Review TRENDS in Plant Science Vol.10 No.11 November 2005

Evolution of diversity: the Cape flora

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Although the environmental correlates of plant species richness have long received attention, research into the genesis of this diversity is in its infancy. The recent development of molecular dating methods and the inference of robust phylogenetic hypotheses have made it possible to investigate this problem. I use the Cape flora as a model to show that much modern diversity could be the result of recruiting diverse lineages over the entire Cenozoic into this flora, followed by *in situ* diversification (thus increasing species richness) of at least some of these lineages over a long period in an environmentally heterogeneous area.

Cape flora

The global distribution of plant diversity and endemism is uneven, with concentrations of species in the Andes, the Atlantic coastal forests of Brazil, the southern tip of Africa, the East Indies and the eastern Himalayas [1]. Species richness has been correlated, among other things, with palaeoclimatic stability [2] and the combination of energy levels and water availability [3], which are all variously correlated with the latitudinal gradient [4]. However, only with the development of robust phylogenetic and molecular dating methods in the past five years has it become possible to address the evolutionary genesis of this diversity. Species diversity is, in many floras, the result of a few species-rich lineages, whereas most other lineages include only a few species [5]. The central question is when, and why, the evolution of these species-flocks started.

Understanding the genesis of plant diversity is important for long-term conservation planning: only by knowing the evolutionary responses of plants to past environmental changes can the consequences of future changes be predicted. Conservation planning should incorporate models of the past diversification of the local floras [6–8].

The flora of the Cape Floristic Region, which comprises ~9000 species in an area of 90 000 km^2, has a species richness comparable to neotropical floras [9,10] and is substantially richer than the other Mediterranean-type ecosystems (e.g. Western Australia, Chile, California and the Mediterranean basin) [11]. The Cape flora can readily be defined by an unusual combination of families: the Proteaceae, Restionaceae, Ericaceae and Aizoaceae are among the most diverse and are also the ecologically dominant families (Figure 1). Furthermore, 67% of the species are endemic to this region [9]. This high level of endemism, the presence of distinctive Cape floral clades [12] and a large variation in the richness of the clades, makes this a suitable flora to use as a model system for an investigation into the genesis of plant diversity.

Assembly of the flora

For many years, the Cape flora was thought to be composed of three components. The 'Antarctic' or Gondwanan component was postulated to be a relict of the Cretaceous Gondwanan flora [13]; possible elements are the gymnosperms *Podocarpus* and *Widdringtonia*, as well as Proteaceae and Restionaceae [9]. The African component, which makes up the bulk of the Cape flora, was shared with tropical Africa, leading to the interpretation of the Cape flora as a specialized African flora [14]. The Eurasian component might have migrated relatively recently southwards along the African mountains from Eurasia [15]. This vicariance view (which seeks to understand biogeography as the result of fragmentation of older distribution ranges [16]) sees the Cape flora as composed predominantly of fragments of two once more widespread floras: a Cretaceous Gondwanan flora and a Tertiary African flora.

However, phylogenetic analyses (Box 1) in the past decade have revealed a much more complex picture. There are several post-Gondwanan intercontinental relationships: for example, *Prionium* with its sister *Thurnia* in South America [17], and *Pelargonium* with the *Peristera* section in Australia [18]. A recent, detailed inventory of the affinities of the Cape flora showed that it contains lineages with closest relatives on all continents but that the most common relationships lie with the Australian flora [19]. The earliest recruitment of an angiosperm lineage into the Cape flora has been dated to the Cretaceous. Since then there has been a regular incorporation of ever more lineages into this flora [19], with migration into the flora not blocked by the opening of the southern oceans. Oceans and geographical distance limit migration in plants (as is evident from the problems with invasive plants transported by humans across diverse barriers) but do not present absolute barriers.

Similar shifts in interpretation have occurred for other floras. In the past, the flora of New Zealand [16] and Australia [20] were interpreted as fragments of the eastern Gondwanan flora, which included South America, Antarctica, New Zealand and Australia. The flora of South America was seen as a mixture of the southern Gondwanan flora and a northern tropical flora [21], itself a fragment of the South American–African–Indian (West Gondwanan) tropical flora [22]. However, more recent

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Figure 1. Selected species of typical Cape floral families: **(a)** *Conophytum speciosus* (Aizoaceae), **(b)** *Phylica plumigera* (Rhamnaceae), **(c)** *Erica glauca* (Ericaceae), **(d)** *Tritoniopsis triticea* (Iridaceae), **(e)** *Mimetes arborea* (Proteaceae), **(f)** *Restio strobilifer* (Restionaceae), **(g)** *Heliophila* sp. (Brassicaceae).

research on the flora of New Zealand suggests that much of the flora was assembled by long-distance dispersal [23] and that most plant lineages arrived in New Zealand during the Neogene, mostly from Australia. A surprising number of lineages in the Australian flora have been recruited from across the oceans [24]. Similarly, the South American flora had received immigrants throughout the Cenozoic from Africa, Laurasia and Australia by long-distance dispersal and stepping-stone dispersal; these immigrants make up more than 10% of the lowland tropical rainforest flora [25].

The Cape flora is thus not unusual in its ability to recruit lineages from all continents. Consequently, it can be confusing to refer to it as a Gondwanan or an African flora. However, individual clades can still be associated with an area where the clade initially or primarily diversified. Proteaceae or Restionaceae could still be referred to as ‘Gondwanan’ without implying that the flora in which they are found is Gondwanan. So we can also recognize Cape floral clades (e.g. the African Restionaceae and the tribe Proteae); these are indeed widespread on many tropical African mountains [26–28] and also in Australia [18] and New Zealand. This reflects a more dynamic biogeographical worldview that does not assign whole floras to categories but rather seeks to understand the evolutionary history of each of its constituent clades.

Age of the modern species flocks

Half of the species richness of the Cape flora can be traced to 30 radiations [12]. This is similar to the Hawaiian flora, where half of the richness is derived from 20 radiations [29], and the Australian flora, where the 10 largest families comprise 50% of the plant species of Australia [30]. With the advent of molecular dating methods it has become possible to estimate the start of each of these radiations. The first published study, which was on the Rhamnaceae genus *Phylica*, indicated a Late Miocene initiation date [31]. However, the investigation of additional Cape lineages returned mostly older dates: *Pelargonium* [32] and *Indigofera* [33] date from the middle Miocene; Irideae, Ixioideae and Nivenioideae (Iridaceae) from Oligocene or early Miocene [34]; and the African Restionaceae radiation was probably initiated in the Oligocene [35]. At the other extreme, the analysis of *Heliophila* suggested an initiation of the radiation in the Pliocene [36]. This implies that some lineages in the Cape flora have been accumulating species over the past 35 million years (My), whereas others started this process much more recently.

The radiation of Australian Restionaceae started substantially earlier (in the Eocene) than that of the African Restionaceae [37]. Eocene to early Oligocene dates were also obtained for the initiation of the radiations of the Australian *Eucalyptus*, *Casuarinaceae* and the *Banksia–Dryandra* group, whereas the radiation of Mirbelieae and Bossiaeeae is somewhat later, in the early Miocene [24]. This suggests that the Australian radiations are even older than the Cape radiations.

Although the radiations in southern Africa might have started in the Early Miocene or earlier, most modern species are much more recent and have evolved during the Pliocene–Pleistocene [34,35], most likely in modern climatic conditions (Figure 2). However, few clades have been sampled adequately to give an insight into the age of the species.

What triggered the radiations?

In the Cape flora, taxonomically isolated species, or species-poor clades, are mostly restricted to forests and along permanent streams (e.g. *Platylophus, Prionium* and *Brabejum*) and to fire-protected habitats (e.g. *Heeria* and *Hyenanche*) [9]. These clades are largely absent from open, regularly burnt, heathy vegetation or open succulent semi-desert habitats dominated by species belonging to the large species-radiations. This indicates that the modern species-rich clades had radiated into these summer-arid habitats when they became established in the Late Miocene, whereas the other groups represent relicts of an earlier flora [12]. In southern Africa, there is an east–west gradient in the severity of the summer drought; for several groups, the greatest diversity, and apparently the most recent radiations, are situated in the more arid west [32,34]. There are no large recent radiations in the more mesic east. This led to the prediction that the earliest species to diverge in each radiation should be found in mesic habitats, which has been confirmed for *Ehrharta* [38] and *Thamnochortus* [39]. For Restionaceae, the combination of anatomical and phylogenetic information also indicates that xerophytic adaptations evolved relatively late in the family [40].

This pattern is also seen in Australia, with the major radiations of *Acacia*, *Eucalyptus* and *Banksia* into the fire-prone seasonally arid environments and the all-year mesic fire-protected habitats occupied by a relictual flora dominated by *Nothofagus*. The Australian fossil record is extensive: the transformation of a mesic *Nothofagus* forest into a fire-prone *Eucalyptus* woodland during the Miocene is well documented [41,42].

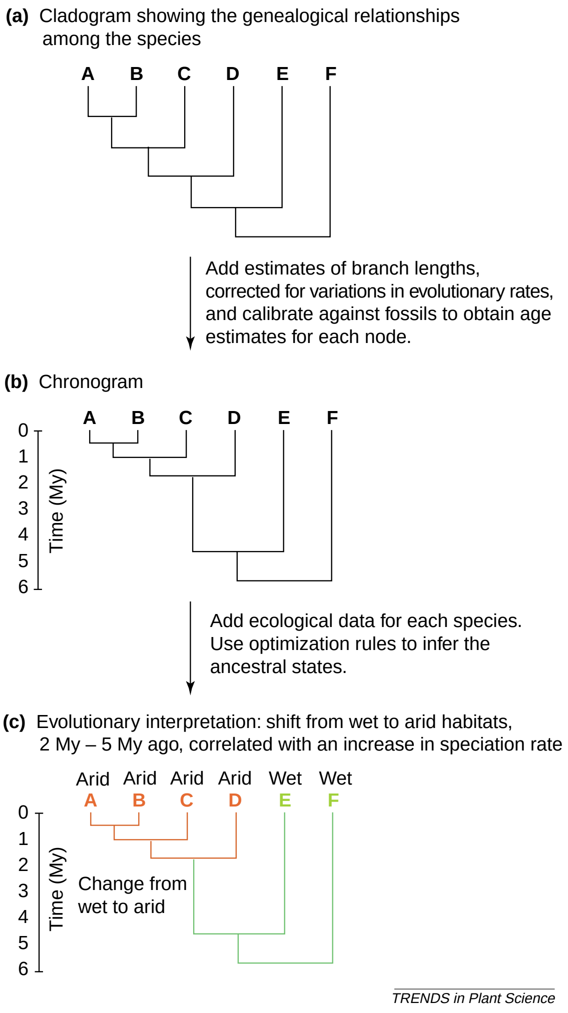
Cenozoic climatic changes in the Southern Hemisphere were complex and were linked to the glaciation history of Antarctica [43], sea surface temperatures [44] and variations in the strengths of the high-pressure cells over the southern oceans [45]. These factors influence both the volume and seasonal distribution of rain in the Cape Floristic Region. Early Oligocene climates might have been similar to modern climates, with low sea-surface

Box 1. Inferring evolutionary history without fossils

Phylogenetic hypotheses specify the genealogical relationships among species. Two recent developments have added much rigour to the construction of phylogenetic hypotheses. The development of cladistic analytical methods provided a logically rigorous method for extracting a phylogenetic signal from comparative data and the development of the polymerase chain reaction and automatic sequencers has provided access to the almost unlimited data locked up in DNA molecules [62].

The molecular divergences among species, appropriately corrected for variations in the molecular evolutionary rate [63–65], provide estimates of the relative time since the speciation events separating the species. If the rate of molecular divergence can be calibrated (against fossils or the occurrence of the species on islands – still a problematic procedure [66,67]), then the absolute divergence dates of the clades can be calculated. However, errors in age estimations can be large [68], so the results of dating analyses should be treated with care.

By mapping distribution and ecological and morphological attributes over phylogenetic hypotheses, the evolution of these attributes can be inferred. Based on this, we can reconstruct the ecologies and distributions of the ancestors of the modern species. However, these optimizations are still problematic and we have little way of knowing how accurate our reconstructions are [69]. Figure I illustrates the analytical progression from cladogram (a) via chronogram (b) to evolutionary interpretation (c).



(a) Cladogram showing the genealogical relationships among the species

Add estimates of branch lengths, corrected for variations in evolutionary rates, and calibrate against fossils to obtain age estimates for each node.

(b) Chronogram

Add ecological data for each species. Use optimization rules to infer the ancestral states.

(c) Evolutionary interpretation: shift from wet to arid habitats, 2 My – 5 My ago, correlated with an increase in speciation rate

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Figure I. From cladogram **(a)** via chronogram **(b)** to evolutionary interpretation **(c)**.

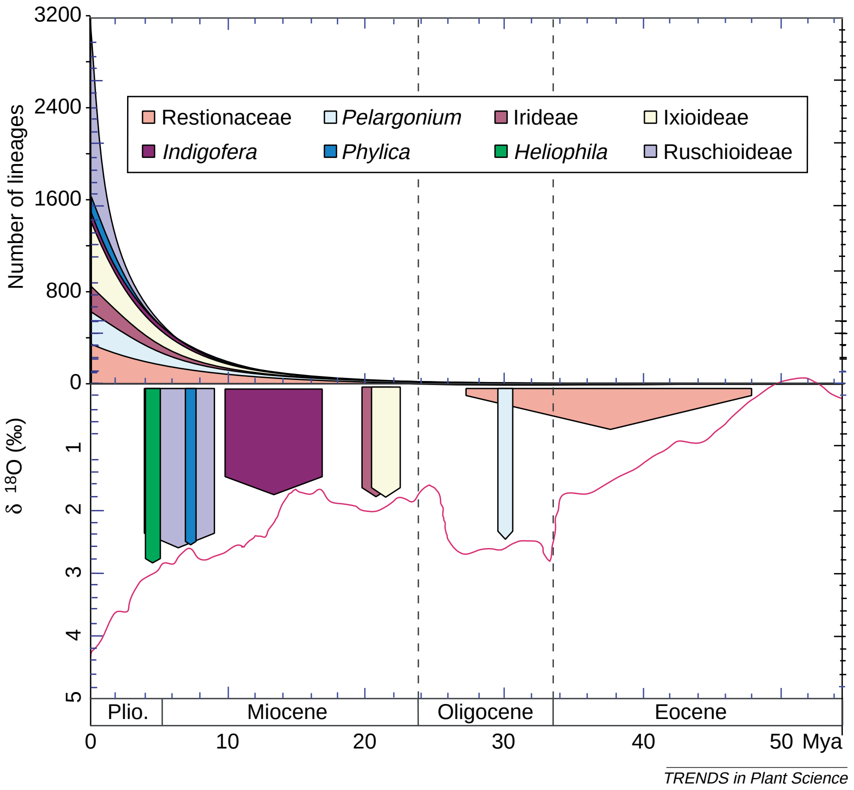

Figure 2. Accumulation of species diversity. The upper half of the diagram shows the accumulated retrojected estimates of diversity for those lineages for which the radiations have been dated, using the rate of lineage increase calculated for Restionaceae. Each lineage is colour-coded, and the total estimated diversity indicated by the upper line. The lower half of the graph shows the δ^{18} O (‰) curve from marine sediments for the Eocene to present, modified from [44]. The degree of $^{18}O/^{16}O$ fractionation between seawater and carbonate ions (incorporated into the shells of marine organisms and so preserved) is influenced by the temperature. In addition, the $^{18}O/^{16}O$ ratio in seawater is affected by the extent of sea-ice. The δ^{18} O (‰) curve can be interpreted as a proxy for oceanic temperatures, and reflects the Oligocene glaciation of Antarctica, the mesic Early and Middle Miocene, and the decreasing temperatures from 14 Mya. The calculated starting dates for each radiation are indicated with colour-coded arrows, the points of which indicate the mean and the width indicates the error of the estimates.

temperatures and extensive Antarctic glaciation. During the early and middle Miocene, climates were more mesic [46]. The increase in Antarctic glaciation from 14 million years ago (Mya) [44], associated with an increase in the strength of the South Atlantic high-pressure cell, initiated a trend towards the modern seasonally arid conditions. This was dramatically accelerated 3 Mya with the closure of the Panama seaway [47,48].

This rather gradual transformation in the climate means that there was no single, obvious trigger for the radiation of the Cape flora. This corresponds with the great spread in the dates of initiation of the radiation of various lineages. Some date back to the putative arid phase of the Early Oligocene and slowly accumulated diversity, others started their radiation after the aridification started 14 Mya, and some generated a large diversity in a short time: typical recent and rapid radiations [49]. In some cases, the presence of a long basal branch in the phylogeny (as in the Australian *Daviesia* [24] or the Africa Restionaceae [37]) indicates that the group was present in the region for a longer period but that only one lineage from this period survives.

The evolution of key innovations allowing the exploitation of new seasonally arid, fire-prone habitats might have been the crucial factor that allowed some groups to radiate while others remained species-poor and restricted to mesic, fire-protected habitats. A rich diversity of such innovations has been suggested: fruit and seedling morphology in Restionaceae [50], stem anatomy in Aizoaceae [49] and Restionaceae [40], the annual habit in the grass genus *Ehrharta* [38], and corms in Iridaceae [34] and *Pelargonium* [32]. However, there seems to be no adequate test to determine whether these attributes were indeed the factors that allowed the survival and radiation of these lineages [51].

What drives speciation?

Diversification in the Cape seems to be more rapid than in other areas, at least for Restionaceae [37] and Iridaceae [52], the only two clades that have been critically investigated. In the past, the drivers of this rapid diversification in the Cape flora were mainly sought in mechanisms that could fragment the distribution ranges of the species and lead to geographically isolated populations, and so to allopatric speciation. Among the postulated mechanisms were sea-level changes and climatic fluctuations, as well as local extinction as a result of inappropriate fires [12].

Recently, the search for the drivers of speciation has shifted from factors promoting allopatry to a search for ecological parameters that could drive diversification between populations as well as select for reproductive isolation [53]. Several selective forces have been proposed for the Cape flora. Pollinator specialization, particularly in the Cape flora where many species have single pollinators [54–57], could lead to ethological isolation as well as result in strong selection for different floral morphologies. This results in reproductively isolated species that can be recognized by their different floral morphologies [58]. Edaphic specialization, with parapatric sister-species restricted to the different soil types has been documented for several groups [56,59,60]. Presumably, specialization to different soils results in hybrids lacking suitable habitats but this has not been tested experimentally. The steep climatic gradients in Southern Africa, with an east–west gradient in the annual distribution of the rain and large orographic effects resulting in wet lee-sides and arid rain shadow interiors, might provide strong disruptive selection [9,12], and numerous sister-species can be separated by their climatic preferences. In most instances, climatic specialization also results in para- or allopatric distribution ranges because climatic variation shows a geographical pattern.

We do not know which ecological parameters are most frequently associated with speciation in the Cape flora. The issue is complicated because we can only determine which parameters are associated with species persistence: the inference that the associations we see in the present day are also associated with speciation might not be justified because both distribution ranges and ecological preferences might have changed since speciation [61]. Furthermore, it seems likely that the factors promoting speciation in biotically pollinated herbs such as orchids would be different from those in wind-pollinated shrubs such as *Cliffortia*.

We are still far removed from a general speciation model for the Cape flora in which the influences of the various factors are quantified. However, it seems clear that heterogeneous environments can play an important role. The steep selective gradients can drive rapid differentiation between populations and the diversity of habitats can provide niches for the numerous species. A comparison of the otherwise similar Mediterranean floras of southern Africa and western Australia suggests that the only possible explanation of the greater species richness of the African flora is the greater environmental heterogeneity [11].

Conclusion

Even though it has become possible to investigate the evolution of plant species diversity, the generality of the interpretations are still limited by four problems. The first is that our methods of molecular dating are still flawed and we have little idea of how large the errors in our estimations are. Second, the poor fossil record of the Cape flora means that we have no independent corroboration of the suggested palaeohistory. Third, the number of clades investigated is still rather small and it is possible that the sample was highly skewed. Finally, our methods of inferring the ecologies and distributions of ancestral taxa are still crude.

The great plant diversity of the Cape flora might be the result of several processes. The incorporation of suitably adapted lineages (to the temperate climates, low-nutrient soils and seasonal drought) from all continents means that the available genetic diversity can be high. Allowing for long-distance dispersal means that with climate change additional lineages can become established in the area. Species richness within this flora is the result of several radiations, some of which started in the middle Tertiary (Eocene–Oligocene), whereas others started only recently. There has been no major extinction similar to the Quaternary glaciations in Europe that massively reduced the diversity in all lineages, at least not since the Oligocene. The final diversity of the flora is the cumulative effect of many lineages radiating, maybe more rapidly than in other areas, over a long period of time, and possibly in response to somewhat different parameters. A flora cannot evolve, it can only reflect the sum of diversities accumulated by its evolving lineages. Environmental heterogeneity appears to be an important factor in promoting speciation and species-persistence, both important contributors to eventual high levels of species diversity. Final species richness might be understood as the product of environmental diversity and the time since the last dramatic, extinction-causing environmental changes.

Acknowledgements

This research was supported by grants from the Swiss Science Foundation, the Claraz Stiftung, the National Geographical Society and the SANW travel grants. I thank Richard Cowling, Chloé Galley, Chris Hardy, Timo van der Niet and three anonymous reviewers for comments on the manuscript, and Alex Bernhard for preparing the figures.

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