# A Biogeographical Analysis of the Freshwater Plants of Australasia

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*Abstract*

Patterns in the distribution of Australasian species of freshwater aquatic plants were sought, to determine whether vicariance, distance dispersal, local speciation, or a mixture of these could best explain the distribution. The distribution was recorded from 10 regions of Australasia that include sizeable areas of wetland: Papua New Guinea, Cape York Peninsula, south-east Queensland, eastern New South Wales, Victoria, Tasmania, New Zealand, northern Northern Territory, the Kimberley, and south-west Western Australia. Matrices of 553 species by 10 regions, 139 genera by 10 regions, and 56 families by 10 regions were analysed using hierarchical fusion, nearest neighbour and ordination techniques. The results indicate that there are two distinct elements in the aquatic flora, tropical and temperate. The diffuse boundary between these two climatic zones could be interpreted as a barrier in the sense used in definitions of vicariance. There is little effective spread between tropical and temperate areas but, within each of these climatic zones, the species are mobile and many spread reasonably readily between regions, provided suitable habitats and dispersal opportunities are available. Where geographic barriers to distance dispersal have been great then these may become as important as the climatic barrier. This is demonstrated, at least in part, by the differences between some of the generic and species dendrograms. Local speciation (not shown by our PATN analyses because of the endemic species being ignored in them) has been important where some primarily aquatic genera have proliferated when conditions have been suitable. Local speciation has occurred in cosmopolitan aquatic genera that have presumably arrived in regions via long distance dispersal. The significance of bird migration and dispersal patterns are discussed. The aquatic flora of the monsoon tropics has evolved mainly from long distance dispersal but with significant local speciation in some genera such as *Nymphoides*, *Utricularia*, *Nymphaea* and *Vallisneria*. The pattern of distribution was compared with those recorded from other ecologically defined groups such as the Australian arid and alpine floras.

## Introduction

Biogeographic studies are mostly based on the distribution of related taxa, looking for some interpretable pattern in the distribution (Jacobs 1982; Parr-Smith 1982; West and Garnock-Jones 1986; Wilson 1986). Others attempt to examine a more or less ecologically defined group of plants (Barker and Greenslade 1982; Barlow 1986a). The present study falls into the latter category and the aims were: to detect patterns in the distribution of native freshwater plants in Australasian regions, determine whether vicariance, distance dispersal, or a mixture of these could best explain the distribution, and compare the pattern of distribution with those recorded from other ecologically defined groups such as the Australian arid (Barker and Greenslade 1982) and alpine (Barlow 1986a) floras. It was hoped that such comparisons would allow the generation of hypotheses on the origins and evolution of the aquatic floras and what type of changes might be expected in the future.

It is difficult to define a waterplant unambiguously. Many attempts have been made at this with Sculthorpe (1967) providing a good summary. Most working definitions have, very sensibly, been left fairly vague (Sculthorpe 1967; Aston 1973; Cook *et al.* 1974; Sainty and Jacobs 1981; Johnson and Brooke 1989) or have, after much thought, been omitted (Leach

and Osborne 1985; Sainty and Jacobs 1988). In many studies, the definitions have been modified to provide a workable size of group and, in others, groups were omitted because of insufficient information. We have no argument with any of these procedures or definitions even though our own definition and procedures differ from some of them. All of the definitions require a degree of interpretation for each species and this seems unavoidable for an ecologically defined group, especially where the main characteristic, water, is one of the most variable in our environment. In this study, a waterplant is defined as a plant that grows in or near water.

For this particular exercise, however, the definition was of only minor significance as the most important task was to rationalise the various sources of information to ensure that, as much as possible, similar entities were being compared. As a result, our source data perhaps contain rather fewer species than if we were able to compile them from scratch. Omissions from one list often meant omitting them from all lists unless the missing information could be obtained from the Herbarium or from our own collections. For this reason, freshwater algae and all marine plant species were not included. Alpine species were excluded since:

(*1*) many of the sources used here excluded them; and
(*2*) it allowed a comparison between the results from the aquatic flora with those obtained from analyses of alpine floras.

The only alpine species included were those that also grew at lower altitudes. Many alpine species grow in waterlogged soil, often with free water on the surface, for 3–6 months of the year. This habitat is difficult to distinguish from a true aquatic habitat other than by altitude. Like mangroves, alpine species are mostly excluded from waterplant studies unless they only grow submerged in high country streams or lakes.

Exotic species were excluded from the study since our interest was in biogeographical relationships. The distributions of naturalised species are, of course, of practical interest as examples of relatively recent dispersal and the species have ecological and economic consequences in their new habitats (Sainty and Jacobs 1981, 1988). These aspects are addressed briefly in the discussion section.

The sizes of the study areas were also considered. The regions were largely pragmatically defined on the basis of obtainable data but we kept them more or less comparable in size, or at least of the same order of magnitude. This is actually of much less significance than the total area of wetland in each region, but that information is difficult to extract. There are generalised maps of the distribution and classification of Australian wetlands (see McComb and Lake 1988; Jacobs and Brock 1993) but they are neither accurate enough nor comparable enough to determine actual areas of wetland in each region. A major problem is that the area of wetland in each region expands and contracts annually, to a different extent each year and at different seasons, so any estimates will have very large error components.

## Methods

The non-arid parts of Australasia (i.e. regions with a reasonably high area of wetlands) were divided into 10 regions that were defined on pragmatic grounds based on the availability of reliable information from our own research and from published and other sources. For tropical Australia, this posed particular problems as there are neither complete published lists nor adequate herbarium collections, and both these problems were compounded by inadequate taxonomic knowledge of many groups. These problems were overcome with the help of colleagues with specialist knowledge of these regions and by our own collections and experience. Clarkson and Kenneally (1988) have discussed the biogeography of two of the tropical areas; these authors generously supplied us with some of their raw data.

Alpine regions were not included, as discussed above. Definitions of the lower limit of the alpine zone approximate fairly closely to the 10°C mean temperature of the warmest month (Costin *et al.* 1979; Royen 1980). In practice, alpine is generally defined in the Australasian region as being the vegetation region above the treeline, although the distinction between alpine and treeless subalpine is not always clearcut (Royen 1980; Kirkpatrick 1986). The altitude at which the treeless zone starts varies with latitude and with distance from the sea. There is relatively little land classified as alpine in Australasia. Alpine areas occur in eastern New South Wales, Victoria, Tasmania, New Zealand, and New Guinea, as biotic 'islands' isolated by extensive areas at lower altitudes and have been mapped by Ramsay *et al.* (1986). The zone in New Guinea is generally referred to as tropicalpine, since the diurnal temperature
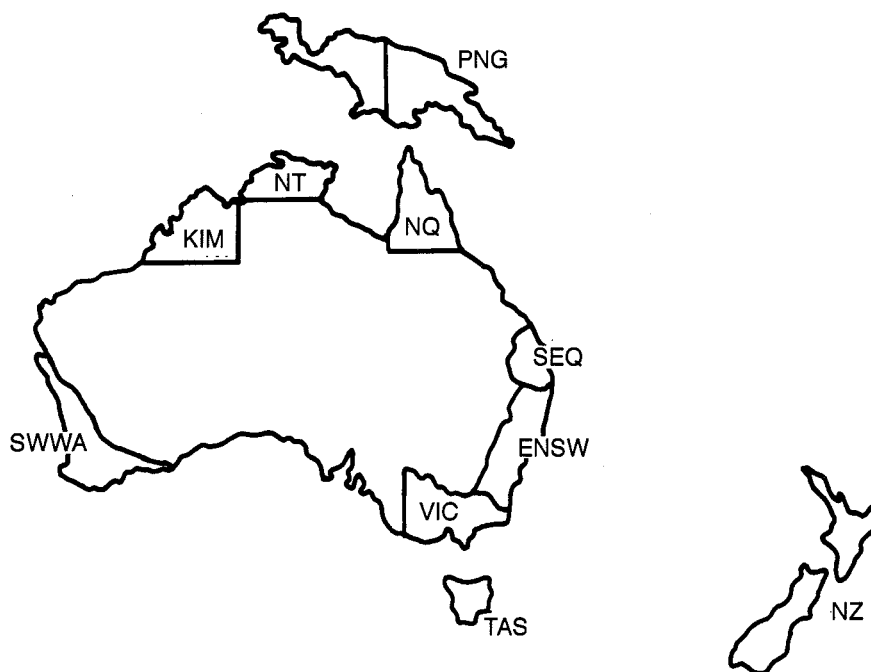
**Fig. 1.**    Regions used in this study. ENSW, Eastern New South Wales (Coast, Tablelands and Slopes botanical divisions); KIM, Kimberley region of Western Australia, north of 19°S and west of 129°E; NQ, Cape York Peninsula region of Queensland north of 18°S and east of 141°E; NT, northern part of Northern Territory north of 15°S; NZ, New Zealand; PNG, Papua New Guinea; SEQ, South-eastern Queensland as defined in Stanley and Ross (1983); SWWA, South-west Botanical Province of Western Australia (Beard 1980); TAS, Tasmania; VIC, Victoria.

and humidity range is more important than the seasonal range, which is the reverse of the situation at higher latitudes (Royen 1980; Barlow 1986a). There is little specific overlap between alpine floras and the aquatic floras of adjoining regions at lower altitude. For example, only eight wide-ranging aquatic species grow at both alpine and non-alpine altitudes in Papua New Guinea and New Zealand.

The 10 regions (Fig. 1) in the study are described below, including comments on the limits of alpine areas with which the freshwater floras at lower altitude are subsequently compared.

(*1*) **Papua New Guinea**, the political area as described by Leach and Osborne (1985; our source of information on the waterplants). Leach and Osborne also describe the geography and climate of Papua New Guinea. Papua New Guinea lies between about 3°S and 10°S, and ranges in altitude from sea level to 4500 m. The tropicalpine zone starts at about 3300 m according to Royen (1980), although it descends to 3000 m in some areas, with a gradual transition from subalpine grasslands to tropicalpine. In general, Papua New Guinea has a relatively high annual rainfall, commonly averaging 2500–3500 mm, with extremes from 1000 to 10 000 mm, and is hot with little seasonality of rainfall except in the drier areas.

(*2*) The **New Zealand** botanical region, including the offshore islands as described in our source of distributional information (Johnson and Brooke 1989), though any species restricted to the subantarctic islands were excluded. New Zealand is a strongly seasonal temperate region with a large altitudinal (sea level to 3700 m) and latitudinal (34–47°S) range. The lower limit of the alpine zone is as high as 1450–1520 m on northern peaks, while in south-west Fiordland it comes down in altitude as low as 900 m (Mark and Adams 1973; Wardle 1986). New Zealand's climate can perhaps best be described as cold and wet, with most of the region having average annual rainfalls of 750–1500 mm, with extremes of 330–7000 mm; Allan (1961) provides a good summary of physical features of the region.

(*3*) **North Queensland** is here defined as Cape York Peninsula lying between 10°S and 18°S, and east of 141°E. The region includes the Atherton Tableland, which rises to 1600 m, but, compared with the previous two regions, there is little altitudinal range over most of the region. The climate is tropical

monsoonal with predominantly summer rainfall with annual averages of mostly 600–2400 mm with extremes to more than 3200 mm. The climate is summarised by Castles (1986) and Bureau of Meteorology (1989). There is little published information on the flora but John Clarkson kindly made his manuscript checklist available to us.

(*4*) **South-eastern Queensland** as described by Stanley and Ross (1983; our source of distributional information). This region lies between latitudes 24°S and 29°S, and east of 149°E, comprising the Queensland pastoral districts Burnett, Wide Bay, Darling Downs and Moreton. Relief is low, with altitudes ranging from sea level to 1300 m. The climate is subtropical with a predominantly summer rainfall and annual averages of about 600–1600 mm. The climate is summarised by Castles (1986) and Bureau of Meteorology (1989).

(*5*) **Eastern New South Wales** comprising the Coast, Tablelands and Slopes Divisions of that State (Jacobs and Pickard 1981), extending between 29°S and 37°S. Altitude ranges from sea level to 2200 m. Alpine vegetation is found only in the Mount Kosciusko region above about 1800 m (Costin *et al.* 1979). The region's climate varies from subtropical with a summer-dominated rainfall in the north to temperate with a more or less even distribution of rainfall in the latitudinally central areas and to a winter-dominated rainfall in the south. Annual averages are mostly in the range of 600–1600 mm with some local extremes. The climate is summarised by Castles (1986) and Bureau of Meteorology (1989). Distributional data were extracted from Jacobs and Pickard (1981) and Sainty and Jacobs (1981).

(*6*) **Victoria**, the political entity, lying between 34°S and 39°S. There are small, scattered alpine and treeless subalpine areas on the highest peaks in eastern Victoria above about 1300 m, descending to 980 m in some areas (Walsh *et al.* 1986). The largest area is associated with Mt Bogong (1986 m). The climate is mostly temperate with a winter-dominated rainfall and annual average rainfalls ranging from 400 to 1200 mm with some local extremes. The climate is summarised by Castles (1986) and Bureau of Meteorology (1989). Our distributional data were obtained from Aston (1973).

(*7*) **Tasmania**, the political entity, including the offshore and Bass Strait islands but excluding subantarctic Macquarie Island. It lies between 40°S and 43°S, and ranges in altitude from sea level to 1600 m. Higher peaks are scattered, with the lower limit of the alpine zone at higher altitude (about 1200 m) in the north-east, descending (as latitude increases) to 700 m in the south-west of the island (Minchin 1981). The distinction between alpine and treeless subalpine is often not clearcut (Kirkpatrick 1986). The climate is temperate with a predominantly winter rainfall annually averaging mostly in the range 600– 3200 mm. The climate is summarised by Castles (1986) and Bureau of Meteorology (1989). Our distributional data were obtained from Aston (1973) and Kirkpatrick and Harwood (1983).

(*8*) The **Northern Territory** south of 11°S and north of 15°S, corresponding to the 'Arnhem' region of Barlow (1986*b*). Topographic relief is low, with altitude ranging from sea level to just under 400 m. The climate is tropical monsoonal with a strong dominance of summer rainfall. Average annual rainfall mostly ranges from 800 to 2400 mm. The climate is summarised by Castles (1986) and Bureau of Meteorology (1989). Our sources of distributional information were Cowie and Finlayson (1986) and Dunlop (1987).

(*9*) The **Kimberley**, Western Australia, lying between 13°S and 19°S and bounded in the east by the Northern Territory–Western Australia border. Topographic relief is low as in the Northern Territory but the highest peaks are just under 1000 m. The climate is tropical monsoonal with a strong dominance of summer rainfall. Average annual rainfall mostly ranges from 400 to 2400 mm. The climate is summarised by Castles (1986) and Bureau of Meteorology (1989). There were no published lists of the Kimberley flora at the time of our analysis, but Kevin Kenneally kindly supplied us with information missing from our own collections.

(*10*) The **South-west Botanical Province** of Western Australia (Beard 1980), the crescent-shaped 'corner' of WA lying between 26°S and 35°S, and ranging in altitude from sea level to 1000 m. The climate is temperate with a strong dominance of winter rainfall. The average annual rainfall mostly ranges from 300 to 2400 mm. The climate is described by Castles (1986) and Bureau of Meteorolgy (1989). Our sources of distributional information were Aston (1973) and Marchant *et al.* (1987).

As well as the specific references above, Aston (1973) provided additional data for the whole of Australia, as did our own collections and others housed at the National Herbarium of New South Wales. Several monographs also provided useful data, notably Taylor (1989) for *Utricularia*, Orchard (1985) for *Myriophyllum*, Aston (1982, 1984, 1986, 1987) for *Nymphoides*, Affolter (1985) for *Lilaeopsis*, Wannan and Waterhouse (1985) for *Limnophila*, Duistermaat (1987) for *Oryza*, Jacobs and Brock (1982) for *Ruppia*, Jacobs and Lapinpuro (1986) for *Amphibromus*.

A matrix of 553 native species by 10 regions was compiled from the above sources. Two subsidiary matrices, 139 genera by 10 regions and 56 families by 10 regions, were derived from the first matrix. Copies of the original species list are available from the authors on request. The matrices were analysed

using hierarchical fusion (PDIV, equivalent to FUSE strategy with flexible UPGMA option), network analysis (NNB nearest neighbour) and ordination (SSH 'semi-strong hybrid' multidimensional scaling, and DCOR incorporating DECORANA) options of PATN (Belbin 1989).

The matrices were also analysed for the number and proportion of species of each of the included major plant groups—Bryophyta, Pteridophyta, Monocotyledonae and Dicotyledonae—in each of the regions. There are no aquatic gymnosperms in Australasia. The number of plant species restricted to a single region and the proportion of these in each of the regions were recorded. This number includes species endemic to a single region and species found also in regions not covered by this study. These species (180 in total) do not contribute to the statistical analyses but clearly are extremely important in any discussion of similarity.

## Results

### The Species Matrix

The nearest neighbour and flexible UPGMA analyses gave very similar results, producing the same four groups of regions. Fig. 2 is a dendrogram from the flexible UPGMA analysis and shows that the major division is between the tropical and temperate regions, these being the last to fuse, with the tropical regions forming a distinct group and the temperate regions producing three groups. The four groups are:

(1)  the four tropical regions: Papua New Guinea (PNG), North Queensland (NQ), Northern Territory (NT) and the Kimberley (KIM);
(2)  the four temperate eastern Australian regions: South-eastern Queensland (SEQ), Eastern New South Wales (ENSW), Victoria (VIC) and Tasmania (TAS);
(3)  New Zealand (NZ); and
(4)  South-west Western Australia (SWWA).

The nearest neighbour analysis differed in having groups (3) and (4) fuse last of all, suggesting, from that analysis, that isolation is slightly more significant than the distinction between tropical and temperate.

The 'semi-strong hybrid' multidimensional scaling ordination (Fig. 3) produced five groups along an axis with the tropical regions at one end, the eastern temperate regions in the centre and the three isolated temperate regions at the other end. The groups are: (1) NT and KIM; (2) PNG and NQ; (3) SEQ and ENSW; (4) VIC; and (5) SWWA, TAS, NZ.

The DECORANA ordination likewise ordered the regions along a latitudinal gradient and the first vector presumably relates to this. It is not clear to what the second vector relates. The first two eigenvalues from the DECORANA ordination account for 81% of the variation.

### The Genus Matrix

The nearest neighbour classification (Fig. 4) essentially produced the same four groups as the species matrix, with the very late fusion of New Zealand and South-west Western
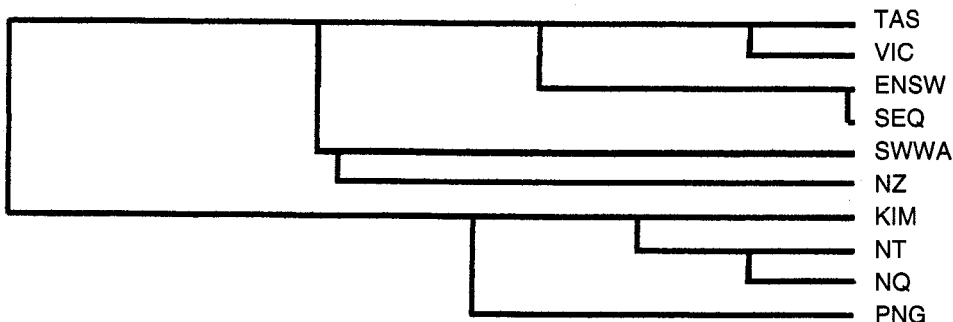


**Fig. 2.** Dendrogram produced from the species matrix by the flexible UPGMA analysis. The nearest neighbour analysis produced a very similar dendrogram.
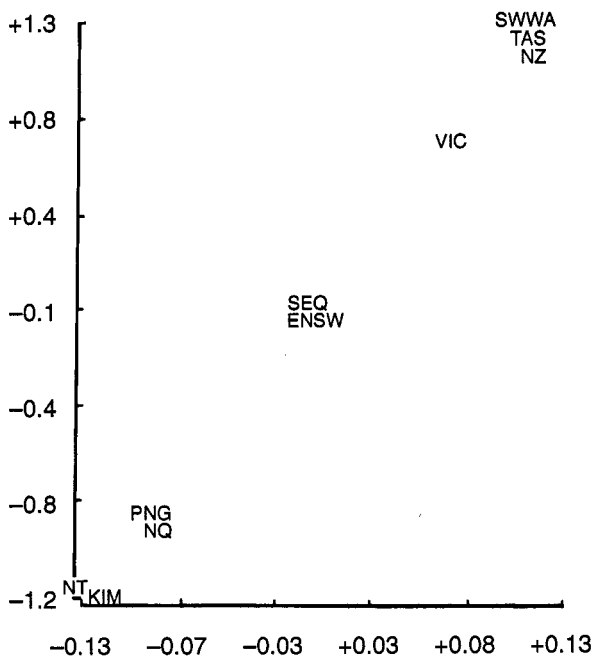
**Fig. 3.** SSH (semi-strong hybrid) multidimensional scaling ordination of the species matrix produced five groups, with the tropical regions at one end and the three isolated temperate regions at the other. The DCOR (incorporating DECORANA) ordination also ordered the regions along a latitudinal gradient.
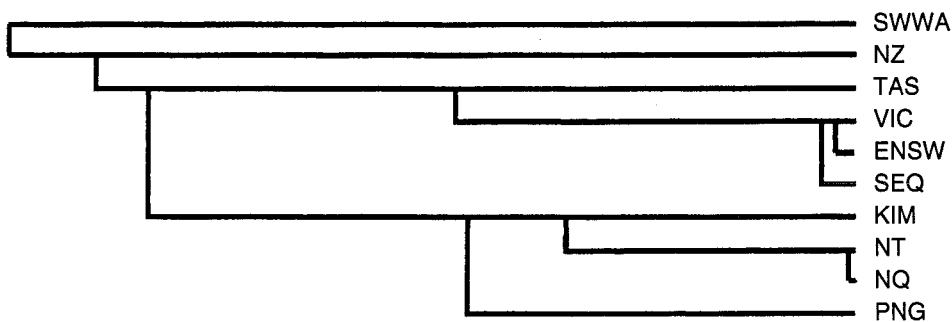


**Fig. 4.** Dendrogram produced from the genus matrix by the nearest neighbour analysis. This is similar to that produced from the species matrix.

Australia again indicating that isolation is slightly more significant than the distinction between the tropical and temperate areas. The flexible UPGMA classification (Fig. 5) did not support this and produced three groups: (1) PNG, NQ, NT, KIM; (2) SEQ, ENSW, VIC; and (3) NZ, TAS, SWWA.

The third group was the last to form but did fuse with the other temperate areas before they fused with the tropical regions.

The eigenvalues for the first two axes of the DECORANA ordination (Fig. 6) account for 98% of the variation with the first axis (84%) again having the tropical regions at one end and TAS, NZ and SWWA at the other; SWWA is widely separated from TAS and NZ by the second vector.
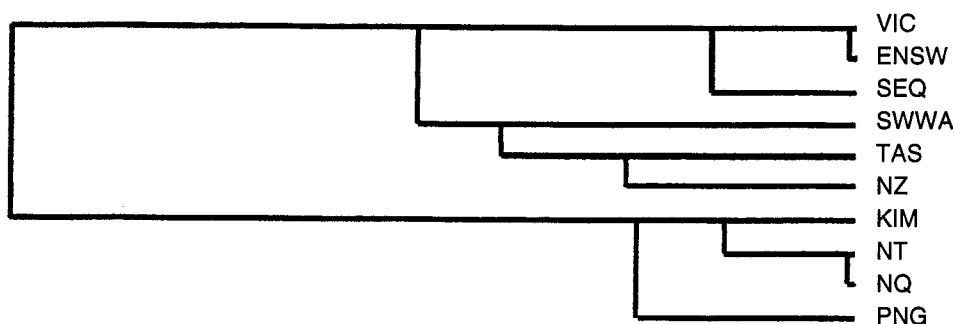
**Fig. 5.** Dendrogram produced from the genus matrix by the flexible UPGMA analysis. This differs from that produced from the species matrix (Fig. 2) in the position of TAS.
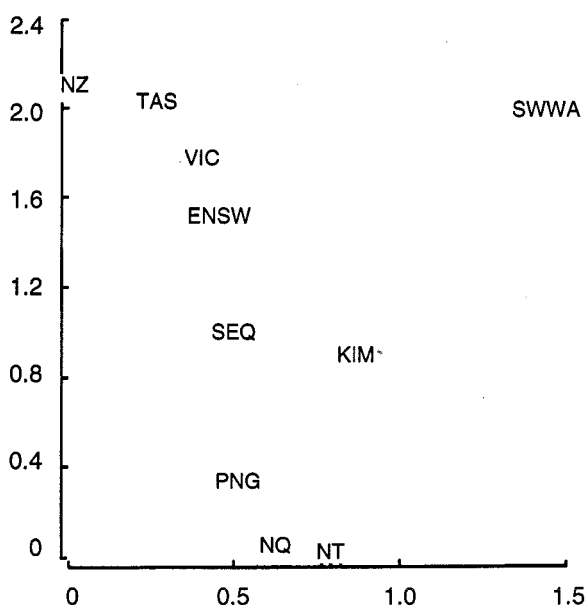


**Fig. 6.** The eigenvalues for the first two axes of the DCOR (incorporating DECORANA) ordination of the genus matrix account for 98% of the variation (84% on the first axis). The first axis has the tropical regions at one end and the three isolated temperate regions at the other (cf.

*Family Matrix*

As would be expected, the fusion groups were less clear at the family level with the nearest neighbour (Fig. 7) and flexible UPGMA (Fig. 8) analyses each producing three (different) groups, although the third group of the nearest neighbour classification could itself equally be treated as three distinct groups. The three nearest neighbour groups are: (1) PNG, SEQ, ENSW, VIC; (2) NQ, NT, KIM; and (3) NZ, TAS, SWWA.

These groups seem to be based on geographical isolation rather than anything else. Most of the fusions occur late and the early fusions are all between neighbouring regions. It is not clear why Papua New Guinea fused with the three temperate east coast regions but the fusion does occur late in the analysis.

The three UPGMA groups are: (1) PNG, NQ, NT, KIM; (2) SEQ, ENSW, VIC; and (3) NZ, TAS, SWWA.
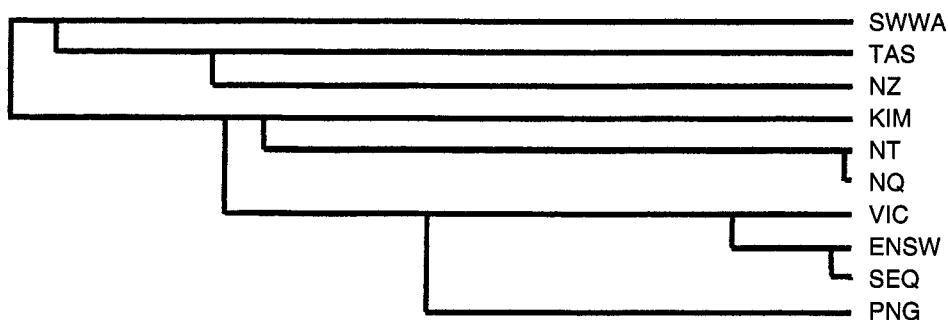
**Fig. 7.** Dendrogram produced from the family matrix by the nearest neighbour analysis has few strong groups. It differs from that produced by the flexible UPGMA analysis (Fig. 8) in the position of PNG and the weaker linkage of the three isolated temperate regions.
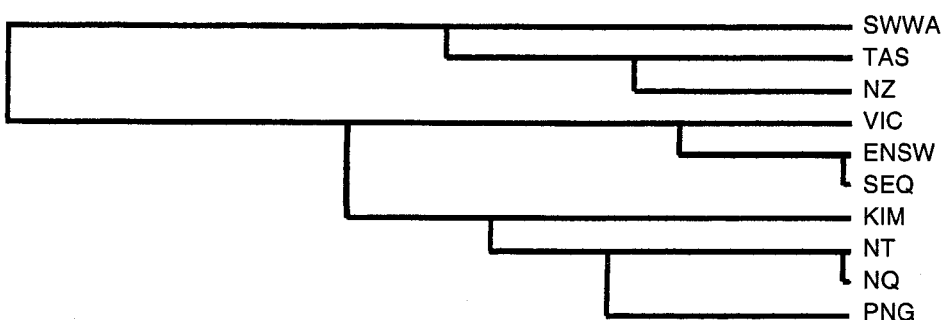


**Fig. 8.** Dendrogram produced from the family matrix by the flexible UPGMA analysis (cf. Fig. 7).

In this case the last group is as strong as the others. The tropical regions form a distinct group but these fuse with the closer temperate regions before this group fuses with the isolated temperate regions. This family analysis recovers the essential elements of the analyses of species and genera.

The first two eigenvalues in the DECORANA ordination (Fig. 9) account for 99% of the variation with the first axis (84%) aligning more or less on a latitudinal gradient but not as clearly as for the generic matrix. SWWA is again well separated from TAS and NZ by the second vector and again it is not clear to what the second axis relates.

*Proportional Composition*

Table 1 summarises the number of species in each region and the number and proportion belonging to each of the major plant groups. The number and proportion of species in only one region are also tabulated. Some of these species are endemic to that region; many others grow outside the region but not in any of the other regions under consideration here. This latter case is particularly so in Papua New Guinea where a large but currently unquantifiable number of species grow elsewhere in the Indo–Malesian region. Four of the genera are each restricted to one of the regions studied but there are no unique families.

Aquatic bryophytes are few and mainly temperate. Aquatic pteridophytes are more or less evenly and thinly distributed with the exception of SWWA where there has been a proliferation of *Isoetes* species. The proportion of monocots is similar in the various regions but the tropical areas do tend to have a slightly lower proportion of monocots then the temperate areas, the exceptions to this being TAS and PNG. The reverse is true for the dicots
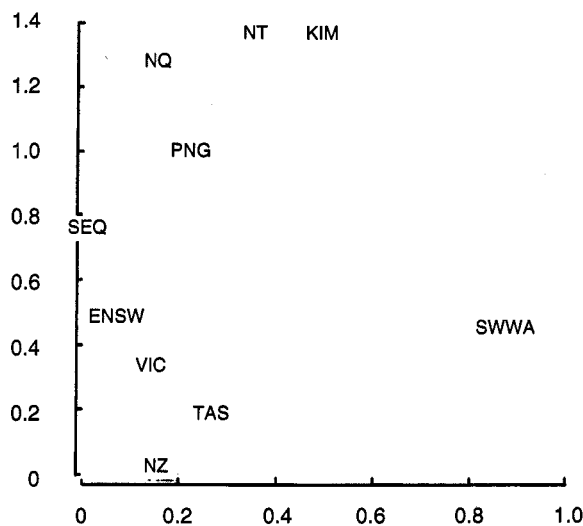
**Fig. 9.** The eigenvalues for the first two axes of the DCOR (incorporating DECORANA) ordination of the family matrix account for 99% of the variation (84% on the first axis, with the tropical groups again separated from the temperate regions).

**Table 1. Total number of aquatic species for each region and the numbers and proportion represented by the major plant groups**

The number and proportion (%) of species restricted to one of these regions is also given; this includes species endemic to a region as well as those growing in only one of the defined regions but also growing in other regions outside those discussed here. Abbreviations for regions are the same as those listed in Fig. 1 caption. –, not recorded from the region

| | PNG | NZ | NQ | SEQ | ENSW | VIC | TAS | NT | KIM | SWWA |
|---|---|---|---|---|---|---|---|---|---|---|
| Bryophytes | – | – | – | 2 | 2 | 1 | 1 | – | – | – |
| | – | – | – | 1% | 1% | 0.5% | 1% | – | – | – |
| Pteridophytes | 7 | 4 | 5 | 4 | 8 | 9 | 5 | 9 | 6 | 11 |
| | 4% | 4% | 3% | 2% | 3% | 5% | 5% | 5% | 5% | 11% |
| Monocots | 138 | 63 | 113 | 131 | 144 | 111 | 62 | 106 | 66 | 55 |
| | 72% | 65% | 60% | 67% | 64% | 63% | 60% | 56% | 54% | 54% |
| Dicots | 46 | 30 | 70 | 59 | 71 | 56 | 36 | 74 | 51 | 35 |
| | 24% | 31% | 37% | 30% | 32% | 31.5% | 34% | 39% | 41% | 35% |
| Total | 191 | 97 | 188 | 196 | 225 | 177 | 104 | 189 | 123 | 101 |
| Species in that | 45 | 43 | 12 | 2 | 5 | 5 | 5 | 15 | 10 | 38 |
| region only | 24% | 44% | 6% | 1% | 2% | 3% | 5% | 8% | 8% | 38% |

as the monocots and dicots together make up 90% or more of the flora in each region. Although PNG has a higher proportion of monocots than expected, the actual figures indicate that PNG really differs in the lower than expected number of dicot species rather than in having high numbers of monocot species. The figures indicate that the more isolated regions have fewer species in total.

The more isolated regions also have higher levels of endemicity (as defined above). The high levels in NZ and SWWA must throw doubt on any grouping of these two since endemics are not effective contributors to hierarchical fusion strategies.

Clarkson and Kenneally (1988) and Bowman *et al.* (1988) present figures for the proportion of ferns, gymnosperms, monocotyledons and dicotyledons in various State floras. Generally, ferns make up approximately the same small proportion of the aquatic flora as they do of the terrestrial. Gymnosperms do not occur in Australasian aquatic floras. The big difference is in the proportion of monocotyledons: in aquatic floras the proportion of monocots ranges from about 50% to 70%, approximately twice the proportion represented in total floras (20–30%).

## Discussion

The results indicate a major disjunction between the tropical and temperate aquatic floras. This distinction is more clearly defined at the species and genus levels than at the family level. The first axis in each of the ordinations (Figs 3, 6, 9) accounted for a very large proportion of the variation and was interpretable as being largely due to latitude. Anyone even vaguely familiar with Australasian aquatic plants would have reached a similar conclusion.

This pattern is similar to that described by Clarkson and Kenneally (1988) who noted that the flora of Cape York Peninsula was more similar to the flora of the Kimberley than the total flora of Queensland was to the total flora of Western Australia. Bowman *et al.* (1988) compared the floras of the other States with that of the Northern Territory but did not compare the tropical Northern Territory flora with that of Cape York and the Kimberley.

*Acacia* shows a similar pattern (Hnatiuk and Maslin 1988; Maslin and Pedley 1988) with different sections of the genus predominating in the tropical and temperate areas. *Triodia* likewise shows a similar pattern (Jacobs 1982). All of these examples suggest a climatic barrier and would support a vicariance model.

Biogeographical studies of two terrestrial genera in Western Australia, *Banksia* (George 1987) and *Lechenaultia* (Morrison 1988), show a different pattern. These two studies show basically southern temperate genera extending north into the tropics. *Plectrachne* shows a similar pattern (Jacobs 1982), although perhaps the path here has been in the opposite direction. However, this pattern may be the exception rather than the rule and may reflect the lack of biogeographical studies on tropical genera.

The level of group fusions before the last fusion in each analysis indicates that regions sort more or less on the distance between them. The distance between regions is possibly one component of the second vector of the ordinations. The comparatively late fusion of Papua New Guinea with the tropical areas of mainland Australia, despite the close proximity to northern Queensland, possibly reflects the higher proportion of wet tropic habitat in Papua New Guinea. There may also be a relationship with the flight paths of the trans-equatorial migratory birds as suggested by studies of the waders (Lane 1987) that indicate that most individuals reaching our northern shores appear to bypass Papua New Guinea. In the northern Australian groups, north Queensland and the Northern Territory always fuse before the Kimberley joins the group. This is a reflection of the greater species richness of the first two and the greater number of shared taxa. The Kimberley is drier than the other two with fewer truly perennial wet areas, reducing the number of aquatic species able to persist there.

The results support a combination of distance dispersal, vicariance, and local speciation. Climate is the most significant vicariance barrier at the species level. The geographically closer the areas are within either the tropical or temperate zones the more similar the floras are. This similarity is maintained by distance dispersal of species. The relative importance of local speciation appears to be directly related to the difficulty of overcoming the isolation barriers. At the generic level, the climatic and distance barriers seem to have been about equally important. At the family level it is less clear, but it appears that the physical barriers have been more important than the climatic, possibly because of past climates being different from those operating today.

Barriers such as the Tasman Sea, Nullarbor Plain, Great Victoria Desert, and the Great Sandy Desert have helped isolate New Zealand, south-eastern Australia, and south-west Western Australia. Local speciation has been important at the species level where some basically aquatic genera have proliferated when conditions have been suitable; examples are *Isoetes*, *Villarsia* and *Utricularia* in southern Western Australia, *Nymphoides* and *Utricularia* in the northern part of the Northern Territory, *Nymphaea* and *Vallisneria* in northern Queensland, and *Carex* and *Crassula* in New Zealand. In all of these examples, speciation has occurred locally in aquatic genera that have presumably arrived in the region via long distance dispersal because the genera are almost cosmopolitan and do not show any pattern interpretable by continental drift.

The mechanisms for long distance dispersal in aquatic plants have been well documented. Bird dispersal is the most significant in terms of movement between catchments, dispersal occurring both in the intestinal tract and externally attached to feet and feathers. Observations abound, with perhaps the most famous by Darwin (1859). Guppy (1906), Ridley (1930), Sculthorpe (1967), Pijl (1972), Wardle (1978) and Cook (1987) provide examples and references to the diverse literature on the subject. There is some debate as to the possibility of dispersal through the intestinal tract with some groups of waterbirds. Loyn and French (1991) regard all ducks and geese as seed predators with only a few seeds likely to escape destruction. This is at odds with work by Papassotiriou (unpublished results) who recovered a large amount of intact seed and fruit of the aquatic *Potamogeton tricarinatus s. lat.* fed to a domestic duck. Germination tests on the recovered material even suggest there may be enhanced germinability of the diaspores under low light conditions (equivalent to being voided in water).

The large number of observations and the number of plant genera and species involved are more than adequate to support the hypothesis of long distance dispersal of many species. The similarity between aquatic floras of different areas has been noted and commented on before. Thorne (1972) notes that more than half of his 'subcosmopolitan' genera are aquatic and, of the very few species that can be described as subcosmopolitan, nearly all are aquatic. Kloot (1984) notes that most (61 of 98) of the native species considered to have disjunct natural distributions between southern Australia and other temperate regions of the world are aquatic (the largest group of the remainder represent taxonomic errors).

In this study, the results reinforce the potential importance of both migratory and nomadic long distance bird movement (Rowley 1974) in dispersal of waterplants. Studies on the migration of birds associated with wetlands (Rowley 1974; Frith *et al.* 1977; Purchase *no date*) show that most of the movement in the Australasian region is between the Northern and Southern Hemispheres rather than between east and west. Several species of birds from the Northern Hemisphere migrate south to the tropics (Danielson and Skov 1989) and may move west to east (or east to west) in that zone. The species of birds that migrate to temperate zones move south down either the east coast or the west coast of Australia, or through the centre (and then head east or west). They may head directly south-east from the Kimberley (Lane 1987) and may return north-west to the Kimberley in their northward migration (Close and McCrie 1986; Minton and Watkins 1989). There is apparently little subsequent movement east or west by these migrants to temperate zones. Only one wetland bird species, the double-banded plover or dotterel regularly migrates across the Tasman Sea (Rowley 1974; Lane 1987). However, nearly 50 species of wader occasionally appear in New Zealand as vagrants, either via tropical Australia or apparently directly from the Northern Hemisphere (Lane 1987; Barter 1989; Davies and Riegen 1989). Number of species alone is not an adequate index, but extrapolating to the number of individuals is difficult and unreliable. An estimated 2 000 000 birds reach the northern shores of Australia (Lane 1987). Thomas (1970) and Rowley (1974) estimate between 250 000 and 500 000 of these spend the Northern Hemisphere winter in south-eastern Australia with about 12 000 of these reaching Tasmania and a similar number reaching South Australia. The south-west of Western Australia is estimated to receive fewer than 20 000. The double-banded plover breeds in New Zealand, and its total population is estimated to be 10 000–12 000, about half of which cross the Tasman to south-eastern Australia in winter (Lane 1987).

Migration within Australia also occurs as studies on the cattle egret (McKilligan *et al.* 1993) indicate, and is also a likely source of dispersal. What little evidence there is suggests that such movement is mostly north–south.

Nomadic movement of our waterbirds is also involved in dispersal of waterplant species. Kingsford (1995) demonstrates that enormous numbers of nomads can be involved, and that these numbers are likely to be very much higher on wetlands with waterplants. What is missing is any information on east–west or west–east movements of these waterbirds between the temperate areas, but that movement may be limited. Banded Stilts, for example, move between the coast and more or less adjacent inland areas in south-eastern and south-western Australia but do not seem to travel between east and west (Hewish 1989).

Our results on the biogeography of waterplants relate well with what is known about waterbird migration. The similarity of the aquatic floras of seasonally dry tropical areas in northern Australia, the slightly lower association of Papua New Guinea, and the consistent grouping along the east coast of Australia are consistent with bird migration patterns, as are the comparative isolation of south-west Western Australia and New Zealand. The nomadic behaviour of the resident native waterbirds could possibly explain the distribution of those plant species that are shared by the more isolated regions and the east coast.

The potential for long distance dispersal is so great that the separation between the tropical and temperate floras could only be maintained if factors other than dispersal were involved. Experience with species in cultivation indicates that the differences are physiological, a mixture of adaptations to temperature and light and specialised adaptations to the highly seasonal monsoonal climates of the Australasian tropics.

The pattern of development of the aquatic flora is quite different from that hypothesised for the Australian arid flora, which is thought to have been derived from elements that either have 'always' been present in arid habitats or have developed from elements growing in more mesic habitats around the arid areas (Carolin 1982; Smith-White 1982). Examples of the former include genera of Chenopodiaceae, Loranthaceae and Asteraceae, *Eremophila* and *Brunonia* (Smith-White 1982). Examples of the latter include *Acacia* (Maslin and Hopper 1982), *Triodia* (Jacobs 1982) and Goodeniaceae (Peacock 1963).

The story about the Australasian alpine floras is rather less clear, Smith (1986) being a strong proponent of long distance dispersal for most taxa, whereas Costin *et al.* (1979) and Macphail (1986) postulate a Gondwanan origin for our alpine flora. Some individual studies support the latter view; for example, Barker (1986) finds evidence for development from a Gondwanan element in *Euphrasia*. Wilson (1986) finds strong evidence of development of alpine species from lower altitude species in Cyperaceae and Juncaceae but also a strong 'peregrine' element, probably derived by long distance dispersal from several other regions of the world. A consensus is difficult to achieve, but the evidence does suggest two elements, a Gondwanan element derived from surrounding plant communities, and a small but significant element originating via long distance dispersal. Even though there may be some long distance dispersal in the alpine flora it is less than that seen for most aquatic floras. The more isolated of the regions defined here for the aquatic floras are possibly similar to the similarly isolated alpine regions.

The higher proportion of monocots than dicots in aquatic floras compared with terrestrial floras has long been known, if not formally commented upon. The percentage of monocot species compared with the total of dicots and monocots is much the same in different areas and apparently independent of the state of taxonomic knowledge. Biswas and Calder (1954) have 58% monocots in their treatment of water and marsh plants of India and Burma, Muenscher (1944) has 64% in his treatment of aquatic plants of the United States, Tarver *et al.* (1978) record 59% for aquatic and wetland plants of Florida, and Spencer-Jones and Wade (1986) record 51% for aquatic plants of the British Isles. Although there is a whole series of related aquatic families in the monocots, the largest numbers of aquatic species are in the Cyperaceae and Poaceae. It is almost as if the monocot syndrome includes the potential to become aquatic in much the same way as the Caryophyllales appears to have gained the potential to develop $C_4$ pathways early in its phylogeny (Carolin *et al.* 1978).

The way in which the Australian aquatic flora has developed does not bode well for the future. Waterplants are particularly well adapted for long distance dispersal; and humans have now added an entirely new and highly efficient dimension to long distance dispersal. We can expect a steady increase in the number of aquatic species being added to our flora. The adaptations of these species are likely to result in comparatively rapid and efficient dispersal between our regions with effective containment of weedy species being more difficult than for many terrestrial species.

## Acknowledgments

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