



Distributional patterns of jumping spiders (Araneae: Salticidae) in Australia

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ABSTRACT

Aim To analyse observed and predicted distributional patterns of selected salticid genera in Australia and to examine these distributions in the light of the origins and attributes of the fauna. To detect and compare the locations of regional hotspots when measured using different scales.

Location Australia.

Methods A total of 4104 locality records for specimens of 51 genera were stored in BioLink. Maps of observed and predicted (using BIOCLIM) distributions were prepared for each genus. The predicted distributions were combined to provide estimates of the number of genera likely to be found at each locality in the raster and for each of a set of landscape regions across Australia. The predictions were tested by comparing them with independent data sets.

Results The Australian salticid fauna consists of radiations based on Oriental, Papuan and possibly Gondwanan forms, plus pantropical and peridomestic species. The predicted distributions of genera fall into a limited number of categories and these reflect the traditional biogeographical regions of Australia. Maximum regional diversity is predicted for central eastern Queensland, though diversity at single locations is highest further south in the New South Wales/Queensland border region. The locations of hotspots are therefore scale dependent. Patterns of distribution are not simply related to particular lifestyles. Fewer genera were predicted from inland Australia; however, recent work has shown that there are a large number of undescribed genera in the drier parts of Australia. The prediction maps allowed lists of genera potentially present in unstudied areas to be developed.

Main conclusions (1) The current distribution of genera is predicted by their bioclimatic profiles rather than by their origins or ecology. Some Oriental genera, however, have not reached south-western Western Australia, though bioclimatic conditions there are predicted to be suitable for them; (2) the highest diversity of genera is predicted to be in south-eastern Queensland; (3) the results highlight the shortcomings of past fieldwork in Australia, which has concentrated on the areas with higher rainfall; (4) it seems likely that inland Australia will support a large, highly endemic, fauna adapted to the region, and ultimately perhaps 40 or more genera could be found in each region; (5) the results show the possibility of using the maps of predicted distribution of genera not only for biogeographical analyses but also for conservation management and survey purposes.

Keywords Australia, BIOCLIM, biodiversity hotspots, BioLink, distribution of genera, Salticidae.

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INTRODUCTION

While the distribution of a species is related to its place of origin, dispersal power, past and present barriers to movement and climate (Gaston, 1991), its occurrence at a particular locality within its range is influenced by micro-climate, vegetation, ground cover, hiding and display places, threatening processes (flooding, drought, fire, snow, frost), hunting strategy, predator–prey relationships, etc. (Duffey, 1978; Rosenzweig, 1991; Gill *et al.*, 1999; Harvey *et al.*, 2000; Tews *et al.*, 2004; review for spiders in Foelix, 1996). To assess the importance of these variables and their interactions, habitats have to be measured and monitored in standardized ways.

In the absence of such detailed studies other approaches to the mapping of distributions for management purposes need to be explored. A commonly used approach has been to predict the distribution of the taxon of interest on the basis of its climate envelope developed using the climate profiles of localities where the species is known to occur (e.g. Nix, 1986; Richardson & McMahon, 1992; Neave *et al.*, 1996; Godown & Peterson, 2000; Fischer *et al.*, 2001; Beaumont & Hughes, 2002; Meynecke, 2004). However, limitations to this approach have been identified (Peterson & Cohoon, 1999; Claridge, 2002; Kadmon *et al.*, 2003). The Australian jumping spiders offer a typical example of the situation faced by workers in poorly studied countries. Only 340 salticid species (in 70 genera) of the likely 1000 or more species (in 100 genera) present have been described (Richardson & Zabka, 2003), and in most cases the species described are represented by relatively few locality records.

A further step towards obtaining useful information when the number of available data are restricted would be to use the set of locality records for a genus rather than a species (given that a genus, in this context, reflects a way of living that is common to all included species). The distribution predicted from such a larger set of records is likely to give a better insight into the probable distribution of the genus (including both known and unknown species) than the sum of the distributions of the few species with extensive locality data. Such an approach allows specimen records identified only to genus, or from undescribed species within the genus, to be used as well.

In this study we analyse the known and predicted distributions of salticid genera in Australia, their diversity and zoogeographical characteristics.

The aims of the study are:

1. to examine predicted distributions of selected genera of jumping spiders (Salticidae) within the continent in relation to climate, landscape and origin,
2. to identify and discuss any biodiversity hotspots for the Australian salticid fauna,
3. to present and discuss regional patterns of similarity in the distribution of genera and of the faunal relationships of different landscape regions.

MATERIALS AND METHODS

The data

A set of 4104 locality records for specimens of salticid species was provided by the Australian Museum, Sydney and the Australian National Insect Collection, Canberra. The data from the publications of M.Z., listed in Richardson & Zabka (2003), and from Harvey *et al.* (2000) were also included. As the described genera have been unequally studied, we used only 51 properly defined and relatively well studied ones (see Table 2 below) where locality records were well distributed. The number of records per genus varied between 6 and 683 (median 30).

The data on locality records was stored in BioLink (version 2.0; Shattuck & Fitzsimmons, 2002) and maps of known distributions were made for each genus. The predicted distribution map for each genus was generated on the basis of its bioclimatic envelope, using the boxcar version of BIOCLIM available in BioLink. An introduction to the logic and accuracy of the method and examples of the use of BIOCLIM to examine the distribution of continental faunas can be found in Nix (1986) and Lindenmayer *et al.* (1991).

Climatic indices

As used here, BIOCLIM estimates 12 bioclimatic indices for the location of each specimen and thence the range found for each variable for the taxon.

The indices estimated are:

1. annual mean temperature (°C),
2. hottest month mean maximum temperature (°C),
3. coldest month mean minimum temperature (°C),
4. annual temperature range (2 minus 3) (°C),
5. wettest quarter mean temperature (°C),
6. driest quarter mean temperature (°C),
7. annual mean precipitation (mm),
8. wettest month mean precipitation (mm),
9. driest month mean precipitation (mm),
10. annual precipitation range (8 minus 9) (mm),
11. wettest quarter mean precipitation (mm),
12. driest quarter mean precipitation (mm).

These variables provide estimates of total energy and water inputs, seasonal extremes and a measure of conditions prevailing during potential active and dormant seasons. The range of values obtained for the taxon are then compared with the values for each point on a 20 second grid covering the continent. The points meeting the criteria for the taxon are identified and mapped. The darker the colour used for each point in the final map, the more likely the taxon is to be present (cut-offs are 25th and 75th percentiles, 10th and 90th percentiles, 5th and 95th percentile, 0th and 100th percentiles for all variables). The quality of the predicted distributions obtained was tested by comparing lists of genera predicted for south-west Western Australia and the Adelaide region of South Australia, based entirely upon records from elsewhere in the

country with the records for these genera from those areas in the collections of the Western Australian Museum and the South Australian Museum respectively.

The generic diversity map was calculated by summing the number of genera predicted at each point on the continental grid, i.e. a diversity measure for each locality with the colour cut-off levels being 75%, 50%, 25% and 0% of the difference between the highest and lowest levels of diversity.

Landscape

A set of landscape regions has been developed for Australia reflecting vegetation, land form and climate (Bridgewater, 1987 after Barlow, 1985) and the number of genera predicted to be present in each region was calculated, i.e. a measure of diversity in each landscape region was obtained. A frequency distribution of the number of genera per region was calculated.

The dissimilarities between landscape regions (in terms of the suites of genera predicted to be present) were calculated using the Bray–Curtis association measure, while the dissimilarities between genera (in terms of the suites of landscape regions in which they are found) were calculated using the two-step association measure (Belbin, 1995). This measure applies to the classification of attributes and was designed specifically to address the problem of frequency bias in species classifications (i.e. species having similar frequencies of occurrence tending to be grouped together). The associations of landscape regions and of genera were fused using an agglomerative hierarchical approach and applying flexible unweighted pair group arithmetic averaging (UPGMA) with a beta of -0.001 . The dendrograms were derived using PATN (Belbin, 1995). A two-way table was prepared by reordering and displaying the rows and columns of the original data matrix in the same order as in the corresponding dendrograms. The table was derived using PATN (G. C. Watson, pers. comm.).

The origin and relationships of the fauna were then considered in the context of its distribution within Australia and earlier taxonomic and biogeographical studies of the Oriental, Papuan and Pacific salticid faunas (Zabka, 1985, 1988, 1990, 1991a,b, 1993; Proszynski, 1996).

The biology of jumping spiders

Beyond the general considerations mentioned above, salticid distributions in Australia depend on some specific variables as listed below.

Habitat preferences

Nearly all species of *Holoplatys*, *Ocrisiona*, *Zebropolitys*, *Afracilla*, *Sandalodes* and *Arasia*, and some species of *Helpis*, *Astia*, *Myrmarachne*, *Tara*, *Clynotis* and *Zenodorus* live on tree trunks and are dependent on bark structure. Representatives of *Sondra*, *Pseudosynagelides*, *Lycidas*, *Gravenulla*, *Adoxotoma* and

'*Neon*' are found on bare ground or in litter, either in various types of forests or in grassland/semi-desert country. Species of *Opisthoncus*, *Cosmophasis*, *Cytaea*, *Mopsus*, *Mopsolodes*, *Euryattus*, *Simaetha*, *Ligonipes* and *Jacksonoides* are also habitat-selective and live on grass, herbs, bushes or in the canopy. Thus, each habitat creates a range of unique microhabitat contexts of microclimate, diet, survival opportunities, shelter, prey, etc., thereby influencing the species/generic composition of the fauna. Such specializations are likely to lead to differences in the distribution of diversity between regions compared with the distribution of diversity between localities (see below).

Dispersal

Most jumping spiders are poor dispersalists but some can 'travel' by rafting, ballooning and human agency (Decae, 1987). Each habitat/microhabitat offers specific dispersal possibilities. For instance, leaf-litter or bark dwellers are poorer candidates for ballooning compared with inhabitants of open areas or tree canopies. In rain forests, the wind currents are too weak and are limited to the highest canopy level, and the majority of species are too narrow niche specialists to 'take a risk' of finding themselves in an 'unknown' and inappropriate place. In open areas the possibilities are better – at least in theory. Some examples of ballooning in Australian species are given by Main (1981), Greenstone *et al.* (1987) and Patoleta & Zabka (1999).

At least six species occurring in Australia (*Plexippus paykulli*, *Plexippus petersi*, *Menemerus bivittatus*, *Hasarius adansonii*, *Frigga crocuta* and *Helpis minitabunda*) live in human habitations and are dispersed by human agency and, consequently, have wide, pantropical distributions.

Extreme climate effects

In Australia, drought and fire are the most influential factors (Gill *et al.*, 1999). In the areas where higher precipitation is the rule, seasonal drought may dramatically decrease the occurrence of jumping spiders. For a fauna that has evolved in warm climates, the cold extremes found in mountain areas, especially in the Snowy Mountains in south-eastern Australia, may be limiting.

RESULTS AND DISCUSSION

The origin of the fauna

According to Main (1981) the Australian spider fauna can be ascribed to the five sources listed below (see Table 1).

Pangean

Possible examples have been suggested from other spider families in Australia (Main, 1981), but not for salticids.

Table 1 Current list of Australian salticid genera and their zoogeographical origin

	Oriental/ Gondwanan	Papuan	Oceania*	Modern endemics	Widespread
<i>Adoxotoma</i> †		<i>Bavia</i>	<i>Ascyrtus</i>	<i>Abracadabrella</i>	<i>Afraflacilla</i>
<i>Neon</i> †‡		<i>Canama</i>		<i>Adoxotoma</i> †	<i>Bianor</i>
		<i>Chalcolecta</i> ‡		<i>Arasia</i>	<i>Cyrba</i>
		<i>Cocalus</i>		<i>Astia</i>	<i>Evarcha</i>
		<i>Coccorchestes</i>		<i>Clynotis</i>	<i>Frigga</i>
		<i>Cosmophasis</i>		<i>Copocrossa</i>	<i>Gangus</i>
		<i>Cytaea</i>		<i>Damoetas</i>	(= <i>Thyene</i>)
		<i>Diolenius</i>		<i>Ergane</i>	<i>Habrocestum</i>
		<i>Euryattus</i>		<i>Grayenulla</i>	<i>Harmochirus</i>
		<i>Mintonia</i>		<i>Helpis</i>	<i>Hasarius</i>
		<i>Ohilimia</i> ‡		<i>Holoplatys</i>	<i>Langona</i> ‡
		<i>Omoedus</i>		<i>Hypoblemum</i>	<i>Menemerus</i>
		<i>Palpelius</i>		<i>Jacksonoides</i>	<i>Myrmarachne</i>
		<i>Phintella</i> ‡		<i>Jotus</i>	<i>Neon</i> †‡
		<i>Zenodorus</i>		<i>Judalana</i>	<i>Pellenes</i> ‡
				<i>Lauharulla</i> §	<i>Plexippus</i>
				<i>Ligonipes</i>	<i>Portia</i>
				<i>Lycidas</i>	<i>Sigytes</i> §
				<i>Maratus</i>	
				<i>Margaromma</i>	
				<i>Megaloastia</i>	
				<i>Mopsolodes</i>	
				<i>Mopsus</i>	
				<i>Ocrisiona</i>	
				<i>Opisthonus</i>	
				<i>Paraphilaeus</i>	
				<i>Paraplatoides</i>	
				<i>Prostheclina</i>	
				<i>Pseudomaevia</i>	
				<i>Pseudosynagelides</i>	
				<i>Rhombonotus</i>	
				<i>Sandalodes</i>	
				<i>Servaea</i>	
				<i>Simaetha</i>	
				<i>Simaethula</i>	
				<i>Sondra</i>	
				<i>Tara</i>	
				<i>Tauala</i>	
				<i>Zebraplatys</i>	

*Genus found primarily in Oceania, doubtfully to Australia (Richardson & Zabka, 2003).

†Genera of uncertain origin.

‡Present but formally not recorded in Australia (for *Chalcolecta* and *Ohilimia* see Gardzinska, 2004).

§Genera of uncertain taxonomic status.

Gondwanan

Australian relict temperate or highland forests with *Nothofagus*, *Dacrydium*, *Podocarpus*, Araucariaceae, Proteaceae, based on precursor floras of the upper Cretaceous, might support salticids that derived from Gondwanan sources. It seems, however, that old (relict) jumping spider faunas have been replaced either by modern neoendemics that evolved in

Table 2 Two way table of genera vs. landscape regions in which they occur. Landscape regions according to Fig. 3 and full genera names are given in Table 1. The associations between landscape regions and genera were developed using UPGMA and PATN and an agglomerative hierarchical approach. Biogeographical regions are: B, Bassian; E, Eremaean; T, Torresian

Region	AKBC	PGT	MWM	GT	LTVN	S	C	CBDMN	DRBLEEOTH	S	N	
<i>Adoxotom</i>									11		111111	8
<i>Phintell</i>											11	4
<i>Arasia</i>									111111		11111111	13
<i>Neon</i>			1						111111	1	111111	13
<i>Saitis</i>									111111	11	111111	13
<i>Servaea</i>									111111	11	111111	13
<i>Pseudosy</i>					1				111111	11	111111	14
<i>Rhombono</i>									111111		1111111111	14
<i>Astia</i>									111111	1	111111	13
<i>Bavia</i>									111111		111111	11
<i>Hypoblem</i>	1	111							111111	111111		15
<i>Opisthon</i> 1		11							1111	1111111111		16
<i>Simaethu</i>			11		1				111111	1111111111		17
<i>Sondra</i>	1	1							111111	1111111111		16
<i>Tara</i>	1111								111111	1	111111	16
<i>Canama</i>									111			13
<i>Jacksono</i>									1111			14
<i>Euryattu</i> 1									1111			15
<i>Hasarius</i> 1									111111			16
<i>Portia</i>	11								111111			17
<i>Ligonipe</i>									111111		1	16
<i>Trite</i>									111111		1	16
<i>Tauala</i>									111111		1	16
<i>Menemeru</i>									1111		111	17
<i>Afraflac</i>	111	111	111	11	1	1	1	11	11	1		20
<i>Grayenul</i>	1	111	111	1	111	1	1	11	11			17
<i>Bianor</i>		111	111	1	11				111111	11111	1	20
<i>Paraplat</i>		111	111	11	1111		1	111111	1111111111			27
<i>Clynotis</i>	1111	111	111						111111	1111111111		24
<i>Helpis</i>	111	111	11		11				111111	1111111111		24
<i>Cytaea</i>	1111	111	111	11		1			111111	111111		24
<i>Zenodoru</i>	1111	111	111	11	1		1		111111	111111		25
<i>Holoplat</i>	1111	111	111	11	1111	1	1	111111	1111111111			32
<i>Lycidas</i>	111	111	111	11	1111		1	111111	1111111111			30
<i>Ocrision</i>	111	111	111	11	1111		1	111111	1111111111			30
<i>Myrmarac</i>	1111	111	111	11	1111				111111	1111111111		30
<i>Zebrapla</i>	111	111	111	11	11	1			111111	11111111	1	27
<i>Simaetha</i>	1111	111	111		1111				111111	1111111111		28
<i>Breda</i>					1111				1111	1111111111		17
<i>Prosthec</i>			11		1111				111111	1111111111		20
<i>Jotus</i>		1	1	111	1111				1111	1111111111		22
<i>Maratus</i>			111	1	1111		1	111111	1111111111			23
<i>Sandalod</i>		1	111		1111				111111	1111111111		22
<i>Margarom</i>		1	111						111	1	11111111	15
<i>Cosmopha</i>	1111	1	1						1111			11
<i>Mopsus</i>	1111								11			16
<i>Gangus</i>	111	111			1		1	111				10
<i>Evarcha</i>	1111								1111			8
<i>Mopsolod</i>	11	1							1111			7
<i>Plexippu</i>	11	1							1111			7
<i>Salpesia</i>		111			1				111111	11		11

sclerophyllous forests and spread to other vegetation types, or/and by Oriental/Papuan immigrants (Zabka *et al.*, 2002). The genera 'Neon' and *Adoxotoma* are so far the only reported suspects of Gondwanan origin (Zabka, 2004). 'Neon' is yet to be formally reported from Australia, though several major subgroups of the taxon have radiated widely in Australia and a few examples of each of these subgroups are found in New Zealand and south-eastern Asia. A further subgroup, including *Neon sensu stricto*, is found in the Palaearctic, Nearctic and Oriental regions. *Adoxotoma* has genitalic structures linking it with other subfamilies (e.g. Heliophaninae) and it seems to be the most 'primitive' member of the Astieae. This subfamily consists of a wide radiation of genera found in Australia and New Zealand (Wanless, 1988). A further possible case of Gondwanan origin consists of species of New Zealand 'Marpissa' and the possibly related Australian genus *Lycidas*; together they could constitute a Gondwanan lineage. All these genera are ground/litter dwellers found in wet sclerophyll forests and rain forests and have restricted dispersal capacities.

Oriental/Papuan

Some Oriental genera have spread to tropical and subtropical coastal Queensland, Northern Territory and the northern part of Western Australia. Widely distributed Oriental genera represented in Australia are *Cytaea*, *Cosmophasis*, *Zenodorus*, *Mintonia*, *Bavia* and *Euryattus*. The genera *Coccorchestes*, *Omoedus*, *Cocalus*, *Palpelius*, *Ohilimia* and *Chalcolecta* seem to have originated in New Guinea and spread southwards. The genus *Ascylus* is widespread in Oceania and may reach Australia (but see Richardson & Zabka, 2003).

Modern endemics

These genera have evolved *in situ*, either from Gondwanan or Oriental precursors. Most of them are adapted to the sclerophyll forests but they are also found (perhaps secondarily) in wetter formations. This group makes up the largest component of the currently described fauna (Table 1) and genera such as *Holoplatys*, *Lycidas*, *Maratus* or *Opisthoncus* have speciated enormously. Some undescribed genera from much drier parts of Australia also belong to this group, having adapted to the increasingly dry conditions that have developed over much of Australia since the Miocene.

Widespread

This category is represented by single pantropical species of *Plexippus*, *Menemerus*, *Hasarius* and *Frigga* – all dispersed by humans – or by suites of Australian endemic species in widespread genera (*Afraflacilla*, *Pellenes*, *Evarcha*).

Actual and predicted distributions

The location records used (Fig. 1) are non-randomly distributed, with most points coming from areas in eastern Australia, Tasmania, south-west Western Australia and the Kimberley region. There are several reasons for this:

1. the east coastal areas have been the best studied, both in the past and nowadays,
2. the data used in this study came from only two collections, both situated in south-east Australia,

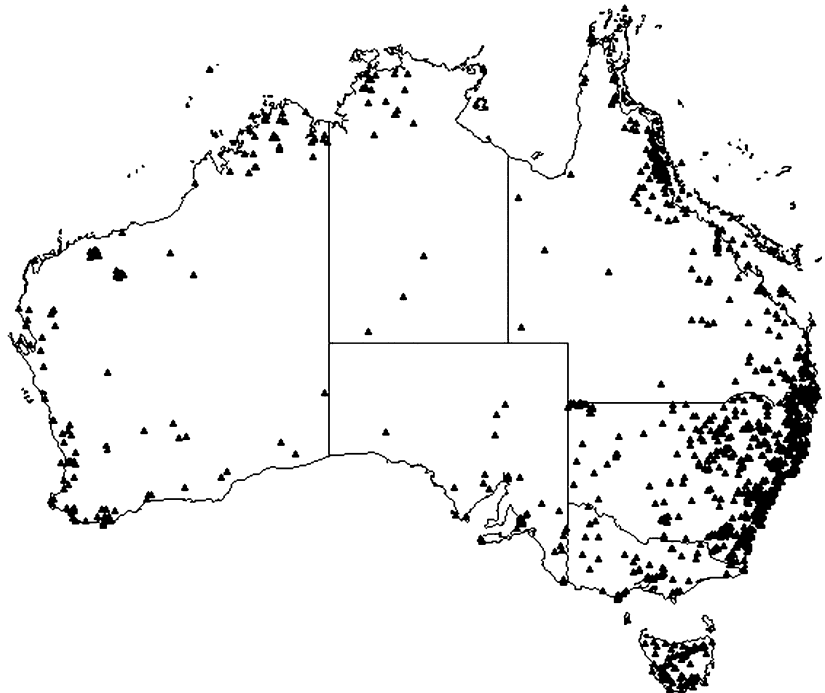


Figure 1 The geographical distribution of the 4104 records from the Australian Museum and the CSIRO Australian National Insect Collection used as the basic data in this study.

3. higher precipitation, along with climatic, topographic and floristic diversity in these areas, makes them more biologically diverse and provides the opportunity for larger numbers of genera to occur,

4. coastal eastern Australia and south-west Australia are under strong Papuan influence or show a high degree of endemism, respectively; both attract intense research activity.

Figures 2 and 3 present the predicted distributions of biodiversity in two ways. In Fig. 2 the relative number of genera predicted to be present at each point is shown, while in Fig. 3 the total numbers of genera predicted in landscape regions are given, i.e. not necessarily found at the same location. Comparison of the two figures shows that more genera are likely to be found at single locations in south-east Queensland and parts of north-east New South Wales (Fig. 2), while area faunas are larger in central eastern Queensland (Fig. 3) than elsewhere. The highest predicted diversity was found for Burdekin and Dawson landscape

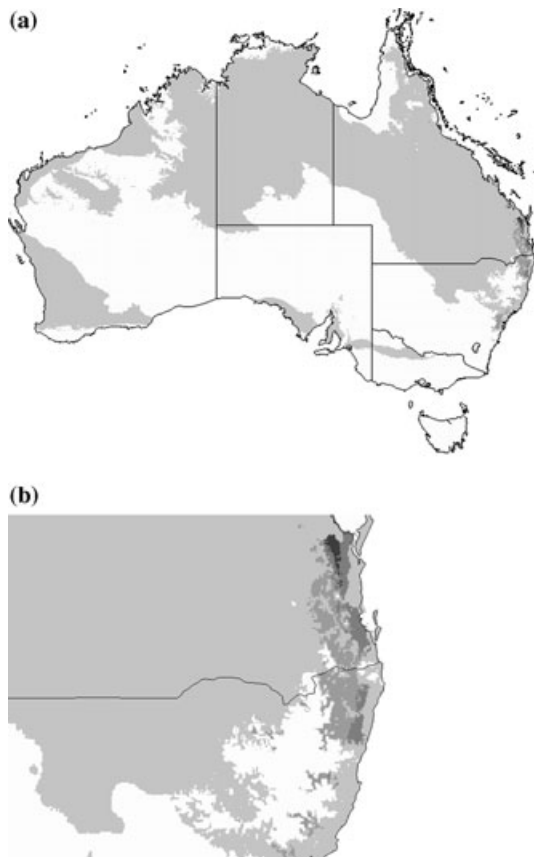


Figure 2 Predicted distribution of generic richness based on all genera studied. The BIOCLIM prediction for each genus was calculated and then the number of genera predicted to be found in each raster calculated using BioLink. The darker the shading, the greater the number of genera predicted to be found (30–40, 20–30, 10–20 and < 10 genera, respectively). (a) Map showing the whole of Australia. (b) Magnified view of the central eastern coastal region.

regions in eastern central Queensland (Fig. 3). These include the drainage areas of the Burdekin, Fitzroy and Dawson rivers, where broken range country is covered by *Corymbia*–*Symphomyrtus* woodland with patches of tropical rain forest. There is some seasonality in mean daily temperature, and rainfall is concentrated into the summer months (Bridge-water, 1987). Thus, the high diversity in these areas is the result of the wider range of habitats present, not the highest diversity at a location. What constitutes a ‘hotspot’ of salticid diversity then depends on how the diversity is measured, in this case by locality (maximum 40) or by area (maximum 48). The three adjacent areas of Cape York, McPherson and Nepean (Fig. 3) also have relatively high predicted diversity. On the other side of the continent, the winter rainfall area of Leeuwin (with *Corymbia*/*Symphomyrtus*/*Monocalyptus* rain forest grading into winter-rain sclerophyll forest) and shrubland and woodland areas in nearby Esperance also support high predicted diversity.

Generally, and interestingly, the highest predicted numbers of genera are neither in the areas with the most data (compare Figs 1 & 2), nor in the mega-diverse (for other groups) biogeographical region of Cape York.

Relatively high numbers are predicted for the MacDonnell geographical area in central Australia (Fig. 3). The ranges in this area and similar parts of the Pilbara carry relatively high predictions of genera otherwise restricted to wetter areas, often of eastern Australia (e.g. *Maratus*, *Helpis*, *Hypoblemum*, see Fig. 6a,c,d).

Other points worth noting are very low predictions for the driest areas, though there are not enough field data to confirm these observations. Simpson (Fig. 3), for example, has no salticid genera predicted – a situation difficult to imagine, especially as large parts of it support vegetation. Elsewhere genera such as *Grayenulla*, *Afraflacilla* and *Pellenes* are known to occur in such habitats.

Few genera were predicted for the Australian Alps and Barrington Tops (see for example Fig. 6c), areas that regularly receive snow. Presumably the climate profile for these areas is outside predicted ranges based on specimens collected at lower altitudes. Our collecting efforts in the Brindabella Ranges at slightly lower altitudes had little success, but specimens of five genera have been found.

The highly biased distribution of localities to the wetter areas of eastern Australia means that predictions for other areas might be underestimated (Peterson & Cohoon, 1999; Claridge, 2002; Kadmon *et al.*, 2003). This possibility can, however, be tested. For example, for seven of the genera predicted for Eyre (Fig. 3) there were no locality records from Eyre used in making the predictions, but specimens of six of these genera were later found in the collection of the South Australian Museum (D. Hirst, pers. comm.). Similarly, of 24 genera predicted for south-west Western Australia, i.e. Bencubbin, Leeuwin and Esperance (Fig. 3), for which no specimen localities from these areas were used to make the predictions, specimens of 12 genera were found from the region in the collections of the Western Australian Museum

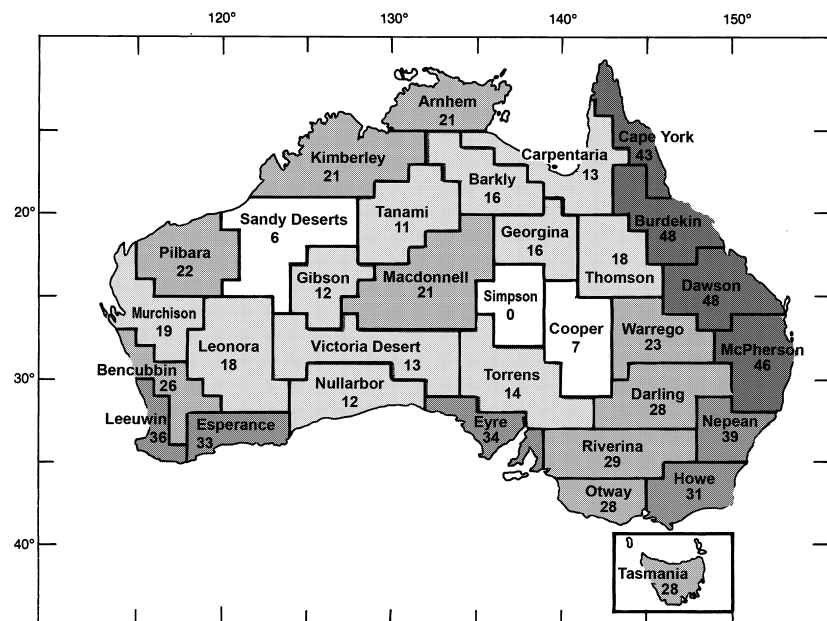


Figure 3 The number of genera predicted to be found in each geographical area of Australia. The BIOCLIM prediction of the distribution of each genus was calculated and then the number of genera predicted to be found in each landscape region was calculated by inspection of these distributions.

(J. M. Waldock, pers. comm.). Most of the remainder are genera represented in eastern Australia as outliers of wide-spread or Oriental genera that presumably have been unable to make their way across the drier Nullarbor region to Western Australia.

It is worth noting that while all 19 genera predicted for the drier Murchison region were found during a detailed biodiversity survey carried out in the area (Harvey *et al.*, 2000), examples of a further 18 undescribed genera were also obtained.

Our results highlight the shortcomings of past fieldwork in Australia, which has concentrated on the areas with higher rainfall. Such systematic bias cannot be offset in a study such as this (Peterson & Cohoon, 1999; Claridge, 2002; Kadmon *et al.*, 2003) and it seems likely that inland Australia will support a large, highly endemic fauna adapted to the region. Ultimately, perhaps 40 or more genera might be found in each region.

The distributional patterns

Two-way relationships between landscape regions and genera are shown in Table 2. The distributional range within the continent does not show any relationships with the entire generic distribution. For instance, the genera *Evarcha* and *Menemerus* of nearly world-wide range are only found in eight and seven regions, respectively, in Australia, while endemic *Holoplatys* or *Ocrisiona* occur in most regions. On the other hand, *Myrmarachne*, which has a cosmopolitan distribution, is widespread in Australia, while endemic *Tauala* is limited to six regions only. Of eight genera predicted for 25 or more regions (Table 2), five (*Holoplatys*, *Ocrisiona*, *Myrmarachne*, *Zebraplatys*, *Paraplatoides*), are eucalypt tree-trunk dwellers, thus their potential presence in many regions is not surprising. The lowest numbers of

regions are predicted for *Canama* (3), *Jacksonoides* (4) and *Euryattus* (5): all are foliage dwellers inhabiting tropical-subtropical forests and, as such, are limited to northern regions. Thus, before any generalization is made, every generic case has to be individually analysed and the available knowledge of its biology (microhabitat preferences) has to be considered.

Relations between genera on the basis of similarity of regional distributions are shown in Fig. 4a and Table 2. It can be seen that the genera are clustered in distinct groups with common distributions, though the groups do not consist of morphologically or ecologically similar forms. The compositions of genera within the clusters result from current climatic and biota profiles and do not reflect areas of origin. The similarities between landscape regions on the basis of genera in common are shown in Fig. 4b and Table 2. The deepest dichotomies separate the faunas into Torresian, Eremaean and Bassian regions. The Bassian region further divides into a northern group of regions reaching as far south as Nepean while the remaining regions form three groups; southern and western coastal groups, and an inland group. The analyses show the potential conservation values of particular regions – even those from which field data are limited.

In most cases, the ultrametric distances between particular regions support the bioclimatic-based analysis. The exceptions refer to the regions where the field data are missing or are incomplete.

Despite the varied age and origin of the fauna, within the continent some genera are distributed according to the patterns that follow the traditional division into Torresian, Eyrean/Eremaean, Bassian and Southwest regions. Most genera, however, show either mixed or trans-Australian distributions related to biotic requirements rather than geographical origin. Selected examples are given below.

Torresian (northern) distribution

This is a distinctive distribution for genera of either Oriental or Australian origin, usually distributed in the northern, tropical part of the continent, with single species found further south in areas of suitable climate and habitats. An example is *Mopsus* (Fig. 5a, Table 2), which is known from tropical forests of Australia, New Guinea and New Caledonia (Patoleta, 2002). The distribution of its closest relatives such as *Mopsolodes* and *Sandalodes* suggests an Australian origin for the group (Zabka, 1991a, 2000). A second genus, *Jacksonoides* (Fig. 5b, Table 2) also seems to be of Australian origin. It is likely to be found further south along the east coast than *Mopsus* – as are related genera in the Astieae subfamily (Wanless, 1988). The genus *Cosmophasis* (Fig. 5c, Table 2) is found from Southeast Asia to the western Pacific islands and is richly represented in Australia [probably *c.* 30 species (M. Zabka, unpubl. data)], mostly in the Torresian region. It inhabits tropical rain forest and similar habitats. Interestingly, the BIOCLIM prediction suggests that it will be ultimately found in drier areas of northern Australia.

Eyrean/Ermaean distribution

Such genera are found in the central, drier, parts of Australia and are represented either by neoendemic genera such as *Grayenulla* (Fig. 5d, Table 2) or widespread ones such as *Pellenes* [present but yet to be formally recorded from Australia (M. Zabka, unpubl. data)].

Bassian distribution (south-eastern or south-eastern and south-western)

These genera are mostly Australian neoendemics and are found both in eastern and western parts of the continent, separated by central and southern dry areas. *Adoxotoma* (Fig. 5e, Table 2) is found in wet sclerophyll and rain forests (Zabka, 2001). It has also recently been found in New Zealand (Zabka, 2004). The genus might be ‘ancestral’ to the entire Astieae subfamily (see above) and is suspected to be of Gondwanan origin. *Opisthuncus* (Fig. 5f) is a modern endemic genus and seems to have a mostly south-eastern distribution in Australia, with an extensive predicted south-western distribution (veri-

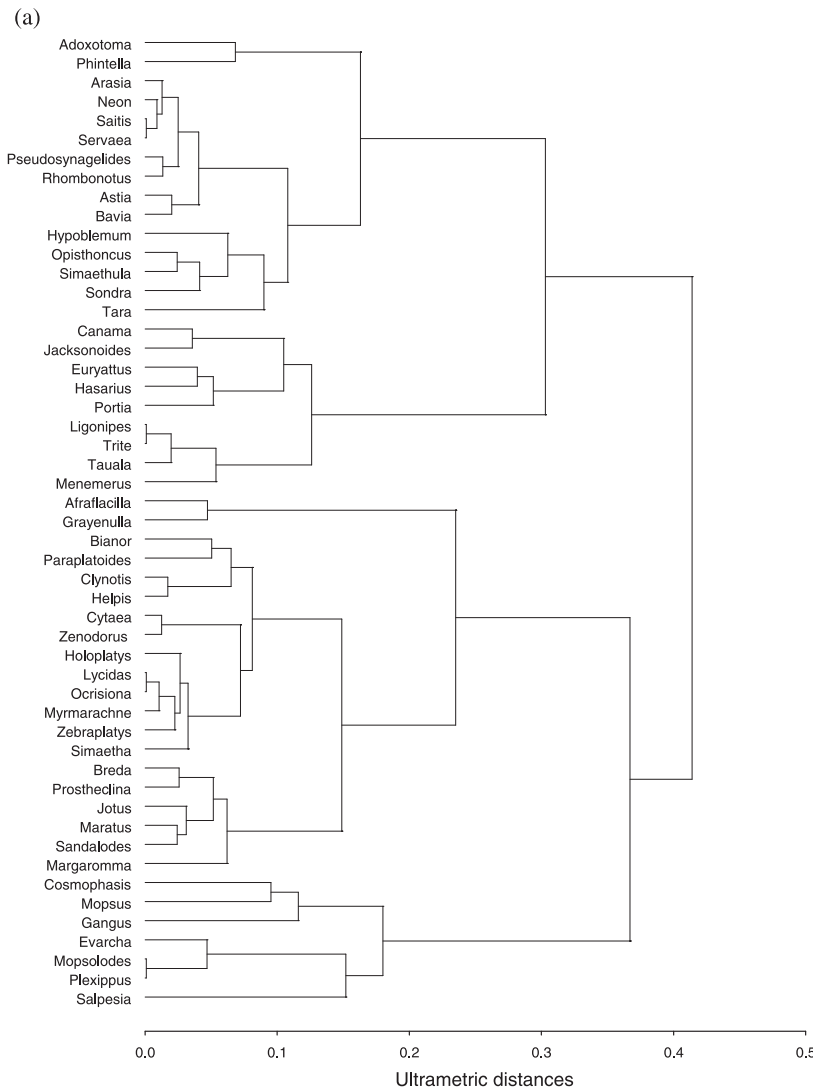


Figure 4 Cluster analyses showing (a) genera clustered according to landscape regions and (b) landscape regions clustered according to genera. The dissimilarities between landscape regions (in terms of genera) were calculated using the Bray–Curtis measure while the dissimilarities between genera (in terms of landscape regions) was calculated as a two-step association measure.

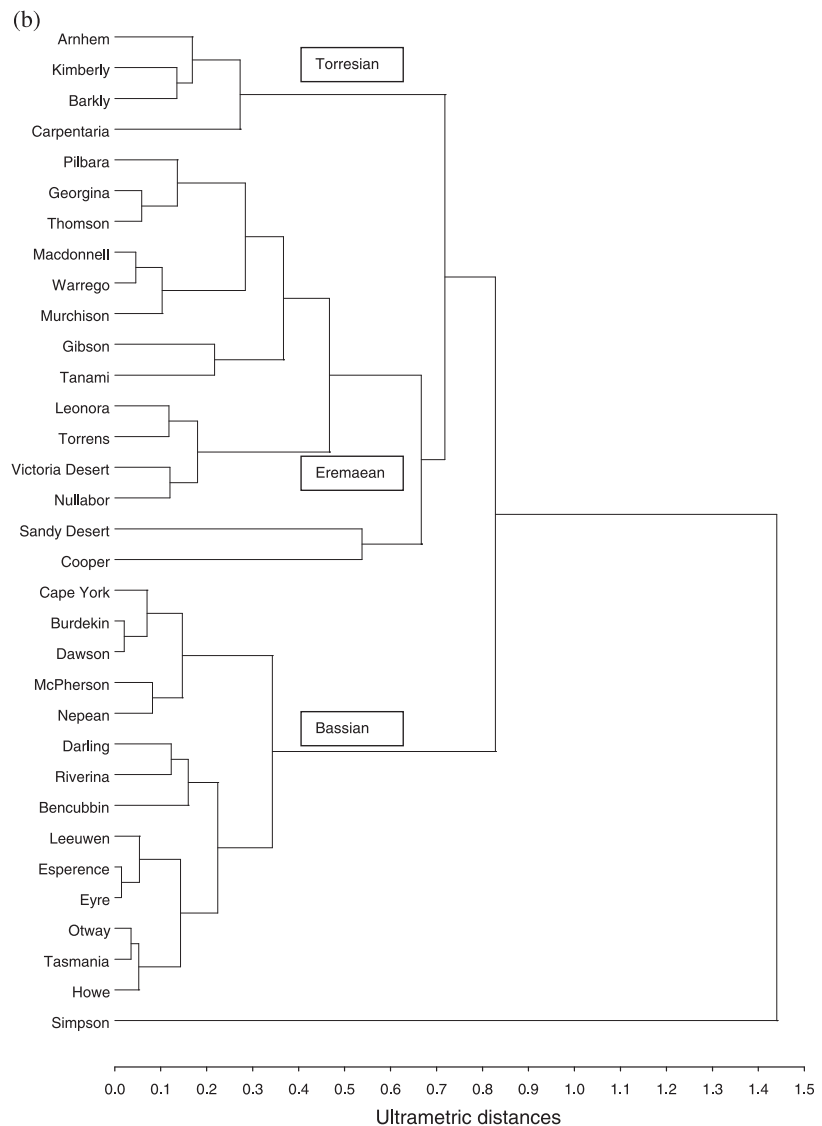


Figure 4 continued

fied by known south-western records). The prediction also spreads into the inland towards north-eastern coastal areas. This group may need to be divided into those found in the south-west and those not. They also tend to be found in arid areas, either in relict habitats or along streams. The genus *Maratus* (Fig. 6a, Table 2) (currently being studied by J. Waldock, unpubl. data), also a modern endemic, has a similar distributional pattern, though it prefers more open habitats and, as such, is also predicted from inland locations.

Trans-Australian distributions

These include several groups of widespread genera. Some, such as *Myrmarachne* (Fig. 6b, Table 2) are found in different biota (habitats) of central, southern and eastern Australia. Others tend to have coastal distributions, such as *Helpis* (Fig. 6c, Table 2), or are found in central latitudes, e.g. *Hypoblemum* (Fig. 6d, Table 2).

Management and conservation issues

The effective management of invertebrates is bedevilled by the problem of a lack of knowledge of the number and distribution of most species. This can be offset to a significant extent by using genera rather than species, along with modelled distributions based on museum records. In the present example, examination of Fig. 2b shows the areas of highest diversity for salticids and points out some interesting facts. Though the highlands in north-eastern New South Wales do not contain a highly diverse fauna, the river valleys that dissect the area are predicted to do so. The diversity in these areas is also higher than that nearer the coast in the same regions. Similarly the higher diversity in the Pilbara and MacDonnell landscape regions compared with surrounding regions (Figs 2a & 3), plus the fact that these areas are predicted to maintain similar suites of genera normally found in eastern Australia (Table 2 and Fig. 4) and that a list of these genera can be obtained in

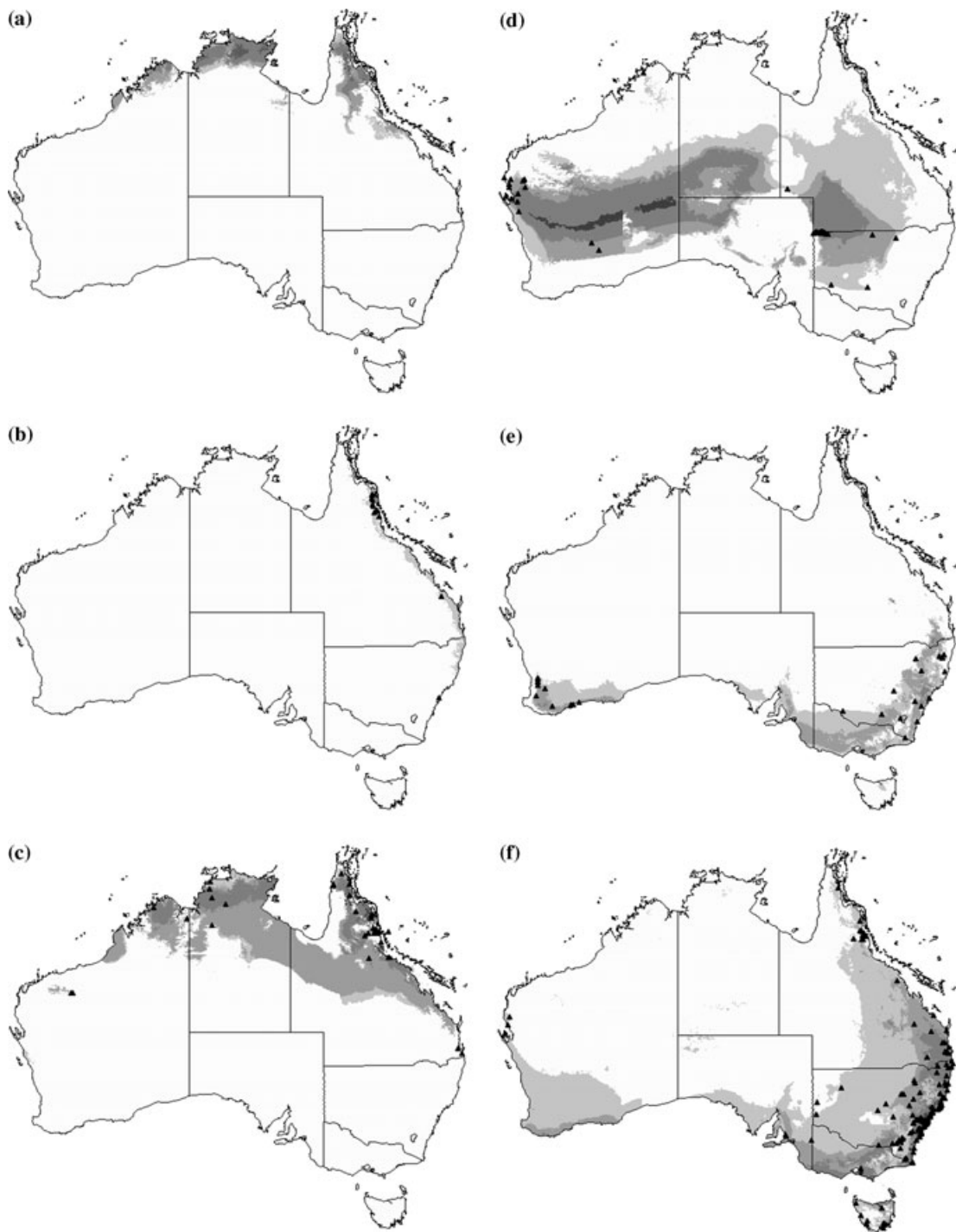
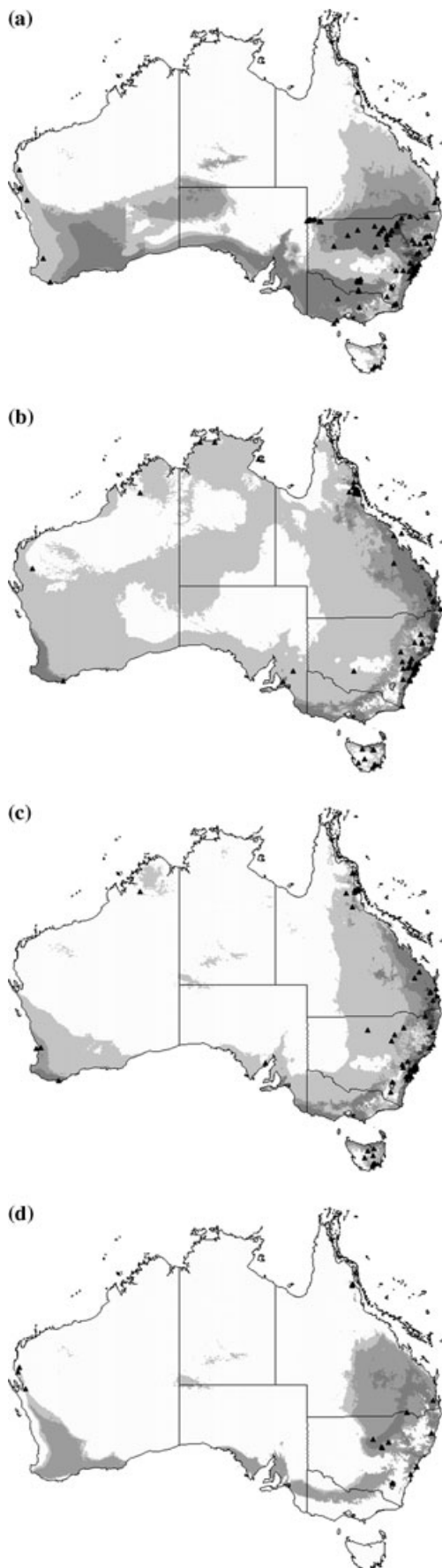


Figure 5 The known and predicted Australian distribution of (a) *Mopsus*, (b) *Jacksonoides*, (c) *Cosmophasis*, (d) *Greyenulla*, (e) *Adoxotoma*, (f) *Opisthoncus*. The localities are those in the primary data set from the museum collections used and the predicted distributions are based on bioclimatic envelopes as calculated using the boxcar version of *BIOCCLIM* available in *BioLink*. The darker the shading, the more likely the genus is to be present (cut-offs are 25th and 75th percentiles, 10th and 90th percentiles, 5th and 95th percentiles, 0th and 100th percentiles, respectively, for each climatic index).

advance to assist planning field work to these areas, provide a more efficient starting point for management and conservation. Mapping genera rather than species allows all records for the genus, including those for undescribed species and for

specimens not identified below genus level, to be used. As a consequence, the distribution map will hopefully identify areas inhabited by undescribed as well as known species. This study also highlights the limitations of such an approach due to the



climatic bias in sampled locations; for example the drier regions of inland Australia and the high country of south-east Australia are under-represented. Again such information can be informative in the strategic development of an effective survey programme.

A further category of genera that were under-represented in the present study are those with highly restricted distributions, for example *Cocalus* and *Coccorchestes*. Because they only occur in small areas, all available specimens come from that small area and the criterion for inclusion used in the present study of 'a set of geographically well distributed specimens' sees such genera removed from the analysis. These genera would, of course, be of significant conservation concern.

While the bioclimatic envelope provides a useful prediction of the distribution of many taxa, other factors, highlighted above, can further restrict the real distribution. The consequence of this is that the predicted distributions given here may overestimate the range of the taxon of interest, which is to be preferred to an underestimate when used in planning biological surveys.

CONCLUSIONS

We can conclude the following:

1. The current distribution of genera is primarily determined by their bioclimatic profiles rather than by their origins. Some Oriental genera, however, have not reached south-western Western Australia, though bioclimatic conditions there are predicted to be suitable for them.
2. The highest diversity of genera is predicted to be in south-eastern Queensland.
3. The results highlight the shortcomings of past fieldwork in Australia, which has concentrated on the areas with higher rainfall.
4. It seems likely that inland Australia will support a large, highly endemic, fauna adapted to the region and ultimately, perhaps 40 or more genera could be found in each region.
5. The results show the possibility of using the maps of predicted distribution not only for biogeographical analyses but also for conservation management and survey purposes.

Figure 6 The known and predicted Australian distribution of (a) *Maratus*, (b) *Myrmarachne*, (c) *Helpis* and (d) *Hypoblemum*. The localities are those in the primary data set from the museum collections used and the predicted distributions are based on bioclimatic envelopes, as calculated using the boxcar version of BIOCLIM available in BioLink. The darker the shading, the more likely the genus is to be present (cut-offs are 25th and 75th percentiles, 10th and 90th percentiles, 5th and 95th percentiles, 0th and 100th percentiles, respectively, for each climatic index).

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