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Species richness and endemism in the Western Australian flora

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Abstract

Aim Estimates of endemic and non-endemic native vascular plant species in each of the three Western Australian Botanical Provinces were made by East in 1912 and Beard in 1969. The present paper contains an updated assessment of species endemism in the State.

Location Western Australia comprises one third of the continental Australian land mass. It extends from 13° to 35° S and 113° to 129° W.

Methods Western Australia is recognized as having three Botanical Provinces (Northern, Eremaean and South-West) each divided into a number of Botanical Districts. Updated statistics for number of species and species endemism in each Province are based on the Census of Western Australian Plants data base at the Western Australian Herbarium (Western Australian Herbarium, 1998 onwards).

Results The number of known species in Western Australia has risen steadily over the years but reputed endemism has declined in the Northern and Eremaean Provinces where cross-continental floras are common. Only the isolated South-West Province retains high rates of endemism (79%).

Main conclusions With 5710 native species, the South-West Province contains about the same number as the California Floristic Province which has a similar area. The Italian mediterranean zone also contains about this number but in a smaller area, while the much smaller Cape Floristic Region has almost twice as many native species. The percentage of endemic species is highest at the Cape, somewhat less in south-western Australia and less again in California. Italy, at 12.5%, has the lowest value. Apart from Italy, it is usual for endemism to reach high values in the largest plant families. In Western Australia, these mainly include woody sclerophyll shrubs and herbaceous perennials with special adaptations to environmental conditions. While those life forms are prominent in the Cape, that region differs in the great importance of herbaceous families and succulents, both of which are virtually absent from Western Australia. In California and Italy, most endemics are in families of annual, herbaceous perennial and soft shrub plants. It is suggested that the dominant factor shaping the South-West Province flora is the extreme poverty of the area's soils, a feature that emphasizes sclerophylly, favours habitat specialization and ensures relatively many local endemic species.

Keywords

Biodiversity, endemism, California Floristic Province, Cape Floristic Region, Italian mediterranean zone, South-West Province, Western Australia.

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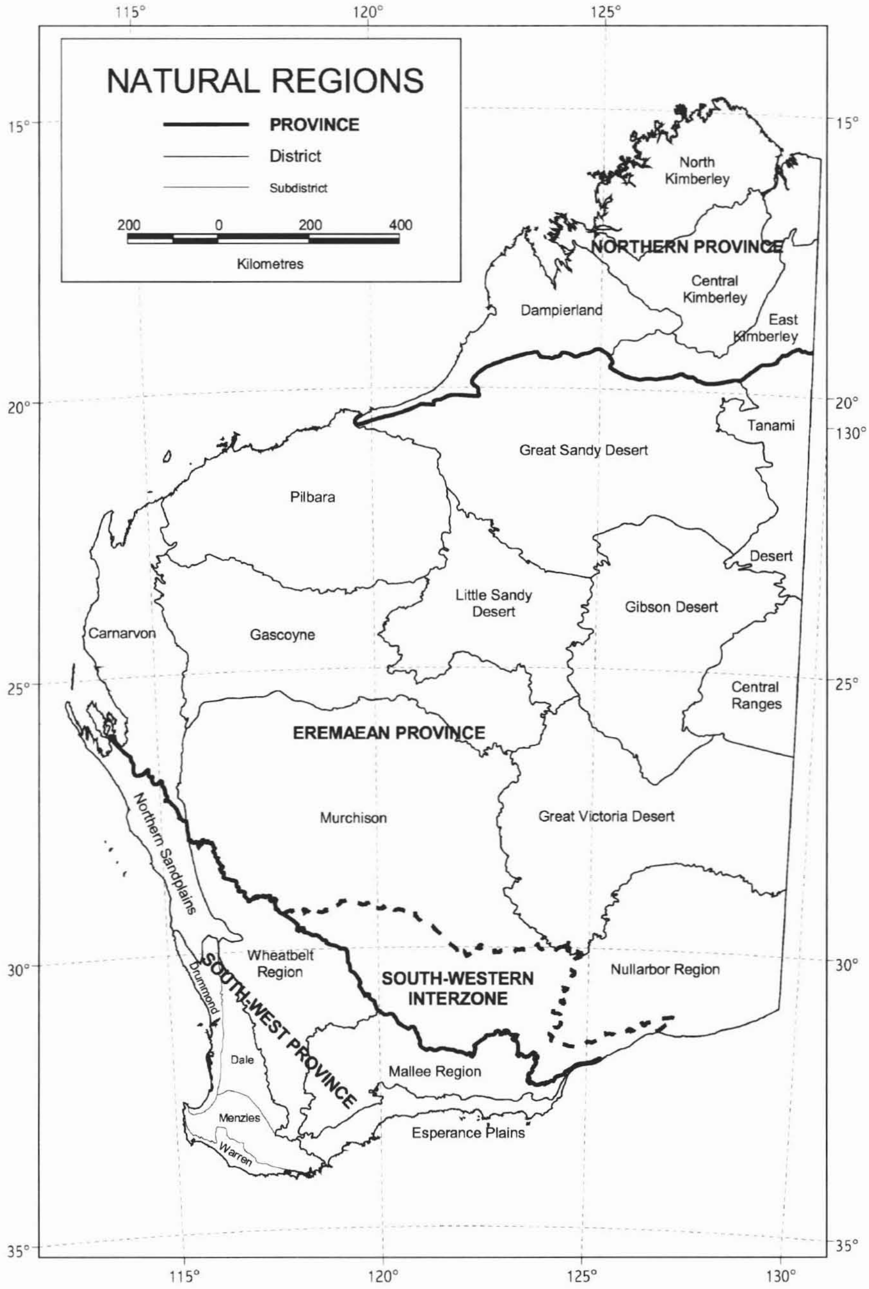

Figure 1 The Natural Regions of Western Australia, otherwise called Botanical Districts, and the Botanical Provinces. After Beard & Sprenger (1984).

INTRODUCTION

The principal object of this paper is to present the results of an updated survey of the Western Australian flora with numbers of native species in the principal biogeographic regions (the Botanical Provinces, Fig. 1) and estimates of endemism. While botanical collections showed that the flora was distinguished by richness and a high degree of endemism, these features could not be quantified. Better estimates were made from time to time, the latest by Beard (1969). However, by employing information systems at the Western Australian Herbarium (Western Australian Herbarium, 1998 onwards), even more reliable statistics were possible.

For comparison, the Western Australian statistics were related to comparable data for other mediterranean regions. The Cape Floristic Region in South Africa is well known and the California Floristic Region a little less so, necessitating some research. A collaborator provided some data for the Mediterranean itself. Only information for the mediterranean region of Chile was unavailable.

Meaningful assessments of endemism must relate to a defined area. Increasingly, geographical definition in Western Australia has come to rely on the ecological regionalizations pioneered by Diels (1906) and Gardner (1944). Beard (1980) described successive treatments which led to the general recognition of three phytogeographic Provinces in Western Australia—Northern, Eremaean and South-West—each divided into a number of Botanical Districts. Beard & Sprenger (1984) (Fig. 1) identified boundaries for these units, based on vegetation mapping (Beard, 1974–81), a treatment that has since been used for the Flora of Central Australia (Jessup, 1981), the Census of Australian Vascular Plants (Hnatiuk, 1990) and largely incorporated in the Interim Biogeographic Regionalization for Australia by Thackway & Cresswell (1995).

The biogeographic treatment of Burbidge (1960) defined a 'South-western Interzone' corresponding to the Coolgardie Botanical District of earlier authors in which floral elements of the South-West and Eremaean Provinces are intermingled. The Interzone has been included here in the Eremaea, maintaining the traditional view of the South-West Province and making comparisons with other mediterranean regions consistent as they have been defined biogeographically in similar terms and exclude semi-desert areas.

METHODS AND APPROACH

Previous Data

Regional estimates of species richness have been difficult to achieve. East (1912) published the estimates incorporated in Table 1. Fifty years later Burbidge (1960) cited 462 genera for the South-West Province, of which 111 were termed endemic, but did not attempt estimates at the species level. Censuses by Gardner (1930) and Green (1985) lack locality details.

Publication of the Descriptive Catalogue of West Australian Plants in 1965 enabled Beard to present estimates of number of species and endemism for all three Botanical Provinces (Beard, 1969).

In East's (1912) figures, endemic species were those 'more or less restricted to each division (province)'. As he was using data from Western Australia only, no account was taken of species extending east over the State boundary, making his estimate of endemism too high. Beard (1969) sought to correct this by adding a study of pan-Australian distributions, so that East's estimate of 64% endemism for the Northern Province was reduced to 29.8%, and further reduced to 14.3% in this study (Table 1). This approach has been important in showing

Table 1 Endemic and non-endemic species of native vascular plants in the Botanical Provinces of Western Australia according to various estimates.

	Species number and percentage of total					
	East (1912)		Beard (1969)		Present authors*	
Northern Province						
Northern only			355	24.6%	241	11.3%
Northern and Eremaean			64	4.4%	47	2.8%
All Provinces			11	0.8%	18	0.8%
Total endemics	780	64%	430	29.8%	306	14.3%
Non-endemic	441		1015	70.2%	1834	85.7%
Total	1221		1445		2140	
Eremaean Province						
Eremaean only			532	29.2%	432	10.9%
Northern and Eremaean			64	3.5%	47	1.2%
Southern and Eremaean			519	28.5%	1506	37.9%
All Provinces			7	0.4%	18	0.4%
Total endemics	614	87%	1122	61.6%	2003	50.4%
Non-endemic	92		700	38.4%	1974	49.6%
Total	706		1822		3977	
South-West Province						
South-West only			2472	68.5%	3000	52.5%
Southern and Eremaean			519	14.3%	1506	26.3%
All Provinces			11	0.4%	18	0.4%
Total endemics	2013	90%	3002	83.2%	4524	79.2%
Non-endemic	226		609	16.8%	1186	20.8%
Total	2239		3611		5710	
Western Australia						
Total endemics	3407	82%	3953	68.0%	5244	62.1%
Non-endemic	759		1849	32.0%	3207	37.9%
Total	4166		5802		8451	

* Figures for endemism are calculated with the Interzone incorporated in the Eremaea.

that the Northern and Eremaean Provinces share pan-Australian floras and are not highly endemic, while the South-West Province is biogeographically isolated from eastern Australia and has developed a specially endemic character. Non-endemic species in the two northern Provinces tend to extend generally through the Tropical & Eremaean Zones of Burbidge (1960), whereas those in the South-West Province have mostly disjunct distributions to the eastern States. This paper continues Beard's previous treatment of endemic species in Table 1.

The *Census of Australian Vascular Plants*

Publication of the *Census of Australian Vascular Plants* (CAVP) (Hnatiuk, 1990) marked a significant step forward. Not only was it the first comprehensive census of the Australian flora since Mueller (1889), it also included data on species distributions for the 97 regions of Australia, 24 of them in Western Australia and corresponding to the divisions of the Botanical Districts of Beard (1980). There were, however, a number of shortcomings in the CAVP. Firstly, the locality data contain omissions for groups of Western Australian species. Secondly, the CAVP has not been updated since 1990 and subsequent work has yielded important additional detail. The taxonomic and distributional information within CAVP was therefore used to supplement recent and more accurate data bases focusing on the Western Australian flora.

Data preparation

The Western Australian Herbarium has an information system allowing it to maintain a comprehensive census of the State's vascular plants (WACensus). It also maintains a specimen record data base for the State collection (WAHerb), with locality details available for most specimens. Information from these systems is available via the FloraBase web site (Western Australian Herbarium, 1998 onwards).

The collections and related research focus on the flora of Western Australia. Thus, while considerable taxonomic and distributional information is available for Western Australian flora, supplementary data were required to establish endemism at a state-wide level. To this end, the CAVP provided distribution information at the national level. That, and flora check lists for South Australia and the Northern Territory, allowed state-wide endemism to be established with some confidence.

Because a study of endemism is as sensitive to species names as to collection sites, steps were taken to ensure precise taxonomic and distributional data.

Substantial processing was required to match names between the various data sources. This was required to accommodate discrepancies in spelling and taxonomic currency. Given the large number of plant names, this process was only feasible with data-base processing technology. Oracle SQL scripts were written to automate this process. Where names did not match perfectly, conservative text-matching algorithms matched names with alternative suffixes or other small differences. This approach struck the balance between achieving true matches and minimizing false positives. Names from sources other than WACensus were checked for synonymy. Where there was clear and unambiguous reference to a more recent name, that change was effected in the data base. A number of mismatches undoubtedly remain, but these are not likely to affect the analysis substantially.

It was also essential to test distributional accuracy. With over 330,000 geocodes to process from WAHerb, a method was required for automatically identifying potential outliers. Outliers could result from positional errors or incorrect identification. They could also represent legitimate populations. Climatic parameters were calculated for each point using BIOCLIM (Nix, 1986; McMahon *et al.*, 1995) including rainfall, temperature and their seasonal variants. Using the environmental envelope described by all available points for a species, a method was developed for identifying extreme outliers and excluding them from further analysis.

Where most climatic parameters for an individual point departed from the mean by at least three standard deviations, that point was excluded from the analysis. To minimize inadvertently excluding disjunct populations, outliers were excluded when they represented fewer than 10% of the points for that species. With this approach a balance was struck between excluding true outliers on the one hand and avoiding inadvertent exclusion of legitimate points on the other. As this methodology is ineffective for species with few records, an arbitrary minimum of 10 records was required before outliers were assessed. Outlier analysis was not performed on species with fewer than 10 records. Distributional information within the CAVP could not be validated using this method as it was recorded at a phyto-geographical district level.

Geographic Information Systems (GIS) technology (ESRI, 1997) was used to intersect species distributional data with Beard's phytogeographic regions (Beard, 1980) for Western Australia and aggregated by botanical province. The resultant data were summarized at different levels to reveal trends and patterns.

Comparison with similar regions

Comparable statistics for other mediterranean regions were obtained where available. These statistics for the Cape Floristic Region in South Africa were available from Bond & Goldblatt (1984) and Cowling & Holmes (1992). For California, the data are less readily applicable since both published floras (Munz & Keck, 1959; Hickman, 1993) cover the State rather than the California Floristic Province. The latter (see Howell, 1957; Raven & Axelrod, 1978, with map) defines the area of mediterranean-type climate and excludes parts of the Great Basin in the north-east and the Mojave and Sonoran deserts in the south-east. On the other hand, it includes small portions of the State of Oregon to the north and of Mexican Baja California in the south. Statistics for the Floristic Province will be available upon completion at Berkeley of an electronic data base (P. Rundel, personal communication).

Statistics for meditterranean biogeographic regions of Italy were provided by Professor Sandro Pignatti (Orto Botanico di Roma, personal communication) and incorporated in Tables 2 and 3. They relate to the zones mapped by Bullini *et al.* (1998). It was not possible to obtain comparable figures for central

Table 2 Attributes of Mediterranean floras of Western Australia, South Africa, California and Italy (native species only)

	South-West Province SWP	Cape Floristic Region CFR	California CFP	Italy IMZ
Area (km^2)	309,840	90,000	324,000*	195,000
No. of families	143	150	154	120
Endemic families	1	6	?	0
No. of genera	711	989	895	1069
Endemic genera	92 (12.9%)	197 (19.5%)	55 (6.1%)*	7 (0.7%)
No. of species	5710	8504	4839	4948
Endemic species	3000 (52.5%)	5783 (68%)	2128 (44.9%)*	628 (12.5%)
Species/genus	8.0	8.6	5.4	4.6
Percentage of flora				
15 largest families	70.3%	64%	66%	70.5%
10 largest genera	27.3%	20.4%	16.0%	11.6%

* Indicates figures for California Floristic Province. Others are for California State.
For SWP, figures are for provincial endemics, for consistency with the other regions.
Sources: South Africa: Bond & Goldblatt (1984), Cowling *et al.* (1992); California Raven & Axelrod (1978) (area); California (endemic genera and species) R. F. Thorne, personal communication (1996); other figures Hickman (1993); Italy: S. Pignatti (personal communication 1999).

Chile. Although it is recognized as a biogeographical region, the *Región del Matorral y del Bosque Esclerófilo* of Gajardo (1993), no separate listing of its flora nor even an estimate of its extent is available.

Taxonomic issues

Different authors apply different taxonomic principles and we needed uniformity for the regional comparisons (Table 3). The Fabaceae and Liliaceae proved the most difficult. The Western Australian Herbarium treats Papilionaceae, Caesalpiniaceae and Mimosaceae as separate families. The CAVP did the same but used Fabaceae as a synonym for Papilionaceae. Bond & Goldblatt (1984) in South Africa and Hickman (1993) in California use Fabaceae as an all-embracing family to include Papilionoideae, Caesalpinioideae and Mimosoideae. For our purposes, we have separated these to follow local practice. Still greater disparity exists in the Liliaceae. The CAVP viewed this as a broad family, excluding only Dasypogonaceae and Xanthorrhoeaceae, while the Western Australian Herbarium recognizes a split into eight families: Alliaceae, Anthericaceae, Asparagaceae, Asphodelaceae, Colchicaceae, Hyacinthaceae, Phormiaceae and Smilacaceae. For comparative purposes we have combined these eight as Liliaceae *sensu lato*. Bond & Goldblatt (1984) regard Liliaceae as exclusively northern hemisphere and recognize seven families: Alliaceae, Asparagaceae, Asphodelaceae, Colchicaceae, Dracaenaceae, Eriospermaceae and Hyacinthaceae. We have combined all seven as Liliaceae *sensu lato*. Hickman (1993) takes a very broad view of Liliaceae, including Liliaceae *sensu stricto* with Alliaceae, Agavaceae, Haemodoraceae and Trilliaceae. We have left the Alliaceae in place but remove the others for uniformity in our Liliaceae *sensu lato*. We use Restionaceae here in the broad sense as the revisionary work of Meney *et al.* (1999) was published subsequent to our data analyses. We follow the Western Australian Herbarium in recognizing the bloodwood group of *Eucalyptus* L. Hér. as the genus *Corymbia* K. D. Hill & L. A. S. Johnson.

RESULTS

Data analysis

A total of 333,416 distributional records for native populations were extracted from WAHerb and aggregated to the species level. Hybrids and unpublished taxa were excluded. In total, 1724 outliers were identified and excluded leaving 331,692 records for further processing. In an attempt to quantify the effects of outlier exclusion, statistics were calculated with and without outlier exclusion.

Percentages of provincial and state level endemism, for all species and at the family level, were unchanged by the exclusion of outliers. However, at the generic level there were modest improvements.

In the case of *Dryandra*, with 91 species in the South-West Province, most of its species are thought to be restricted to that province. With outliers not excluded, analysis showed 10 species extending into the Eremaean Province. Manual inspection of the data showed half of these extensions to be erroneous outliers. After exclusion of outliers, the number of bi-provincial species was reduced to five. Of these, at least two or three species were close to the boundary between provinces. Another bi-provincial species had been derived from incorrect CAVP distributional data which could not be automatically validated. The exclusion methodology seems to have reduced distributional error without excluding important or debatable points.

Flora of the Provinces

Western Australia

Table 1 summarizes endemism values compared with the earlier data of East (1912) and Beard (1969). While the number

Table 3 Number of species and endemism in the 15 largest families and 10 largest genera in comparable mediterranean regions. Columns show the number of native species and the percentage endemism of these. Figures for SWP are for provincial endemism.

South-West Province SWP			Cape Floristic Region CFR			California (State)			Italy IMZ		
	Spp.	Endemism		Spp.	Endemism		Spp.	Endemism		Spp.	Endemism
Families											
Myrtaceae	807	(54%)	Asteraceae	986	62%	Asteraceae	627	31%	Asteraceae	624	23%
Proteaceae	681	(73%)	Ericaceae	672	97%	Papilionaceae	285	38%	Poaceae	419	10%
Papilionaceae	424	(67%)	Mesembryanthemaceae	660	77%	Scrophulariaceae	257	35%	Papilionaceae	378	8%
Mimosaceae	398	(53%)	Papilionaceae	639	82%	Poaceae	251	16%	Brassicaceae	239	16%
Asteraceae	263	(19%)	Iridaceae	612	79%	Liliaceae *sensu lato*	214	49%	Caryophyllaceae	216	16%
Epacridaceae	187	(84%)	Liliaceae *sensu lato*	418	57%	Brassicaceae	197	29%	Apiaceae	211	13%
Goodeniaceae	180	(45%)	Proteaceae	320	96%	Polygonaceae	196	42%	Lamiaceae	188	12%
Orchidaceae	167	(62%)	Restionaceae	310	94%	Cyperaceae	193	13%	Scrophulariaceae	176	18%
Cyperaceae	164	(51%)	Scrophulariaceae	310	52%	Polemoniaceae	168	37%	Liliaceae *sensu lato*	171	13%
Stylidiaceae	154	(75%)	Rutaceae	259	93%	Boraginaceae	140	35%	Rosaceae	162	3%
Poaceae	141	(19%)	Campanulaceae	222	71%	Hydrophyllaceae	139	32%	Ranunculaceae	151	14%
Rutaceae	120	(64%)	Orchidaceae	206	60%	Onagraceae	137	37%	Boraginaceae	95	20%
Chenopodiaceae	118	(6%)	Cyperaceae	203	61%	Rosaceae	136	29%	Cyperaceae	88	6%
Liliaceae *sensu lato*	111	(52%)	Poaceae	181	42%	Apiaceae	132	32%	Orchidaceae	87	3%
Sterculiaceae	99	(65%)	Polygalaceae	139	84%	Lamiaceae	105	48%	Campanulaceae	84	19%
Genera											
Acacia	397	(53%)	Erica	526	96%	Carex	131	17%	Carex	80	6%
Eucalyptus*	254	(47%)	Aspalathus	245	93%	Eriogonum	113	39%	Ranunculus	70	14%
Grevillea	182	(58%)	Ruschia	138	79%	Astragalus	96	47%	Trifolium	66	5%
Stylidium	146	(77%)	Phylica	133	89%	Phacelia	94	38%	Centaurea	60	45%
Melaleuca	106	(48%)	Agathosma	130	96%	Lupinus	71	54%	Silene	57	18%
Leucopogon	104	(87%)	Oxalis	129	70%	Mimulus	63	46%	Euphorbia	57	12%
Hakea	93	(62%)	Pelargonium	125	51%	Arctostaphylos	56	84%	Allium	49	8%
Verticordia	93	(63%)	Senecio	113	52%	Juncus	53	45%	Festuca	46	35%
Dryandra	91	(93%)	Cliffortia	106	90%	Penstemon	52	38%	Galium	45	33%
Daviesia	90	(76%)	Muraltia	106	90%	Cryptantha	52	37%	Vicia	43	7%

* Excludes *Corymbia*.

Sources: South Africa, Bond & Goldblatt (1984); California, Hickman (1993); Italy, S. Pignatti (personal communication 1999).

of recorded species has grown steadily for all Provinces, reputed endemism has declined substantially in the Northern Province and to a lesser degree in the Eremaean but has been maintained in the South-West. The Northern and Eremaean Provinces share in a common Australian flora whereas the South-West has a largely unique biota.

The known flora has grown from 5802 to 8451 published species (46% increase) since 1969, and this process will continue since the Western Australian Herbarium contains representatives of many as yet unpublished taxa. As the number of published species increases most, if not all, of those added will be endemic, further raising percentage endemism. Whenever a genus is revised many new species are normally published. Total endemism figures for Western Australia, however, have decreased to 62.1% now, from 82.0% in 1912 and 68.0% in 1969 (Table 1). That decrease can be attributed to increased knowledge and the greater numbers of collection vouchers and extensions to species distributions, principally affecting the Northern and Eremaean Provinces.

The figures given here are for numbers of native species validly recorded up to January 2000 from WACensus. The number of known species in the state (8451) is at odds with sources such as Hopper *et al.* (1996; Table 2) who give a total of *c.* 12000 plant species, although the taxonomic unit is unclear in that reference. Inspection of the original data base this statistic was based on (WACensus) shows there are *c.* 12000 plant *taxa*, not species.

Northern Province

The Northern Province is now firmly established as an integral part of Burbidge's (1960) Tropical Zone, sharing its flora with the Northern Territory and Queensland. It has a dry tropical climate with summer maximum rainfall and a long dry season. The vegetation consists of savannas with Poaceae and scattered *Eucalyptus* trees. Some endemic species are likely, but at 14.3% the rate is low (Table 1). A few species are shared with the adjacent Eremaean Province and about half the flora is found elsewhere.

A Flora for the Kimberley Region (equivalent to the Northern Province) was published by Wheeler *et al.* (1992) and lists 167 families with 660 genera. Data from WAHerb (January 2000) show 162 families with 645 genera. Variation between the Kimberley Flora and the current data are due to ongoing research and changes in taxonomic concepts.

As may be expected for a savanna region, Poaceae is the largest family in terms of species but there are no large genera. Papilionaceae and Mimosaceae are common in the shrub layer, the latter almost entirely represented by *Acacia* P. Miller. Similarly, the trees are almost entirely *Eucalyptus* and *Corymbia*. Cyperaceae, with two large genera, are numerous. They are typically associated with wet and swampy places such as exist in the Kimberley, e.g. in clay pans and black soil plains. Petheram & Kok (1983) remarked that most sedges occur in areas that are wet for at least part of the year, although some grow in dry sandy soils. Euphorbiaceae may be shrubs or subshrubs, while the remaining four large families tend to be grassland forbs. Apart from Poaceae, there are no large families and the only large genus is *Acacia*. The 10 largest families comprise 50.3% of the flora, the number of species per genus averages 3.3, and endemism is low. Our data record six genera as provincially endemic to the Kimberley, although only one, *Monodia* S. Jacobs (Poaceae, monotypic, *M. stipoides*), was sustained in the Kimberley Flora (Wheeler *et al.*, 1992).

Eremaean Province

The Eremaean Province forms part of Burbidge's (1960) Arid Zone and has a desert climate without an assured growing season. Because average annual rainfall in Western Australia is about 200 mm there is an extensive plant cover with no unvegetated sandhills. Rainfall seasonality varies from summer maximum in the north to evenly distributed in the south. There is no winter-rainfall desert. The vegetation cover varies from dry spinifex grassland (*Triodia* R.Br. and *Plectrachne* Henrard) in the north to low *Acacia* woodlands in the south. On the limestone Nullarbor Plain Chenopodiaceae are dominant.

Species recorded for the Eremaean Province have more than doubled in number since 1969 and show the strong influence of the species-rich, highly endemic flora of the South-West Province. A total of 1506 of the 2003 endemic species are shared with the South-West Province and inflate the overall endemism, which is otherwise quite low (Table 1). Apart from this influence, the Eremaea shares species with the Arid Zone and is not distinctly western in character. We now record 701 genera in 138 families for the Province. Nine genera may be provincially endemic although only two (*Symphiobasis* K. Krause and *Hemiphora* (F. Muell.) F. Muell.) are confirmed in the Flora of Central Australia (Jessup, 1981).

Asteraceae reflect the abundance of spring annuals and Poaceae partly so. Chenopodiaceae characterize the widespread alkaline and saline habitats. Goodeniaceae and Myoporaceae typically contain many arid-zone plants. Mimosaceae are almost entirely represented by *Acacia*. *Eucalyptus* swells the numbers of Myrtaceae but these, together with Papilionaceae and Proteaceae, largely show the influence of the South-West Province. There are no large genera other than *Acacia* and *Eucalyptus*. The 10 largest families comprise 59% of the flora and the number of species per genus averages 5.7. Some families and genera are highly endemic, notably those with South-West affinities, and this results in large differences in number of endemics between the provincial and state lists.

South-West Province

The South-West Province is characterized by winter-rainfall maximum, making it comparable with California, Chile, South Africa and the Mediterranean border lands. Annual rainfall ranges from 1200 mm in the south-west to 300 mm at the provincial boundary in the interior. The vegetation cover consists of eucalypt woodlands and forests, with mixed shrubland (kwongan) on poor sandy soils. There are no grasslands.

The South-West Province is approximately the same area as the Northern but differs in other respects. There are fewer families (143), more genera (711), and more than twice as many species (5710). One family, Cephalotaceae (monotypic,

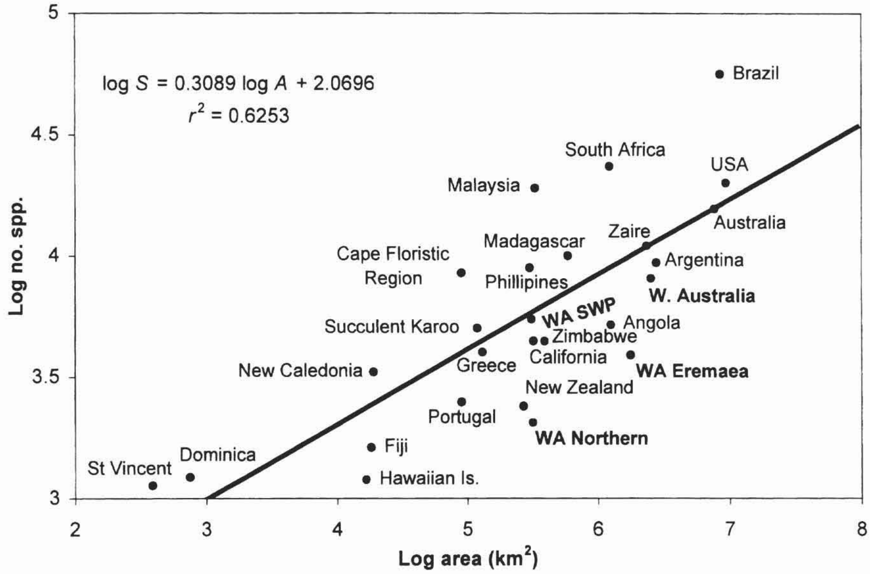

Figure 2 Species–area relationships for Western Australia and other regions (WA, Western Australia).

Cephalotus follicularis Labill.) and 92 genera are provincially endemic. The 15 largest families and 10 largest genera are listed in Table 3. From this table it is seen that families of woody, sclerophyll shrubs predominate (Myrtaceae, Proteaceae, Papilionaceae, Mimosaceae and Epacridaceae) each with many species and very high endemism. Asteraceae are still prominent, but mainly in the drier parts of the Province, as are Chenopodiaceae and Poaceae. These three families show low levels of endemism. Orchidaceae and Liliaceae *sensu lato* are common in the ground layer and Cyperaceae are common mainly in wet places. The 10 largest families comprise 60% of the flora and the number of species per genus averages 8.0; although the 10 largest genera far exceed that.

Out of 5710 species native to the Province, 3000 (53%) are provincial endemics with another 1524 (26%) endemic to Western Australia (by inclusion of species shared with the Eremaea), making the total endemism 4524 (79%, see Table 1). Endemism is barely expressed at the family level, it becomes significant at the generic level, and is strongly exhibited at the species level. High rates of endemism may be seen in many families of the South-West Province, in marked contrast to the Eremaean Province.

Floristic Richness

Western Australia contains 8451 native species (Table 1) and the South-West Province contains 5710 of these, but are these figures high, average or low? According to Cowling *et al.* (1992) 'species diversity is a complex phenomenon which has eluded general explanations'. Estimates of the total world flora of vascular plants vary from 250,000 to 400,000 (Davis *et al.*, 1995). By taking a conservative estimate of 300,000 species, Western Australia contains 3% and the South-West Province just 2%. Local or alpha richness and regional richness are normally distinguished. The former is the number of species occurring together in relatively small sample areas. Regional richness, on the other hand, is the total number of species in a heterogeneous landscape. It is difficult to compare regions on the basis of richness but the difficulty can be overcome by regressing log species number against log area (e.g. Rosenzweig, 1995).

Total numbers of species by country have been published by Davis *et al.* (1995). Figure 2 shows the graph of log species against log area and the fitted regression line with the equation is $\log S = 2.0696 + 0.3089 \log A$ (S = species number, A = area) and $r^2 = 0.63$, $P < 0.0001$. In general, tropical countries have higher than average richness, although the oceanic islands of Fiji and Hawaii are exceptions. South Africa as a whole and its Cape Floristic Region in isolation enjoy high values. All Australian regions are below the line, notably Western Australia's Eremaea and Northern Provinces. The South-West Province compares with other mediterranean regions, e.g. Portugal, Greece and California. Even South Africa's semi-arid Karoo is richer than Western Australia's Eremaean Province.

The tropical countries with high richness are characterized by favourable environments, often allowing the growth of rain forest. As limiting factors take effect, species richness declines: falling temperatures, increasing seasonality of rainfall, aridity, shallow or waterlogged soils. Certain mediterranean climate regions provide striking exceptions to these trends (Cowling *et al.*, 1992) and have remarkably high species densities and levels of endemism despite relatively adverse climatic conditions. While no acceptable general explanations have been advanced for this, reliable figures are now available to describe the floras of mediterranean regions in South Africa, California, Western Australia and the Mediterranean basin (Table 2).

Comparative data for mediterranean regions

The South-West Province of Western Australia (SWP) is about the same size as the California Floristic Province (CFP). The

Italian Mediterranean Zone (IMZ) is about two-thirds the area, while the Cape Floristic Region (CFR) is less than one-third the size of SWP. The number of families represented is similar between all four, with the number of endemic families negligible throughout.

The Cape Floristic Region (CFR) is much richer than the others at the species level in number of species and percentage of endemics, less so at family and generic levels. At the other extreme, Italy is remarkably low in endemics.

Some families in the SWP contain many genera and species, others only few, while endemism varies widely. In numerical order of species (authors' unpublished tables), using figures for total endemics, the first 14 families which have > 100 species per family comprise 9.7% of the total of families, yet they contain half the genera (including half of the endemic genera) and two-thirds of the whole flora (68.6%), with 72.4% of all species endemic to Western Australia. Species endemism in these families is high, averaging 84%. Nine of the families have a very high endemism, up to 97% in the Proteaceae, while three families (Asteraceae with 53%, Chenopodiaceae with 32% and Poaceae with 31%) are less prominent. Cyperaceae are intermediate with 65%. Continuing down the list, the next 46 families have between 10 and 100 species each and account for 27.1% of the total flora and 25.5% of total endemics; the average species endemism is 74.5%. The remaining 83 families, with less than 10 species each, provide only 4.3% of the whole flora with 247 species, of which 94 are endemic (38.1%).

A comparison with other mediterranean regions shows that their floras exhibit similar trends. Table 3 lists the 15 largest families and 10 largest genera for the Cape, California and Italy. Figures for the families at the Cape were published by Bond & Goldblatt (1984), those for the genera were extracted by the senior author. California data were extracted from Hickman (1993) and therefore relate to California State. Figures for Italy were provided by S. Pignatti (personal communication) and relate to the mediterranean portion of that country as shown by Bullini *et al.* (1998; Fig. 6.8). Table 2 shows that the 15 largest families comprise 64% of the total native flora at the Cape, 66% in California, 70% in the South-West Province and 71% in Italy. The 10 largest genera comprise 20.4%, 16.0%, 27.3% and 11.6%, respectively. The regions are not exactly comparable. CFR and SWP are phytogeographically defined. CFP is a political unit, while Italy forms only a small proportion of the Mediterranean.

In families of the South-West Province, woody sclerophyll shrubs are characteristic of the vegetation with high rates of endemism. Herbaceous perennials such as Orchidaceae, Stylidiaceae and Droseraceae tend to high rates, and have evolved special adaptations (Pate & Dixon, 1982; Pate *et al.*, 1984). Low endemism is exhibited by annuals, readily disseminated herbaceous plants and halophytes. Similar trends are shown in the CFR. The Australian family Epacridaceae is of importance in the SWP but at the Cape the related family Ericaceae becomes the dominant one. Proteaceae, Papilionaceae and Rutaceae are equally well represented at the Cape, as are Orchidaceae and Cyperaceae. Restionaceae assume much greater importance at the Cape, and are a diagnostic element in fynbos (Taylor, 1978; Cowling & Holmes, 1992). South Africa differs in the greater importance of Asteraceae (mainly woody plants in fynbos), in the prominence of herbaceous families such as Iridaceae, Scrophulariaceae and Campanulaceae, and in the prominence of succulents, with Mesembryanthemaceae as the third largest family. Succulents are scarcely represented other than by halophytes in SWP. Conversely, Chenopodiaceae are a minor element in the Cape. Succulence in the Cape is also seen in Orchidaceae, Liliaceae *sensu lato* and Iridaceae, most of which produce bulbs and corms and in many cases succulent leaves. Species in these families are much fewer in SWP, and typically produce root and stem tubers, with bulbs and corms being quite rare (Pate & Dixon, 1982). This has led us to the conclusion that factors favouring leaf and stem succulence also operate to favour soft and fleshy underground perennating organs.

In California, woody sclerophyll shrubs are likewise characteristic of the mediterranean shrubland, chaparral, but their families, except for Papilionaceae, are not represented among the top 15 where the trend is towards herbaceous annuals and perennials. *Arctostaphylos* Adans. (Ericaceae) is one of the 10 largest genera but the family does not rank highly, with 95 species. Even among Papilionaceae some genera, e.g. *Astragalus* Tourn. ex L., consist of annuals, herbaceous perennials and soft shrubs. Unlike in South Africa, succulence is not a feature of the California Floristic Province. There are for example 32 species of Cactaceae listed in the *California Flora* (Hickman, 1993) but these belong rather to the desert areas outside the Province. Orchidaceae in the Province are exclusively terrestrial and perennate with rhizomes. Liliaceae are treated in the *Flora* with a somewhat broad concept in 36 genera. Three of these (*Agave* L., *Nolina* Michx., *Yucca* Dill.ex L.) are caulescent woody perennials with rosetted leaves, sometimes succulent; 12 genera produce bulbs, 12 rhizomes, seven corms, and two a stem tuber or caudex. Iridaceae are similarly bulbous. California is therefore similar to South Africa in the underground organs of herbaceous perennials, and differs from Western Australia. In Italy, the largest families show a close similarity to California; 11 of the 15 being the same. The genera are not taxonomically similar, but similar life-forms are represented, e.g. annuals, herbaceous perennials and soft shrubs. As in California, woody sclerophyll shrubs, macchia, dominate the mediterranean shrubland but are not taxonomically diverse. In both areas the intensity of sclerophylly is much less than in SWP or CFR. In California succulence is not a feature, and although *Euphorbia* L. appears among the largest genera its species do not form stem succulents as seen in many parts of Africa. The characteristics of Orchidaceae, Liliaceae *sensu lato* and Iridaceae are also similar to California.

DISCUSSION

Origin and composition of floras

The floristic composition of an area depends on its origins and on local environmental pressure favouring certain families. The Mediterranean and Californian floras share a Laurasian

origin and similar mountainous country frequently with nutrient-rich volcanic and limestone soils. The CFR and SWP share a Gondwanan origin but have very different topography and soils. The CFR is essentially mountainous with steep slopes and shallow soils, while the SWP is an ancient plateau, its surface rocks deeply weathered and covered with highly leached nutrient-poor material.

Endemism

High levels of endemism are often considered characteristic of mediterranean regional floras and our data confirm this, except for Italy where endemism is low at 12.6%. The SWP is biogeographically an island: temperate, relatively humid, cut off for a long period from eastern Australia by the desert. It is one principle of island biogeography that 'given enough time, all insular populations will evolve away from one another and from the mother population' (MacArthur & Wilson, 1963). In this way they develop their own endemic character. This theory was evoked for South Africa by Linder *et al.* (1992) who argued that the region has comprised an edaphic and climatic 'island' since the end of the Tertiary. Recent environmental deterioration has brought about the extinction of many genera and families and stimulated explosive speciation within a limited number of pre-adapted sclerophyllous genera. This argument was applied to the SWP by Hopper (1979) suggesting speciation as a response to repeated climatic fluctuations in the Quaternary. On the other hand, McLoughlin & Hill (1996) cited palaeobotanical studies indicating that south-western Australia has been a major centre of diversity for Myrtaceae and Proteaceae since at least the Eocene. They suggested that the Australian sclerophyll flora evolved initially in response to low soil nutrient levels and was pre-adapted to developing xeric conditions.

Applying the same argument to California and the Mediterranean, the generally lower levels of endemism shown in Table 3 may be attributed to the richer soils, so the low-nutrient factor does not apply. For Italy, it may be that the long period of exposure to human disturbance has eliminated many endemic species that had restricted habitats and that were particularly vulnerable.

Another factor affecting SWP and CFR, in particular, is most likely to have been habitat specialization. Another principle of island biogeography (MacArthur & Wilson, 1963) states that endemic species, not only of plants but of insects and other organisms on relatively species-rich islands, often occur in restricted populations adapted to specialized local habitats. So many endemics tend to distribute in this pattern that it can be inferred that in some way restriction conveys greater stability and mean survival time to the population (MacArthur & Wilson, 1963). Richardson *et al.* (1995) noted that edaphic specialization and associated beta-diversity are extremely high both in fynbos and kwongan (kwongan: see Beard, 1976). As a local example, Taylor & Hopper (1988) recorded that of 60 *Banksia* spp. in Western Australia, 39 occurred only in single specialized habitats. As a means of adapting to extreme nutrient deficiencies this strategy may be expected to have contributed to speciation in the predisposed families.

Sclerophylly and succulence

While all mediterranean-type shrublands are generally described as sclerophyllous, this character is far more pronounced in Australia than elsewhere. Pate *et al.* (1984) published data for the life- and growth-form characteristics of south-western kwongan vegetation, establishing the predominance of simple, microphyllous sclerophyllous leaves (68%). No comparative measurements of sclerophylly appear to have been made in other mediterranean regions. However, it is a matter of common observation that the leaves of Australian Proteaceae, for example, can be rated as several degrees of magnitude more sclerophyllous than those in CFR and CFP. The predominance of sclerophylly in the South-West Province is also shown by the large numbers of species of sclerophyll shrubs and their high endemism, compared with the Cape and California.

Sclerophylly is frequently held to be a response to low availability of nutrients (Beadle, 1966; Rice & Westoby, 1983), and other peculiarities of the Western Australian flora may also be ascribed to this factor. Virtual absence of succulents on poor sandy soils, the lack of bulbous and cormous geophytes, and the small numbers of annuals except immediately after fire when nutrients have been liberated, all suggest the same basic factor, nutrient deficiency. It may be supposed, therefore, that this has operated to select initially those genera which were predisposed to tolerate it, leading to active speciation.

Tree cover

One feature not adequately discussed in the literature is the relative treelessness of the CFR (however, see Cowling & Holmes, 1992). Forest covers only 4.5% of the region (Cowling & Holmes, 1992) and consists of relics of Afromontane rainforest. There are no sclerophyll woodlands or forests; Cape shrublands cover 83% of the region (Cowling & Holmes, 1992). In California and the Mediterranean, low forest dominated by *Quercus* L. spp. is a common vegetation type at lower altitudes, while taller forest of gymnosperms is found at higher levels. Shrubland (chaparral, macchia and matorral) is normally confined, as potential natural vegetation, to dry and shallow soils, although it commonly forms a secondary vegetation following disturbance. The SWP forms the greatest contrast to the CFR where sclerophyll forest and woodland, as original vegetation, covered 41% of the province, mallee 22% and kwongan 33% (Beard & Sprenger, 1984). Mallee is a eucalypt-dominated shrubland considered by Beard (1981) to represent a fire-degraded low forest. Kwongan comprises several types of shrubland, all confined to dry shallow or sandy soils (Pate & Beard, 1984).

A deeply weathered regolith covering most of the SWP provides a deep moisture storage zone favouring widespread tree cover. Much of the CFR consists of mountain slopes with shallow soils, but the readiness of introduced tree species, especially *Pinus* L., to invade fynbos shows that there is somehow an empty niche here. In California, sites with annual precipitation comparable to many fynbos sites are forested (Keeley, 1992). The missing element today may be a forest or woodland dominated by *Widdringtonia* Endl. This is a

formation tolerant of low nutrient status. The present-day distribution suggests that it existed widely in the past, as relics remain scattered from the Cedarberg to Mt. Mulanje. This vegetation has been eliminated by fire aided by climatic change to greater seasonality in rainfall during the Quaternary. A similar situation exists in Australia with the related genus *Callitris* Vent. (Beard, 1974–81).

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BIOSKETCHES

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