

---

CSIRO PUBLISHING

---

# Australian Journal of Botany

Volume 47, 1999

© CSIRO Australia 1999

An international journal for the publication of  
original research in plant science

**[www.publish.csiro.au/journals/ajb](http://www.publish.csiro.au/journals/ajb)**

All enquiries and manuscripts should be directed to

*Australian Journal of Botany*

**CSIRO PUBLISHING**

PO Box 1139 (150 Oxford St)

Collingwood

Vic. 3066

Australia

Telephone: 61 3 9662 7624

Facsimile: 61 3 9662 7611

Email: [simone.farrer@publish.csiro.au](mailto:simone.farrer@publish.csiro.au)



Published by **CSIRO PUBLISHING**  
for CSIRO Australia and  
the Australian Academy of Science



## Is Geographic Range Correlated with Climatic Range in Australian *Spyridium* Taxa?

Fiona Coates<sup>ABC</sup> and J. B. Kirkpatrick<sup>A</sup>

<sup>A</sup>School of Geography and Environmental Studies, University of Tasmania, GPO Box 252-55, Hobart, Tas. 7001, Australia.

<sup>B</sup>Present address: Flora and Fauna Branch, Department of Natural Resources and Environment, GPO Box 500, East Melbourne, Vic. 3002, Australia.

<sup>C</sup>Corresponding author; email: Fiona.Coates@nre.vic.gov.au

### Abstract

The major centres of local endemism and richness at the species level and below in *Spyridium* Fenzl are located on the southern coast of Western Australia and in south-eastern South Australia. There are only a few *Spyridium* taxa with ranges that transgress the boundaries of the following four regions: south-western Western Australia; south-eastern South Australia and western Victoria; eastern Victoria, New South Wales and southern Queensland; Tasmania. Synthetic climatic variables were generated for all recorded populations of *Spyridium* taxa. Variabilities in these were related to the maximum geographic ranges of taxa in Australia as a whole, and within the regions, in order to test the hypothesis that narrow endemism is explained by climatic restriction since the last glacial. In Australia as a whole, local endemics are both narrowly and widely distributed climatically, as are more widespread *Spyridium* taxa, and there were no significant relationships between the climatic and geographic ranges of taxa confined to the Australian mainland regions. However, Tasmanian taxa exhibited a strong positive relationship. Restriction of range as a result of climate change is an unlikely explanation for local endemism in *Spyridium* in mainland Australia, where topographic and climatic gradients are generally subdued, and which apparently experienced less severe climatic oscillations during the Quaternary. However, this hypothesis cannot be rejected for Tasmania, which experienced more extreme Quaternary climatic fluctuations than the present-day areas of mediterranean climate, and hence more severe fluctuations in the area and location of climatically suitable habitats.

### Introduction

Australian species in the Rhamnaceae are notable for their tendency towards rarity, with approximately 30% classified as nationally rare or threatened (Briggs and Leigh 1996; Coates 1996). Rarity in the family is also significant in most state floras, with roughly 30% of Rhamnaceae taxa rare in Western Australia, 25% in New South Wales, 23% in Tasmania, 21% in Queensland, 18% in South Australia and 18% in Victoria (Rye 1995; Briggs and Leigh 1996; Coates 1996; Walsh and Coates 1997). In most cases, rarity can be attributed to a high incidence of narrow endemism in the family, local endemics being defined as taxa that have a maximum geographic range of less than 100 km (Rye 1995; Briggs and Leigh 1996; Walsh and Coates 1997). *Spyridium* is one of the most diverse genera in the Australian Rhamnaceae and also contains a high proportion of narrow endemics (Briggs and Leigh 1996; Coates 1996). The genus is widely distributed in temperate, non-arid Australia, from southern Tasmania to southern Queensland and from eastern New South Wales to the south-west of Western Australia.

Biogeographical approaches to rarity have sought to explain local endemism as an age-related phenomenon primarily linked to long-term climate change. Taxa with narrow range distributions have been interpreted as representing environmental conditions widespread in the past, but less common in the Holocene (e.g. Kirkpatrick and Brown 1984; McGlone 1985; Nimis and Bolognini 1993). An alternative hypothesis associates narrow endemics with

relatively localised refugial environments or microsites which have allowed the persistence of ancient taxa (Stebbins and Major 1965; Raven and Axelrod 1978; Hopper 1979, 1992; Kruckeberg and Rabinowitz 1985). In such sites speciation can occur over considerable time frames, and extinction is a rare event.

These hypotheses imply that rare species are restricted to environments that are rare or restricted in the Holocene, or have arisen in response to pre-Holocene geological or climate change. Given that climatic and edaphic conditions are the major environmental correlates of the present-day range of individual species (Busby 1986a; Grace 1987; Hill *et al.* 1988; Pease *et al.* 1989; Austin *et al.* 1990; Lamont and Connell 1996; but see Hughes *et al.* 1996), and that climate change is a major driving force determining the ranges of species (Bennett 1988; Huntley and Webb 1989), it could be reasonably hypothesised that the geographic ranges of closely related species should be strongly related to their climatic and edaphic ranges.

This paper tests the hypothesis that one aspect of environmental heterogeneity (climate) is related to the geographical extent of individual taxa in *Spyridium* in Australia. The null hypothesis is that there is no difference between widely and narrowly distributed species in terms of the breadth of their climatic envelopes. *Spyridium* is a useful genus to test because it includes an unusually high number of rare or restricted taxa, as well as widespread and disjunct taxa. The genus is confined to southern Australia (113°07'E–152°51'E), and, excluding Tasmanian taxa, nearly all members of the family are concentrated between latitudes 32°00'S and 36°46'S.

## Methods

### Data Collection

The distributions of 47 *Spyridium* taxa, including species, subspecies and varieties, in mainland Australia and Tasmania were identified from records held in State Herbaria and from flora survey records stored on electronic databases in State Government nature conservation agencies. Victorian records were taken entirely from the Department for Natural Resources and Environment's Flora Information System. Where possible, general habitat and environmental information was noted. Tasmanian records were extracted from the Tasmanian Herbarium, from flora survey data, from communication with reliable sources and from personal observation. Most records for Tasmanian *Spyridium* populations were verified in the field.

Locations of taxa recorded on herbarium sheets with any degree of accuracy were geocoded (Kershaw and Nix 1988) by conversion to latitude, longitude and elevation above sea level (in metres) by using 1:100 000 or 1:25 000 topographic maps. Precision was to the nearest minute.

### Taxonomy

A revision of *Spyridium* is currently being prepared (F. Udovicic and K. Thiele, Centre for Plant Biodiversity Research, Canberra; B. Rye, Western Australian Herbarium; and W. R. Barker, Adelaide Herbarium). As a result of this work, a number of new species or taxonomic changes have occurred since publication of the Census of Australian Vascular Plants (Hnatiuk 1990). Some taxa were excluded owing to too few data available at the time of analysis, and some unpublished taxa were included. The latter are currently known as *Cryptandra* sp. A, *C. buxifolia* and *C. scortechinii*, and are referred to here as *Spyridium* sp. A, sp. B and sp. C, respectively. Nomenclature follows Hnatiuk (1990), Barker and Rye (1993) and Rye (1995).

### Distributional Classification of Taxa

Latitudinal and longitudinal ranges for each taxon were converted to their geographic ranges (km) from 1:100 000 topographic maps. A taxon was deemed to be a narrow endemic if it had both a north–south and east–west range of less than 100 km following Brown *et al.* (1983), Hopper and Muir (1984) and Briggs and Leigh (1988). A taxon was deemed to have a disjunct distribution where populations were separated by at least 100 km.

### Bioclimatic Analysis

BIOTCLIM Version 2.0 (Busby 1986b) was used to generate 16 climatic parameters for all locations of *Spyridium* taxa. These were used as predictors in a multivariate discriminant functions analysis after arcsin transformation to fit the assumption of normal distribution. Some widespread taxa were subsampled where numerous records were available: *S. parvifolium*, *S. vexilliferum* var. *vexilliferum*, *S. eriocephalum* var. *eriocephalum* and *S. globulosum*. *Spyridium villosum* and *S. riparium*, which contained only one record at the time of the study, were excluded from the analysis. In some cases there were very few data for some narrow endemics (Table 1), a hazard commonly experienced when dealing with rare species. However, these were retained to maintain as complete a data set as possible and prior probabilities specified according to group size.

As most species had distributions confined to one of four regions, identified by the above analysis, it was possible to test for regional variation in the species range–climatic range relationship. Thus, geographic subsets of the climatic data were analysed in the same manner as the total data set. These subsets were Western Australia, South Australia/western Victoria (west of 142°E), Victoria (east of 142°E)/New South Wales/south-eastern Queensland, and Tasmania.

The degree of climatic variability within the range of each taxon was indicated by calculating the standard deviations from the mean score on each of the first two functions of the climatic ordination. Spearman's coefficient of rank correlation (two-tailed) was used to test the relationships between the maximum of east–west and north–south geographic ranges and the maximum standard deviations of the axis scores on the climatic ordination, for both the total data set and the regional subsets.

The storage, manipulation and analysis of data were carried out by using SYSTAT® Version 7.0 (SPSS Inc. 1997).

## Results

### Geographic Distribution Patterns

Sixteen of the 47 taxa had distributions confined to, or centred on, the south-west of Western Australia. A further 20 taxa occurred from southern South Australia mainly east of the Great Australian Bight, to western Victoria. Thirteen of these taxa occurred on Kangaroo Island and 10 on the Eyre Peninsula. Only three taxa occurred in New South Wales where they are distributed on the seaward slopes of the Great Dividing Range. Nine taxa occurred in Tasmania, with a concentration of six of these on the east coast.

The most widespread taxa were a Western Australian coastal endemic, *S. globulosum*, and the south-eastern Australian taxa *S. vexilliferum* var. *vexilliferum*, *S. parvifolium* and *S. eriocephalum* var. *eriocephalum* (Table 1).

Six taxa had disjunct distributions: *S. tricolor*, *S. subochreatum* var. *subochreatum*, *Spyridium* sp. A, *S. cinereum*, *S. gunnii* and *S. eriocephalum*.

Fourteen species, subspecies and varieties of *Spyridium* of 47 (30%) were local endemics. At the species level, 11 of 37 (30%) had both latitudinal and longitudinal ranges of less than 100 km (Table 1). Local endemic taxa occurred in all regions. However, there were strong concentrations of local endemics in the Stirling Range to Ravensthorpe region of Western Australia and on Kangaroo Island.

Western Australia had six local endemic species and one variety out of a total of 18 taxa (39%). South Australia/western Victoria had two narrow endemic species and two narrow endemic varieties out of a total of 21 taxa (19%). Eastern Victoria/New South Wales/south-east Queensland contained one narrow endemic out of a total of 7 taxa (14%). *Spyridium microphyllum* and *S. obcordatum* were the only narrow endemics in Tasmania, out of a total of nine taxa (22%).

There are very few *Spyridium* taxa that exhibit any degree of edaphic, topographic or altitudinal constancy. *Spyridium globulosum* was the only taxon endemic to mainland Australia with soil/geological descriptions available from two or more sites that was edaphically restricted. All of the Tasmanian endemics occur on a variety of soil and rock types, but are mainly associated with relatively fertile soils (Coates 1996). Most *Spyridium* taxa were concentrated in heathland or shrubland (Coates 1996).

**Table 1. Minimum (lat. min.; long. min.) and maximum (lat. max.; long. max.) latitudinal and longitudinal distributions of *Spyridium* populations, and their corresponding geographic ranges**

Regional representation defined by the first bioclimatic analysis is shown in parentheses. WA, taxon occurs in Western Australia; SA/V, taxon occurs in South Australia/western Victoria; E, taxon occurs in eastern Australia; TAS, taxon occurs in Tasmania; n/a, not available

Taxon	Populations ( <i>n</i> )	Lat. min.	Lat. max.	North–south	Long. min. range (km)	Long. max	East–west range (km)
<i>S. glaucum</i> (WA)	2	33°28′	33°30′	4	120°00′	120°01′	2
<i>S. montanum</i> (WA)	2	34°22′	34°23′	2	118°03′	118°20′	24
<i>S. oligocephalum</i> (WA)	5	33°41′	34°03′	41	118°31′	119°40′	97
<i>S. spadiceum</i> (WA)	4	34°42′	35°02′	37	117°51′	117°55′	6
<i>S. villosum</i> (WA)	1 <sup>A</sup>	n/a	n/a	0	n/a	n/a	0
<i>S. mucronatum</i> var. <i>multiflorum</i> (WA)	3	33°05′	33°36′	57	121°44′	123°18′	94
<i>S. majoranifolium</i> var. <i>pediacum</i> (WA)	3	34°31′	34°35′	7	118°02′	118°13′	15
<i>S. mucronatum</i> var. <i>recurvum</i> (WA)	3	33°45′	34°05′	35	118°16′	119°58′	143
<i>S. mucronatum</i> var. <i>mucronatum</i> (WA)	14	32°57′	33°26′	54	120°05′	123°12′	262
<i>S. globulosum</i> (WA)	101	28°44′	35°08′	710	114°37′	126°28′	995
<i>S. majoranifolium</i> var. <i>majoranifolium</i> (WA)	32	33°29′	35°06′	180	117°41′	123°17′	470
<i>S. microcephalum</i> (WA)	29	32°10′	34°13′	228	117°47′	126°18′	715
<i>S. minutum</i> (WA)	13	32°22′	33°45′	154	120°44′	122°41′	117
<i>S. cordatum</i> (WA)	15	32°59′	33°53′	100	119°23′	123°38′	357
<i>S. riparium</i> (WA)	3 <sup>B</sup>	n/a	n/a	30 <sup>B</sup>	n/a	n/a	30 <sup>B</sup>
<i>S. polycephalum</i> (WA)	11	32°24′	33°59′	176	118°00′	123°52′	493
<i>S. erymnocladum</i> (SA)	2	33°33′	33°37′	7	136°14′	136°26′	17
<i>S. leucopogon</i> (SA/V)	6	34°44′	35°13′	54	135°30′	136°01′	43
<i>S. halmaturinum</i> var. <i>integrifolium</i> (SA/V)	27	35°42′	36°02′	37	136°34′	137°08′	48
<i>S. eriocephalum</i> var. <i>glabrisepalum</i> (SA/V)	5	35°35′	35°47′	22	137°29′	137°56′	38
<i>S. halmaturinum</i> var. <i>halmaturinum</i> (SA/V)	28	35°45′	36°03′	33	136°36′	138°06′	126

<i>S. halmaturinum</i> var. <i>scabridum</i> (SA/V)	7	35°43'	35°53'	19	136°35'	137°52'	108
<i>S. tricolor</i> (WA/SA)	11	31°47'	33°45'	218	123°17'	133°19'	867
<i>S. bifidum</i> var. <i>bifidum</i> (SA/V)	25	32°07'	36°44'	513	135°14'	141° 51'	472
<i>S. bifidum</i> var. <i>integrifolium</i> (SA/V)	9	33°09'	36°10'	335	134°16'	140°27'	519
<i>S. subochreatum</i> var. <i>subochreatum</i> (SA/V)	101	32°20'	36°33'	468	135°46'	142°21'	553
<i>S. subochreatum</i> var. <i>laxiusculum</i> (SA/V)	7	35°11'	36°46'	176	139°14'	140° 22'	95
<i>S. coactilifolium</i>	15	33°38'	35°38'	222	138°28'	138°37'	13
<i>S. nitidum</i> (SA/V)	29	34°21'	36°49'	274	135°27'	140°30'	424
<i>S. phlebophyllum</i> (SA/V)	30	30°20'	33°04'	303	137°58'	139°52'	160
<i>S. phyllicoides</i> (SA/V)	83	31°49'	36°04'	472	132°15'	140°08'	662
<i>S. spathulatum</i> (SA/V)	51	33°39'	36°21'	300	135°33'	141°00'	458
<i>S. thymifolium</i> (SA/V)	91	35°00'	36°32'	170	136°33'	140°19'	316
<i>S. vexilliferum</i> var. <i>latifolium</i> (SA/V)	22	35°47'	36°46'	109	136°48'	140°25'	304
<i>S. sp. A</i> (E)	47	34° 09'	34°17'	14	150°16'	150°21'	8
<i>S. sp. B</i> (E)	4	32°02'	33°22'	150	149°33'	151°21'	160
<i>S. sp. C</i> (E)	11	28°35'	36°43'	900	149°44'	152°51'	280
<i>S. cinereum</i> (E)	11	36°55'	37°40'	83	142°27'	149°57'	630
<i>S. microphyllum</i> (TAS)	17	41°45'	42°37'	96	147°45'	148°15'	42
<i>S. obcordatum</i> (TAS)	8	41°04'	41°13'	17	146°31'	146°46'	21
<i>S. obovatum</i> var. <i>obovatum</i> (TAS)	46	41°01'	43°12'	242	147°11'	148°20'	97
<i>S. obovatum</i> var. <i>velutinum</i> (TAS)	28	41°56'	43°05'	128	147°13'	148°14'	85
<i>S. ulicinum</i> (TAS)	38	41°27'	43°15'	200	146°47'	147°48'	85
<i>S. gunnii</i> (TAS)	18	40°12'	43°09'	327	144°26'	148°05'	307
<i>S. vexilliferum</i> var. <i>vexilliferum</i> (SA/V/TAS)	75	31°05'	42°50'	1304	135°39'	148°20'	1065
<i>S. parvifolium</i> (E/SA/V/TAS)	102	32°43'	41°19'	955	137°15'	149°58'	1068
<i>S. eriocephalum</i> var. <i>eriocephalum</i> (E/SA/V/TAS)	101	32°15'	42°50'	1175	135°41'	147°20'	979

<sup>A</sup>Data obtained from Rye (1995); <sup>B</sup>data not available at the time of the analysis.

### Climatic Distribution Patterns

#### Full data set

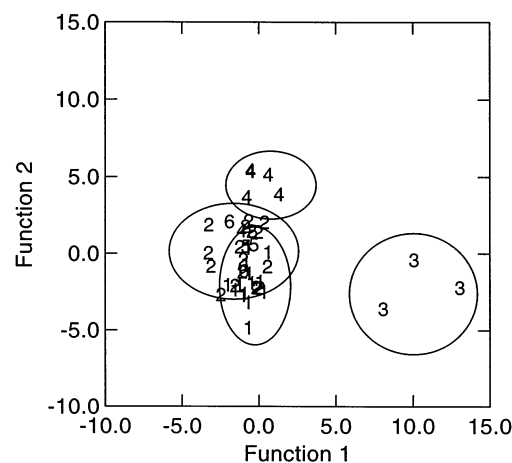
The first discriminant function maximally separated eastern Australian taxa from all other groups (Fig. 1), and accounted for 30% of between-group variability. The most significant predictors for distinguishing groups were precipitation of the warmest quarter (0.6) and mean temperature of the driest quarter (−0.5). The second discriminant function, which also accounted for 30% of between-group variability, maximally separated taxa confined to Tasmania from all other regions (Fig. 1). There was some overlap in the ordination space on Function 2 between taxa distributed in Western Australia and those distributed in South Australia/western Victoria and in eastern Australia. The most significant predictors that distinguished groups were mean annual temperature (0.6) and coefficient of variation of monthly precipitation (−0.6).

There was no significant rank order correlation between the maximum geographic extent of a taxon and its maximum standard deviation from the mean score of the first two discriminant functions of the climatic ordination ( $R_s = 0.3$ , d.f. = 44,  $P > 0.05$ ) (Fig. 2).

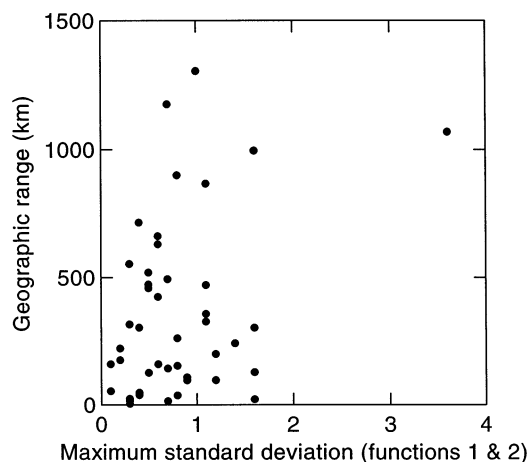
#### Regional data sets

The most significant predictors on the first function of the Western Australian discriminant functions analysis were mean precipitation in the wettest month (−0.8), mean precipitation in the wettest quarter (−0.8), and mean precipitation in the coolest quarter (−0.8). This function accounted for 45% of the between-group variability. On the second function, which accounted for 20% of the between-group variability, significant predictors were mean temperature of the coolest quarter (0.6), mean temperature of the wettest quarter (0.6), and mean minimum temperature of the coolest month (0.5).

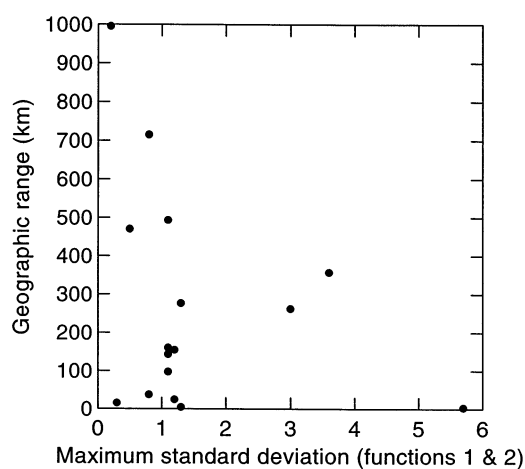
There was not a significant rank order correlation between maximum geographic extent and the highest standard deviation for the first two discriminant functions ( $R_s = -0.3$ , d.f. = 15,  $P > 0.05$ ) (Fig. 3).



**Fig. 1.** First bioclimatic analysis for all populations of *Spyridium* taxa. Numbers represent the mean canonical score for each taxon according to region. 1 = Western Australia; 2 = South Australia/western Victoria; 3 = eastern Australia; 4 = Tasmania; 5 = disjunct between regions; 6 = widespread between regions.



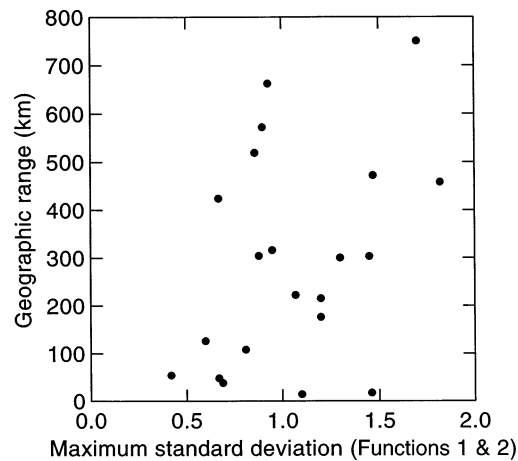
**Fig. 2.** Spearman's coefficient of rank correlation between geographic range and maximum standard deviation from the mean score on each of the first two axes of the first bioclimatic analysis using all *Spyridium* population data ( $R_s = 0.3$ , d.f. = 44,  $P > 0.05$ ).



**Fig. 3.** Spearman's coefficient of rank correlation between geographic range and maximum standard deviation from the mean score on each of the first two axes of the first bioclimatic analysis using population data for *Spyridium* distributed in Western Australia ( $R_s = -0.3$ , d.f. = 15,  $P > 0.05$ ).

For the South Australian/western Victorian analysis, taxa were maximally separated along the first function by seasonality (0.8); mean precipitation in the wettest month (0.7), wettest quarter (0.7) and coolest quarter (0.7); and mean maximum temperature in the warmest month (−0.7). This function accounted for 43% of the between-group variability. Predictors best explaining the separation of taxa on the second function, which accounted for 19% of the between-group variability, were mean temperature in the coolest quarter (−0.6), mean precipitation in the driest month (0.6), and mean precipitation in the driest quarter (0.6).





**Fig. 4.** Spearman's coefficient of rank correlation between geographic range and maximum standard deviation from the mean score on each of the first two axes of the first bioclimatic analysis using population data for *Spyridium* distributed in South Australia/western Victoria ( $R_s = 0.3$ , d.f. = 20,  $P > 0.05$ ).

There was not a significant rank order correlation between the maximum geographic extent of a taxon and its maximum standard deviation from the mean score of the first two discriminant functions of the climatic ordination ( $R_s = 0.3$ , d.f. = 20,  $P > 0.05$ ) (Fig. 4).

The most significant predictors on Function 1 for the eastern Australian discriminant analysis, which accounted for 62% of the between-group variability, were mean temperature of the wettest quarter (0.5) and mean temperature of the driest quarter (−0.4). Significant predictors on Function 2 were mean temperature of the warmest quarter (0.6) and mean maximum temperature of the warmest month (0.6). This function accounted for 20% of the between group variability.

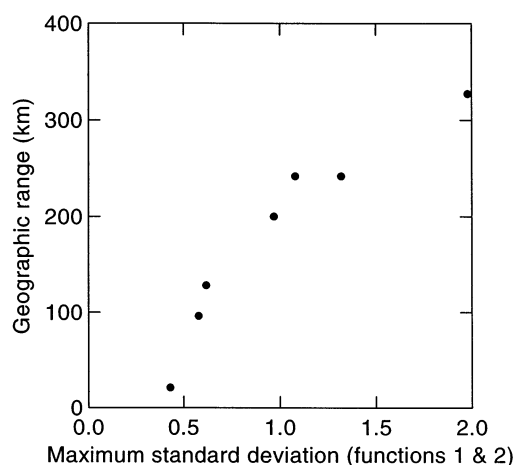
There were insufficient data for correlations.

There were no significant predictors on Function 1 in the Tasmanian discriminant analysis. Taxa were widely separated into two groups consisting of one outlying taxon, *S. vexilliferum*, and all other taxa, which were compressed at the opposite end of the axis, accounting for 98% of the between-group variability. Consequently, a second analysis was carried out, excluding *S. vexilliferum*. The first two discriminant functions from this analysis accounted for 56 and 35%, respectively, of the between-group variability. Taxa were maximally separated on the first function by variation of monthly precipitation (−0.8) and rainfall in the coolest quarter (−0.5). Significant predictors on the second axis were mean precipitation of the driest month (−0.6) and driest quarter (−0.5), and annual rainfall (0.5).

There was a strongly positive rank order correlation between the maximum geographic extent of a taxon and its maximum standard deviation from the mean score of discriminant Functions 1 and 2 of the climatic ordination ( $R_s = 0.99$ , d.f. = 6,  $P < 0.005$ ) (Fig. 5).

## Discussion

The lack of any significant relationship between geographic extent and climatic range in regional mainland Australian *Spyridium* taxa contrasts markedly with the strong positive relationship in Tasmanian *Spyridium* taxa.



**Fig. 5.** Spearman's coefficient of rank correlation between geographic range and maximum standard deviation from the mean score on each of the first two axes of the first bioclimatic analysis using population data for *Spyridium* distributed in Tasmania ( $R_s = 0.99$ , d.f. = 44,  $P < 0.005$ ).

One hypothesis to explain this inter-island difference could be that the critical environmental variables controlling *Spyridium* distribution patterns, and in particular, those of narrow endemics, tend more to the physical than the climatic on mainland Australia and the reverse in Tasmania. However, information on environmental conditions that was gleaned from herbarium specimens, databases, the literature and observation, suggests that there are very few *Spyridium* taxa that exhibit any degree of edaphic, altitudinal or topographic constancy. Only one (wide ranging) coastal species was apparently restricted by soil type.

The lack of any relationship between geographic extent and climatic range in the mediterranean climatic regions and its contrasting strength in Tasmania might alternatively be related to the relative impacts of Quaternary climatic fluctuations on the areas and locations of climatically suitable habitats.

In Tasmania, there is good palynological and geomorphic evidence of temperature fluctuations in the order of 6–7°C and a halving of precipitation during the late Last Glacial Maximum compared with the present (Bowden 1983; Goede *et al.* 1990; Colhoun *et al.* 1996; Kirkpatrick and Fowler 1998). Alpine vegetation and ice are thought to have covered a large proportion of the then Tasmanian Peninsula at the height of glacial periods (Kirkpatrick 1986; Colhoun *et al.* 1996; Kirkpatrick and Fowler 1998), forests were dramatically reduced in area compared with the present, and woodlands and lowland treeless vegetation were much more extensive than today. *Spyridium* is seldom encountered as a component of the forest vegetation of Tasmania. As forests expanded from glacial refugia (Macphail and Jackson 1978; Macphail 1979; Thomas and Kirkpatrick 1996), woodland and lowland treeless vegetation was likely to have become dramatically reduced in area and more highly fragmented. One explanation for the close relationship between area and climate in Tasmania may be that *Spyridium* taxa were associated with treeless plant communities which have since become relictual.

Unfortunately, fossil evidence is limited or non-existent for regions where endemic *Spyridium* taxa are concentrated in Tasmania at present. Past floras of the east coast region in particular are not known, and the history of the shrubby east coast endemic flora in particular

is poorly understood. There is some evidence in the north of the state to suggest that the vegetation of at least parts of the south-western Bassian Plain during the last glacial included phases of heathland and shrubland (Colhoun 1977; Hope 1978). These communities are not represented in contemporary vegetation. However, patterns of coexistence within communities can change over time (Huntley and Webb 1989; Valentine and Jablonski 1993; Thomas 1994; Roy *et al.* 1996). Thus, the Tasmanian *Spyridium* taxa may occur within subsets of their past environmental ranges and within communities that have no past analogues.

The part of the south-west of Western Australia that forms the heartland of *Spyridium*, and other genera (Groom and Lamont 1996; Lamont and Connell 1996), has some of the highest levels of species richness recorded within the temperate zone (George *et al.* 1979; Lamont *et al.* 1984). This richness may indicate an accumulation of species in response to relatively constant environmental conditions (Diels 1906 in Beard 1984; Marchant 1973; George *et al.* 1979; Hopper 1979, 1992), a conclusion consistent with gentle topographic and climatic gradients and apparently less severe climatic fluctuations than that which occurred in Tasmania. The region has remained unglaciated since the Permian (Hopper 1979), with the development of a mediterranean-type climate from the late Tertiary (Bowler 1982). The forests of the far south-west of Western Australia, although probably reduced in area, certainly survived glacial times, and the kwongan belt, in which almost all the *Spyridium* taxa are found, is likely to have moved towards the coast in response to Arid Zone encroachment during cooler, drier climatic phases and lower sea levels (Hopper 1979), but may not have been dramatically reduced in area. Nevertheless, given the lack of relative relief over most of the present and putative past potential range of *Spyridium* species and gentle climatic gradients, individual species may have migrated over substantial distances. In the present mediterranean climate, it is unlikely that shrub-dominated vegetation was displaced or forced onto marginal sites by post-glacial forest expansion, as was likely to have been the case in Tasmania.

In the south-east of South Australia, *Spyridium* taxa were concentrated in areas known for levels of local endemism which are relatively high for the state, and which also experience a mediterranean-type climate. There is very little Quaternary palaeoenvironmental evidence for the region but it is highly likely that none of these areas was alpine during glacial maxima. The extremes of climatic fluctuation hypothesised for Tasmania are unlikely to have been felt in the lower latitudes of the South Australian/western Victorian region. Except for the Lofty and southern Flinders Ranges, topographies as well as climatic gradients are relatively gentle. Forest species survived in the Mt Lofty Range and losses of range to increased aridity would have been partly compensated for by exposure of the continental shelf.

Thus, in contrast to Tasmania, where the area occupied by vegetation suited to extant *Spyridium* species is likely to have dramatically contracted in the transition from glacial to interglacial environments, the area of vegetation suited to extant *Spyridium* species on the mainland is likely to have remained relatively constant, or even been larger in glacial times.

*Spyridium* taxa are obligate seed regenerators with poor dispersal abilities (Coates 1996). This suggests that they would have had limited opportunity to migrate in response to the climatic amelioration of the last 10 millennia. In the mediterranean zone of south-western and southern mainland Australia, the locations of glacial populations may have had more of an influence on present ranges than the present climate, simply because many species have not been able to occupy their potential ranges in the time available to do so. In contrast, a reduction from a more widespread range, as in Tasmania, could have occurred *in situ*, especially given the major influence of topography on microclimate at mid-latitudes (Kirkpatrick and Nunez 1980). Thus, in Tasmania reductions in the climatic ranges available to species as a result of the displacement of open, lowland vegetation by forest with climatic amelioration has resulted in concomitant reductions in geographic ranges.

The largely coincident locations of centres of richness and local endemism in *Spyridium*, *Hakea* and *Banksia* (this study; Groom and Lamont 1996; Lamont and Connell 1996) in

south-western Australia may indicate a part of the ranges of the component species that are at the humid end of their potential at the moment and the dry end of their potential during glacial times. Incomplete dispersal from varying last glacial ranges would account for the lack of correspondence between present climatic range and geographic range.

In South Australia/western Victoria concentrations of *Spyridium* species are generally in areas with relatively high rainfall. These are also highly likely to have been the higher-rainfall areas during the heights of glacials. Colonisation of other areas following the likely expansion of suitable habitat is probably incomplete, or in some moist, elevated areas, restricted by local forest expansion. In the case of Kangaroo Island, the potential for expansion was truncated in the mid-Holocene when the rise in sea levels cut off access to climatically similar areas on the mainland of Australia. The mainland species have had a longer time to occupy their potential climatic ranges, but are unlikely to have done so in most cases.

Our results support the notion that local endemism in *Spyridium* is related to pre-Holocene climatic events. However, only in Tasmania can climatic fluctuation be nominated as a possible underlying cause of narrow range distributions, resulting in the hypothesised present situation of localised climatic confinement. Alternative hypotheses, such as confinement to localised refugial environments not markedly affected by climate change or restriction to microsites, might explain narrow endemism in mediterranean-zone *Spyridium* taxa.

Clearly there is a need for a more complete palaeoenvironmental record in the Australian mediterranean zone. Further comparisons of the relationship between geographic range and climatic range in other large genera with a Tasmania/mediterranean zone pattern of distribution are also necessary to determine whether the differences documented herein are general. If they are, the historical hypothesis outlined above would be given greater veracity.

### Acknowledgments

This work was funded by an Australian Postgraduate Research Award. We thank John Busby (Environmental Resources Information Network, Canberra) for providing a copy of BIOCLIM and Fiona Cross (Arthur Rylah Institute, Department of Natural Resources and Environment, Victoria) for extracting Victorian site records. Bill Barker (Adelaide Herbarium), Barbara Rye (Western Australian Herbarium), Frank Udovicic and Kevin Thiele (Centre for Plant Biodiversity Research, Canberra) also provided species records. The Botany School, University of Melbourne, kindly provided FC with facilities to complete the study.

### References

- Austin, M. P., Nicholls, A. O., and Margules, C. R. (1990). Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs* **60**, 161–177.
- Barker, W. R., and Rye, B. L. (1993). *Spyridium tricolor* (Rhamnaceae), a disjunct new species from the Great Australian Bight. *Journal of the Adelaide Botanic Gardens* **15**, 153–157.
- Beard, J. S. (1984). Biogeography of the Kwongan. In 'Kwongan, Plant Life of the Sandplain'. (Eds J. S. Pate and J. S. Beard.) pp. 1–26. (University of Western Australia Press: Nedlands, Western Australia.)
- Bennett, K. D. (1988). Post-glacial vegetation history: ecological considerations. In 'Vegetation History'. (Eds B. Huntley and T. Webb III.) pp. 699–725. (Kluwer Academic Press: Dordrecht.)
- Bowden, A. R. (1983). Relict terrestrial dunes: legacies of a former climate in coastal northeastern Tasmania. *Zeitschrift für Geomorph.* N. F. Suppl.-B. D. **45**, 153–174.
- Bowler, J. M. (1982). Aridity in the late Tertiary and Quaternary of Australia. In 'Evolution of the Flora and Fauna of Arid Australia'. (Eds W. R. Barker and P. M. J. Greenslade.) pp. 35–46. (Peacock Publications in association with the Australian Systematic Botany Society and ANZAAS South Australian Division Inc.: Frewville.)
- Briggs, J. D., and Leigh, J. H. (1996). 'Rare or Threatened Australian Plants.' (CSIRO: Australia.)
- Brown, M. J., Kirkpatrick, J. B., and Moscal, A. (1983). 'An Atlas of Tasmania's Endemic Flora.' (Tasmanian Conservation Trust: Hobart.)

- Busby, J. R. (1986a). A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in south-eastern Australia. *Australian Journal of Ecology* **11**, 1–7.
- Busby, J. R. (1986b). 'Bioclimate Prediction System (BIOCLIM). User's Manual Version 2.0.' (Australian Biological Resources Study Leaflet: Canberra.)
- Coates, F. (1996). Ecological and biogeographical correlates of rarity in *Spyridium microphyllum* and *Spyridium obcordatum*. Ph.D. Thesis, University of Tasmania.
- Colhoun, E. A. (1977). Late Quaternary fan gravels and slope deposits at Rocky Cape, northwestern Tasmania: their palaeoenvironmental significance. *Papers and Proceedings of the Royal Society of Tasmania* **11**, 13–39.
- Colhoun, E. A., Hannan, D., and Kiernan, K. (1996). Late Wisconsin glaciation of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **130**, 33–45.
- George, A. S., Hopkins, A. J. M., and Marchant, N. G. (1979). The heathlands of Western Australia. In 'Ecosystems of the World. Vol. 9A. Heathlands and Related Shrublands. Descriptive Studies'. (Ed. R. L. Specht.) pp. 211–230. (Elsevier Scientific Publishing Company: Amsterdam.)
- Goede, A., Veeh, H. H., and Ayliffe, L. K. (1990). Late Quaternary palaeotemperature records for two Tasmanian speleothems. *Australian Journal of Earth Sciences* **37**, 267–278.
- Grace, J. (1987). Climatic tolerance and the distribution of plants. *New Phytologist* **106** (Suppl.), 113–130.
- Groom, P. K., and Lamont, B. B. (1996). Ecogeographic analysis of *Hakea* (Proteaceae) in south-western Australia with special reference to morphology and life-form. *Australian Journal of Botany* **44**, 527–542.
- Hill, R. S., Read, J., and Busby, J. R. (1988). The temperature-dependence of photosynthesis of some Australian temperate rainforest trees and its biogeographical significance. *Journal of Biogeography* **15**, 43–49.
- Hnatiuk, R. J. (1990). 'Census of Australian Vascular Plants.' (Australian Flora and Fauna Series Number 11: Canberra.)
- Hope, G. S. (1978). The Late Pleistocene and Holocene vegetational history of Hunter Island, northwestern Tasmania. *Australian Journal of Botany* **26**, 493–514.
- Hopper, S. D. (1979). Biogeographical aspects of speciation in the southwest Australian flora. *Annual Review of Ecology and Systematics* **10**, 399–422.
- Hopper, S. D. (1992). Patterns of plant diversity at the population and species levels in south-west Australian mediterranean ecosystems. In 'Biodiversity of Mediterranean Ecosystems in Australia'. (Ed. R. J. Hobbs.) pp. 27–46. (Surrey Beatty and Sons Pty Ltd: NSW.)
- Hopper, S. D., and Muir, B. G. (1984). Conservation of the Kwongan. In 'Kwongan, Plant Life of the Sandplain'. (Eds J. S. Pate and J. S. Beard.) pp. 253–266. (University of Western Australia Press: Nedlands, Western Australia.)
- Hughes, L., Cawsey, E. M., and Westoby, M. (1996). Geographic and climatic range sizes of Australian eucalypts and a test of Rapoport's rule. *Global Ecology and Biogeography Letters* **5**, 128–142.
- Huntley, B., and Webb, T., III (1989). Migration: species' response to climatic variations caused by changes in earth's orbit. *Journal of Biogeography* **16**, 5–19.
- Kershaw, A. P., and Nix, H. A. (1988). Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant taxa. *Journal of Biogeography* **15**, 589–602.
- Kirkpatrick, J. B. (1986). Tasmanian alpine biogeography and ecology and interpretations of the past. In 'Flora and Fauna of Alpine Australasia'. (Ed. B. A. Barlow.) pp. 229–242. (CSIRO Australia in association with the Australian Systematic Botany Society: Australia.)
- Kirkpatrick, J. B., and Brown, M. J. (1984). The palaeogeographic significance of local endemism in Tasmanian higher plants. *Search* **15**, 112–113.
- Kirkpatrick, J. B., and Fowler, M. (1998). Locating likely glacial refugia in Tasmania using palynological and ecological information to test alternative climatic models. *Biological Conservation* **85**, 171–182.
- Kirkpatrick, J. B., and Nunez, M. (1980). Vegetation-radiation relationships in mountainous terrain: eucalypt-dominated vegetation in the Risdon Hills, Tasmania. *Journal of Biogeography* **7**, 197–208.
- Kruckeberg, A. R., and Rabinowitz, D. (1985). Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* **16**, 447–479.
- Lamont, B. B., and Connell, S. W. (1996). Biogeography of *Banksia* in south-western Australia. *Journal of Biogeography* **23**, 295–309.

- Lamont, B. B., Hopkins, A. J. M., and Hnatiuk, R. J. (1984). The flora—composition, diversity and origins. In 'Kwongan, Plant Life of the Sandplains'. (Eds J. S. Pate and J. S. Beard.) pp. 27–50. (University of Western Australia Press: Nedlands, Western Australia.)
- Macphail, M. K. (1979). Vegetation and climate in southern Tasmania since the last glaciation. *Quaternary Research* **11**, 306–341.
- Macphail, M. K., and Jackson, W. R. (1978). The late Pleistocene and Holocene history of the Midlands of Tasmania. *Proceedings of the Royal Society of Victoria* **90**, 287–300.
- Marchant, N. G. (1973). Species diversity in the south-western flora. *Journal of the Royal Society of Western Australia* **56**, 23–30.
- McGlone, M. S. (1985). Plant biogeography and the late Cenozoic history of New Zealand. *New Zealand Journal of Botany* **23**, 723–749.
- Nimis, P. L., and Bolognini, G. (1993). Quantitative phytogeography of the Italian beech forests. *Vegetatio* **109**, 125–143.
- Pease, C. M., Lande, R., and Bull, J. J. (1989). A model of population growth, dispersal and evolution in a changing environment. *Ecology* **70**, 1657–1664.
- Raven, P. H., and Axelrod, D. I. (1978). 'Origin and Relationships of the Californian Flora.' (University of California Publications in Botany 72.)
- Roy, K., Valentine, J. W., Jablonski, D., and Kidwell, S. M. (1996). Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends in Ecology and Evolution* **11**, 458–463.
- Rye, B. L. (1995). New and priority taxa in the genera *Spyridium* and *Trymalium* (Rhamnaceae) of Western Australia. *Nuytsia* **10**, 119–140.
- Stebbins, G. L., and Major, J. (1965). Endemism and speciation in the Californian flora. *Ecological Monographs* **35**, 1–35.
- SPSS Inc. (1997). 'Systat® 7.0 for Windows. Statistics.' (SPSS Inc.: Evanston IL, USA.)
- Thomas, C. D. (1994). Extinction, colonization, and metapopulations: environmental tracking by rare species. *Conservation Biology* **8**, 373–378.
- Thomas, I., and Kirkpatrick, J. B. (1996). The roles of coastlines, people and fire in determining the development of heathlands in northeast Tasmania. *Journal of Biogeography* **23**, 717–728.
- Valentine, J. W., and Jablonski, D. (1993). Fossil communities: compositional variation at many time scales. In 'Species Diversity in Ecological Communities'. (Eds R. E. Ricklefs and D. Schluter.) pp. 341–349. (University of Chicago Press: IL.)
- Walsh, N. G., and Coates, F. (1997). New taxa, new combinations and an infrageneric classification in *Pomaderris* (Rhamnaceae). *Muelleria* **10**, 27–56.

Manuscript received 4 August 1997, accepted 14 July 1998