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Phytogeography and speciation in the vegetation of the eastern Cape

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ABSTRACT

The eastern Cape is a region of variable environmental factors, with a flora estimated at about 3 600–4 000 species and encompassing 21 of Acocks's (1975) veld types. It lies at the edges of the major phytochoria present in southern Africa, with many tropical species reaching the southern and western limits of their distribution, and many south-western Cape and Karoo species reaching the northern and eastern limits of their distribution. The apparently low incidence of species endemic to the eastern Cape may be the result of selection for 'generalist' genotypes and the close proximity of different phytochoria, which may allow species to migrate between phytochoria to fill niches resulting from environmental change.

RÉSUMÉ

PHYTOGÉOGRAPHIE ET SPÉCIATION DE LA VÉGÉTATION DU CAP ORIENTAL

Le Cap oriental est une région de milieux à facteurs variables, avec une flore estimée à environ 2 600–4 000 espèces et renfermant 21 des types champêtres Acocks (1975). Il repose aux bords de la phytochoria majeure présent en Afrique australe, avec beaucoup d'espèces tropicales atteignant les limites australes et occidentales de leur distribution, et beaucoup d'espèces du Cap sud-occidental et du Karoo atteignant les limites septentrionales et orientales de leur distribution. L'incidence apparemment faible d'espèces endémiques au Cap oriental peut être le résultat de sélection pour génotypes 'généraliste' et la proximité étroite de différents phytochoria, lesquels peuvent permettre aux espèces d'émigrer entre phytochoria pour remplir des niches résultant de changement de milieu.

INTRODUCTION

The eastern Cape, here defined as the area south of 32°S and between 24°E and the Great Kei River, has long been known as an area rich in species and communities and one of phytogeographical interest and complexity. To date, however, little systematic work has been done and the flora remains poorly understood. This paper presents data illustrating species and community diversity within the eastern Cape, and between it and other areas of southern Africa, and discusses some aspects of speciation in the eastern Cape flora.

DESCRIPTION OF THE AREA

The region covers an area of about 88 000 km^2, and is climatically and topographically very variable. Much of the range of climate and many landforms found elsewhere in southern Africa can be encountered in the eastern Cape.

The land rises from sea level in the south and south-east to about 2 100 m in the north-west and 1 500 m in the north-east (Fig. 1). There are two major mountain ranges, the Winterberg roughly in the centre of the area (with a maximum height of 2 360 m), and the coastal ranges north and west of Port Elizabeth, which are about 1 500 m high. The terrain is much dissected by numerous small and a few large rivers, so that there is little flat country, except in the west, and this naturally produces marked environmental heterogeneity over short distances.

Rainfall varies in amount and seasonality. As a general rule, amount decreases from the coast inland and from east to west (Fig. 1), with the highest precipitation being recorded from the southern slopes of the central mountain ranges. An appreciable proportion of the area is semi-arid. Furthermore, over much of the area rainfall is unreliable and droughts are not uncommon. Of greater phytogeographical significance, is the seasonal pattern of rainfall. In the southern third of the eastern Cape, a considerable proportion of the rain falls in winter, whereas in the north-eastern part the rainfall has a summer pattern; therefore over much of this region there can be some rain at nearly any time of the year. Also, the line denoting equal probability of spring or autumn rainfall runs through the northern part of the area. Some places receiving summer rains have a bimodal distribution of rain, with peaks in late spring and autumn. A further aspect of rainfall distribution which adds to environmental heterogeneity is illustrated in Fig. 2. Here the month-by month movement of the 50 mm rainfall isohyet is plotted for the summer rainfall region, and it can be seen that it converges on the area of Grahamstown, with the result that in the centre of the eastern Cape there is a concentration of seasonal rainfall changes into narrow bands. (Weather Bureau, 1965).

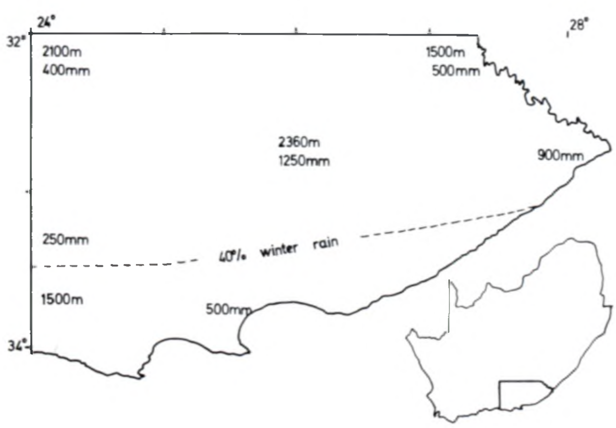

FIG. 1.—Generalized diagram of rainfall and altitude in the eastern Cape.

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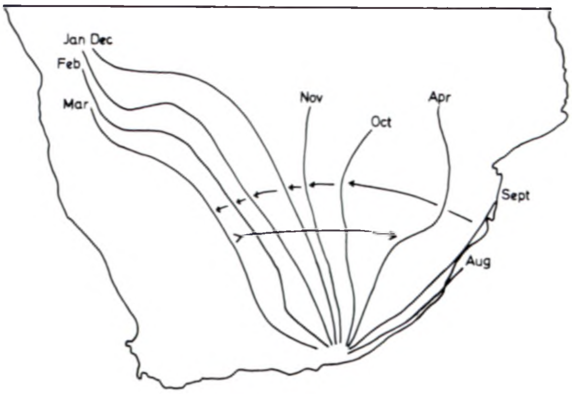

FIG. 2.—Seasonal movement of the 50 mm rainfall isohyet in the summer rainfall area, showing its convergence on the eastern Cape (Weather Bureau, 1965).

Temperatures also vary from the coast inland, with summer mean daily minima of 14–19°C and maxima of 25–32°C, and winter mean daily minima of 2–10°C and maxima of 16–21°C. The more extreme temperatures occur in the north and west of the area. Frost occurs in winter at higher altitudes, particularly at sites where temperature inversions occur. Snow has been recorded occasionally from a few localities at low altitude (e.g. Grahamstown in 1976) and is rather regular in mountainous parts of the area (Weather Bureau, 1965).

Geologically much of the eastern Cape is underlain by Karoo System rocks (Haughton, 1963). These consist mainly of shales and sandstones of the Beaufort and Ecca Series, with dolerite dykes and intrusions common to the whole Karoo System. Silcrete 'cappings' produce many of the highest hills. In addition, a number of outcrops of Witteberg Quartzite of the Cape System are found and their occurrence is biogeographically very important. Even small and isolated outcrops, such as that forming Mount Coke near King William's Town, support 'islands' of fynbos vegetation of the Cape Floral Kingdom deep within vegetation of tropical origin.

The soils derived from these rocks differ considerably. The most noticeable fine-scale variations attributable to the underlying rocks are those produced by the dolerite intrusions and the quartzites. Change from one soil type to another can be abrupt, and because the soil type can affect water availability there is considerable interaction between climatic and edaphic parameters, producing a wide range of habitats over short distances.

A further environmental factor which must be mentioned is the impact of man. Over the past 100 years or so European farming has changed the pattern of utilization of the vegetation and has introduced many alien species. There are records that by 1705 the Xhosa had settled on the banks of the Great Fish River and were in possession of large herds of cattle (Soga, 1931). Grazing and overgrazing by sheep, goats and cattle, and more recently the introduction of alien plants, must have had considerable influence on species composition and plant speciation in the area.

FLORISTICS, PHYTOGEOGRAPHY AND PHYTOSOCIOLOGY

Floristics and phytogeography

To date there is no complete flora for the area. A preliminary check list is in preparation, and extrapolation from this list and Martin & Noel's (1960) Flora of Albany and Bathurst gives an estimated number of 3 600 to 4 000 vascular plant species. This estimate agrees reasonably well with the number of species in areas of similar size, such as Natal (Gibbs Russell, 1975; Oliver, 1977). Floristic information for the present paper has been obtained from monographs and other works dealing with various groups, and data collected by the authors in the course of other studies.

The eastern Cape has long been known to botanists as an area where major vegetation units meet in southern Africa. Here the Indian Ocean Coastal Belt, Zambezian Domain, Afromontane, Karoo-Namib and Capensis phytochoria of the sub-continent are adjacent to one another (Werger, 1978; Goldblatt, 1978; U.N.E.S.C.O./A.E.T.F.A.T., 1980). At many sites the mixing is so intimate that species of different phytochoria intermingle in a single stand of vegetation. Detailed examination of distributions of taxa show clearly that the elements composing the eastern Cape flora have their centres elsewhere (Tables 1–3). The distribution of both grasses and trees (Table 1) reflects their tropical origin. The majority reach their south-western limits in the eastern Cape and range to the north and east. A minority of species are of southern derivation and extend no further north than our area. Nearly all the species that extend in both directions from the eastern Cape are those with extremely wide ranges in southern Africa. Taxa characteristic of the south-western Cape (Table 2) and the Karoo (Table 3) also show a drop in numbers of species across our area, with many taxa that come as far as the eastern Cape but go no further to the north or east. In general then, the tropical elements of the southern African flora extend no further to the south and west than the eastern Cape, and the south-western Cape and Karoo species do not extend further to the north and east. The eastern Cape, therefore, is a region where many taxa of diverse phytogeographical units reach their limits of distribution. However, the flora of the region has apparently a rather low proportion of endemics (Table 4), suggesting that there has been little speciation here in the recent past.

It is not possible to determine the number of endemic species in a flora whose composition is not yet well known. However, when the number of endemics are found for certain plant groups in the eastern Cape it is shown in Table 4 that the percent of endemic species in these groups falls far below the percent of endemic species in areas well known for high levels of endemism. Furthermore, extracting data from Goldblatt's (1978) list of genera endemic to southern Africa, it is seen (Table 5) that the numbers of species per genus is much lower for genera restricted to the eastern Cape than for endemic genera in all of southern Africa. Moreover, the high number of species per genus in endemic genera which reach the eastern Cape, but have the greater part of their distribution elsewhere, emphasizes once again that the eastern Cape is on the edge of major distribution patterns.

In summary, the diversity of taxa in the eastern Cape is due to combinations of species from different phytochoria meeting at the ends of their ranges, and not a result of speciation taking place in the area.

Phytosociology

Plant community data complement the phytogeographical picture. Acocks (1975) describes 70 veld

TABLE 1.—Distributions of 'tropical' taxa

	EC* endemic spp.	Spp. extending to EC from S&W	Spp. extending from EC both S&W and N&E	Spp. extending to EC from N&E
Grasses (Chippindall, 1955)	11 (5%)	33 (16%)	44 (22%)	116 (57%)
Trees (Coates Palgrave, 1977)	4 (1%)	31 (10%)	82 (25%)	207 (64%)

*Eastern Cape

TABLE 2.—Distributions of south-western Cape taxa

	(Adamson & Salter, 1950) Cape Pen.	(Martin & Noel, 1960) Alb. & Bath.	(Ross, 1972) Natal	(Jacot Guillarmod, 1971) Lesotho
Restionaceae				
Species	86	21	6	2
Genera	10	8	2	1
Proteaceae				
Species	39	10	16	5
Genera	9	4	5	1
	Caledon	Uitenhage	Alb. & Bath.	All Africa
Erica (Baker & Oliver, 1967) Species	220	112	12	25

TABLE 3.—Distributions of Karoo-Namib taxa

Mesembryanthemaceae (Herre, 1971)	Karoo-Namib		W. Cape		E. Cape		Natal
Genera	122		46		30		6
Pteronia	NW Cape	SW Cape	Karoo	Little Karoo	S Cape	E Cape	Natal
Species	33	18	16	14	13	9	0

TABLE 4.—Percentages of endemic taxa

	%
Eastern Cape	
Southern African endemic genera (Goldblatt, 1978)	5
Grasses (Chippindall, (1955)	5
Aloe (Reynolds, 1950)	6
Gladiolus (Lewis, Obermeyer & Barnard, 1972)	0
Crassulaceae (Tölken, 1977)	18
Oxalis (Salter, 1944)	3
Trees (Coates Palgrave, 1977)	1
All seed plant species in published volumes of Flora of Southern Africa (Dyer *et al.*, 1963; Codd *et al.*, 1966, 1970; Ross 1975, 1976, 1977; Leistner, 1979, 1980)	5
Other areas, of high endemism	
SW Cape (Weimarck, 1941)	83
Cape Floristic Region (Goldblatt, 1978)	73
Namib Desert (Robinson, 1978)	35
All of southern Africa (Goldblatt, 1978)	80

types, which are plant communities or aggregations of communities. Of the 70 veld types, 21 (30%) occur in the eastern Cape. Therefore a region with only about 6,5% of the area of South Africa has more veld types than any other single region (the next most diverse areas of comparable extent are Natal with 16 and the south-western Cape with 10 veld types). Furthermore, no single veld type extends both south-west and north-east from the eastern Cape. Acocks only considered six of the 21 veld types to be restricted to the eastern Cape, and four of these he terms 'false' (man-induced). Edwards's (1977) map of South African biomes shows the same pattern. Eight of the 11 biomes occur in the eastern Cape, not one of which is restricted to the area. All the biomes extend into our area either from the west or from the north and east, and none extends in both directions from the eastern Cape.

As well as the spatial variation in communities, the eastern Cape vegetation is unstable through time. It is all too well known by agriculturalists that many communities are prone to rapid changes in floristic

TABLE 5.—Numbers of species in genera endemic to southern Africa (Goldblatt, 1978)

	No. genera	No. species	Spp./gen.	Standard deviation
Genera restricted to E. Cape	6	7	1,2	0,41
All endemic genera in sth. Afr.	557	4 802	8,6	28,40
Genera reaching E. Cape but not restricted	127	1 841	14,5	28,40

TABLE 6.—Numbers of weed species in various areas of South Africa (Henderson & Anderson, 1966)

Area	Species
Transvaal	116
Orange Free State	69
Natal	82
Eastern Cape	104
Southern Cape	37
Northern Cape	54
Central Cape	33
South-western Cape	51
Widely distributed species	84

TABLE 7.—Weeds, aliens and species of disturbed sites in Albany and Bathurst (Martin & Noel, 1960)

Plant group	Species
Aliens	180
Weeds	40
Of disturbed sites	15
	235
Total flora	2 390
Aliens, weeds, etc	ca. 10%

composition as soon as they are disturbed. The data of Henderson & Anderson (1966) and Martin & Noel (1960) show clearly how readily weeds and alien species become established over much of our area. (Tables 6 & 7). This suggests that many communities may be very sensitive to changes. Of perhaps even greater interest is the way elements of different phytochoria (for example, *Pteronia incana* and *Elytropappus rhinocerotis* of the winter rainfall area, *Pentzia incana* and *Felicia* spp. of the Karoo, and the tropical species of the scrub woodland communities) can invade communities of a range of phytochoria. Although at least some of these invasions are initiated or encouraged by man's activities, the fact that elements of different regions can replace one another emphasizes the dynamic nature of the vegetation as a whole and gives a clue to the possible reason for the apparent lack of speciation in the area.

FACTORS PROMOTING SPECIATION

At this point it is worth reviewing briefly the kinds of environmental and other factors that lead to fragmentation of gene pools and subsequent divergence of sub-populations under various selection pressures. Data for the eastern Cape flora can then be examined in the light of prevailing environmental conditions and the currently accepted theories of the kinds of environment which favour micro-evolution.

The fragmentation of populations into sub-units as a factor likely to promote speciation has been widely accepted since it was proposed by Wright in 1931. If the sub-units are sufficiently isolated from one another to become differentiated by selection pressures but there is still limited gene flow to retain variability, it may be expected that species complexes will develop (Stebbins, 1972). This condition will be found in regions of marked, fine-scale environmental heterogeneity. Related to this is environmental, particularly climatic, instability over time. Changes in climate can serve to restrict populations to favourable areas, thereby fragmenting the gene pool. As pointed out by Stebbins (1952, 1972 & 1974), as far as higher plants are concerned, water availability is here of critical importance. Raven (1964) showed the effect of edaphic variability and the way it will interact with climatic fluctuation.

The above conditions together underlie the idea that speciation is likely to be rapid at the limits of species distribution ranges. Here, marginal populations are likely to become genetically isolated from the general gene pool and may undergo differentiation. This idea was elegantly proposed by Valentine (1967) under the title of the 'species pump' hypothesis, and has been discussed at some length by Stebbins (1974).

By taking the above points into account, we can describe one sort of environment in which speciation should be actively occurring. This would be a place in which there is considerable variation, in space and time, of a variety of parameters (climate, soil, landscape, etc.) and where many taxa are nearing the limits of their geographical ranges. In addition, the balance of evidence suggests that the climate should be semi-arid (but see Simpson, 1977, for a discussion of speciation in tropical forests). From the description of the physical environment and the vegetation, the eastern Cape seems to meet the above conditions for speciation. However, the flora does not show the expected pattern of diversity in terms of numbers of endemic species.

DISCUSSION

When one looks at the species and communities of the eastern Cape, three features are apparent. First, physiographic and climatic variability result in spatial and temporal heterogeneity on a fine scale. This allows many different species and vegetation types to exist in close proximity to one another and at the same time results in instability of the communities. Second, the distribution ranges of a large number of taxa end here, confirming the recognition of the eastern Cape as the boundary for a number of phytochoria. Third, neither taxa nor syntaxa seem to have become differentiated enough to be recognized as separate despite the operation of factors that elsewhere lead to speciation or the development of distinct plant communities. There are relatively few plant taxa that are endemic or restricted to the area, and of the six veld types restricted to the eastern Cape only two (Alexandria Forest and Eastern Province Thornveld) are not the result of invasion apparently initiated by man. It must be stressed that much more taxonomic and syntaxonomic information is needed for the area. At present neither the flora nor the communities are adequately treated in any work and the data presented above are crude. In spite of this, it may be in order to examine the situation a little more closely, if only to suggest possible directions for further investigation.

At present there is only scanty palaeoclimatic or floristic data for the eastern Cape, so we have no real idea of how long the conditions now experienced in this area have continued. However, when one considers the changes that have occurred over southern Africa [see for instance Livingstone (1975), Tankard & Rogers (1978) and Lancaster (1979)], and the decade to century long fluctuations commented on by May (1979), there can be little doubt that the eastern Cape climate must have been unstable for a very long time. As indicated earlier, the area is the boundary between the winter and summer rainfall zones, so any change in macroclimate over southern Africa would lead to a dramatic change in conditions. However, on the west coast of southern Africa there is a region which is climatically similar in some ways to the eastern Cape in that the summer and winter rainfall zones meet and there is a variety of habitats. In this area of the north-western Cape and southern Namib a number of taxa show active speciation (Robinson, 1978, Moffett, 1979).

Why then has the eastern Cape not developed a distinctive flora as a result of active speciation? It is possible that the nature of the dominant life forms, the variability of the environment and the position of the eastern Cape between the major phytochoria have all resulted in selection for 'generalist' genotypes rather than producing 'specialists'. Hamrik *et al.* (1979) have shown that woody plants and wind pollinated plants (grasses) show greater genetic diversity within a species on average than do herbaceous and entomophilous ones. Hedrik *et al.* (1976) have shown that heterogenous environments encourage or maintain high levels of genetic diversity in taxa. Furthermore, it would be expected that of the species making up a phytochorion, the generalists would be more likely to extend to the ends because of their wider tolerances. Therefore, the species in the eastern Cape may tend to be the most genetically diverse representatives of their respective phytochoria.

In other areas where speciation is rapid, it is single species or communities that are reaching the ends of their ranges, whereas in our area it is phytochoria (i.e., assemblages of many species and communities) that are reaching their distribution limits. It is important to remember that the species making up the different phytochoria have evolved under very different selection pressures. This may mean that in an area such as the eastern Cape where a number of phytochoria are adjacent to one another there is a species already present (perhaps most likely a 'generalist') which can occupy virtually any niche that becomes available. Therefore a change in environmental factors will simply lead to movements of species populations to new sites rather than the evolution of new genotypes. This idea is supported by the effects of fire on macchia vegetation reported by Trollope (1973) and Downing *et al.* (1978). In the Amatole Mountains fynbos species (*Cliffortia linearifolia, C. paucistaminea* and *Erica brownleeae*) form dense closed communities. When such fynbos is burned on a regular basis the community changes to grassland dominated by tropical grasses of the genera *Themeda, Tristachya* and *Panicum*. At the community level, although Acocks's treatment is too broad to allow more detailed discussion, it may be significant that the 'false' veld types of the eastern Cape are the result of Cape and Karoo phytochoria invading disturbed areas in phytochoria of tropical origin.

This reasoning leads to the conclusion that there is a saturation of the environment by species in such a region, which is apparently contradicted by the large number of weeds and aliens found in most communities in our area. However, most of the weedy species are annuals, a life form that is not well represented in Africa generally, and there may be niches, particularly those produced by man's activities, to which alien taxa are better adapted than any indigenous species.

CONCLUSION

The eastern Cape is floristically rich, with an estimated 3 600 – 4 000 species, and is phytogeographically and phytosociologically complex, and yet there are few endemic or restricted taxa or vegetation types. We suggest two hypotheses to explain this situation. First, selection pressures, particularly climatic instability, have acted to produce a flora in which 'generalist' genotypes predominate; and second, close proximity of phytochoria of different evolutionary histories ensures that somewhere there is a species already present that can fill, by migration, any new niche which may result from environmental change. Studies to confirm these hypotheses would be of great interest not only to evolutionary biologists but also to agriculturalists because of the practical implications. Much of the eastern Cape is only marginally suitable for agronomy and the natural vegetation is therefore of great significance for agricultural production. Management of such inherently unstable ecosystems for sustained productivity demands detailed knowledge of the environment. The information given in this paper shows that the eastern Cape is a very complex place and that our understanding of its vegetation is far from complete. Studies of the species and communities making up the vegetation will greatly increase the chances that management plans can be made that will take account of the long-term variability which this area exhibits.

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UITTREKSEL

Die Oos-Kaap is 'n gebied met veranderlike omgewingsfaktore, 'n flora wat na beraming 3 600–4 000 spesies bevat en 21 van Acocks (1975) se veldtipes in-

sluit. Dit lê op die grense van die hoof fitochoria wat in suidelike Afrika verteenwoordig is, verskeie tropiese spesies wat die suid- en westelike grense van hulle verspreiding bereik kom voor, terwyl baie suidwestelike Kaap en Karoo spesies wat die noord- en oostelike grense van hulle verspreiding bereik, daarin gevind word. Die skynbaar lae voorkomssyfer van spesies endemies in die Oos-Kaap kan wees as gevolg van seleksie vir 'algemene' genotipes in die teenwoordigheid van verskillende fitochoria waar immigrasie van spesies tussen fitochoria kan plaasvind om sodoende nisse te vul wat as gevolg van veranderings in omgewingstoestande kan ontstaan.

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