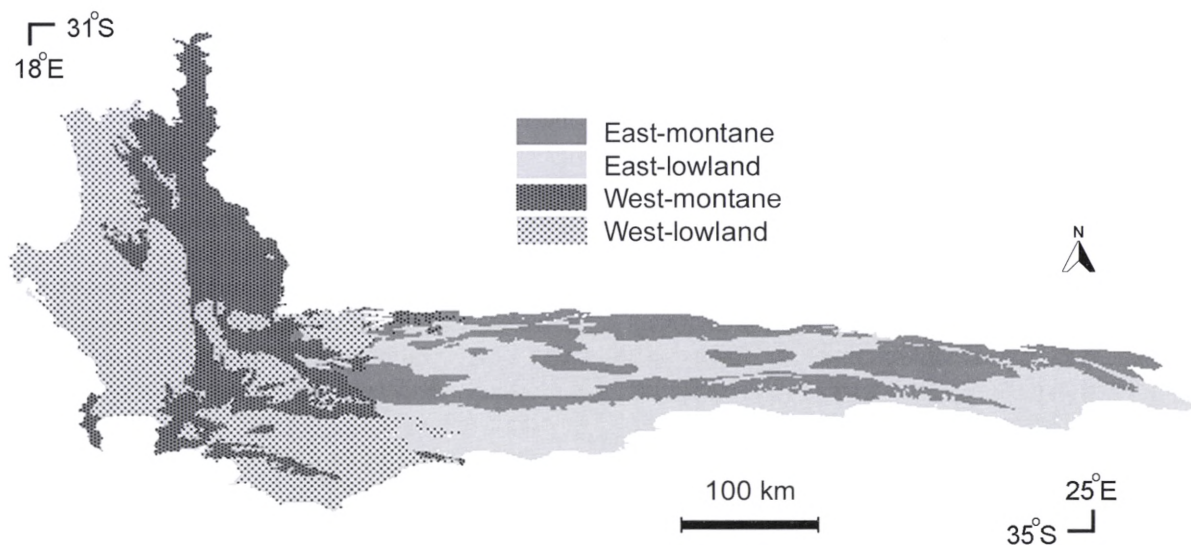
Fig. 1. The Cape Floristic Region showing the subregional classification used in this paper. Reproduced with permission from Cowling and Lombard (2002).

tled by calcareous marine sediments (aoelian sand and limestone). These areas we define as lowland.

While the sediments and orogeny associated with the Cape Folded Belt are very old (450-340 Myr and 280-215 Myr, respectively), the contemporary landscapes are much younger, and this has an important bearing on the evolution of plant diversity. Since Africa and South America began to separate about 140 Myr, there followed a period of relative tectonic stability in southern Africa that persisted until the early Miocene (Partridge 1997). In the region that is now the CFR, this long (African) cycle of erosion resulted in extensive planation; landscapes then were considerably less heterogeneous edaphically and topographically, than those of today.

This stability was interrupted in the early Miocene (20 Myr) by an uplift that was greatest in the eastern part of southern Africa where it approached 300 m (Partridge 1997). A second and much greater event – concentrated in the south-east – was initiated during the Pliocene,

probably between 3 Myr and 5 Myr. As a result of these tectonic events, the landscapes of the CFR were dissected as sediments were scoured from ancient the fault basins, hardpans of silcrete and ferricrete, which covered the gently sloping plains, were consumed, and softer sediments and deeply-weathered soils stripped from the mountains. However, owing to the eastern location of the epicentres of these two events, landscape dissection was greatest in the eastern CFR. Interestingly, there are no significant differences in topographical heterogeneity – measured as the ratio of the three-dimensional surface area of digital terrain model (100 m resolution) to planimetric surface area – between eastern and western landscapes, be they lowland or montane (P.G. Desmet & R.M. Cowling unpublished data).

The soils of the CFR are mostly sandy, infertile lithosols on the upper slopes of the mountains, with somewhat more fertile and deeper soils of colluvial origin on the foothills (Deacon *et al.* 1992). Lowland soils are mostly derived from shales and are moderately fertile

and relatively fine-grained. Sandy soils of marine origin, including those derived from Tertiary limestone, mantle the coastal margin. There is a gradient from west to east, of increasing soil fertility and texture across all sediment types in montane landscapes (Campbell 1983).

Climate

Most of the CFR receives an annual rainfall of between 300 mmyr^{-1} and 2000 mmyr^{-1}, although some montane sites in the west receive as much as 3000 mmyr^{-1} (Deacon *et al.* 1992). In the west, rainfall, which is associated with cold fronts budded off from the circumpolar westerly system, is concentrated in the winter months (*i.e.* mediterranean-type conditions prevail). In the east, rainfall is less seasonal; post-frontal events, especially the advection of moist air across a relatively warm Indian Ocean, produce rain throughout the year, but especially in the spring and autumn. Overall, orographic effects on rainfall are massive and the associated gradients are extremely steep (Deacon *et al.* 1992).

Surprisingly, the effect on diversity of the dramatically different rainfall seasonality regimes in the CFR has only been explored relatively recently (Cowling *et al.* 1992). However, of similar importance is the much less well-known pattern in the reliability of seasonal rainfall. Regarding the winter-rainfall component, which is essential for the reproductive and physiological processes of most of the CFR's plant life, amount and reliability is significantly greater in the west than the east; the opposite holds true for summer rainfall (unpublished data). We show later in this paper that these patterns have an important bearing on plant diversity patterns across the CFR (see also Cowling *et al.* 1997a).

On the lowlands, temperatures are generally mild: frost is rarely recorded and summer maxima seldom exceed 30°C, except in the interior

valleys. In montane landscapes temperature minima are more extreme than the adjacent lowlands: frost is widespread on upper peaks where snow may lie for several weeks in the winter months. Summer maxima seldom exceed 25°C.

Palaeoclimatic reconstruction in the CFR is hampered by a lack of suitable data, especially for the Tertiary. Linder (2003) provided the most recent summary of paleoclimates and associated vegetation. A picture emerges of mesothermic and humid climates throughout most of the Late Cretaceous and Tertiary, with relatively rapid cooling and drying in the terminal Pliocene (ca. 3 Myr), followed by the sawtooth cool-warm cycles of the Pleistocene. Fossil data, scanty as they are, suggest warm temperate to subtropical forest throughout the Tertiary, followed by the rapid emergence of elements typical of the contemporary Cape flora after Pliocene climatic deterioration (Linder *et al.* 1992). This somewhat simplistic scenario, which is consistent with patterns from other Mediterranean-climate regions (Deacon *et al.* 1992), needs to be tempered by considering at least the following four points. (1) There are no fossil data from the Oligocene, a period of pronounced cooling and drying (Willis & McElwain 2002) that must have profoundly influenced plant diversity and evolution in southwestern Africa (Goldblatt & Manning 2002; Linder 2003). (2) The difference in Pleistocene climates between the east and the west, which has only recently been emphasized (Cowling *et al.* 1999), must have had an important impact on the evolution of diversity in these two geographic subregions (Cowling & Lombard 2002). Available palaeodata suggest that glacial climates were somewhat moister than present in the west and drier than present in the east. Furthermore, moist conditions capable of supporting Cape floral elements appear to have extended deep into the present succulent karoo and Namib Desert environ-

ments along southern Africa's west coast during glacial times (Linder 2003). In contrast, the Cape flora was probably quite restricted in extent during glacial conditions in the east (Cowling *et al.* 1999), although more data are required to test this assertion. (3) Owing possibly to its peninsula-like configuration within an extensive area of ocean, glacial temperature regimes in southwestern Africa were amongst the mildest of all continental land masses (Markgraf *et al.* 1995). (4) As a consequence of (2) and (3), Pleistocene climates in the western CFR were probably unusually stable, at least for mid-latitude regions across the globe.

Flora and vegetation

The CFR is an extraordinarily diverse biogeographical region comprising a mere 90,000 km^2. The flora, which is relatively well known compared to other species-rich regions in the developing world, comprises about 9000 vascular plant species, 69% of which are endemic (Goldblatt & Manning 2002). The flora includes five endemic plant families and 160 endemic genera. A spectacular feature of the flora is the massive diversification of some genera: 13 of them have more than 100 species (*Erica* has 658 spp.). Other distinctive features include the large number of geophytes (1552 spp.), especially among the petaloid monocots, and the relative paucity of annuals (6.8% of the flora) and trees (2.4%).

Vegetation patterns are relatively well understood and documented (Cowling *et al.* 1997b; Cowling & Heijnis 2001). The predominant vegetation types are fynbos and renosterveld, while subtropical thicket, forest and succulent karoo occupy much smaller areas. Fynbos, which harbours about 70% of the CFR's plant species, is a hard-leaved, evergreen and fire-prone shrubland characterized by four major plant types: restioids (Restionaceae), ericoids, proteoids (tall shrubs in the Proteaceae) and geophytes (Cowling *et al.* 1997b). Seedling and

ramet recruitment are largely confined to the immediate post-fire period. Fynbos thrives on rocky, nutrient-poor soils of the sandstone mountains, on leached, wind-blown sands of the coastal forelands, and on the nutritionally imbalanced coastal dune and limestone sands of the coastal margin.

Unlike fynbos, renosterveld lacks restiods, and proteoids are very rare (Cowling *et al.* 1997b). This vegetation type, also fire-prone, comprises a low shrub layer (1-2 m tall) of mainly ericoids, usually dominated by the renosterbos (*Elytropappus rhinocerotis*, Asteraceae), with a ground layer of grasses and seasonally active geophytes. Renosterveld always grows on the fine-grained, shale-derived soils of the coastal plain and inland valleys where the annual rainfall is between 250 mm and 650 mm. At rainfalls higher and lower than this, it is replaced by fynbos and succulent karoo, respectively.

Subtropical thicket and forest, which are most extensive in the eastern lowlands, are dominated by shrubs and trees of palaeotropical affinity, although species of Gondwanan, Cape and Karoo-Namib affinity are often locally dominant (Cowling 1983b). These formations are not fire-prone and regeneration from ramets and vertebrate-dispersed propagules is not linked to disturbance. In comparison with the other formations in the CFR, thicket and forest are poor in species and endemics (Cowling 1983b). However, the warm-temperate forests of southern Africa (including those in the CFR) are the richest temperate forests in the world at both the species and genus levels (Silander 2001). Moreover, when assessed in terms of its overall distribution in southern Africa, subtropical thicket has very high levels of diversity and endemism (Vlok *et al.* 2003).

Succulent karoo occupies a small part of an interior basin (Little Karoo) in the eastern CFR. This is a dwarf, succulent shrubland,

dominated by Aizoaceae, Asteraceae and Crassulaceae (Milton *et al.* 1997). Diversity at all scales is extremely high (Cowling *et al.* 1998). Owing to its limited occurrence in the CFR, diversity in succulent karoo is not discussed further in this paper.

Patterns and explanations of diversity

Patterns

It has long been known that the richness of species belonging to Cape clades (sensu Linder 2003) peaks in the mountains of the southwestern CFR, and diminishes rapidly eastwards and more gradually northwards, and is generally higher in montane than lowland subregions (Weimark 1941; Levyns 1964; Oliver *et al.* 1983). However, this pattern does not hold for all lineages represented in the Cape flora. For example, *Euryops* (Asteraceae), in addition to the southwestern peak, shows a pronounced peak in the extreme east (Nordenstam 1969). For many thicket and forest genera, species richness declines from east to west. Given these contrasting patterns, it is reasonable to ask: what are the overall patterns of richness at the regional scale? How do these vary along geographical and topographical gradients? Can these patterns be explained by variation in the contemporary environment? What evolutionary processes produced these patterns? We attempt to provide answers to these questions in this paper.

Using species-area analysis of regional-scale data sets (Fig. 2a), and analysis of covariance, Cowling and Lombard (2002) (see also Cowling *et al.* 1992) showed a clear geographic diversity pattern (Fig. 2b): the intercept of the regression for western sites was significantly higher than that for the eastern ones, and the ratio of the intercepts for these two data sets was 2.11, indicating that western sites have slightly more than double the number of species than eastern sites. The topographic pattern was non-significant (Fig. 2c). However,
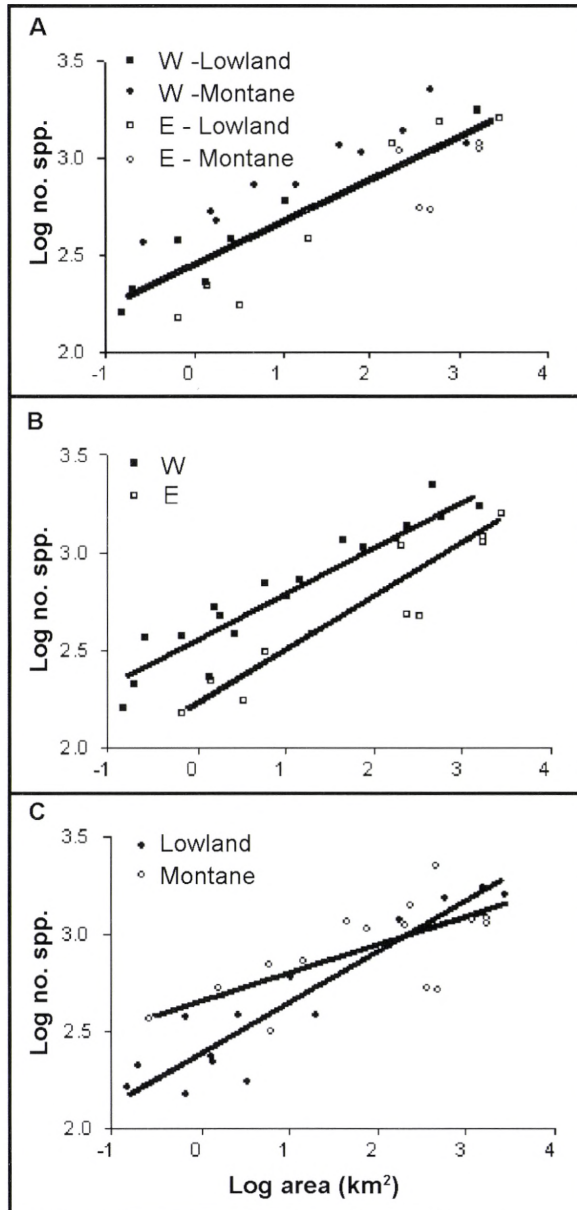
Fig. 2. Plant species-area curves for a) combined data from all subregions in the Cape Floristic Region, b) eastern (E) and western (W) subregions (geography effect), and c) lowland and montane subregions (topography effect). Redrawn from Cowling and Lombard (2002).

there was a weakly significant interaction between geography and topography, a result of the fact that while western montane sites were about 1.5 times richer than corresponding lowland sites (see also Linder 1991), there was no difference between the richness of lowland and montane sites in the east. (West-montane sites were 2.5 times richer than montane sites in the east, while lowland sites in the west were about 1.8 times richer than corresponding sites in the east.

Explanations

What explains these patterns? We can think of at least three groups of explanations: (1) differences in the contemporary environment, (2) differences in other components of diversity (local richness and turnover), and (3) differences in speciation and extinction histories. We discuss each of these below.
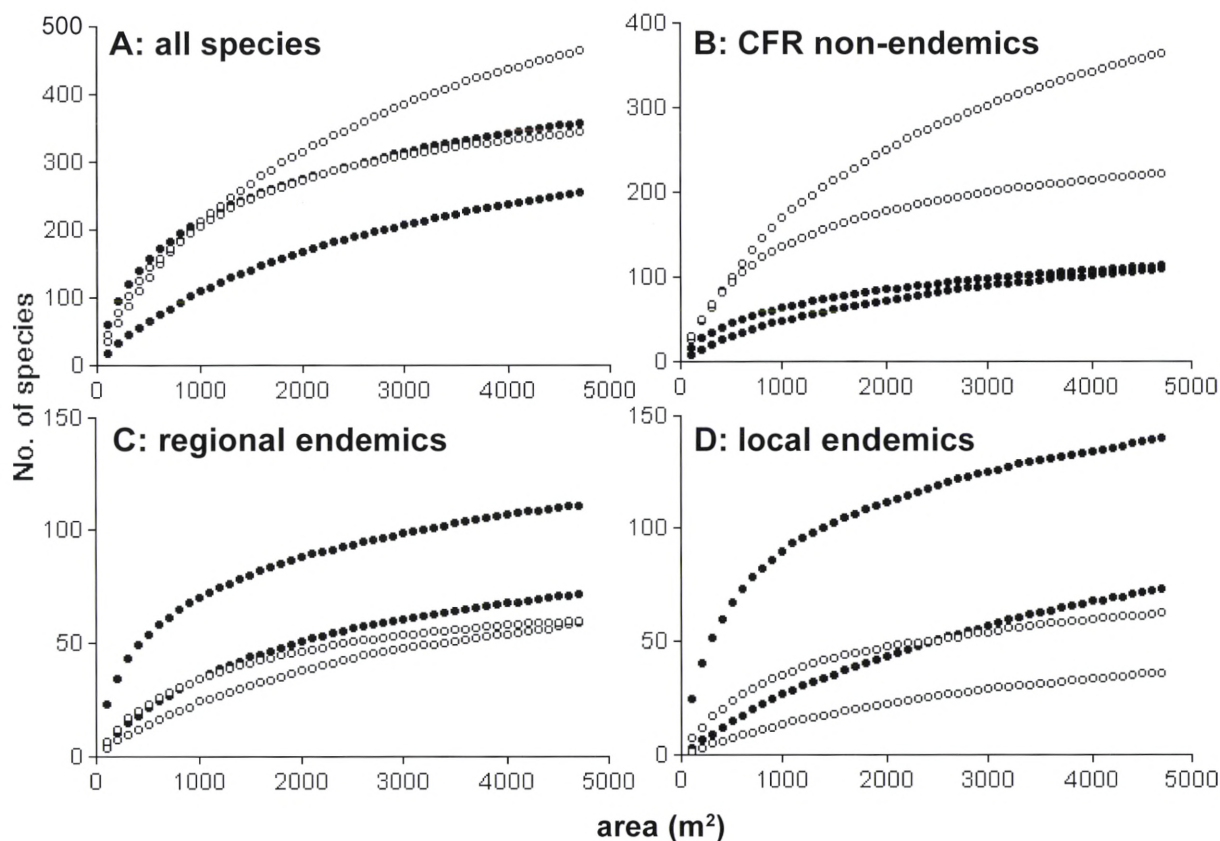
Fig. 3. Species-area curves for two localities in the eastern Cape Floristic Region (CFR) (Baviaanskloof and Humansdorp, open symbols) and two in the western CFR (Cape Point and Cedarberg, closed symbols). A) Includes all species; B) includes only those not endemic to the CFR; C) includes only those endemic to the CFR but present in both the eastern and western subregions; and D) includes CFR endemics that are restricted to either the western or the eastern subregion. The curves are based on relevé data (Proches *et al.* 2003), the area being plot size multiplied by the number of pooled plots.

Differences in the contemporary environment
Cowling *et al.* (1997a) used multiple regression to assess environmental determinants of regional-scale diversity, *i.e.* inventory data from areas between one and several thousands km² in size. In addition to area, only rainfall reliability and topographical heterogeneity, emerged as significant predictors. The variables used comprised three measures of environmental heterogeneity, three measures of favourableness, three measures of available energy, two measures of seasonality, and one measure of irregularity (rainfall reliability). Clearly, rainfall reliability contributes to explaining the west-east geography effect while the emergence of topographic heterogeneity is consistent with the topography effect in the west (Linder 1991).

However, the measure of topographical heterogeneity used by Cowling *et al.* (1997a) – being based on contours of 100 m – is very crude, as are the other region-wide measures of heterogeneity used in their analyses. These measures are certainly not representative of the scale of species packing in Cape vegetation. For this reason, Cowling and Lombard (2002) used community diversity, defined as the actual number of phytosociologically circumscribed communities within study areas of 1-1200 km² of an area, as a surrogate for its biologically meaningful heterogeneity or habitat diversity (Rosenzweig 1997). They compiled 34 data sets, distributed across all subregions, that had adopted the Zürich-Montpellier approach to phytosociological survey and analysis, and sampled, in relevés of 50 m² or 100 m², the full range of community-level variation in their respective study areas. After establishing that the number of phytosociologically defined communities in an area was significantly related to size of the study area and number of relevés sampled, Cowling and Lombard (2002) used analysis of covariance to test for geography and topography effects on community

diversity. No significant relationships were found. They concluded that biological heterogeneity showed no significant variation across the CFR and, therefore, could not explain the geography or topography effects on regional richness.

In conclusion, the only environmental variable that contributes significantly to explaining regional richness in the CFR is rainfall reliability: western areas that receive predictable winter rains are richer in species than eastern areas that receive less predictable non-seasonal rainfall.

Differences in other components of diversity
Regional richness is a product of local richness (or alpha diversity) and turnover along habitat gradients (beta diversity) and geographic gradients (gamma diversity) (Whittaker 1972; Cody 1986). Perhaps variation in these components of diversity can explain the regional patterns observed in the CFR? Not so for alpha diversity: there are no consistent patterns across the region at either the 1m² or 0.1 ha scales (Cowling *et al.* 1992). Using Wilson and Shmida's (1984) turnover measure, Cowling *et al.* (1992) showed that beta diversity was 1.7 times higher, and gamma diversity 2.2 times higher in a western lowland than a physiographically similar eastern lowland area. Substituting values for all three diversity components in a simple formula to predict regional richness, they showed that a hypothetical western area would support about 1.6 times as many species as a similar sized eastern one. This figure is very close to the value of 1.8 identified in the species-area analysis for lowland regions of Cowling and Lombard (2002).

Higher turnover along environmental and geographical gradients should be reflected in a higher incidence of range-restricted rares (Cody 1986). Therefore, it is reasonable to predict that there would be a positive relationship between regional richness and the incidence of
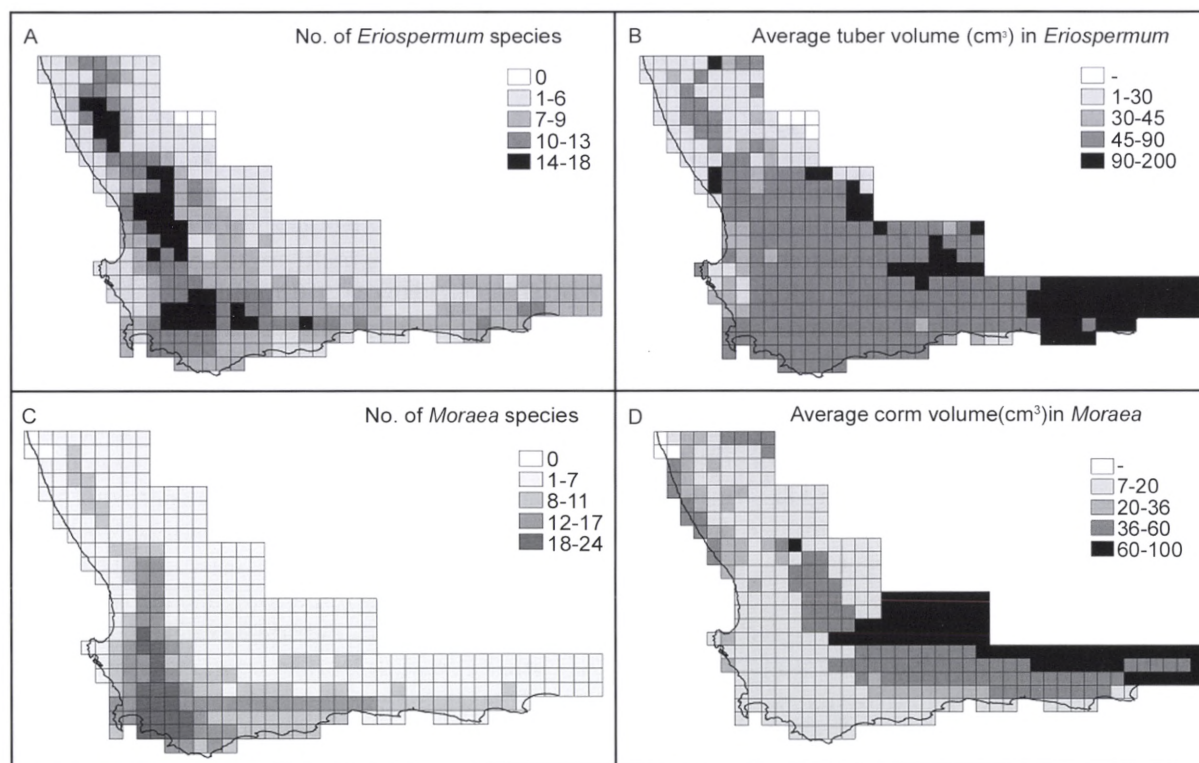
Fig. 4. Species diversity (A and C) and storage organ size (B and D) patterns for two genera of geophytes: *Eriospermum* (Convallariaceae) (A and B) and *Moraea* (Iridaceae) (C and D). Storage organ size is the average size for all the species with ranges intersecting a quarter degree square (data from Procheş *et al.* 2005).

naturally rare species. Cowling and Lombard (2002) tested this prediction by analysing the abundance in quarter degree squares (QDS – approx. 66 km^2) of 1,034 naturally rare taxa (*i.e.* Red Data Book taxa excluding those whose rarity status is due to anthropogenic factors) in relation to categories of topography and geography. They found that diversity patterns of rare species mirrored exactly the diversity patterns at the regional scale: on average, there was double the number of rare plants per QDS in the western, as compared to the eastern subregions, and lowland QDS had significantly fewer rare plants than montane ones, although this topographic pattern was evident only in the western subregion where the incidence of

rare plants was 1.5 times higher in montane than lowland QDS.

Further support for the hypothesis that regional diversity patterns in the CFR are paralleled by rarity patterns, comes from an analysis of species-area relations using phytosociological relevés of between 25 m^2 and 100 m^2 in size, sampled in study areas across the CFR (Procheş *et al.* 2003.). Simulated species-area curves (using EstimateS; Colwell 2001), based on the relevé data, did not show any consistent differences between western and eastern subregions when all species were included in the analysis (Fig. 3a). Thus, at the scale of about 5-20 ha, comprising the cumulative area of relevés sampled to capture vegetation patterns

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in relatively large (70-1500 km^2) areas, the east is no poorer than the west. Proches et al. (2003) suggested that this is because eastern landscapes include larger areas and higher diversity of non-Cape vegetation and, therefore, harbour a large number of "pseudorares", i.e. species seldom sampled in the study area but that are actually widespread outside of the CFR (Fig. 3b). However, when the analysis was restricted to CFR endemics (Fig. 3c) and regional endemics (Fig. 3d), the two western sites were significantly richer than the two eastern ones. This, argue Proches et al. (2003), results from the higher number of rare species (i.e. species encountered in one to few relevés) in the west, among those species restricted to the CFR or subregions thereof.

In conclusion, we suggest that variation in regional-scale richness across the CFR appears to be a consequence of differences in the richness of CFR endemics that are locally rare. This conclusion is supported by analyses across a range of spatial scales. Thus, in species-rich western, montane landscapes one would expect to find a greater number of plants restricted to spatial scales ranging from a few ha to the entire subregion, than in the species-poorer parts of the CFR.

Differences in speciation and extinction histories
A third explanation for the diversity patterns, and one that addresses the root causes of these patterns, is that they are a consequence of differences in speciation and extinction histories across the CFR.

Do the patterns in the diversity of rare species tell us anything about differences in speciation and extinction histories across the CFR? Assuming that rarity is associated with the early (post-speciation) and late (pre-extinction) phases of the lifespan of a taxon (Rosenzweig & Lomolino 1997), it is reasonable to assume that areas with a high incidence of rare

species (e.g. in the western montane subregion) have experienced higher rates of speciation and/or lower rates of extinction, than areas with fewer rare species.

Based on a biological profile of rare species in the CFR, Cowling and Lombard (2002, see also Cowling et al. 1992) developed a speciation model that invoked post-fire regeneration mode, gene dispersal and rainfall reliability. Many studies have shown that rare species are not a random subset of the flora of a region. They are significantly associated with a limited number of plant lineages, most of which are Cape clades (sensu Linder 2003) (e.g. Erica, Rutaceae: Diosmoideae, Leucadendron). Non-sprouting (post-fire) and limited gene dispersal (associated with short seed dispersal distance and insect pollination) are traits that are over-represented among them (Cowling & Holmes 1992; McDonald et al. 1995; Trinder-Smith et al. 1996). These biological traits, especially non-sprouting, have favoured increased speciation rates and lower extinction rates. Thus, fire-induced plant mortality increases generation turnover and produces discrete generations, thereby providing potential for more rapid evolution than sprouters (Wisheu et al. 2000). The higher allocation of resources by non-sprouters to reproduction (Bond & Midgley 2001) increases their numeric dominance locally, and lowers extinction rates (Wisheu et al. 2000). Limited gene dispersal promotes isolation and hence speciation of daughter populations in marginal or unusual habitats: most rare species are habitat specialists (Cowling & Holmes 1992; Trinder-Smith et al. 1996).

Predictable winter rainfall will favour non-sprouting species since the survival of germinants would be enhanced by reliable rain after the summer fire season. Furthermore, non-seasonal rainfall may favour sprouters – at least in small-seeded taxa – since rainfall distributed throughout the year would facilitate the sur-

vival of their seedlings that need to allocate large amounts of resources to below-ground storage organs (Ojeda 1998). The higher incidence of sprouters in the eastern subregion (Schutte *et al.* 1995; Ojeda 1998) may have negatively influenced the potential for speciation, owing to lower seedling production (Bond & Midgley 2001), overlapping generations and longer generation times (Wisheu *et al.* 2000). As a result of these differences in climate, and their influence on the success of different post-fire regeneration biologies, speciation rates may have been higher, and extinction rates lower, in the west than the east.

A preliminary analysis of recent molecular phylogenies for woody taxa in the CFR and the environmental similar SW Australia seems to support the hypothesis that non-sprouting leads to greater diversification than sprouting in the genus *Protea* (Cape) and, to a lesser extent, in the genus *Banksia* (Proteaceae) (SW Australia), but not in *Cliffortia* (Rosaceae), another large genus of the Cape flora (Bond & Midgley 2003). While there is some evidence that non-sprouting clades are more speciose than sprouting ones, sprouting has evolved many times and is associated in some cases with rapid evolutionary divergence. Reeves (2001) suggests that the apparently higher rates of diversification among non-sprouting versus sprouting clades in Cape *Protea* spp. might be consequence of high extinction rates of resprouters. This is not the case in SW Australian *Banksia* (Proteaceae) where sprouters are well represented in many clades, including speciose ones (Bond & Midgley 2003). Clearly more research is required on the relationships between regeneration mode, generation time and speciation rates.

This generation time hypothesis is unlikely to explain geophyte diversity patterns since all these species sprout after fire from underground storage organs. Geophytes, which comprise about 17% of the Cape flora, have diversi-

fied in several clades, especially Iridaceae, Hyacinthaceae, Amaryllidaceae, Asphodelaceae and Convallariaceae among monocots, but also Geraniaceae and Oxalidaceae in the eudicots (Goldblatt & Manning 2002). Like many other Cape taxa, geophytes show a pronounced concentration of species in the western montane subregion (Figs 4a & c). Procheş *et al.* (2005) recorded a negative correlation between average storage organ size and species diversity of certain geophyte taxa at the QDS scale (Figs 4b & d). They suggest that these patterns are a consequence of patterns of winter rainfall amounts and their reliability, both of these measures peaking in the southwestern Cape. Predictable and ample winter rains would require less allocation of resources to persistence, making large organs unnecessary. It remains to be demonstrated whether there is a relationship between storage organ size, generation time, and population size, and whether any of these factors have a bearing on speciation and extinction rates.

Pollinator specificity is widespread among certain geophytic taxa and many have argued that specialization to a single pollinator is the driving force in the evolution of this (*e.g.* Johnson *et al.* 1998; Goldblatt & Manning 2000) and other plant guilds (Johnson 1996). It appears, however, that for some geophytic taxa, habitat specialization is the major selective force and that pollinator specificity is of secondary importance in speciation (Goldblatt & Manning 1996). Also, it is intriguing that the diversity of particular specialization syndromes is overwhelmingly concentrated in the western subregion; eastern members of particular genera are often pollinated by a wide range of species, even though the pollinator associated with the syndrome may occur there (*e.g.* for *Lapeirousia*: Iridaceae, Goldblatt *et al.* 1995).

Finally, we consider another hypothesis – historical rather than biological – that invokes differential speciation and extinction rates to

explain regional-scale diversity patterns. While less parsimonious than the biological hypothesis, this historical explanation is nonetheless complementary rather than alternative to the one based on the contemporary selective regime. The hypothesis states that the geographic pattern of diversity results from differences in Pleistocene climatic conditions and associated differences in the extent of Cape vegetation (Cowling *et al.* 1992, 1999). In the west, fynbos and allied shrublands were not disrupted during wetter glacial periods; in the east, however, drier glacial conditions (Deacon & Lancaster 1988; Parkington *et al.* 2000; Linder 2003) probably restricted Cape vegetation to mesic refugia (Cowling *et al.* 1999). Not only could this have caused the extinction of many species, it may also have disrupted speciation (Dynesius & Jansson 2000).

We know little about rainfall reliability during glacial times in the CFR. However, given that conditions were drier in the east than the west, it is reasonable to assume that rainfall reliability was lower there. It appears, therefore, that stability not only of the contemporary environment, but also of Pleistocene conditions, could be very important for understanding differential patterns of diversification and diversity in the CFR. There is evidence to support a climate stability-diversity hypothesis from other species – and endemic-rich parts of the world (*e.g.* Fjeldså *et al.* 1997).

On the evolution of plant diversity in the CFR

The speciation model that we have presented is essentially an ecological one in which a subset of clades has radiated – sometimes massively – by subdividing ecological space, often edaphic, but also climatic (Rourke 1972; Linder 1985; Linder & Vlok 1991; Cowling & Holmes 1992; Goldblatt & Manning 1996; Linder & Hardy in press). Until recently, the general consensus was that this ecological radiation was initiated in the late Miocene-Pliocene, concomitant with the development of mediterranean-climate conditions (Linder *et al.* 1992). However, not all lineages have biogeographies that are consistent with ecological diversification; indeed, many patterns are suggestive of geographic speciation (Goldblatt 1978) that may have predated the Mio-Pliocene radiation.

Fortunately a number of molecular phylogenies have been produced in the past few years and these enable an assessment of the timing of radiation of the Cape flora (see Linder 2003 for an overview). Thus far, the molecular clock estimates suggest relatively recent (late Miocene) radiation for the shrubby, ant-dispersed genus *Phylica* (Rhamnaceae) (Richardson *et al.* 2001), the geophytic sect. *Hoarea* of *Pelargonium* (Geraniaceae) (Bakker *et al.* 1999), the grass genus *Ehrharta* (Verboom 2000), and the geophytic genus *Moraea* (Iridaceae) (Goldblatt *et al.* 2002). This diversification would have coincided with the onset of cooler and summer-dry climates (at least in the west), and the development of greater topographic and edaphic diversity in response to Late Tertiary uplift. However, other lineages appear to have diversified in the mid to early Miocene, namely the *Gladiolus-Watsonia* clade of the geophytic Iridaceae (Reeves *et al.* 2001), and the Restionaceae (Linder 2003). Putative climates at this time were moist and warm, with widespread evidence of rainforest vegetation (Linder *et al.* 1992; Willis & McElwain 2002), at least on the lowlands where fossil sites are located (Linder 2003). The Antarctic ice-sheet began expanding in the mid Miocene, and this was accompanied by a cooling and drying of the climate of south-western Africa (Deacon *et al.* 1992). Other lineages appear to have radiated in the Oligocene, namely the shrub genus *Protea* (Proteaceae) (Reeves 2001) and the geo-

phytic *Androcymbium* (Colchicaceae) (Caujapé-Castells *et al.* 2002). Climatic conditions during the Oligocene were probably similar to those at present (Linder 2003) but the scenery of the CFR was considerably more subdued than now, having endured 100 million years of planation (Partridge 1997).

For many groups, ecological factors, especially soil characteristics, played an important role in diversification (Verboom 2000; Caujapé-Castells *et al.* 2002; see also Rourke 1972; Goldblatt 1979; Linder & Vlok 1991; Goldblatt & Manning 1996). For both *Disa* sect. *Herschelia* (Orchidaceae) (Linder 1995) and *Thamnochortus* (Restionaceae) (Linder & Hardy in press), basal species grow in mesic montane habitats while younger species are found in the lowlands. In the case of *Thamnochortus*, the most recently evolved species grow on substrata of marine origin that would only have been exposed after Pliocene regression (Deacon *et al.* 1992), and on upper mountain slopes where skeletal and highly infertile soils overlie quartzitic sandstone. The latter surface may only have become exposed after uplift and associated erosion in the early to mid Pliocene. However, while ecological factors have played an important role in the diversification of some lowland clades of *Protea*, most speciation in this genus has been geographic (Reeves 2001).

The evolution of thicket and forest lineages in the CFR has received little attention. In two recent reviews (Goldblatt & Manning 2002; Linder 2003), mention is made of monotypic and presumably phylogenetically basal elements that possibly represent extant components of ancient thicket and forest formations. These include Anacardiaceae (*Harpephyllum, Heeria, Loxostylis, Laurophyllis*), Celastraceae (*Empleuridium, Gloveria, Maurocenia, Mystroxylon*), Cornaceae (*Curtisia*), Cunoniaceae (*Platylophus*), Euphorbiaceae (*Lachnostylis*), Flacourtiaceae (*Kiggelaria, Pseudoscolopia*), Picrodendraceae (*Hyenanche*), Santalaceae (*Rhoiacar-pos*), Sapindaceae (*Hippobromus, Pappea, Smellophyllum*), and Rutaceae (*Calodenrum*). Furthermore, the thickets of southern Africa, much of which fall in the eastern CFR, are a global centre of diversity and endemism for numerous genera, including *Rhus, Ozoroa* (Anacardiaceae), *Cussonia* (Araliaceae), *Cassine, Gymnosporia, Pterocelastrus, Putterlickia, Robsodendron* (Celastraceae), *Rhoicissus* (Vitaceae), *Schotia* (Fabaceae) and *Encephalartos* (Zamiaceae). We have no idea when and how these lineages diversified. Distribution patterns suggest that geographic factors were important in speciation. It has been suggested that these thickets are extremely ancient and include many elements basal to the Cape and succulent karoo floras (Vlok *et al.* 2003). The same may be true of wet forests. Thus, *Schotia* (Fabaceae), from Cape thickets, is sister to old lineages well represented in the rainforests of Madagascar and Central Africa (Schrire *et al.* 2005).

Conclusions

We draw five conclusions from this overview. Those dealing with patterns and explanations of diversity are relatively well supported, while those dealing with the evolution of diversity are very tentative. Clearly, there is an urgent need for better fossil data, many more reliably dated phylogenies spanning the full array of lineages in the Cape flora, a better integration of ecological and phylogenetic data, and a better understanding of the implications of landscape evolution for speciation. We conclude as follows:

1. Contemporary patterns of plant diversity in the CFR are reasonably well quantified and described across a broad range of spatial scales.

2. Diversity at the regional scale is largely a consequence of rarity associated with a limited number of lineages and biological traits.

3. This pattern can be explained by a biological-climate and a historical hypothesis that predict patterns of rare plant diversity as a consequence of differential speciation and extinction rates.

4. Most of these rare species have evolved relatively recently, after climatic deterioration in the Mio-Pliocene. Owing to greater climatic stability in the west, rates of speciation have been higher, and rates of extinction lower than in the east.

5. The Cape flora also comprises elements associated with earlier diversification events. Many lineages may have started radiating in the Oligocene, when climates were similar to those of today. Others, especially thicket and forest taxa, may have an even earlier origin. Finding this out is will make an interesting research project.

Acknowledgements

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