

Endemism in the Australian flora

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Abstract

Aim To detect centres of vascular plant endemism at a continental scale by analysis of specimen-based distributional data and to relate any pattern to environmental factors and history.

Location Australia.

Methods Presence of 8468 seed plant species-level taxa throughout continental Australia and Tasmania was mapped on a 1° grid to visualize the pattern of species richness. This sample comprises half the known flora. Three indices of endemism were calculated but we preferred one that is unrelated to species richness, so that these two concepts could be distinguished in practice. Centres of endemism were detected by simple mapping and by spatial autocorrelation analysis (SAC). Linear regression was used to examine the relationship of the patterns of species richness and endemism to latitude, topography and climate.

Results Both species richness and endemism vary greatly across the continent but in most cases the same centres were high in both richness and endemism. Twelve distinct centres were identified. The major centres of both diversity and endemism are south-west western Australia, the Border Ranges between New South Wales and Queensland, the Wet Tropics near Cairns, Tasmania and the Iron-McIlwraith Range of eastern Cape York Peninsula. The last centre appears to be more significant than recognized by past authors. Whether this is a true Australian centre of endemism, or is largely an outlier of the flora of Papua New Guinea, is explored. Another centre, in the Adelaide–Kangaroo Island region, has been overlooked altogether by previous authors. Regression analysis did not find a simple climatic explanation of the observed patterns. There was a suggestion that topographic variation within the 1° cells may be positively correlated with endemism, which is consistent with mountainous regions functioning as refugia. One clear result is that all the major centres of endemism are near-coastal. A likely explanation is that Pleistocene expansions of the central desert have been a powerful limitation on the viability of refugia for narrowly endemic species. All the centres of endemism lie outside the estimated limits of the expanded arid zone at the last glacial maximum (18,000 yr BP). In particular, the ‘Central Australian Mountain Ranges centre of plant diversity and endemism’ of Boden & Given (1995) is detected as a strong centre of species richness, but not at all as a centre of endemism. This is despite good sampling of this region.

Main conclusions Endemism can be distinguished from species richness by using an appropriate index and mapping of such indices can detect centres of endemism. This study demonstrates the value of specimen based distributional data, such as is held in state herbaria and museums.

Keywords

Biodiversity, endemism, species richness, Australia, Pleistocene, refugia, extinction, climate.

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INTRODUCTION

The concept of endemism is central to the study of biogeography. A taxon (e.g. a species) is considered endemic to a particular area if it occurs only in that area (Anderson, 1994). It has often been observed that quite small areas have a high concentration of endemics, irrespective of the overall richness of taxa (Wallace, 1855; Gentry, 1986; Hill & Read, 1987; Major, 1988; Gess, 1992; Barrington, 1993; Anderson, 1994; Ceballos & Brown, 1995; Williams & Pearson, 1997). Ecologists are interested in areas of endemism because of their importance in conservation – narrowly endemic species are by definition rare, and therefore potentially threatened (Crosby, 1994; Fjeldsa, 1994; Linder, 1995; Blackburn & Gaston, 1996; Ceballos *et al.*, 1998; Myers *et al.*, 2000). Biogeographers are interested in explaining why areas of endemism occur, whether by a unique combination of ecological factors restricting the ranges of taxa, or because of a history of vicariance and speciation in isolation followed by continued range restriction (Nelson & Platnick, 1981; Wiley, 1981; Major, 1988; Anderson, 1994; Brown & Lomolino, 1998; Humphries & Parenti, 1999). Some authors have argued that biogeographic analysis should not be linked explicitly to delimited areas (Henderson, 1991; Hovenkamp, 1997), and panbiogeographers use tracks, not areas, as units of analysis (Craw *et al.*, 1999). However, these are minority views, and the area of endemism is the standard unit of historical biogeography (Nelson & Platnick, 1981; Wiley, 1981; Myers & Giller, 1988; Crisp *et al.*, 1999; Humphries & Parenti, 1999).

Definition of areas of endemism is contentious (Axelius, 1991; Platnick, 1991; Harold & Mooi, 1994; Morrone, 1994). It is usually accepted that endemism minimally means ‘restricted to a particular area’ (Anderson, 1994). Often there is the rider that the area should be ‘small’, but this is a relative term, and entirely dependent on the geographical scale of interest. More importantly, if *general* biogeographic patterns are being sought, then an area of endemism is interesting only if multiple taxa are restricted to it, especially if these taxa are unrelated. Therefore, we have adopted the definition of ‘the smallest area to which two or more taxa are restricted in distribution’ (Platnick, 1991; Harold & Mooi, 1994).

Few attempts have been made to delimit areas of endemism objectively. (This discussion excludes islands and continents, whose limits are self-evident.) For example, in analysing historical biogeographic patterns of vertebrates within Australia, Cracraft (1991) derived his areas from the phytogeographic map of Burbidge (1960), which was an intuitive classification based largely on climatic zonation. Subsequent authors (Crisp *et al.*, 1995; Ladiges, 1998) accepted the Burbidge–Cracraft areas with minor modification. Although Crisp *et al.* (1995) recognized that area definition was a problem, they did not pursue the matter.

In studies of geographical pattern of species richness, a commonly used approach has been to map species counts in grid cells, and then to use numerical methods such as clustering algorithms to classify grid cells, or to detect

centres or hotspots of species richness (Hnatiuk & Pedley, 1985; Hnatiuk & Maslin, 1988; Lawton *et al.*, 1994; Cope & Simon, 1995; Lamont & Connell, 1996; Puente *et al.*, 1998; Saiz *et al.*, 1998). This approach has seldom been used with measures of endemism. Morrone (1994) subjected species-in-grid-square data to parsimony analysis and interpreted clades as areas of endemism, however, one of us found serious problems in attempting to apply it to plant distribution data in western Australia (Monro, 1997). In particular, Morrone’s method is over-sensitive to scale effects and empty grid squares. Non-hierarchical methods, e.g. using ordination or Twinspan, seem more promising, being better able to handle the continuously overlapping nature of biotic distributions (Andersson, 1988; Bibby *et al.*, 1992; Dzwonko & Kornas, 1994; Blackburn & Gaston, 1996; Long *et al.*, 1996). This is analogous to using phenetics to delimit species-level taxa as units for cladistic analysis (Theriot, 1992; Crisp & Weston, 1993; Thiele & Ladiges, 1994), although the analogy between phylogeny and biogeography is limited (Sober, 1988).

The advent of specialist geographical software such as Geographic Information Systems (GIS) and Worldmap has made possible very large-scale studies in which variables such as species richness are mapped on a grid, and hotspots or centres are usually identified by eye (McAllister *et al.*, 1994; Williams *et al.*, 1994; Long *et al.*, 1996). This is the approach used in the present study. An alternative approach uses similar analytical methods to identify boundaries or transitional zones, rather than centres (Blackburn *et al.*, 1999; Williams *et al.*, 1999). Note that the first approach recognizes areas of species richness (or endemism) by their central hotspots, whilst the second attempts to delimit areas by their edges. Ideally perhaps, the two criteria should be combined, or at least compared. This was carried out by McAllister *et al.* (1986), who devised a method to define the edges of ranges and sum the edge values in grid cells to detect transition zones. This approach was not very successful, because most of the range sizes were small, and most of the range edges fell within species hotspots. Thus, cells with high-value edge counts also tended to be high in species richness counts. In the present study, areas of endemism are identified by their centres alone, because the methods for doing this are better developed at present.

As the concept of endemism is tied to particular areas, recognition of centres of endemism is dependent on scale (and the density of sampling). The continent of Australia as a whole is recognized as a centre of endemism of global significance (Major, 1988). Large regions within the continent also are recognized as centres of endemism, e.g. the south-west (Hopper, 1979), the north-eastern rainforests (Webb & Tracey, 1981), and Tasmania (Kirkpatrick & Brown, 1984a). Most Australian studies have focused narrowly on patterns within these regions (e.g. Kirkpatrick & Brown, 1984a; Lamont & Connell, 1996; Main, 1996; Williams & Pearson, 1997; Hill & Orchard, 1999). However, to date there have been no formal analyses of the whole of Australia aimed at identifying intermediate-scale centres of endemism.

The present study analyses restricted-plant distributions in grid squares over the whole of Australia with the aim of identifying intermediate-scale centres of endemism.

Phytogeographic regions have been mapped in Australia but mostly at an intuitive level (Burbidge, 1960; Herbert, 1967; Beard, 1981; Schodde, 1989). Studies using formal pattern analysis methods and species-in-grids as data (phytochorology) are few, and have concerned either an individual taxonomic group, or regions within Australia, or both. Most of these have focused on patterns of species richness, rather than of endemism (Hnatiuk & Pedley, 1985; Whiffin & Hyland, 1986; Hnatiuk & Maslin, 1988; Williams, 1991; Bowman, 1996; Jacobs & Wilson, 1996; Lamont & Connell, 1996; Simon & Macfarlane, 1996; Linder *et al.*, in press). The present study analyses plant distributions (both restricted and widespread) over the whole of Australia with the aim of identifying general patterns of species richness as a context for interpreting the centres of endemism.

In contrast to Australia, Africa has been studied extensively using phytochorology. Through a series of analyses, White (reviewed in 1993) identified and mapped phytochoria (floristic regions) which laid the basis for further work. Subsequently, Linder (2000) has analysed species-in-grid-square data aimed specifically at identifying centres of plant endemism in sub-Saharan Africa. The centres of narrow endemism found by Linder appear to be correlated to climatic stability, rather than to high rainfall *per se*. Notably, the region between the Sahara Desert and the equatorial rainforest belt (which is rich in endemics), is deficient in centres of endemism. Linder suggested that expansions of the desert during the past arid cycles have extinguished centres of endemism in this region, even in apparently suitable refugia such as mountain ranges.

Australia likewise has a large central desert, which is known to have expanded greatly during Pleistocene glaciations (Nix, 1982; White, 1994). The question arises whether, like the Sahara, it has extinguished refugia during periods of maximum aridity, as has been suggested for vertebrates in south-western Australia (Archer, 1996). A comparative analysis of African and Australian centres of plant endemism is needed to determine whether Pleistocene extinction of refugia has been a global phenomenon. This study analyses the relationship of identified centres of endemism to ecological factors, especially climate and past cycles of aridity.

MATERIALS AND METHODS

Choice of taxa and source of data

The primary source of data is vascular plant distributional records data based at the Environmental Resources Information Network (ERIN) in Canberra. These data were provided to ERIN cooperatively by the majority of the Australian State and Commonwealth herbaria. Each data point is derived from a herbarium specimen; thus all

identifications are vouchered. An introduction to this resource is given by Chapman & Busby (1994).

There are more than 17,000 named vascular plant species in Australia (Hnatiuk, 1990), and the ERIN data base includes a sample of about half the flora (*c.* 8320 species). Ideally, the sample of taxa used in this study should be broadly representative of the diversity of habitats and regions in Australia, to maximize the chance of detecting all major centres of endemism, and to avoid bias in those detected. However, choice is also limited by availability of data based distributions of higher plant taxa (e.g. genera, families) which are complete for Australia. The ERIN has Australia-wide records for two groups of taxa: ecological dominants and rare or threatened taxa (Chapman & Busby, 1994). The community dominants include *Eucalyptus*, *Acacia*, Casuarinaceae, conifers, rain-forest taxa, and from inland areas, grasses and Chenopodiaceae. Most (but not all) of the rare or threatened taxa are narrowly endemic, and this is clearly an advantage for the present study. However, it is important to view the narrow endemics in the context of their more widespread relatives – endemism is a relative concept. Therefore the inclusion of community dominants tends to balance the sample. We added data for *Daviesia*, which is being monographed (Crisp, 1995), and helps to fill a sampling gap in south-west Western Australia (see below). Athero-spermataceae and Monimiaceae were also included (D. Foreman, unpublished monograph) to improve sampling of south-east Australian rainforest trees. This brought the total sample to 8468 terminal taxa (species or infraspecific taxa).

The ERIN data suffer some sampling biases (Chapman, 2000). One of these is the absence of data from the Western Australian Herbarium, which did not participate in the ERIN project. The ERIN sample does include Western Australian plants, from specimens in other Australian herbaria, but this sample is deficient relative to the rest of Australia. We estimate that our sample includes 33% of all Western Australian plants, compared with 47% of the entire Australian flora. The sample of rare or threatened plants from Western Australia is better than this because national legislation requires that all states provide these data to ERIN. The ratio of rare to widespread species is 0.60 for western Australia, and 0.42 for the whole of Australia. Thus the particular Western Australian bias in our data is a deficiency of widespread species. This becomes evident in our results. The second main bias is the 'roadmap effect'. In remote areas such as the arid inland, plant collecting has been mostly restricted to the vicinity of the few good roads through the region (Chapman & Busby, 1994). This is evident when the raw point record data are mapped, as inland areas resemble a road map. Another potential bias is inconsistency of taxonomy between the institutions contributing the data, but coordinated efforts were made to minimize these in compiling the ERIN data base. Errors in identification are presumably random in distribution and should not have biased the sampling. The ERIN data include some introduced species (not indigenous to Australia) but

these are mostly grasses and their proportion of the total data set is minor (< 5%). Weeding these out would have been difficult and time consuming and their presence was not expected to bias the analysis.

Pattern analysis

Scale

It is known that patterns of endemism are scale-dependent (Major, 1988; Anderson, 1994; Ruggiero & Lawton, 1998; Vilkenkin & Chikatunov, 1998). We chose the relatively coarse 1° latitude × 1° longitude grid size, partly for ease of data manipulation and partly to reduce the effects of sampling artifacts such as mapping errors and unsampled grids in sparsely inhabited areas (the roadmap effect). A smaller scale grid would include many artificially empty (= unsampled) cells which are likely to bias the regression analysis used in the climatic comparisons (below). Chapman & Busby (1994) suggest correcting sampling bias using bioclimatic analysis, but this would lead to circularity when later relating the pattern to climate. By sampling at a larger scale, we expect and intend to detect only the major centres of endemism, such as those described by Boden & Given (1995). Smaller scale centres of endemism such as those found at a 10 × 10 km scale within Tasmania (Kirkpatrick & Brown, 1984b; Hill & Orchard, 1999) are expected to slip through our net.

Cell dimensions are about 110 km from north to south, and vary between 109 km (northern Australia) and 81 km (Tasmania) from east to west. Thus, those in northern Australia are 30% larger than those in Tasmania. This inequality results from convergence of the meridians of longitude towards the poles. Consequently the northernmost cells appear artificially richer in any area-dependent variable, such as endemism, than the southern cells. A similar problem affects any cell that overlaps the coast. The solution of constructing an equal-area grid (McAllister *et al.*, 1994) was beyond the scope of this study.

Measures of species richness and endemism

Species richness is measured simply as the total count of species within each grid cell. Measurement of endemism is less straightforward. The simplest approach is to count range-restricted species per cell. Range-restriction is specified by an upper distributional limit, e.g. one or a small number of grid cells (Kirkpatrick & Brown, 1984b; Usher, 1986; Long *et al.*, 1996). We tested scale effects by making separate maps with limits of endemism set at 1, 2, 3 and 4 grid cells. Having found little difference among these, we set an upper limit of 4 cells for further analysis (termed 1–4-cell endemism). This measure has two problems. First, it is correlated related with species richness ($r^2 = 0.60$ in the ERIN data). We return to this problem below. The second problem with this measure is that it sets an arbitrary limit on endemism.

Some authors have avoided arbitrary limits on endemism by counting *all* species (no matter how widespread) in each

cell, but weighting each by the inverse of its range (Dony & Denholm, 1985; Usher, 1986; Williams & Humphries, 1994; Williams *et al.*, 1994). Thus, a single-cell endemic has the maximum weight of 1, a species occurring in two cells has a weight of 0.5, and a species occurring in 100 cells has a weight of 0.01. To obtain an endemism score for a cell, these weights are summed for all species occurring in the cell. We term this measure *weighted endemism*. However, this measure correlates even more with species richness than does 1–4-cell endemism ($r^2 = 0.76$), because it counts every species in the cell.

Correlation between species richness and endemism is an empirical observation that reflects a roughly similar log-normal distribution of species-range sizes over a wide range of biota and over scales from regional to global (Gaston *et al.*, 1998 and references therein). However, this relationship varies among communities (Vilkenkin & Chikatunov, 1998) and major taxonomic groups (Gaston *et al.*, 1998), and it is these deviations from the more general relationship that are of most interest in the study of endemism. Therefore, we considered it important to find a measure of endemism that is least related to species richness. We did this by dividing the weighted endemism index by the total count of species in the cell, thus deriving a new index termed *corrected weighted endemism* (cf. Linder, 2000). This index corrects for the species richness effect by measuring the *proportion* of endemics in a grid cell. In our data it is scarcely correlated with species richness ($r^2 = 0.11$). Dony & Denholm (1985) made a similar correction, but applied it to a measure of endemism of the first kind, defined by an arbitrary upper distributional limit.

Detecting patterns of species richness and endemism

The data were manipulated and mapped using the GIS software Arc/Info (ESRI, 1999) on a Sun computer. In the first instance, patterns of species richness and endemism were examined by mapping the four indices described above and inspecting the maps for concentrations of cells with high values. In addition, spatial autocorrelation analysis (SAC) (Ord & Getis, 1995; Getis & Ord, 1996) was used to test for geographical clustering of cells with high values of endemism.

Spatial autocorrelation analysis tests whether values in each cell correlate with those in adjacent cells. In other words, this tests whether the geographical pattern of endemism is essentially random, or whether there are centres or 'hotspots' of endemism. We used two different SAC statistics: G^* and Moran's I (Getis & Ord, 1996). G^* measures degree of deviation of the neighbourhood from the mean, irrespective of whether this is positive or negative, and is alternatively known as 'hotspot' analysis. By contrast, Moran's I indicates direction (positive or negative) and degree of SAC. Our strategy was first to use Moran's I to test for any unusual pattern of positive vs. negative autocorrelation, and then to use G^* to diagnose and rank hotspots, which is the principal aim of this analysis. Spatial autocorrelation analysis can be tested for increasing spatial scales,

but for our analysis we only used the four N, E, S and W cells.

Relationship to environmental and historical factors

The relationship of species richness and endemism to climate and topography was investigated by linear regression analysis. In Australia there is an excellent set of climatic models available which have been used extensively for climatic modelling of biotic distributions (e.g. Nix & Kalma, 1972; Nix, 1982; Lindenmayer *et al.*, 1996), although never before on an Australia-wide scale with such a large set of distributions. Using these, we calculated appropriate climatic indices for each grid square. Linear bivariate regressions were then carried out using species richness, 1–4-cell endemism and corrected weighted endemism as the dependent (*y*) variables, and elevation, latitude, moisture seasonality and rainfall in the driest quarter as the independent (*x*) variables. As within-cell variability was high for elevation and the climatic variables, the mean, maximum, minimum and standard deviation of these were tested as separate variables. Western Australia was excluded from the analyses because of the unbalanced sampling from that state. Additionally, we compared and interpreted the maps of species richness and endemism with reconstructions of Australian Quaternary climates.

RESULTS

Species ranges

Altogether, 823 grid cells were sampled, and these included 118, 850 occurrence records for 8468 species-level taxa. Species range sizes show a poisson (or lognormal) distribution, as would be expected from comparable studies (McAllister *et al.*, 1994; Blackburn & Gaston, 1996; Brown & Lomolino, 1998; Gaston *et al.*, 1998). The mean range is 14 grid cells, whilst the median is 5 cells, and the mode is a single cell (1333 species). At the other extreme, one species (*Eucalyptus camaldulensis*) is recorded in 375 grid cells. Given the small range of most species, any attempt to apply the method of McAllister *et al.* (1986) to detect areas of endemism by their edges would probably have failed to distinguish edges from centres, as experienced by these authors.

Species richness

It is evident in Fig. 1 that species richness concentrates into eight distinct centres, plus a few other minor or doubtful ones. Following the nomenclature of Boden & Given (1995) where applicable, the distinct centres are: Kakadu–Alligator Rivers, Central Australian Ranges, Adelaide–Kangaroo Island, Cape York Peninsula, Wet Tropics, McPherson–Macleay, Sydney Sandstone and Tasmania (Fig. 1, Table 1: centres 3–8 and 11). The centres at Cape York Peninsula (6) and the Wet Tropics (7) almost merge

to form a 1300-km strip of high species richness running down the Queensland coast from Cape York to Eungella. This strip contains the two richest grid cells, which together comprise the core of the Wet Tropics. They are located at Atherton Tableland (17.5° S, 145.5° E; 1633 species) and Cairns–Daintree (centred on 16.5° S, 145.5° E; 1420 species). The two next richest cells are both in the Border Ranges (New South Wales–Queensland border; centre 8) and have, respectively, 1194 species (27.5° S, 152.5° E) and 1100 species (27.5° S, 153.5° E). After these the number of species per cell drops away sharply.

The centres in Fig. 1 correspond well with the ‘centres of plant diversity and endemism’ mapped by Boden & Given (1995), with some exceptions (Table 1). The most conspicuous difference can be seen in the two Western Australian centres recognized by Boden & Given: (1) the South-west and (2) North Kimberley. The South-west is the richest centre recognized by these authors, with 5500 species. By comparison, their next richest centre, the Wet Tropics, has about 3500 species. Yet in Fig. 1, the South-west appears minor compared with the Wet Tropics. The reason for the incongruence between Boden & Given and this analysis is the absence of any data in ERIN from the Western Australian Herbarium. For the same reason, the North Kimberley is recorded as a centre by Boden & Given, but scarcely differs from the background in Fig. 1. Boden & Given consider the North Kimberley (2), Kakadu–Alligator Rivers (3), Central Australian Ranges (4) and Border Ranges (8) about equally rich with 1200–1500 species each. Comparison of these centres in Fig. 1 clearly shows that our sample is deficient for North Kimberley.

Another difference between the two studies, this one apparently real, is that Boden & Given have missed the Adelaide–Kangaroo Island centre (Fig. 1, centre 5), as have previous authors. Two other centres have been recognized but apparently underrated by these authors: Cape York Peninsula (6) and McPherson–Macleay (8). The Cape York Peninsula centre contains a local centre at Iron Range–McIlwraith Range that is recognized but not mapped by Boden & Given. Similarly, our McPherson–Macleay centre contains the much smaller Border Ranges centre of Boden & Given. Conversely, Boden & Given appear to have overrated the Australian Alps (10), which scarcely appears as a centre in Fig. 1. However, in considering these differences, it should be remembered that Boden & Given do not distinguish species richness from endemism. Some of their centres that differ from our centres of species richness (e.g. South-west Western Australia, North Kimberley, Australian Alps and Border Ranges) are much more comparable with our centres of endemism (below).

Endemism

1–4-cell endemism

The observed pattern of endemism does not vary with the change in scale from 1-cell endemics to 4-cell endemics. The same centres appear in each map, although for 1- and

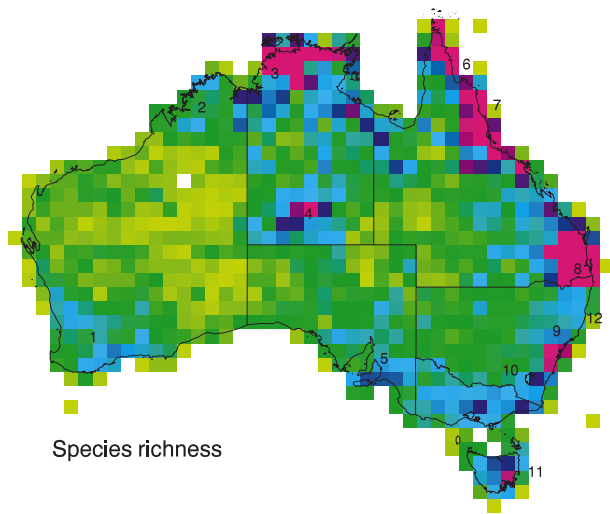


Figure 1 Species richness mapped in $1 \times 1^\circ$ grid cells. Numbers on centres correspond with Table 1.

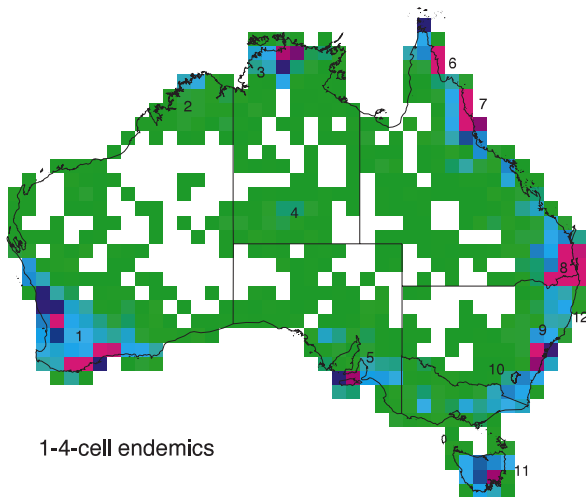


Figure 2 Endemism as represented by species with a range of 1–4 grid cells. Numbers are as in Fig. 1 and Table 1. White grid cells are empty.

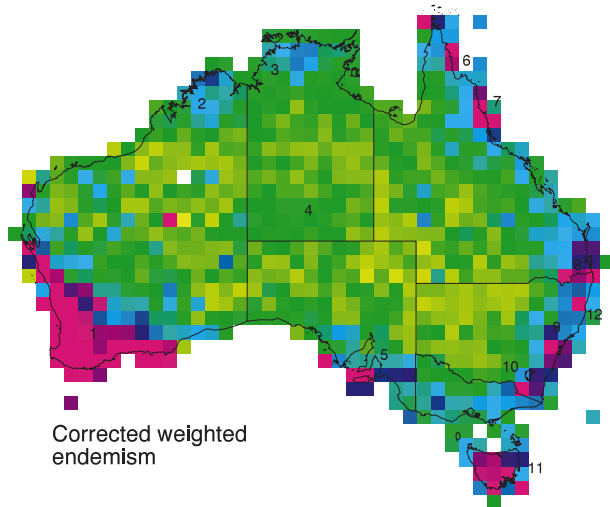


Figure 3 Corrected weighted endemism (measured by summing the inverse of all species' ranges, and corrected for species richness). Numbers are as in Figs 1 and 2 and Table 1.

2-cell endemism, this pattern is weakly visualized, with many empty cells. Therefore, only cumulative endemism in 1–4-cells is shown (Fig. 2). This map is very similar to the map of species richness, which should be expected given the high correlation between these variables. For instance, the two cells richest in endemics (in the entire map) are those at the core of the Wet Tropics (7), and these are the same two that are richest in species, namely Atherton Tableland (485 endemics) and Cairns–Daintree (432 endemics). The next five richest cells, between 140 and 158 endemics, are all located in the three Queensland centres (6–8).

However, there are two important differences between the maps of species richness (Fig. 1) and endemism (Fig. 2). First, South-west Western Australia (1) shows strongly as a double centre of endemism, reflecting the better sampling of range-restricted species from that state, compared with the poor sampling of widespread species. The two centres, north- and south-east of Perth, are the ‘northern sandplains’ and ‘southern sandplains’, which have long been recognized as centres of floristic diversity and endemism (Erickson *et al.*, 1986). The latter includes the particularly rich Stirling Range at its western end. The second difference is that the Central Australian Ranges (4) have very few endemics, and scarcely stand out from the uniformly depauperate background of the central Australian arid zone.

Another difference is that the centres of endemism in Fig. 2 are much more restricted in area than the centres of species richness in Fig. 1. This is to be expected because the number of range-restricted species is only a small proportion of the total species in the flora.

Weighted endemism

The measure of endemism that counts all species in inverse proportion to their range produces a map that resembles the pattern of species richness (Fig. 1) even more closely than does 1–4-cell endemism (Fig. 2), and is not shown. This is unsurprising, given the high correlation between weighted endemism and species richness. However, like Fig. 2, it shows the South-west as a distinct double centre.

Corrected weighted endemism

When weighted endemism is corrected for the correlation with species richness, a rather different pattern is seen (Fig. 3). It emphasizes areas that, while not necessarily high in species richness, have a high proportion of flora with restricted distributional range. This map resembles that of Boden & Given (1995) more closely than do either Fig. 1 or Fig. 2. It differs strikingly from the map of species richness (Fig. 1) in several details.

South-west Western Australia (1) is by far the most significant centre on the map. The entire region south of a line from Shark Bay to Israelite Bay is shown as having a high level of endemism and its boundaries map exactly to those of Boden & Given and earlier authors (e.g. Burbidge, 1960; Beard, 1979). In our data, this region shows up far more strongly as a centre of *endemism* (Fig. 3) than it does as a centre of *species richness* (Fig. 1). In fact, 9 of the 10 grid cells scoring highest for corrected weighted endemism are in this region. Whilst this difference is partly the result of undersampling of widespread species in this region, it also accords with a longstanding recognition of the south-west as a centre of endemics in particular (Diels, 1906; Burbidge,

Table 1 Centres of plant species richness and endemism in Australia found in the present study, and for comparison, the centres of ‘plant diversity and endemism’ recognized by Boden & Given (1995). Numbers correspond with Figs 1–3

Centre	Present study				Boden & Given (1995) Plant diversity and endemism
	Species richness	1–4-cell endemism	Weighted endemism	Corrected weighted endemism	
1. South-west Western Australia	?	+(double centre)	+(double centre)	++	++
2. North Kimberley	?	?	?	+	+
3. Kakadu–Alligator Rivers	++	+	+	+	+
4. Central Australian Ranges	+	–	?	–	+
5. Adelaide–Kangaroo Island	+	+	+	+	–
6. Iron Range–McIlwraith Range (Cape York Peninsula)	++	+	+	+	+
7. Wet Tropics	++	++	++	++	++
8. Border Ranges (McPherson–Macleay)	++	++	++	+	+
9. Sydney Sandstone	+	+	+	+	+
10. Australian Alps	?	?	?	+	+
11. Tasmania	+	+	+	++	+
12. New England–Dorrigo	–	?	?	+	–

+, Centre; ++, major centre; ?, weak or doubtful centre; –, no centre distinct from background.

1960; Hopper, 1979; Boden & Given, 1995; Crisp *et al.*, 1999).

There is no indication of a centre of endemism in the Central Australian Ranges (Fig. 3), although it shows strongly as a centre of species richness (Fig. 1). We return to this point in the Discussion below.

In Queensland and the 'Top End' of the Northern Territory, the centres of endemism (3, 6, 7 and 8) are small in area, rather than forming the extended, interlinking regions of richness seen in Fig. 1. This localization should not be taken to indicate that these centres are unimportant; rather, it shows the effect of correcting high species richness. Despite this correction, the 9th and 11th highest-scoring cells for corrected weighted endemism remain the two most species-rich cells in the entire data set – those at the core of the Wet Tropics.

By contrast with these tropical centres, those in New South Wales are relatively more significant as centres of endemism than of species richness. There is an elongated 'ridge' of high endemism running down eastern side of the Great Dividing Range from the Queensland border to the Victorian border. Embedded in this ridge are four 'peaks' of endemism: the Border ranges (8), New England–Dorrigo (12), Sydney–Blue Mountains (9) and the Australian Alps (10). Corrected weighted endemism is our only index that supports the Australian Alps centre (10) of Boden & Given (1995). Also, it highlights a New England–Dorrigo (12) centre not recognized by previous authors, although it does sit at the southern extremity of Burbidge's 'McPherson–Macleay overlap' (which also takes in the Border Ranges).

The two southern centres, Adelaide–Kangaroo Island (5) and Tasmania (11), show up as larger and more significant in Fig. 2 than by the other measures of species richness and endemism. Interestingly, the Tasmanian centre incorporates almost all of the island, except the extreme north-east and north-west. This contrasts with the map of Boden & Given

Table 2 Distributional details of 230 species of 1–4-cell 'endemics' occurring in the four richest grid cells on CYP

True narrow endemics*	46	20%
CYP and overseas†	91	40%
CYP and elsewhere in Australia‡	32	14%
CYP and overseas and elsewhere in Australia	23	10%
Unresolved§	36	16%

* Occurring only on Cape York Peninsula. † For example, Papua New Guinea, Indonesia. ‡ For example, the 'Top End' of the Northern Territory or farther south in Queensland. § As a result of problems in identification or obtaining distributional data.

(1995: map 15), which considers only the south-west of the island to be significant. According to Fig. 3, the centre and eastern side of Tasmania also rank highly as centres of endemism, which is more consistent with the analyses of Kirkpatrick & Brown (1984a, b).

Corrected weighted endemism appears to be sufficiently sensitive to identify some recognized but very localized centres of endemism (Fig. 3) that have been missed by the other indices (Figs 1 & 2). These include the Cape Range, near Exmouth in western Australia (22.5° S, 113.5° E) and the Grampians in western Victoria (37.5° S, 142.5° E).

Spatial autocorrelation analysis of hotspots (not shown) confirms all the numbered centres in Fig. 3 – except the Central Australian Ranges (4), which although numbered for comparison with other maps, do not appear as a centre of corrected weighted endemism. As in Fig. 3, North Kimberley (2) and Kakadu–Alligator Rivers (3) are supported only weakly as hotspots. On the other hand, the South-west (1), Tasmania (11) and Wet Tropics (7) receive strong support.

It should be noted that corrected weighted endemism is subject to sampling artifacts. Several cells have artificially

Independent (x) variable	Dependent (y) variable		
	Species richness	1–4-cell endemism	Corrected weighted endemism
Latitude	0.0417	0.0031	0.0303
Elevation, SD (relief)	0.0893	0.0864	0.2382
Elevation, mean	0.0025	0.0013	0.0090
Elevation, max	0.0566	0.0424	0.1346
Moisture seasonality, SD	0.1351	0.1654	0.0869
Moisture seasonality, min	0.0054	0.0389	0.1044
Moisture seasonality, max	0.0034	0.0032	0.0537
Moisture seasonality, mean	0.0001	0.0158	0.0721
Rainfall, driest quarter, SD	0.0747	0.1313	0.2244
Rainfall, driest quarter, min	0.0171	0.0208	0.2438
Rainfall, driest quarter, max	0.0686	0.0916	0.3062
Rainfall, driest quarter, mean	0.0293	0.0496	0.2721

Table 3 Bivariate linear regressions of indices of species richness and endemism (y) against environmental variables (x). Cell entries are r^2 values

high values because the sample is very small (usually < 5), but by chance includes one or more narrow endemics. Examples can be seen along the coast, where only a small area of land (often small islands) is taken in by the cell (e.g. western tip of Cape York Peninsula at 10.5° S, 141.5° E; western tip of Eyre Peninsula at 34.5° S, 134.5° E), or in remote regions (e.g. in the Gibson Desert at 24.5° S, 123.5° E). In these cells, the 'endemism' may also be an artifact of undersampling.

Sampling artifacts on Cape York Peninsula

We have already mentioned that the centres of species richness and endemism on Cape York Peninsula, especially the hotspot at the Iron and McIlwraith Ranges (6) have been overlooked by previous authors. This may be partly because of the lack of serious botanical exploration of the area until recently (Frith & Frith, 1995). A number of endemic taxa from this area in the present data set have not yet been described formally. Alternatively, the high scores may be a sampling artifact, inflated by species that extend outside Australia into adjacent countries, especially Papua New Guinea, whose mainland is only 150 km to the north, across Torres Strait. This strait is shallow and was continuous land linking Australia and New Guinea < 21,000 yr BP (Hope, 1996; Williams *et al.*, 1998). Such species may appear 'endemic' only when sampling is restricted to Australia.

To test the effect of extra-limital species we examined the three grid cells that scored the highest numbers of 1–4-cell 'endemics' on Cape York Peninsula (CYP). These are centred on the Iron Range, McIlwraith Range and the tip of Cape York (Fig. 2). These cells also scored highly for corrected weighted endemism. Together these three cells included 230 endemics restricted to 1–4 cells, and we checked the distribution of each, both in Australia and overseas (Table 2). At least 64% of the 'endemics' occurring in these three grid cells also occur outside CYP (Table 2: lines 2–4), and at least 50% also occur overseas (Table 2: lines 2 and 4). Interestingly, the seasonal megatherm environment of the eastern coastal strip of CYP (including Iron–McIlwraith Range) has more affinity with the Trans-Fly and Port Moresby 'dry' strips in Papua New Guinea (Nix, 1982, p. 56, Fig. 10) than with any other part of mainland Australia. This predicts floristic links between these areas, such as we appear to have found.

This result may have implications for all the centres of endemism, as for 24% of the above species, the occurrences outside CYP are elsewhere within Australia. Such species may be genuinely restricted in range, but to disjunct habitats (e.g. mountain peaks). Alternatively, they may have a wider, more continuous distribution, but may be undersampled in the intervening localities. Therefore, the four northern-most centres of endemism (2, 3 and 6) may be less important relative to the more southerly centres than Figs 2 and 3 suggest. However, all these centres appear even when 1-cell endemics are mapped, and their magnitude relative to the other centres is about the same as in

Fig. 2. Consequently, none of these centres should be considered an artifact.

Relationship to environment

Regression analysis

Results of the regressions of species richness and endemism against environmental variables (Table 3) were generally poor, with either low r^2 values, slopes nearly parallel to an axis, or both. Species richness and 1–4-cell endemism returned low r^2 values against all variables, with most < 0.1 and none > 0.2. Corrected weighted endemism fared only slightly better, showing a slight relationship to all measures of rainfall in the driest quarter ($0.22 < r^2 < 0.31$). Additionally a slight relationship was shown between corrected weighted endemism and standard deviation of elevation, which is a measure of topographic relief ($r^2 = 0.24$). Topographic relief indicates habitat variability and availability of specialized sites (slopes with different aspect, gullies, peaks) that may harbour a range of narrowly endemic species with specialized habitat requirements. A relationship between endemism and relief is therefore expected.

DISCUSSION

Detecting centres of endemism

Among the three indices of endemism tried in this study, 'corrected weighted endemism' appears the most useful. It detected centres of endemism that were highly congruent with those found by previous authors using different criteria. Additionally, and very importantly, it is uncorrelated with species richness and so separates the pattern of range-restricted species from that of more widespread species. Moreover, this index seems to have the advantage of subtlety: it detects minor centres that are missed by the other indices, e.g. New England–Dorrigo, Australian Alps, Grampians, Cape Range. There are a couple of minor problems with this index: it does not give a simple count of endemic species within an area and it is sensitive to artifacts of poor sampling. The latter problem can be minimized by eliminating from consideration any site with very low species richness, especially where unbalanced sampling is suspected.

It is clear from this study that range-restricted species are not distributed randomly over the landscape, but do aggregate into centres or hotspots. This is demonstrated amply by simple mapping (Figs 2 & 3), and is confirmed by SAC. Why this phenomenon occurs is properly the subject of historical biogeography, and beyond the scope of this paper. It is not a simple byproduct of geographical aggregation of species richness because corrected weighted endemism, which is uncorrelated with species richness, finds a different pattern of centres (cf. Figs 1 & 3).

One of the principal questions addressed by this study is whether centres of endemism can be detected objectively and repeatably by analysis of species-in-grid-cell data. The

answer seems to be 'yes', for two reasons. The first is the above-mentioned congruence of centres in Figs 2 and 3 with those described by previous authors, most of whom used subjective, non-analytical methods. Second, although we have good reasons for preferring 'corrected weighted endemism', all three indices found more or less the same set of centres. Repeatability of the method should be tested using independent data, e.g. from different groups of organisms, such as non-vascular plants, animals and fungi. It is sometimes expected that major groups of organisms should have different patterns of endemism because their environmental tolerances, behaviours and mobilities differ (Wilson, 1992; Brown & Lomolino, 1998). Nevertheless, cladistic biogeography is founded on the observation that areas of endemism are fundamentally the same for a wide range of organisms (Nelson & Platnick, 1981; Wiley, 1981; Humphries & Parenti, 1999).

Do the centres of endemism detected in this study have value as units ('areas of endemism') for historical biogeography? We have already drawn an analogy between this method and the use of phenetics to define species-level units for phylogenetic reconstruction. However, this analogy is no more than an empirical convenience. Rather, this question should be addressed by cladistic biogeographic analyses using these centres as units, to see whether congruent and meaningful historical patterns can be reconstructed among them.

Endemism is a scale-dependent phenomenon, and this study was carried out at a single, broad scale. Scale differences can account for different findings in different studies. For example, Boden & Given (1995) missed the elongated south-east Australian area of endemism (Fig. 3), probably by focusing too narrowly. Within that area (thus at a smaller scale) they recognized three centres: the Border Ranges, the Sydney Sandstone and the Australian Alps. They also described, but did not map, a fourth centre within this area: 'sclerophyll forests of far south-east New South Wales'. In Tasmania, the present study detected a single area of endemism incorporating all the island except the far north-east and north-west. This is consistent with the results of Kirkpatrick & Brown (1984b), however, by sampling at a much finer scale, they resolved this area into three major and four minor centres of plant endemism. Also in the present study, the entire South-west Province (Beard, 1990) of Western Australia was shown to be a large-scale centre of endemism (Fig. 3). However, the present data also contain the suggestion of two centres within the south-west (Fig. 2), and more resolution still may be found using a more detailed sample than we have at present. Future studies of plant endemism within Australia should focus on smaller scales, with the aim of resolving more localized centres.

Relationship to environment

Climatic regressions

Other studies, both in Australia and elsewhere have found good relationships between species richness and environ-

mental variables, especially latitude, altitude and climate (Nix, 1982; Brown & Lomolino, 1998; Cueto & Lopez de Casenave, 1999; Rathert *et al.*, 1999). Such analyses have seldom been made for endemism. Thus it is somewhat surprising that the regression analyses in the present study found little relationship among these variables. The reasons are probably to do with sampling artifacts and scale.

False absences appear to be frequent in the ERIN data, especially in the more remote areas. This kind of sampling bias strongly perturbs regression analysis. Additionally, considerable topographic (and hence climatic) variation can occur within the 10,000 km² area of a 1° × 1° grid cell, such that the single value calculated for each variable per cell may fail to reflect any relationship with richness or endemism.

All the studies cited above, where relationships were found between climate and species richness, were made at a much smaller scale than the present study. In particular, Nix (1982) first classifies the Australian flora into three major temperature-response groups (megatherm, mesotherm and microtherm) and argues that species richness – climate relationships are only likely to be found within such a group. He finds two bioclimatic predictors of species richness: (1) weekly mean growth index (GI), which is equivalent to potential site productivity and (2) seasonality of growth response, which is equivalent to environmental stability. His models make much better predictions at fine geographical scales (where data were available) than at coarse scales such as 1° grid cells.

Nix (1982, p. 56) notes that, in eastern Australia at least, overlap between major climatic zones coincides with some centres of endemism and diversity. In Queensland there are three major zones of overlap between mesotherm and megatherm environments with favourable conditions for growth (GI > 0.45): the Wet Tropics, McPherson–Macleay and the Eungella Range. Also, Tasmania is an overlap zone of mesotherm and microtherm climates with good growth index. However, the major centre in south-west Western Australia cannot be explained in this way, because it shows no such overlap. The explanation of this centre is more likely historical.

Pleistocene extinction in Central Australia?

The single major anomaly in the Australian patterns of species richness and endemism is the absence of any suggestion of a centre of endemism in the species-rich Central Australian Ranges (centre 4; contrast Fig. 1 with Figs 2 & 3). This seems especially surprising given the presence of some well-known endemics in the area such as *Livistona mariae* F. Muell., *Macrozamia macdonnellii* (Miq.) A.D.C. and *Sedopsis filsonii* (J.H. Willis) J.H. Willis. This region is well collected and data based, so it is safe to conclude that both the number and proportion of endemics in this centre is much lower than expected by comparison with the rest of Australia. Consider the cell that scores highest for species richness in Central Australia (489 species). It includes Alice Springs and the

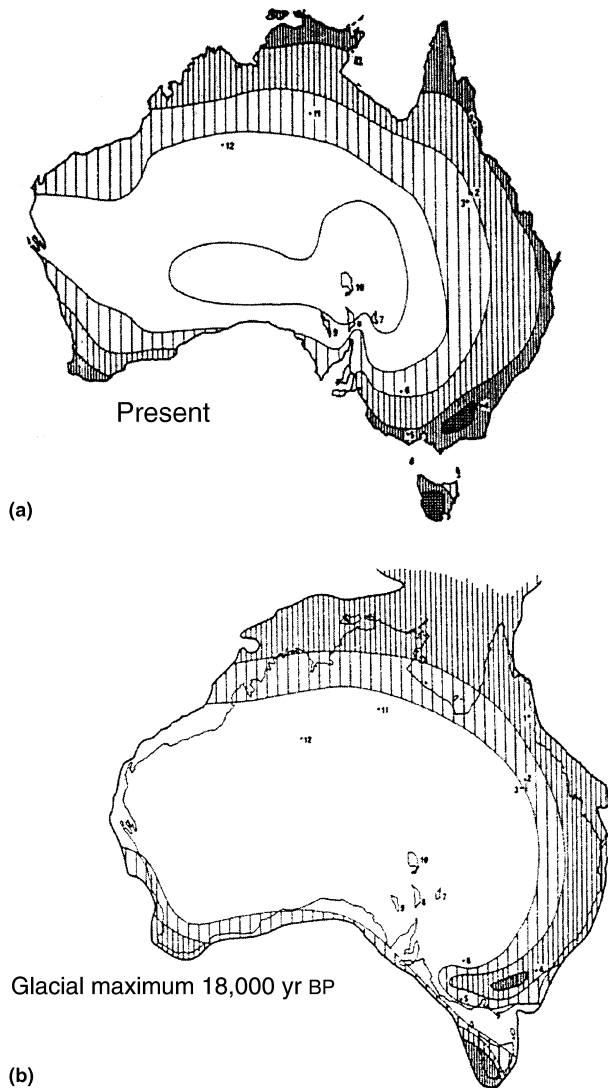


Figure 4 Australian coastline and climatic zones (a) at present and (b) reconstructed for 18,000 yr BP, at the last glacial maximum, when the central desert was at its maximum extent. The central, unshaded zones are desert with mobile sand dunes. Reproduced from Jones & Bowler (1980).

central Macdonnell Ranges and is centred at 33.5° S, 133.5° E. This cell ranks 31st (out of 823 cells) for species richness, but 339th for corrected weighted endemism and 128th for 1–4-cell endemism (15 endemics). An adjacent cell (23.5° S, 132.5° E) ranks slightly higher for corrected weighted endemism (326th), and also has fifteen 1–4-cell endemics (128th). All other species-rich cells in this centre rank lower for endemism, with 9–12 endemics each.

We suggest that this anomaly has a historical cause – a selective extinction (or series of extinctions) of narrowly endemic species in inland Australia. During the Pleistocene glaciations, the central Australian desert was much

larger in extent and much more hostile to plant growth and survival than at present (Fig. 4, Jones & Bowler, 1980). At last glacial maximum (18,000 yr BP), the edges of the desert extended to the coast in the west, to the Kimberley and the (present-day) Gulf of Carpentaria in the north, to the western slopes of the Great Dividing Range in the east, to Bass Strait and northern Tasmania in the south-east, almost to the coast in the south, and to the edge of the south-western Province of Western Australia (Fig. 4b). All the present-day centres of endemism in Fig. 3 are near-coastal and lie outside this reconstructed desert (cf. Figs 3 & 4b). The severity of this desert is indicated by mapping of mobile (essentially unvegetated) sand-dunes deriving from this period (Hope & Kirkpatrick, 1988; Wasson *et al.*, 1988). These dune systems filled nearly the whole of the expanded arid zone as shown in Fig. 4(b). Moreover, this was an extremely cold desert, even in latitudes near Alice Springs (Miller *et al.*, 1997).

During the extremely arid periods of the glacial maxima, the wide-ranging inland flora and fauna with broader environmental tolerances probably tracked the climatic changes and retreated to the edges of the desert, and perhaps to refugia deep in the mountain ranges. However, narrowly endemic species, most of which may have been adapted to specific sites occurring only in the central mountain ranges (as are those few that exist in this region today), would have had nowhere to go, and most would have gone extinct. After climate ameliorated during the interglacials, the wide-ranging species would have re-expanded their ranges out of refugia, and the species-richness of central Australia would have recovered to approximately its previous level (minus the extinct endemics). This would explain the selective extinction of endemic species.

Note that we are suggesting that it is not the aridity *per se* of central Australia that accounts for the lack of endemics; rather, it is the *instability* of the arid climate that has mitigated against their survival. Deserts are known elsewhere with high numbers of endemic plants, but these are old deserts whose climate has been stable over a long period, e.g. the Horn of Africa (Lovett & Friis, 1996). Some authors have suggested that climatic stability favours the development of both high species diversity and high endemism (Fjeldsa & Lovett, 1997a, b; Brown & Lomolino, 1998). Fjeldsa and Lovett suggest that this may be because of continued speciation and accumulation of neoendemics in the areas of high richness and endemism, rather than to extinctions outside these areas. However, they were considering rainforests, not deserts. Gaston (1998) suggests that, in general, range-restricted species are more sensitive than widespread species to climatic change.

Tropical Africa is known to be floristically poorer than tropical South America and south-east Asia, and this has been ascribed to extinctions caused by glacial aridity (Axelrod & Raven, 1978; Brennan, 1978). Using essentially the same approach as in this study, Linder (unpublished data) has demonstrated a similar deficit of endemic flora

in centres of species richness adjacent to the Sahara Desert in Africa. He too ascribes this effect to Pleistocene expansion of the desert, which was a world-wide phenomenon (Williams *et al.*, 1998). He found that the areas with fewer than expected endemics were all on the northern side of mountain ranges, where they were exposed to severe arid winds (the Harmattan winds) blowing out of the centre of the Sahara.

How might this hypothesis of selective extinction of arid-zone endemics be tested? First, evidence of the pattern of fewer than expected endemics could be sought in deserts elsewhere that have been subject to Pleistocene fluctuations, and these could be compared with the patterns in stable deserts. Within Western Australia, there are areas which should be investigated further because the ERIN sample is inadequate to elucidate the pattern. The Pilbara is a mountainous region in arid north-west Western Australia and, with a balanced sample, it could be tested for a deficit of endemics. The patterns shown by other biota could also be mapped and compared with the floristic pattern. An ideal test would be evidence for the pre-Pleistocene levels of endemism in the arid zone, such as from fossils, but this would be extremely difficult to obtain, at least for plants. Interestingly, it appears that the south-west of Western Australia is deficient in endemic vertebrates, and it has been suggested that this is the result of Pleistocene extinction (Archer, 1996). The south-west, although outside the boundaries of the desert at glacial maxima, was right on the edge, and would undoubtedly have been affected by the severe climate of the time.

CONCLUSIONS

Endemism can be distinguished from species richness by using an appropriate index calculated from presence of species in grid cells. Mapping of this index for seed plants can detect centres of endemism. Within Australia, we have confirmed several previously identified centres of floristic endemism (south-west western Australia, Wet Tropics, Border Ranges, North Kimberley, Kakadu–Alligator Rivers, Sydney Sandstone, Australian Alps, Tasmania). Our analysis also identified centres that have been either overlooked or underrated in the past (Adelaide–Kangaroo Island, Iron–McIlwraith Ranges, New England–Dorrigo). In general, centres of species richness coincide with centres of endemism. However, the Central Australian Ranges region is found to be no centre of endemism, although it is confirmed as a centre of species richness. This anomaly is ascribed to selective extinction of narrow endemics (but not of widespread species) in arid inland Australia, driven by extreme climatic conditions during the Pleistocene glacial maxima.

This study is probably unique in being a continent-wide analysis of the distributional pattern of a high proportion (*c.* 50%) of the known species in a major group of organisms, and at a relatively small scale. It is a compelling demonstration of the value of specimen-based

data, such as are held in herbaria and museums worldwide. Yet, such data are only useful if they are available, and availability depends on coordinated data basing of data at a continental and international scale. The Australian ERIN data are unusually comprehensive and accurate at this scale. Nevertheless, they have serious deficiencies, such as the sampling biases already described. Additionally, they are ‘fossilized’ because, whilst additional data are progressively being added, at least for rare and threatened species, there is no updating of the existing data, e.g. of new records for taxa already data based. Therefore, this study should be considered a first approximation of what is possible.

Future studies of this kind might take a somewhat different approach. Ideally, the sample should be structured more evenly than the ERIN data with respect to life-form, range size, region of distribution and habitat of the organisms. Also, the taxa should be recently monographed, to minimize taxonomic and identificational errors. Monographers usually go to considerable trouble to record distributions comprehensively and accurately, often by making new collections in areas where the species was unknown previously. Such data would be much less subject to sampling artifacts than the ERIN data. The Virtual Australian Herbarium will make these data accessible. It is a web-based flora information system which is being developed cooperatively by all the major Australian herbaria (Barker, 1998). It will provide direct access to the primary specimen-based data, which are continuously updated, and will supersede the ERIN data base.

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BIOSKETCHES

Mike Crisp's research concerns the systematics of various taxa, especially legumes (Fabaceae). His main interest is estimating phylogenies and applying these to evolutionary and ecological questions in biogeography, speciation and the evolution of adaptive traits.

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Peter Linder works on the systematics of the large African orchid tribe, Deseae, as well as on Restionaceae and the southern temperate grass tribe, Danthonieae. Developing from these taxonomic researches he developed an interest in biogeography, and especially African biogeography, and has addressed the problems of plant distribution both from a historical, and a descriptive, approach.

Anna Monro is a PhD student working on the systematics of the Australian members of the plant family Polygalaceae. This study includes a phylogenetic analysis and taxonomic revision.