Endemism and speciation in a lowland flora from the Cape Floristic Region

2 authors:

Richard M Cowling
Nelson Mandela University
479 PUBLICATIONS   **24,166** CITATIONS

SEE PROFILE

Patricia Holmes
Stellenbosch University
69 PUBLICATIONS   **3,055** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Project   Gouritz Initiative View project

Project   Palynological and sedimentological investigation of early Neogene deposits at saldanha Bay/South Africa View project

Endemism and speciation in a lowland flora from the Cape Floristic Region

R. M. COWLING AND P. M. HOLMES

Botany Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa

Taxonomic, edaphic and biological aspects of endemism were studied in a phanerogamous flora from the Agulhas Plain, a coastal lowland area of the Cape Floristic Region. Of the 1751 species in the flora, 23.6% were regional endemics and 5.7% were local endemics. Families which were over-represented in terms of endemics included the Ericaceae, Rutaceae, Proteaceae and Polygalaceae. Under-represented families included the Poaceae, Cyperaceae, Scrophulariaceae and Orchidaceae. Highest levels of local endemism were recorded on limestone and colluvial acid sand. Sixty-nine percent of regional endemics and 85% of local endemics were confined to a single substratum. An analysis of the frequency of biological traits associated with species with different categories of endemism enabled the establishment of a biological profile of a local endemic: a dwarf to low, non-sprouting shrub with soil stored seeds which are ant-dispersed and/or form a symbiotic relationship with microbes. It is argued that lineages with these characteristics are vulnerable to severe population reduction or even local extinction. An effect of this would be the promotion of rapid, edaphic speciation as a result of catastrophic selection. Thus, certain traits (e.g. non-sprouting) prevail or even predominate in the flora not because of any adaptive advantage but because high speciation rates of lineages which possess them, overwhelm low survival rates.

KEY WORDS:—Cape Floristic Region – edaphic specialization – endemism – extinction – fynbos – speciation.

CONTENTS

367

INTRODUCTION

Certain mediterrannean-climate regions provide a striking exception to the trend for plant geographical range size to decline with decreasing latitude (Cody, 1986; Gentry, 1986; Major, 1988; Stevens, 1989). The most notable of these is the Cape Floristic Region of South Africa which has one of the highest known levels of plant species endemism of any continental tropical or temperate area (Goldblatt, 1978; Gentry, 1986; Cowling, Holmes & Rebelo, 1992). Despite the flora being relatively well studied, and the region's accessibility for research, patterns and determinants of endemism have been poorly studied in the Cape Floristic Region.

We identified three main questions regarding endemism in the Cape Floristic Region: are endemics a heterogeneous group taxonomically; what is the relationship between endemism and habitat specialization; and is it possible to develop a biological profile of an endemic? Some of these question have been addressed in the Cape Floristic Region (Thoday, 1925; Dahlgren, 1968; Cowling, 1983) and elsewhere (Stebbins & Major, 1965; Kruckeberg, 1969; Raven & Axelrod, 1978; Kruckeberg & Rabinowitz, 1985; Major, 1988), but we know of no study which has addressed all three.

A major aim of our study was to identify the relationship between endemism and speciation. In order to do this, it was necessary to distinguish between paleoendemism and neoendemism (Favarger & Constandriopoulos, 1961; Stebbins & Major, 1965; Major, 1988). Paleoendemics are taxonomically isolated taxa, usually monotypic sections, genera or subgenera, which may be regarded as evolutionary relicts. Neoendemics are subspecies, semi-species or sibling species: they usually have close relatives in the same or adjacent areas. Neoendemics are the products of recent speciation reflecting contemporary selective forces (Major, 1988). Thus, pattern associated with the characterization of neoendemics in terms of taxonomic, biological and habitat attributes should provide important insights into speciation processes. Specifically, these patterns should identify selective forces and biological traits associated with speciation, as well as lineages which are prone to speciation (Vrba, 1980).

This paper is an attempt to address these questions by studying patterns and determinants of endemism in the phanerogamous flora of the Agulhas Plain (Thwaites & Cowling, 1988), a coastal lowland area of the Cape Floristic Region. In most respects the Agulhas Plain is a highly suitable study area: it has a rich flora (Cowling & Holmes, 1992); floristic pattern is under strong habitat (edaphic) control (Thwaites & Cowling, 1988; Cowling, 1990); and it has a large, neoendemic flora (Cowling et al., 1992). Evidence for neoendemism is that the Agulhas Plain was largely inundated by a marine transgression in the early to mid-Pliocene (4 Myr) (Hendey, 1983). Since most local endemics are confined to sediments and soils deposited after this transgression, it is reasonable to assume they are younger than this event (Nordenstam, 1969; Deacon, 1983; Midgley, 1987). Secondly, nearly all of the endemics belong to speciose genera and there is good evidence that many have sympatric or parapatric sister species (Rourke, 1972; Midgley, 1986, 1987; Williams, 1972, 1982a; E.G.H. Oliver, personal communication).

STUDY AREA

Physiography

The study area is on the Agulhas Plain, and comprises a gently rolling, coastal lowland landscape occupying 1609 km^2 at the southern tip of Africa (Fig. 1). Virtually the entire area was inundated by transgressions during the mid-Miocene (15 Myr) and the early–mid-Pliocene (4 Myr) (Hendey, 1983). Most sediments and soils postdate the regression (Hendey, 1983). The geology of the region is complex and there is a high diversity of geomorphic land units and associated soil types (Thwaites & Cowling, 1988). The Agulhas Plain is largely underlain by Palaeozoic sediments of the Cape Supergroup. Sandstones and quartzites of the Table Mountain Group form the low mountains and coastal ridges; soils derived from these rocks are acidic and highly infertile. Landscapes underlain by Bokkeveld Group Shales comprise the broad vales and low, rolling surfaces between the mountain ridges. Soils are non-hydromorphic and duplex with an acid topsoil and a sodic, clayey B horizon. They are more fertile than the sandstone-derived soils. Numerous siliceous ferricrete outcrops supporting shallow, infertile soils are scattered across this landscape. These are remnants of a ferricrete-veneered surface of late Pliocene age. Mio-Pliocene limestones and associated colluvial deposits of the Bredasdorp Group form distinctive relief features in the coastal zone. Soils on the limestone bedrock are shallow, well-drained, calcareous sands. Colluvial sands which apron the limestone hills are deep, weakly acid and infertile. The Quaternary is represented by an extensive cover of calcrete and dunes comprising calcareous aeolian quartz and shelly sand. Soils are poorly developed alkaline sands which are moderately fertile, especially under thicket and forest. The valley floodplains, with many vleis and pans, form the youngest identifiable surface. Soils are duplex with alluvial or colluvial acidic topsoils over residual or transported clays. These different soils
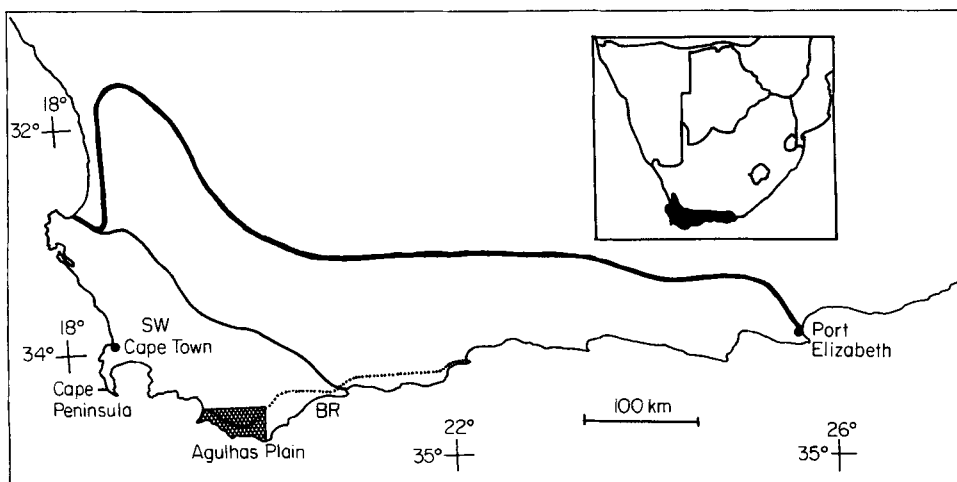

Figure 1. Location of the Cape Floristic Region (enclosed by thick, solid line), regional centres of endemism (SW = South Western Centre and BR = Bredasdorp—Riversdale centre) and the Agulhas Plain study area.

are juxtaposed in a complex mosaic so that up to five types may be encountered along a transect of 5 km (Cowling, 1990). Further details on the geology, geomorphology and soils (including physical ahd chemical data) of the Agulhas Plain are given in Thwaites (1987) and Thwaites & Cowling (1988).

The climate of the area is relatively uniform. Mean annual rainfall along the coast ranges from 445 mm in the east to 540 mm in the west, and rises to about 650 mm in the low hills that form the region's northern boundary (Weather Bureau, 1986). Rainfall seasonality is typical of a mediterranean-type climate with between 65% and 75% of annual precipitation falling in the winter months (May–October). At Cape Agulhas (34°50'S, 20°01'E) potential evaporation exceeds rainfall from November to March. Mean annual temperature at this station is 16.9°C; the highest mean monthly temperature is in January (26.6°C) and the lowest in August (6.6°C). Frost is extremely rare and snowfalls have not been recorded (Weather Bureau, 1986).

Vegetation and flora

The Agulhas Plain falls within the Cape Floristic Region (Bond & Goldblatt, 1984) and is dominated by fynbos, a sclerophyllous, heath-like shrubland associated with nutrient-poor soils which cover most of the region (Cowling & Holmes, 1992). These shrublands are fire-prone and usually burn at six to 40 year intervals. A structural classification employing limited floristic data (dominant species) recognized nine major vegetation categories in the area (Cowling et al., 1988). Non-fynbos types included forest, thicket and renoster shrubland; fynbos types comprise variations of proteoid fynbos, asteraceous fynbos, restioid fynbos, and ericaceous fynbos (Table 1). Soil type is the major determinant of the distribution of the communities (Thwaites & Cowling, 1988). Details are given in Cowling et al. (1988).

The Agulhas Plain has a rich phanerogamous flora estimated at 1751 species. The composition is typical of floras from the Cape Floristic Region (Cowling & Holmes, 1992). The flora has six genera with more than 25 spp. including Erica (Ericaceae) with 91 spp. and Aspalathus (Fabaceae) with 60 spp. There are 3.6 spp. per genus and 19.8% of the spp. occur in the ten largest genera (Cowling & Holmes, 1992). The taxonomic reliability of taxa is generally good: nomenclature follows Bond & Goldblatt (1984).

METHOD

Categories and centres of endemism

We recognized three categories of endemism: species confined to the Cape Floristic Region (Goldblatt, 1978); regional endemics confined to either Weimarck's (1941) South Western Centre or the Bredasdorp-Riversdale centre (Dahlgren, 1963; Nordenstam, 1969); and local endemics, more-or-less confined to the study area (Fig. 1). The Cape Floristic Region and South Western Centre are well established centres of endemism (Oliver, Linder & Rourke, 1983; Cowling et al., 1992). The Bredasdorp-Riversdale centre, which was not recognized by Weimarck (1941), comprises a well-defined centre for the calcicole fynbos taxa confined to the Bredasdrop formation limestone and associated

TABLE 1. Plant community and soil characteristics of transect and other sites on the Agulhas Plain

Site	Community*	Dominant species[+]	Soil (parent material)	Soil fertility index**
Geelrug transect				
G1	Proteoid fynbos[1]	Protea compacta, Elegia filiacea	Deep, colluvial podzol (TMG sandstone)	−0.25
G2	Proteoid fynbos[2]	Leucadendron platyspermum, Restio similis	Gravelly, leached lithosol (TMG sandstone)	−0.19
G3	Proteoid fynbos[3]	Leucadendron elimense, Blaeria klotzschii	Lithosol (Sil-ferricrete)	−0.17
G4	Asteraceous fynbos[4]	Disparago anomala, Thoracosperma interruptum	Duplex-loam on clay with ferricrete stoneline (Bokkeveld shale)	0.59
G5	Renoster shrubland[5]	Elytropappus rhinocerotis, Ischyrolepis caespitosa	Alluvial sand over transported clay	0.36
Hagelkraal transect				
H1	Proteoid fynbos[1]	Protea compacta, Willdenowia glomerata	Deep, colluvial podzol (TMG sandstone)	−0.22
H2	Proteoid fynbos[6]	Protea susannae, Euchaetes burchellii	Deep, colluvial podzol (Bredasdorp limestone)	−0.14
H3	Proteoid fynbos[7]	Leucadendron meridianum, Phylica sp. nov.	Calcareous lithosol (Bredasdorp limestone)	0
H4	Asteraceous fynbos[8]	Passerina paleacea, Euclea racemosa	Deep, calcareous dune sand	0.16
H5	Forest[9]	Sideroxylon inerme, Stipa dregeana	Deep, colluvial, calcareous sand (Bredasdorp limestone)	0.69
Soetanysberg transect				
S1	Proteoid fynbos[1]	Protea compacta, Staavia radiata	Deep, colluvial podzol (TMG sandstone)	−0.23
S2	Ericaceous fynbos[10]	Syndesmanthus globiceps Erica coccinea	Leached lithosol (TMG sandstone)	−0.12
S3	Restiod fynbos[11]	Leucadendron linifolium, Chondropetalum deustum	Shallow, calcareous sand (TMG sandstone)	−0.05
S4	Asteraceous fynbos[8]	Agathosma collina, Ischyrolepis eleocharis	Deep, calcareous dune sand	−0.03
S5	Thicket[12]	Olea exasperata, Euclea racemosa	Deep, calcareous dune sand	0.31
Miscellaneous plots				
HN1	Proteoid fynbos[7]	Leucadendron meridianum, Thamnochortus paniculatus	Calcareous lithosol (Bredasdorp limestone)	0.02
S6	Ericaceous fynbos[10]	Blaeria ericoides, Thamnochortus lucens	Leached lithosol (TMG sandstone)	−0.09

*Sites with the same superscript belong to the same community (sensu Cowling et al., 1988).

[+]Nomenclature according to Bond & Goldblatt (1984).

**Derived from a multivariate analysis of soil data (see Thwaites & Cowling, 1988; Cowling, 1990).

colluvial deposits which have their maximum exposure in this area (Hendey, 1983). The Agulhas Plain is roughly coincident with the Bredasdorp centre of local endemism recognized for the Proteaceae and other Cape taxa (Rebelo & Siegfried, 1990). Additional discussion of these centres appears in Cowling *et al.* (1992).

We categorized endemics on the basis of distributional data gleaned from several sources. These included: PRECIS, a computerized data bank managed by the National Botanical Institute (Gibbs Russell, 1985); relatively recent (i.e. post-1960) monographs; Bond & Goldbatt's (1984) catalogue of the Cape flora; specimen localities in three south-western Cape herbaria; and the collections and observations of R.M. Cowling. Data from these sources were also used to categorize local and regional endemics in terms of substratum specificity. This list of endemics, classified by category and substratum specificity, is available on request.

Taxonomic aspects of endemism

We asked the question: are endemics in the Agulhas Plain flora a heterogeneous group taxonomically or do certain taxa have a higher than expected probability of being endemic? We addressed this question by using χ^2 analysis to test the null hypothesis that the frequency of endemics in a family would not be significantly different from the frequency for the remaining flora (independent sample) from which it was drawn. Owing to problems with minimum expected cell count frequencies, we were only able to analyze families with more than 35 species.

Edaphic aspects of endemism

Here we explored the relationships between levels of endemism, and substratum type and edaphic variables. We categorized all local and regional endemics in terms of substratum specificity. The substrata included quartzite, colluvial acid sand, limestone, calcareous dune sand and shale/ferricrete. These are fairly crude categories but a finer subdivision was not feasible. Shale and ferricrete were combined since, in the study area, ferricrete always overlies shale-derived saprolite and other shale-derived soils usually have substantial amounts of ferricrete in the A horizon or as a stone line (Thwaites & Cowling, 1988). Very few endemics were exclusive to either shale or ferricrete.

In order to quantify the relationship between soil variables and level of endemism we sampled 17 1000 m^2 (20 X 50 m) plots in the study area. Five plots were located along three transects, chosen to include the widest possible range of edaphic habitats on the Agulhas Plain. Two non-transect plots were also sampled. In all, twelve different soil and associated vegetation types were sampled (Table 1). Each of the transects represented crude gradients of increasing soil fertility, from fynbos at leached upland sites to non-fynbos at more fertile bottomland sites. A soil fertility index, which generally increased along all the transects, was computed for each plot. The indices were derived from a covariance biplot ordination (Greenacre & Underhill, 1982) of a plot X topsoil (chemical and physical) data matrix (Cowling, 1990). This ordination technique is essentially similar to principal components analysis employing a covariance

matrix except that axes are weighted to facilitate simultaneous plotting of both sample sites and variables. The actual soil data and the results of the analysis are presented in Thwaites & Cowling (1988). The first axis of the ordination, which accounted for 34% of the variance, was strongly associated with increasing total nitrogen, pH, available phosphorus, organic carbon, clay content and available cations (particularly calcium). This was taken to represent a gradient of increasing soil fertility. The ordination score of this axis for each plot was used as its soil fertility index (more negative is less fertile) (see Table 1).

Sampling was carried out between 1983 and 1987 and confined to the spring (Sept-Nov). Therefore, species lists include most ephemerals (geophytes and annuals). All species were allocated to categories of endemism as described above.

Biological aspects of endemism

We compared the association between endemism and biological attributes of species in order to determine whether endemics were a random assemblage with respect to growth form, dispersal mode, dispersal distance etc. We used the combined flora (1121 spp.) from the 17 1000 m² plots for this analysis.

The categorization of species with respect to attributes (these are self evident in Table 5) was based on data in Phillips (1951), Bond & Slingsby (1983), Bond & Goldblatt (1984), Rebelo (1987) and our own unpublished observations. In some cases the categories were possibly too broad to be biologically meaningful (e.g. soil-stored seed, insect pollination) but data were unavailable for finer subdivisions.

Relationships were investigated using two-way frequency tables (BMPD Program 4F; Dixon, 1988). χ^2 was used to test for independence between the variables. Adjusted standardized deviates (Haberman, 1973) exceeding 3.0 in absolute value were taken to indicate cells with unusually large deviations from the expected. Three-way frequency tables were computed to examine how some of these variables interact. Unfortunately log-linear modelling could not be used because the data were over-dispersed (i.e. there was insufficient data in many of the variable classes).

RESULTS

Of the 1751 species in the Agulhas Plain flora, 413 (23.6%) were regional endemics and 100 (5.7%) were local endemics (Table 2).

Taxonomic aspects

Of the larger families in the flora, the Ericaceae, Rutaceae, Proteaceae, Polygalaceae and Mesembryanthemaceae were strongly over-represented in terms of both regional and local endemics (Table 2). Under-represented families included the Poaceae, Cyperaceae, Scrophulariaceae, and Orchidaceae. In the Restionaceae only regional endemics were over-represented. Among the larger genera (> 20 spp.) higher than average (> 30%) levels of regional endemism were recorded for *Erica* (Ericaceae) (44.9%), *Thesium* (Santalaceae) (47.8%), *Leucadendron* (Proteaceae) (47.1%), *Muraltia* (Polygalaceae) (45.8%), *Agathosma*

TABLE 2. Frequency of local, regional and non-endemics in the Agulhas Plain flora. The χ^2 tests the null hypothesis that the frequency of species in the endemic categories would not be different from the frequency in the whole flora, excluding that family. Only large (> 35 spp.) families were used in order to avoid excessively low predicted cell frequencies. NS, Not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

| Family | No. endemics (%) | | | χ^2 |
	Non	Regional	Local	
All	1238	413 (23.6)	100 (5.7)	
Asteraceae	151	50 (24.6)	2 (1.0)	9.53 NS
Campanulaceae	38	13 (25.0)	1 (1.9)	1.44 NS
Cyperaceae	56	6 (9.5)	1 (1.6)	10.56*
Ericaceae	44	58 (46.8)	22 (17.8)	82.16***
Fabaceae	89	41 (30.0)	8 (5.8)	3.20 NS
Iridaceae	111	31 (20.8)	7 (4.7)	1.16 NS
Liliaceae[+]	63	11 (14.7)	1 (1.3)	7.23 NS
Mesembryanth	32	17 (29.3)	9 (15.5)	12.98***
Orchidaceae	36	2 (5.3)	0 (0)	10.92*
Poaceae	62	3 (4.6)	0 (0)	19.97***
Polygalaceae	16	12 (34.3)	7 (20.0)	17.66**
Proteaceae	19	28 (47.5)	12 (20.3)	46.17***
Restionaceae	53	34 (38.6)	1 (1.1)	13.73**
Rutaceae	13	23 (48.9)	11 (23.4)	52.29**
Scrophulariaceae	48	8 (14.3)	0 (0)	7.27*
Thymeleaceae	21	14 (38.9)	1 (2.8)	12.01**

[+] Sensu lato.

(Rutaceae) (37.9%) and *Aspalathus* (Fabaceae) (31.7%). High levels of local endemism (> 15%) were recorded for *Phylica* (Rhamnaceae) (26.9%), *Muraltia* (25.0%), *Leucadendron* (23.5%), *Agathosma* (16.7%) and *Erica* (15%).

Edaphic aspects

The proportion of all categories of endemism in the 17 1000 m² plots were negatively correlated with soil depth and most measures of soil fertility. However, these relationships were, on the whole, significant only for the Cape Floristic Region endemics (Table 3). This trend was also evident along the three soil fertility gradients where the incidence of Cape Floristic Region endemics dropped sharply in the non-fynbos plots (G5, H5 and S5) (Fig. 2). The pattern was less pronounced for regional and local endemics: plot H3, a limestone site mid-way along the Hagelkraal transect had the highest proportion of both regional and local endemics. Local endemics were very poorly represented in the non-fynbos plots.

The proportion of regional and local endemics in the combined floras of fynbos plots on different substrata were similar except for calcareous dune sand (Table 4) (χ^2 excluding calcareous dune sand $= 6.5$, $P = 0.35$). Inclusion of the calcareous dune sand data resulted in a significant test ($\chi^2 = 21.9$, $P < 0.01$).

At the whole flora level, the highest proportion of regional endemics were confined to quartzite and the lowest proportion confined to shale/ferricrete (Table 4). Local endemics confined to limestone comprised a massive 37% of the total. Only 31% of regional endemics and 15% of local endemics occurred on more than one substratum. Local endemics confined to one substratum were
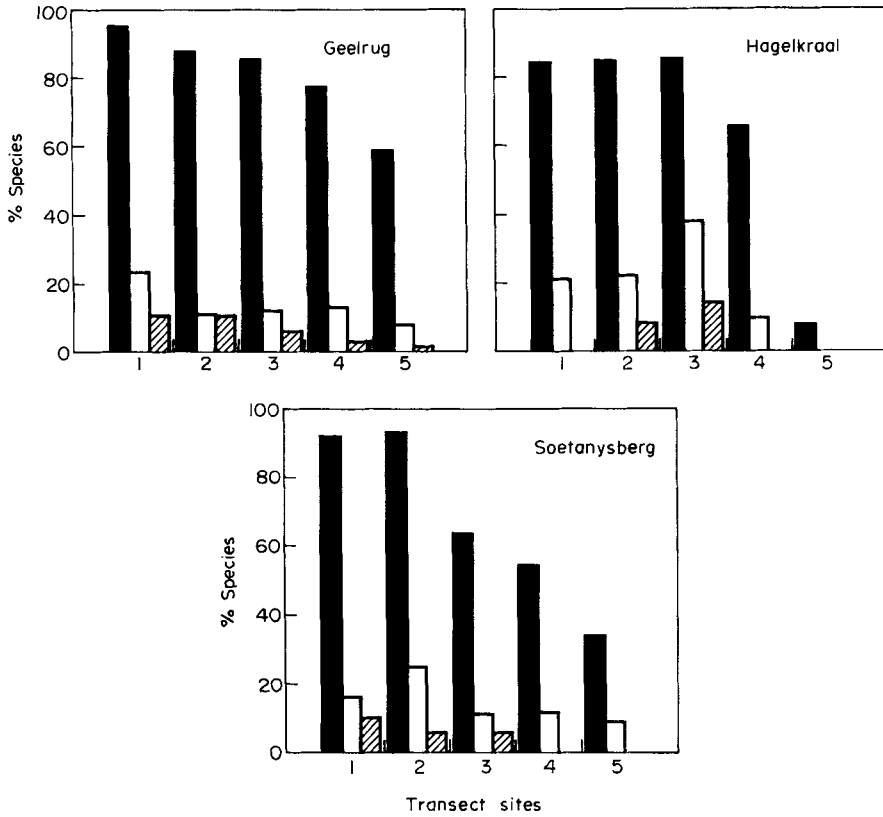
Figure 2. The percentage occurrence of Cape Floristic Region endemics (■), regional endemics (□) and local endemics (▨) in 1000 m² plots located along three soil fertility gradients on the Agulhas Plain. See Table 1 for a description of the three transects. Note that all regional and local endemics are included in the Cape Floristic Region endemic category.

TABLE 3. Correlations (Spearmans r) between percentage endemism and soil variables in 1000 m² plots ($n = 17$, see Table 1) on the Agulhas Plain. Soil data from Thwaites & Cowling (1988). $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

Soil variable	Cape Floristic Region endemic[+]	Regional endemic	Local endemic
Soil depth	−0.29	−0.58*	−0.51*
% Rock cover	−0.25	0.34	0.46
% Sand	0.36	0.15	0.01
pH	−0.55*	0.34	−0.39
% Organic carbon	−0.24	0.21	0.11
Total nitrogen	−0.11	0.18	−0.23
Available phosphorus	−0.83***	−0.29	−0.47
Available calcium	−0.63*	−0.25	−0.34
S-value[++]	−0.53*	−0.14	−0.38
Soil fertility index[§]	−0.71**	−0.30	−0.53*

[+]Includes both local and regional endemics.
[++] = sum of exchangeable bases (Ca, Mg, Na and K).
[§]From Cowling (1990) (see text).

TABLE 4. Substratum specifity of endemics in (a) 1000 m^2 plot from fynbos communities on the Agulhas Plain, and (b) for the entire Agulhas Plain flora (= 1751 spp.)

	Substratum					
	Quartzite	Colluvial acid sand	Shale/ ferricrete	Limestone	Calcareous dune sand	> 1 substratum
(a) Plot data						
No. pots	3	3	2	2	2	
Total spp.	154	97	126	97	96	
Regional endemics (%)	20.1	22.7	19.0	27.8	12.5	
Local endemics (%)	7.8	9.3	5.6	11.3	0	
(b) Whole flora						
Regional endemic	127 (30.7)[+]	55 (13.3)	14 (3.4)	55 (13.3)	33 (8.0)	129 (31.2)
Local endemic	12 (12)[++]	14 (14)	13 (13)	37 (37)	9 (9)	15 (15)

[+] = % of total regional endemics (= 413 spp.).
[++] = % of total local endemics (= 100 spp.).

significantly over-represented relative to regional endemics ($\chi^2 = 10.5$, $P < 0.05$).

Biological aspects

The χ^2 tests were significant for all endemic category-biological attribute relationships with the exception of woody plant pollination (Table 5). Amongst the local endemics woody plants and dwarf shrubs in particular, were over-represented. Widespread species had a higher than expected frequency of forbs and trees. In general, taller woody growth forms were over-represented amongst the widespread species. Local endemics had a higher than expected frequency of ant-dispersed species—the inverse held for widespread species. Vertebrate dispersed species were massively over-represented in the widespread category as were species with long-distance dispersal and non-storage of seeds.

An analysis of three-way frequency tables showed that 56% of local endemic shrubs (comprising 84% of all local endemics) were ant-dispersed as were 41% of regional endemics. All of these species had soil-stored seed banks. Furthermore, 71% of local endemic shrubs and 61% of regional endemic shrubs had short-dispersal distances.

DISCUSSION

Levels of endemism

The level of local endemism in the Agulhas Plain flora is extraordinarily high for a lowland continental region. About 8% of the 2256 spp. on the nearby island-like Cape Peninsula (Fig. 1) are endemics (Cowling et al., 1992). When compared with similar sized continental areas higher levels of endemism than the Agulhas Plain are recorded only from some mountainous areas in the Mediterrannean Basin, the Caucasus and certain tropical mountains (Gentry, 1986; Major, 1988).

TABLE 5. The association between endemism and biological attributes of species in the Agulhas Plain ($n = 1121$ spp.). Observed frequencies are listed with adjusted standardized deviates in parentheses (see text). LE, Local endemics; RE, regional endemics; CE, Cape Floristic Region endemics; WD, widespread species. In this case CE species exclude LE and RE species

(a) Grown form

	Vine	Geophyte	Graminoid	Forb	Shrub and tree+
LE	0 (−1.0)	1 (−2.6)	2 (−2.7)	2 (−1.7)	41 (5.5)
RE	0 (−1.0)	10 (−1.9)	28 (2.1)	4 (−2.9)	61 (2.1)
CE	5 (−0.6)	59 (3.3)	58 (0.4)	29 (−1.4)	132 (−1.6)
WD	7 (2.9)	19 (−0.5)	24 (−0.6)	34 (5.4)	49 (−3.5)

$\chi^2 = 80.3$, $P < 0.0001$

(b) Woody plant height

	Dwarf shrub (<0.25 m)	Low shrub (0.25−1 m)	Medium shrub (1−2 m)	Tall shrub (2−5 m)	Tree (>5 m)
LE	14 (4.3)	21 (−1.3)	5 (−0.9)	1 (−1.0)	0 (−1.3)
RE	7 (−0.4)	41 (1.2)	9 (−0.6)	4 (0.2)	0 (−1.6)
CE	14 (−1.2)	91 (2.7)	24 (0.4)	3 (−2.5)	0 (−2.9)
WD	2 (−2.1)	18 (−3.7)	11 (4.0)	9 (4.0)	9 (6.7)

$\chi^2 = 85.9$, $P < 0.0001$

(c) Dispersal mode

	Wind	Vertebrate	Ant	Ballistic	Passive/Unknown
LE	13 (−0.1)	1 (−1.3)	25 (4.6)	1 (−0.4)	6 (−3.3)
RE	36 (1.5)	0 (−3.0)	37 (2.6)	3 (−0.2)	27 (−2.1)
CE	86 (0.7)	6 (−4.3)	70 (−0.6)	12 (1.4)	109 (1.5)
WD	29 (−2.1)	30 (8.5)	14 (−4.6)	2 (−1.3)	58 (2.3)

$\chi^2 = 117.5$, $P < 0.0001$

(d) Dispersal distance

	Short (<10 m)	Medium (10−50 m)	Long (>50 m)
LE	32 (0.8)	13 (−0.1)	1 (−1.3)
RE	67 (0.2)	36 (1.4)	0 (−3.0)
CE	190 (1.4)	87 (0.8)	6 (−4.3)
WD	74 (−2.4)	29 (−2.1)	30 (8.5)

$\chi^2 = 74.6$, $P < 0.0001$

(e) Seed storage

	Canopy-storage	Soil-storage	Non-storage
LE	5 (1.2)	41 (0.5)	0 (−1.9)
RE	10 (1.4)	93 (1.2)	0 (−3.1)
CE	20 (0.5)	254 (2.2)	9 (−3.5)
WD	2 (−2.7)	101 (−4.1)	30 (8.1)

$\chi^2 = 73.6$, $P < 0.0001$

(f) Woody plant pollination

	Wind	Insect	Bird
LE	1 (−1.5)	37 (1.1)	3 (0.0)
RE	4 (−0.5)	47 (−1.2)	10 (2.0)
CE	12 (0.4)	107 (−0.3)	13 (0.0)
WD	7 (1.4)	41 (0.6)	1 (−2.1)

$\chi^2 = 10.3$, $P > 0.10$

+Trees (9 spp.) were included with shrubs.

Endemism and edpahic specialization

Nutritionally unusual substrata such as serpentine, limestone, quartzite etc. provide a strong selective force for the evolution of neoendemic plant species throughout the world (Kruckeberg, 1969; Raven & Axelrod, 1978; Hopper, 1979; Cowling, 1983; Kruckeberg & Rabinowitz, 1985; Major, 1988). Our results suggest a high degree of edaphic specialization of Agulhas Plain endemics. The generally low nutrient status of most of the soils (Thwaites & Cowling, 1988), and subtle differences in nutrient and moisture status between soil types on the Agulhas Plain (Mustart & Cowling, 1992), probably represents a major selective force for plant speciation. Many Agulhas Plain local endemics have edaphically differentiated hypothetical sister taxa (Cronk, 1985) with sympatric or parapatric distributions (Cowling et al., 1992). These patterns are consistent with Linder's (1985; Linder & Vlok, 1991) suggestion that speciation in the Cape Floristic Region is predominantly ecological (e.g. edpahic) rather than geographical.

Taxonomic and biological profile of an endemic

It is possible to provide a reasonably comprehensive profile of species endemic in the Agulhas Plain. There is a higher-than-average chance that locally endemic species will be dwarf to low shrub with ant-dispersed and soil-stored seeds belonging to one of a relatively low number of taxa, especially Rutaceae, (Agathosma), Polygalaceae (Muraltia) and Rhamnaceae (Phylica). These species also have short-dispersal distances (Slingsby & Bond, 1985), a trait correlated with endemism in other floras (Lewis, 1962; Gentry, 1986).

Locally endemic species not characterized by this profile are more than likely members of the Ericaceae and certain genera in the Fabaceae (Aspalathus). These shrubby taxa with soil-stored seed banks both have microsymbiont-mediated (ericoid mycorrhiza and rhizobia respectively) nutrient uptake. Cowling, Straker & Deignan (1990) have suggested that specificity for microbes could explain edpahic specialization and local endemism and speciation in these groups.

For lack of data, we were not able to explore the association between mode of post-fire regeneration and endemism in our data. Wells (1969) has shown that endemism and speciation in the Californian chaparral shrub genera, Arctostaphylos and Ceanothus, is related to the post-fire, non-sprouting habit. In the Cape Floristic Region, only 10% of locally endemic and 20% of regionally endemic Proteaceae are sprouters as opposed to 47% of widespread species (Cowling et al., 1992). Similar patterns exist for other Cape taxa. For example, all local endemics in Acmadenia (Rutaceae), a shrubby, ant-dispersed genus, are non-sprouters (Williams, 1982b). Le Maitre & Midgley (1992) estimate that > 90% of Cape Floristic Region Ericaceae, 80% of Proteaceae, and > 50% of Rutaceae, are non-sprouters. All these families in the Agulhas Plain flora and elsewhere in the Cape Floristic Region (Cowling et al., 1992) are associated with higher than average levels of endemism.

An expanded biological profile of a local endemic in the Agulhas Plain flora would read thus: a dwarf to low, non-sprouting shrub with soil-stored seeds which are ant-dispersed and/or form a symbiotic relationship with microbes.

Below we explore the implications of biological and other aspects of endemism for speciation on the Agulhas Plain.

Implications for speciation

The dominant paradigm for speciation in the Cape Floristic Region is that it has been largely allopatric (Rourke, 1972; Goldblatt, 1978). The high floristic turnover between fynbos landscapes is suggestive of geographic speciation (Kruger & Taylor, 1979). However, there is much evidence for patterns, such as occur on the Agulhas Plain, of geographic overlap in the distribution of closely related species. Linder (1985; Linder and Vlok, 1991) suggests that sympatric speciation in response to steep ecological gradients is prevalent in the Cape flora. The following requirements must be met for sympatric speciation to occur: short gene flow distances; strong disruptive selection on sufficiently polymorphic traits in relation to spatially heterogeneous resources; the evolution of reproductive isolation either as a result of selection or pleiotropy; the extinction of intermediate individuals to minimize selection-recombination antagonisms under a wide range of ecological conditions; occasional and drastic reduction of marginal populations facilitating rapid speciation as a result of catastrophic selection or genetic drift (Lewis, 1962; Grant, 1981; Templeton, 1981; Linder, 1985; Kondrashov & Mina, 1986; Rice & Salt, 1988). Much of the debate concerning allopatric or sympatric speciation is centred on the meaning of the word 'geographical' (Templeton, 1981). Bearing in mind that most fynbos species have short gene dispersal distances (Linder, 1985; Slingsby & Bond, 1985), each distinctive habitat could represent a "geographic' region without the usual physical barriers associated with allopatric speciation (Linder & Vlok, 1991).

Stated thus, conditions are highly conducive to rapid 'sympatric speciation' in an area such as the Agulhas Plain. The high level of edaphic specialization indicates that the complex mosaic of edaphic environments represents an important selective regime. Populations of edaphically restricted species would be subject to drastic reduction as a result of fire in the short-term (Van Wilgen, Bond & Richardson, 1992) and climatic change in the long term (Goldblatt, 1978). These processes would result in the extinction of intermediates (Cowling, 1987) and a reduction in the population sizes of genetically divergent isolates in marginal habitats (e.g. limestone). The result could be rapid speciation. We now elaborate this model to explain why speciation has been so prolific in lineages which possess such traits as non-sprouting, ant-dispersed seed or microbe-mediated nutrient uptake. We begin with the non-sprouting, ant-dispersed combination.

There is a strong selective force to produce large protein-rich seeds in the fire-prone and nutrient-poor fynbos environment (Le Maitre & Midgley, 1992). Large seeds enable rapid seedling growth and the avoidance of drought-induced mortality during the dry summer months. However, the commonly observed trade-off between seed size and number (Le Maitre & Midgley, 1992) means that seed production is often low and highly variable. Ant-dispersal has evolved to ensure that precious seeds are dispersed to sites safe from vertebrate predators (Bond & Breytenbach, 1985). Low seed production results in small soil-stored

seed banks which are often dependent on the current year's seed crop for their maintenance (Pierce & Cowling, 1991). Fire may severely reduce the population sizes of non-sprouting, ant-dispersed species and thus promote population fragmentation and isolation, especially if the species are edaphically restricted to small habitat patches. In other words, these species are vulnerable to local extinction (Parker & Kelly, 1989). Cowling & Bond (1991) have shown that shrubs with ant-dispersed seeds and Ericaceae were the species groups most vulnerable to local extinction on small limestone habitat fragments on the Agulhas Plain. However, lineages that are extinction-prone are also prone to speciation. This certainly seems to be the case for *Clarkia*, a richly diversified genus of annuals in the California Floristic Province (Lewis, 1962). Populations of *Clarkia* species, which have transient seed banks, are vulnerable to local extinction or severe population reduction as a result of environmentally extreme events. Speciation of populations at the margin of the species' distribution or on unusual substrata (Raven, 1964) occurs as a result of catastrophic selection whereby exceptionally adapted individuals survive extreme events (Lewis, 1962; 1972). Similarly, the lack of buffering provided by persistent seed banks is thought to have contributed to diversity, endemism and habitat specialization among non-sprouting species of the Californian chaparral genera, *Arctostaphylos* and *Ceanothus* (Wells, 1969; Stebbins, 1974; Parker & Kelly, 1989).

Of relevance to our argument is Vrba's (1980; 1984) effect hypothesis, which states that 'selection for proximal fitness may also, and incidentally, drive speciation' (Vrba & Gould, 1986). Habitat specialists are more likely to be subject to directional selection in the event of environmental change leading to fragmentation, population divergence, vicariant speciation and extinction. Thus, for fynbos shrubs, selection for non-sprouting and large, ant-dispersed seeds, which may be adaptive at the organism-level, incidentally causes the multiplication of species. The potential of non-sprouting lineages for speciation probably has nothing to do with rapid generation turnover (cf. Wells, 1969) which suggests a gradualist mode of speciation (Vrba, 1980). Speciation occurs in punctuated events when populations of non-sprouting lineages undergoing strong selection are driven to very low numbers. Thus, traits prevail or even predominate in a flora because high speciation rates may overwhelm low survival rates. Microevolution at the organism level is uncoupled from macroevolution at the species level (Vrba & Eldredge, 1984; Vrba & Gould, 1986). The effect hypothesis is not an example of species selection since it does not require units of selection above the level of the species (Vrba, 1980, 1984; Vrba & Gould, 1986).

It could be argued that in a fire-prone environment, sprouting ability is a more adaptive trait under a wider range of fire regimes that non-sprouting (James, 1984; Le Maitre & Midgley, 1992). However, selection for this trait will reduce the probability of population fragmentation and, thus, rates of lingeage turnover. Clades which possess sprouting ability produce species that are resistant to extinction and hence, speciation: in Vrba's (1980) terminology these are survivors. The corollary is more interesting: the prevalence of nonsprouting in fynbos shrub lineages may have resulted not from any immediate adaptive advantage to the organism, but rather from their greater potential for speciation. The preponderance of species with particular traits in communities and landscapes may be a stronger reflection of incidental speciation events than

contemporary or historical ecological conditions (Fowler & MacMahon, 1982; cf. Le Maitre & Midgley, 1992).

This model similarly explains the tremendous diversification of lineages with microsymbiolent-mediated naturient uptake (e.g. Ericaceae and *Aspalathus*). Epaphic specialization would result from strong selection at the organism level to acquire new microsymbionts in different soil types (Cowling *et al.*, 1990). It is appealing to suggest that the massive speciation of *Erica* in the Cape Floristic Region (526 spp.) is an effect of selection on seedlings for capturing more efficient microsymbionts in new edaphic environments.

ACKNOWLEDGEMENTS

REFERENCES

BOND, P. & GOLDBLATT, P., 1984. Plants of the Cape Flora. A descriptive catalogue. *Journal of South African Botany Supplementary Volume, 13:* 1–455.

BOND, W. J. & BREYTENBACH, G. J., 1985. Ants, rodents, and seed predation in Proteaceae. *South African Journal of Zoology, 20:* 150–154.

BOND, W. J. & SLINGSBY, P., 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *South African Journal of Science, 9:* 231–233.

CODY, M. L., 1986. Diversity, rarity and conservation in mediterranean-climate regions. In M. E. Soule (Ed.), *Conservation Biology. The Science of Scarcity and Diversity:* 122–152. Sunderland: Mass: Sinauer.

COWLING, R. M., 1983. Phytochorology and vegetation history in the south eastern Cape, South Africa. *Journal of Biogeography, 10:* 393–419.

COWLING, R. M., 1987. Fire and its role in coexistence and speciation in Gondwanan shrublands. *South African Journal of Science, 83:* 106–112.

COWLING, R. M., 1990. Diversity components in a species-rich area of the Cape Floristic Region. *Journal of Vegetation Science, 1:* 699–710.

COWLING, R. M. & BOND, W. J., 1991. How small can reserves be? An empirical approach in Cape flynbos. *Biological Conservation, 55:* 243–256.

COWLING, R. M. & HOLMES, P. M., 1992. Flora and vegetation. In R. M. Cowling (Ed.), *The Ecology of Fynbos. Nutrients, Fire and Diversity:* 23–61. Cape Town: Oxford University Press.

COWLING, R. M., HOLMES, P. M. & REBELO, A. G., 1992. Plant diversity and endemism. In R. M. Cowling (Ed.), *The Ecology of Fynbos. Nutrients, Fire and Diversity:* 62–112. Cape Town: Oxford University Press.

COWLING, R. M., CAMPBELL, B. M., MUSTART, P., MCDONALD, D., JARMAN, M. L. & MOLL, E. J., 1988. Vegetation classification in a floristically complex area: The Agulhas Plain. *South African Journal of Botany, 54:* 290–300.

COWLING, R. M., STRAKER, C. J. & DEIGNAN, M. T., 1990. Does microsymbiont specificity determine plant species turnover and speciation in Gondwanan shrublands? A hypothesis. *South African Journal of Science, 86:* 118–120.

CRONK, Q. C. B., 1985. The history of endemic flora of St Helena: a relictual series. *New Phytologist, 105:* 509–520.

DAHLGREN, R., 1963. Studies on *Aspalathus:* phytogeographical aspects. *Botaniska Notiser, 116:* 431–472.

DAHLGREN, R., 1968. Distribution and substrate in the South African genus, *Aspalathus*. Botaniska Notiser, 121: 504–534.

DEACON, H. J., 1983. The comparative evolution of mediterranean-type ecosystems: a southern perspective. In F. J. Kruger, D. T Mitchell & J. U. M. Jarvis (Eds), *Mediterranean-type Ecosystems: The Role of Nutrients:* 3–40. Springer: Berlin.

DIXON W. J., 1988. *BMDP Statistical Software Manual.* Berkeley: University of California Press.

FAVARGER, R. C. & CONSTANDRIOPOULOS, J., 1961. Essai sur l'endemissme. *Bulletin Society Botanique Suisse, 71:* 384–408.

FOWLER, C. W. & MACMAHON, J. A., 1982. Selective extinction and speciation: their influence on the structure and functioning of communities and ecosystems, *American Naturalist, 119:* 480–498.

GENTRY, A. H., 1986. Endemism in tropical vs temperate plant communities. In M. E. Soule (Ed.), *Conservation Biology. The Science of Scarcity and Diversity:* 153–181. Sunderland: Mass: Sinauer.

GIBBS RUSSELL, G. E., 1985. PRECIS, the National Herbarium's computerized information system. *South African Journal of Science, 81:* 662–665.

GOLDBLATT, P., 1978. An analysis of the flora of southern Africa: Its characteristics, relationships and origins. *Annals of the Missouri Botannical Garden, 65:* 369–436.

GRANT, V., 1981. *Plant Speciation,* 2nd edn. Columbia University Press, New York.

GREENACRE, M. J. & UNDERHILL, L. G., 1982. Scaling a data matrix in low dimensional Euclidean space. In D. M. Hawkins (Ed.), *Topics in Applied Multivariate Analysis:* 181–268. Cambridge: Cambridge University Press.

HABERMAN, S. J., 1973. The analysis of residuals in cross-classified tables. *Biometrics, 29:* 203–229.

HENDEY, Q. B., 1983. Palaeontology and palaeoecology of the fynbos region: an introduction. In H. J. Deacon, Q. B. Hendey & J. J. N. Lamprechts (Eds), *Palaeoecology of the Fynbos Landscape: a Preliminary Synthesis:* 100–115. *South African National Scientific Programmes Report, 75:* Pretoria: CSIR.

HOPPER, S. D., 1979. Biogeographical aspects of speciation in the south-west Australian flora. *Annual Review of Ecology and Systematics, 10:* 399–422.

JAMES, S., 1984. Lignotubers and burls—their structure, function and ecological significance in mediterranean ecosystems. *Botanical Review, 50:* 225–266.

KONDRASHOV, A. S. & MINA, M. V., 1986. Sympatric speciation: when is it possible? *Biological Journal of the Linnean Society, 27:* 201–223.

KRUCKEBERG, A. R., 1969. Soil diversity and the distribution of plants with examples from western North America. *Madrono, 20:* 129–154.

KRUCKEBERG, A. R. & RABINOWITZ, D., 1985. Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics, 16:* 449–479.

KRUGER, F. J. & TAYLOR, H. C., 1979. Plant species diversity in Cape fynbos: gamma and delta diversity. *Vegetatio, 47:* 85–93.

LE MAITRE, D. C. & MIDGLEY, J. J., 1992. Reproductive ecology of fynbos plants. Enigmas in a fire-prone, nutrient-poor environment. In R. M. Cowling (Ed.), *The Ecology of Fynbos. Nutrients, Fire and Diversity:* 135–174. Cape Town: Oxford University Press.

LEWIS, H., 1962. Catastrophic selection as a factor in speciation. *Evolution, 16:* 257–271.

LEWIS, H., 1972. The origin of endemics in the California flora. In D. H. Valentine (Ed.), *Taxonomy, Phytogeography and Evolution:* 179–189. London: Academic Press.

LINDER, H. P., 1985. Gene flow, speciation and species diversity patterns in a species-rich area: the Cape Flora. In E. S. Vrba (Ed.), *Species and Speciation:* 53–57. Pretoria: Transvaal Museum.

LINDER, H. P. & VLOK, J., 1991. The morphology, taxonomy and evolution of *Rhodocoma* (Restionaceae). *Plant Systematics and Evolution, 175:* 139–160.

MAJOR, J., 1988. Endemism: a botanical perspective. In A. A. Myers, & P. S. Giller (Eds), *Analytical Biogeography. An Integrated Study of Animal and Plant Distributions:* 117–146. New York: Chapman and Hall.

MIDGLEY, J. J., 1986. Aspects of phylogeny, evolution and biogeography of the genus *Leucadendron* (Proteaceae). *Palaeoecology of Africa, 17:* 193–200.

MIDGLEY, J. J., 1987. The derivation, utility and implications of divergence index for the fynbos genus *Leucadendron* (Proteaceae). *Botanical Journal of the Linnean Society, 95:* 137–152.

MUSTART, P. J. & COWLING, R. M. 1992. Seed size: phylogeny and adaptation in two closely related Proteaceae species-pairs. *Oecologia, 91:* 292–295.

NORDENSTAM, B., 1969. Phytogeography of the genus *Euryops* (Compositae): a contribution to the phytogeography of southern Africa. *Opera Botanica, 23:* 1–77.

OLIVER, E. G. H., LINDER, H. P. & ROURKE, J. P., 1983. Geographical distribution of present day Cape taxa and their phytogeographical significance. *Bothalia, 14:* 427–440.

PARKER, T. & KELLY, V. R., 1989. Seed banks in California chaparral and other mediterranean climate shrublands. In M. A. Leck, V. R. Parker & R. L. Simpson (Eds), *Ecology of Soil Seed Banks:* 231–255. San Diego: Academic Press.

PHILLIPS, E. P., 1951. *Genera of South African Flowering Plants.* Pretoria: Government Printer.

PIERCE, S. M. & COWLING, R. M., 1991. Dynamics of soil-stored seed banks of six shrubs in fire-prone fynbos. *Journal of Ecology, 79:* 731–747.

RAVEN, P. H., 1964. Catastrophic selection and edaphic endemism. *Evolution, 18:* 336–338.

RAVEN, P. H. & AXELROD, D. I., 1978. Origin and relationships of the California flora. *University of Californian Publications in Botany 72:* 1–134.

REBELO, A. G. (Ed.), 1987. A preliminary synthesis of pollination biology in the Cape flora. *South African National Scientific Programmes Report, 141:* Pretoria: CSIR.

REBELO, A. G. & SIEGFRIED, W. R., 1990. Protection of fynbos vegetation: ideal and real-world options. *Biological Conservation, 54:* 15–31.

RICE, W. R. & SALT, G. W., 1988. Speciation via disruptive selection on habitat preference: experimental evidence. *American Naturalist, 131:* 911–917.

ROURKE, J. P., 1972. Taxonomic studies on *Leucospermum* R. Br. *Journal of South African Botany Supplementary Volume, 8:* 1–194.

SLINGSBY, P. & BOND, W. J., 1985. The influence of ants on the dispersal distance and seedling recruitment of *Leucospermum conocarpodendron* (L.) Buek (Proteaceae). *South African Journal of Botany, 51:* 30–35.

STEBBINS, G. L., 1974. *Flowering Plants, Evolution above the Species Level.* Cambridge, Mass: Harvard University Press.

STEBBINS, G. L. & MAJOR, J., 1965. Endemism and speciation in the California flora. *Ecological Monographs, 35:* 1–31.

STEVENS, G. C., 1989. The latitudenal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist, 133:* 240–256.

TEMPLETON, A. R., 1981. Mechanisms of speciation—a population genetic approach. *Annual Review of Ecology and Systematics, 12:* 23–48.

THODAY, D., 1925. The geographical distribution and ecology of *Passerina. Annals of Botany 39:* 175–208.

THWAITES, R. N., 1987. Preliminary investigation into the geomorphological history of the Agulhas Plain. *South African Geographical Journal, 69:* 165–168.

THWAITES, R. N. & COWLING, R. M., 1988. Soil-vegetation relationships on the Agulhas Plain, South Africa. *Catena, 15:* 333–345.

VAN WILGEN, B. W., BOND, W. J. & RICHARDSON, D. M., 1992. Management of fynbos ecosystems. Principles and scenarios. In R. M. Cowling (Ed.), *The Ecology of Fynbos. Nutrients, Fire and Diversity:* 345–371. Cape Town: Oxford University Press.

VRBA, E. S., 1980. Evolution, species and fossils: how does life evolve? *South African Journal of Science, 76:* 61–84.

VRBA, E. S., 1984. Evolutionary pattern and process in the sister group Alcelaphini-Aepycertini (Mammalia: Bovidae). In N. Eldredge & S. M. Stanley (Eds), *Living Fossils:* 62–79. New York: Springer.

VRBA, E. S. & ELDREDGE, N., 1984. Individuals, hierarchies and processes: towards a more complete evolutionary theory. *Paleobiology, 10:* 146–171.

VRBA, E. S. & GOULD, S. J., 1986. The hierarchical expansion of sorting and selection: sorting and ecological selection cannot be equated. *Paleobiology, 12:* 217–228.

WEATHER BUREAU, 1986. *Climate of South Africa. Statistics up to 1984.* Pretoria: Government Printers.

WEIMARCK, H., 1941. Phytogeographical groups, centres and intervals within the Cape Flora. *Acta University Lund, 37:* 5–143.

WELLS, P. V., 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. *Evolution, 23:* 264–267.

WILLIAMS, I. J. M., 1972. A revision of the genus *Leucadendron. Contributions to the Bolus Herbarium, 3:* 1–425.

WILLIAMS, I. J. M., 1982a. Studies in the genera of the Diosmeae (Rutaceae): 14. A review of the genus *Diosma* L. *Journal of South African Botany, 48:* 329–407.

WILLIAMS, I. J. M., 1982b. Studies in the genera of the Diosmeae (Rutaceae): 13. A revision of the genus *Acmadenia* Bartl. Wendl. *Journal of South African Botany 48:* 169–240.