

Patterns in the composition of the jumping spider (Arachnida: Araneae: Salticidae) assemblage from the wheatbelt region, Western Australia

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Abstract – A survey of the salticid spider fauna of the wheatbelt revealed a total of 41 genera and 121 species, of which 17 genera and 106 species are undescribed. Patterns in the species composition of assemblages across the survey area were broadly correlated with environmental gradients, particularly Maximum Temperature in the Warmest Period. High proportions of apparently localised endemic species dominated the geographical patterns in species composition. A rare, widely distributed, compositionally discrete, saline-associated fauna was detected. Taxonomic revisions taking into account fauna collections from surrounding areas are required to understand the relationships between localised endemics and environmental gradients.

INTRODUCTION

The Salticidae is a large and diverse family with members on every continent (except Antarctica) and on most oceanic islands (c. 5000 described species, Dippenaar-Schoeman and Jocqué, 1997; Platnick, 2003). They are easily recognised by their characteristic anteriorly squared-off head and large forward facing eyes in addition to their often jerky 'stop and go' movements. Jumping spiders live in habitats ranging from rain forests to deserts and from 80 m below sea level in Death Valley to 6400 m above sea level on Mt Everest. These spiders are a major component of most terrestrial faunas (Jackson and Hallas, 1986).

Salticids have been described as classic examples of cursorial hunting spiders that, instead of building webs to ensnare their prey, use vision to stalk, chase, and leap on active insects (Drees, 1952; Land, 1974; Forster, 1977, 1982a,b in Jackson and Hallas, 1986). Web or silk production is generally limited to forming temporary silk shelters for protection during moulting, for occupation during times of inactivity, or as mating or brood chambers (Main, 1976; Dippenaar-Schoeman and Jocqué, 1997).

Most species are predatory although some have been recorded consuming insect eggs, while others open nests of other spiders and feed on the eggs they contain (Jackson, 1986a). Consumption of flower nectar has also been observed and the behaviour may be widespread, if not routine (Jackson *et al.*, 2001). Predatory technique is variable, with both ambush (sit and wait) and hunting (actively searching for prey) being used

(Jackson, 1986c). Some hunting species exhibit preferences for certain prey, such as ants, but Jackson and Li (2001) considered it valid to recognize dietary specialisation only if the spiders exhibited a preference for particular prey over alternative 'easier' prey and had adopted special prey-capture tactics. *Portia fimbriata* sometimes builds its own capture webs, in addition to hunting cursorially. This species uses a wide repertoire of other predatory behaviour, including aggressive mimicry whereby it performs vibratory behaviours on alien webs to deceive the host spider; (Jackson and Blest, 1982; Jackson and Hallas, 1986) and, in certain populations in Queensland, specialized 'cryptic stalking' behaviour for capturing other salticids (Jackson and Blest, 1982).

Many salticids readily move from leaf litter on the ground into shrubs (e.g. *Lycidas* spp. and *Maratus* spp.), although other species are more constrained in habitat use and live under loose bark of living trees (e.g. *Holoplatys* spp., *Zebraplatys* spp.) or under rocks around outcrops (e.g. *Adoxotoma* spp.). Species such as *Grayenulla australensis* may be found running on bare ground between *Triodia* tussocks.

The Australian salticid fauna comprises three broad groups: (1) cosmopolitan/pan tropical species generally distributed by human activity, (2) 'orientals' that are common in the northern coastal rainforests, and (3) endemic species (about 60% of the fauna) concentrated towards the southern and central-western regions of the continent (Patoleta and Žabka, 1999). The expansion and contraction of *Eucalyptus* and *Acacia* communities, in response to

periodic climatic change since the Tertiary (Hill *et al.*, 1999), may have led to vicariant speciation of the endemic salticid fauna. A similar mechanism has been proposed for plants (Hopper *et al.*, 1996; Cowling and Lamont, 1998; Beard *et al.*, 2000) and mygalomorph spiders (Main, 1996, 2000).

Recent large-scale biogeographic surveys in Australia have collected many new undescribed forms of salticid, suggesting the fauna is much more diverse than previously estimated (Davies and Žabka, 1989; Main, 1991; Harvey *et al.*, 2000). A large number of specimens from previous collections of salticids in the wheatbelt, based on opportunistic and sporadic sampling, are lodged in the Western Australian Museum awaiting appropriate taxonomic revisions (Harvey *et al.*, 2000).

This paper reporting results of the recent biogeographic survey of the wheatbelt, as part of the Western Australian Government's Salinity Action Plan, presents an opportunity to assess patterns in composition of salticid species assemblages and relate them to geographic, climatic and substrate attributes. The survey consisted of a pitfall-trapping program at 304 quadrats positioned to sample all major geomorphological and geographical units of the wheatbelt region of Western Australia. By assessing the compositional patterns, we aim to determine whether salticid assemblages reflect differences in environmental variables between the quadrats.

METHODS

Study area

The wheatbelt study area occupies 205 000 km². It covers the semi-arid areas of Western Australia's South West Botanical Province (Beard, 1980, 1990) and encompasses all or part of five IBRA bioregions (Figure 1, Thackway and Cresswell, 1995): Avon Wheatbelt, Mallee, Geraldton Sandplains, Jarrah Forest and Esperance Plains (see McKenzie *et al.*, 2004). Vegetation communities are highly diverse across the study area. Coastal scrub heaths, *Acacia-Casuarina* thickets and *Acacia* scrub with *Eucalyptus loxophleba* on sandy laterite-derived soils occur in the north, to *Acacia-Casuarina* thickets on ironstone gravels, *E. loxophleba*, *E. salmonophloia* and *E. wandoo* woodlands on loams with halophytes on saline soils in the central regions (Beard, 1990; Gibson *et al.*, 2004). In the south-eastern part of the study area *Eucalyptus eremophila* woodlands occur on clay soils, with *Casuarina* thickets on residual plateau soils and a variety of heaths and *Eucalyptus* woodlands on sandy soils overlying clays or ironstones (Beard, 1990; Gibson *et al.*, 2004).

The climate in the northern part of the study area is semi-arid with temperate weather patterns and

an annual rainfall of c. 300–500 mm. The central part has seasonal temperate to semi-arid (in the east) weather patterns with an annual rainfall of c. 300–650 mm. The south-east part has an arid non-seasonal to semi-arid climate with an annual rainfall of c. 200–300 mm. Alluvial and aeolian processes have produced a highly complex undulating landscape mosaic overlying the granitic rock strata of the Yilgarn Craton (McKenzie *et al.*, 2003). Spillway sands derived from duricrust occur on uplands and slopes associated with the 'old' Tertiary plateau, while duplex soils derived from the bed rock occur on slopes and floors of broad 'dissection' valleys. In addition, calcareous clays and loams are also present on valley floors (Figure 2; McKenzie *et al.*, 2003). Low gradients, high potential salt loads and high flow variability characterise the hydrology of the regions (Dirnbock *et al.*, 2002).

Sampling strategy

The survey was based upon 304 quadrats distributed in remnant bushland patches across 24 survey areas (Figure 1) that together covered the geographical extent of the study area. Twelve or 13 quadrats were positioned to sample the main components of the geomorphic profile in each survey area, including one or two quadrats in geomorphic units affected by rising groundwater. Otherwise, quadrats were placed in least-disturbed examples of each habitat-type as far as possible from vegetation clearing, wheatfields, gravel extraction and rubbish dump sites.

Landform units of the Yilgarn Craton were assigned numbers 1 to 12 (Figure 2), according to their position in the landscape profile. The dissection profile corresponded with units 1–7, while the 'old plateau' profile was associated with 9–12. Unit 8 (Belmunging) consisted of spillway sand mantling a clay belonging to the dissected valley profile. Units at the bottom of the profile included freshwater swamps (1) and saline flats (2). Quadrats situated in the Esperance Plains and Geraldton Sandplains bioregions were positioned using relevant 1:250 000 surface lithology maps and assigned arbitrarily to the 12-class landform series according to their soil profile and origin and the landscape profile (see McKenzie *et al.*, 2003).

Field sampling

Five pitfall traps were placed in each of the 304 quadrats. Each pitfall trap consisted of a 2 L plastic container (80 mm neck diameter) dug into the ground, the top flush with the ground surface. Each trap contained approximately 400 ml preserving fluid (320 ml ethylene glycol, 64 ml tap water, 16 ml formaldehyde). Sampling of quadrats in HY, KL, KN, MN, NR, QU, WK and YR survey areas occurred from October 1997 to September 1998.

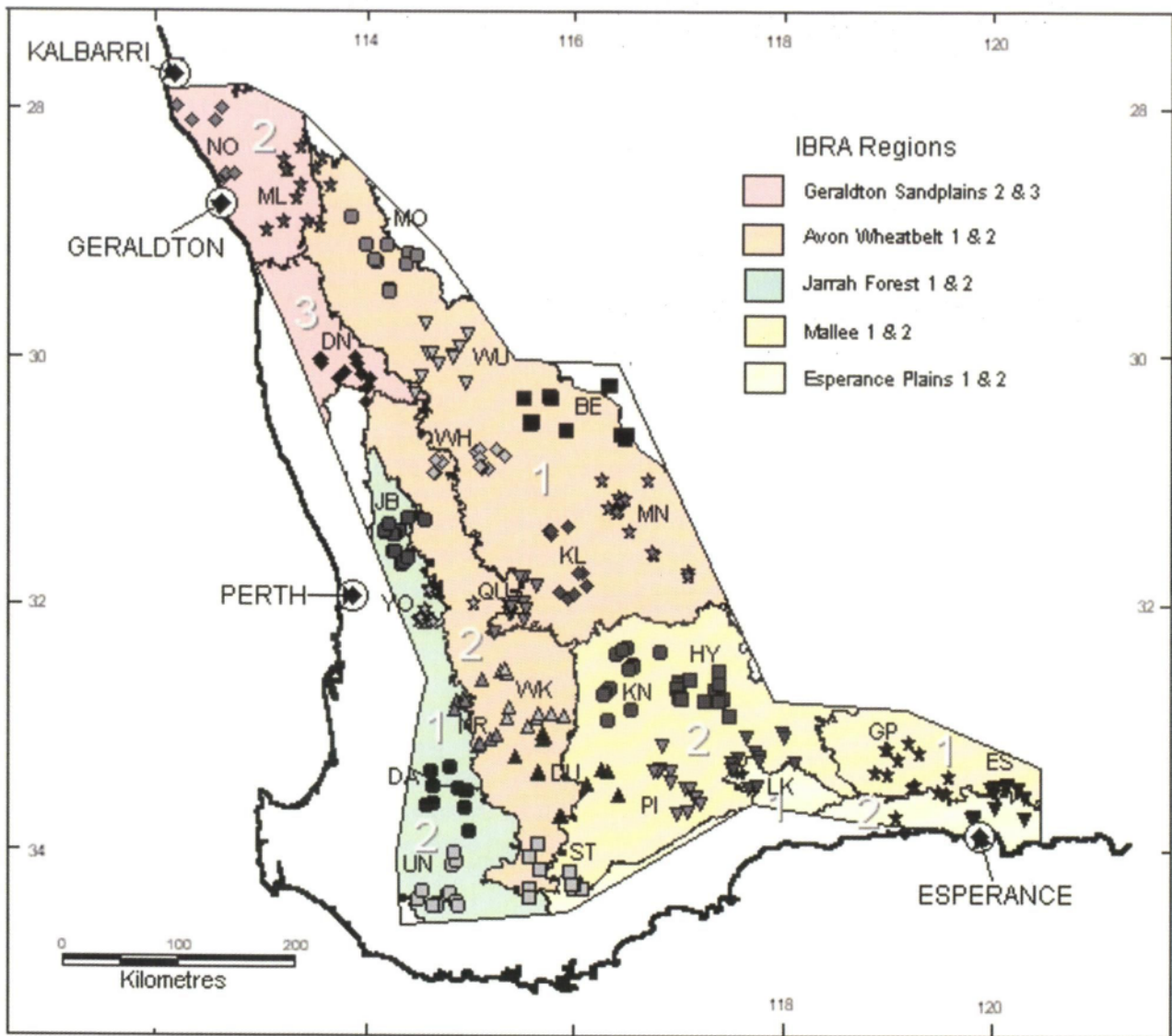


Figure 1 The wheatbelt study area, showing the 304 quadrats, and the five relevant IBRA biogeographical region boundaries (Thackway and Cresswell, 1995). The different symbols indicate the 12 or 13 quadrats in each of the 24 survey areas (BE- Beacon; DA- Darkin; DN- Dandaragan Plateau; DU- Dumblyung; ES- Esperance; GP- Grass Patch; HY- Hyden; JB- Julimar-Bolgart; KL- Kellerberrin; KN- Kulin; LK- Lake King; ML- Mullewa; MN- Merredin; MO- Morawa; NO- Northampton; NR- Narrogin PI- Pingerup; QU- Quairading; ST- Stirling; UN- Unicup; WH- Wongan Hills; WK- Wickepin; WU- Wubin; YO- York).

Quadrats in BE, JB, ML, MO, NO, WH and WU survey areas were sampled between September 1998 and October 1999. Sampling of quadrats in southern survey areas DA, DU, ES, GP, LK, PI, ST and UN occurred from October 1999 to October 2000 (Harvey *et al.*, 2004). Thus, each quadrat was sampled for a year, with about 1800 pit trap nights per quadrat, and all sampling occurred in three consecutive years. This reduced the bias associated with sampling for short periods (such as a few weeks in a single season). Samples were returned to the laboratory, washed in water and stored in 75% ethyl alcohol until sorting and identification. All specimens have been lodged in the Western Australian Museum, Perth.

A set of 18 climatic attributes were derived for

each quadrat using ANUCLIM (McMahon *et al.*, 1995); these comprised annual and seasonal range and average values for temperature and precipitation, and are listed in Appendix 1. Fifteen soil chemical and texture values were derived for each quadrat using the methods of Wyrroll *et al.* (2000) (see Appendix 2). In addition, a variety of landform, secondary salinization and vegetation attributes (modified from Newsome and Catling, 1979) were assessed for each quadrat (Appendix 2). Significant inter-correlations between the environmental attributes were identified using Kendall's rank correlation coefficient (Appendix 3).

Taxonomy

Adult salticid specimens were identified based on

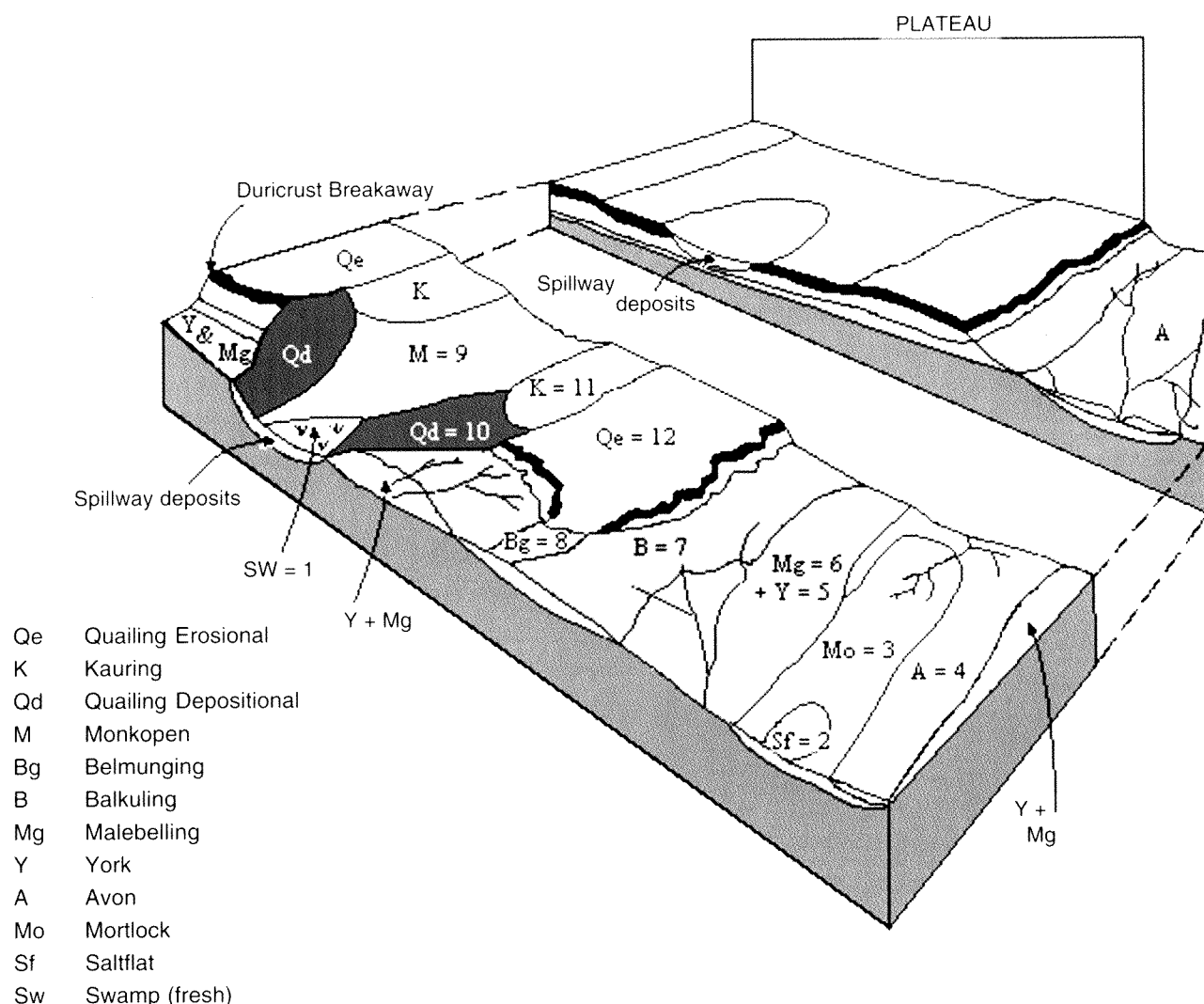


Figure 2 Wheatbelt landforms, adapted from McKenzie *et al.* 2003 (modified from Mulcahy and Hingston, 1961). The plateau profile comprises the duricrust Tertiary laterite plateau and its derived spillway sands, while the dissection profile comprises finer textured soils derived from bedrock and pallid-zone clays beneath the duricrust.

genital characters of the male palp and female epigynum as described in current taxonomic literature (e.g. Žabka, 1990, 1991, 1992a,b, 2000, 2001; Waldock, 2002). Where original descriptions were too ambiguous to assign specimens confidently to known taxa, a morphospecies approach using male and female genitalic characters was adopted (see Harvey *et al.*, 2000). These taxa are considered in this paper to be 'unassociated'. The position of many of the currently unassociated taxa, either as entirely new taxonomic entities or as known species, will be resolved when these groups are revised.

Analysis

To determine patterns in the salticid fauna across the wheatbelt landscape from our dataset, we needed to minimise distortions due to under-sampling and/or disturbances such as secondary

salinization. Thus, two categories of quadrats were excluded from analyses:

1. Freshwater swamps that were poorly sampled because pit traps were inundated for long periods of time.
2. Salt-affected quadrats that, internally, were mosaics of living and dead vegetation at various stages in the transition to obvious salinization (see Cramer and Hobbs, 2002; Dirnbock *et al.*, 2002). These were the non-salt flat quadrats in salinity categories 3 or 4 (Appendix 2).

The presence and absence of species at quadrats was explored using the computer package PATN (Belbin, 1995). The Czekanowski association measure was used to compare quadrats according to similarities in their species composition, and the Two-Step association measure was used to compare species on the basis of distribution among quadrats. Dendrograms were constructed from these

association matrices using an unweighted pair group arithmetic averaging (UPGMA) hierarchical clustering strategy (Sneath and Sokal, 1973; Belbin, 1995), and the reordered data were displayed as a two-way table. Quadrat dendrogram structure was assessed statistically in terms of the 51 physical attributes of the quadrats using Kruskal-Wallis tests. In order to maintain to an overall significance level of $\alpha = 0.05$, a Bonferroni correction was used so that the P -value used for each of the 51 individual tests was 0.009. The relationship between environmental variables and quadrat groups defined by clustering was further examined using canonical analysis of principal co-ordinates (CAP, Anderson and Robinson, 2003).

Each of the 24 survey areas contained quadrats in 12 equivalent units of the geomorphic profile (McKenzie *et al.*, 2004), which allowed each survey area to be treated as a single landscape-scale relevé. Broad biogeographical patterns in the distribution of salticids were examined by classifying survey areas, using the Czekanowski association measure and UPGMA, according to similarities in their overall species composition. The resulting classification structure was examined statistically in terms of the average climatic attributes of the quadrats in each survey area using Kruskal-Wallis tests.

RESULTS

Species richness

A total of 121 salticid species were collected from the 304 quadrats. Of these, 106 species could not be associated with described species. Twenty-four named genera were recorded and it appeared that a further 17 new genera had been collected, so that current information suggests at least 41 salticid genera occur in the study area.

The most speciose genus was *Lycidas* with 29 species (27 unassociated and two described species: *L. chrysomelas* and *L. michaelsoni*). Three southern quadrats were the most speciose with seven species each but 73 quadrats had only one *Lycidas* representative. These quadrats were northern, arid and/or low in the landscape. The two most common species were *L. chrysomelas* and *L. sp. 1*, found at 81 and 145 quadrats, respectively. They occurred in allopatry in the northern areas and in sympatry in the central and southern regions.

The *Lycidas* assemblage in the southern parts was dominated by *Lycidas michaelsoni*, and three unassociated species. Populations of *L. michaelsoni* were scattered across Darkin, Narrogin, Stirling, Pingrup and Wickpin survey areas in addition to several Grass Patch and Esperance quadrats. Other species' distributions ranged from widespread and scattered to highly localized.

Eleven species of *Clynotis* were disjunctly distributed across the Wheatbelt study area. Four species had distributions extending from the northern regions to central and southern parts of the study area. The remaining seven species had disjunct but localised distributions across southern sub-coastal survey areas.

Three unassociated and three described allopatric species represented *Maratus*: *M. mungaich*, *M. pavonis* and *M. vespertilio*. *Maratus pavonis* occurred on the western and southern peripheries of the study area whereas the more semi- to arid-adapted *Maratus vespertilio* occurred in the central parts. *Maratus mungaich*, known to occur in jarrah and banksia woodlands, was found at two central western quadrats, and neither *M. pavonis* or *M. vespertilio* was present at these localities. Two undescribed species were found at one quadrat each.

Holoplatys was represented by three unassociated and two described species (*H. chudalupensis* and *H. dejongi*). *Zebraplatys* was represented by four unassociated species and *Z. fractivittata*, and *Adoxotoma* with two unassociated species plus *A. chinopogon* and *A. nigroolivacea*. Both *Simaetha* and *Simaethula* were represented by three unassociated species. Seven genera were represented by two species (*Bianor maculatus* and *B. sp. 1*; *Ocrisiona leucocomis* and *O. sp. 1*, and *Grayenulla australensis* and *G. nova*; *Hypoblemum*, *Margaromma*, *Myrmarachne* and *Opisthoncus* were represented by unassociated species. Nine recognised and 14 unassociated genera were represented by single species. Three unassociated genera were represented by seven, six and four species respectively.

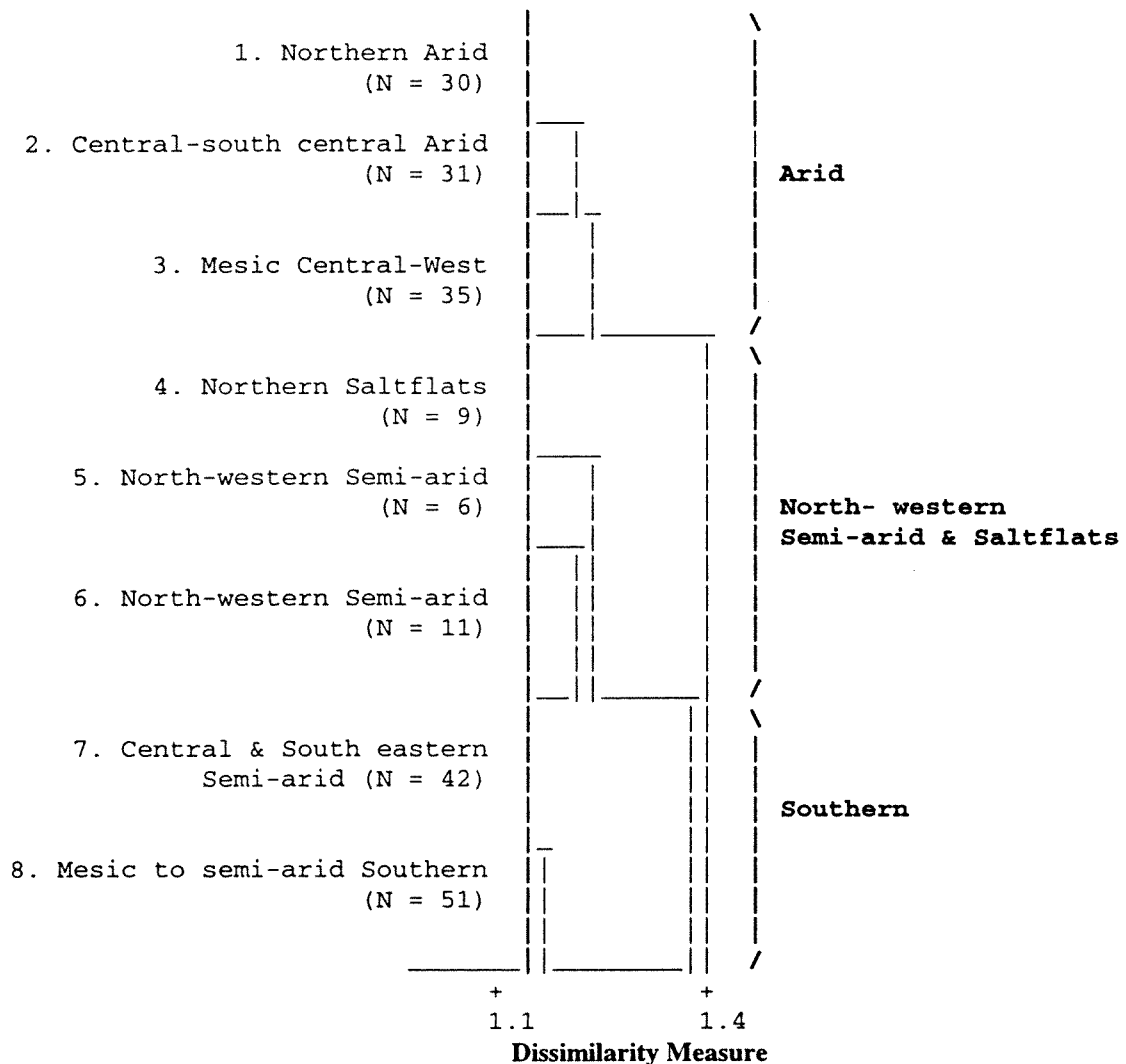
The average species richness per quadrat across the landforms did not vary significantly, ranging between 1.6 (freshwater swamps, s.d. = 1.71, n = 10) and 5.46 (Balkuling, s.d. = 3.13, n = 24; see Figure 2 for position of the landforms in the landscape).

Quadrat analysis

After removing singletons and quadrats in fresh water swamps or affected by salinization, the data matrix comprised 77 species and 215 quadrats (Table 1). The eight groups of quadrats recognized in the quadrat classification (Table 1, Figure 3) reflected climatic gradients. In general, groups 1 and 2 comprised quadrats in more arid parts of the study area, its northern and eastern survey areas. Quadrats from the mesic central-western areas formed group 3. Northern saltflats, plus three drainage slopes, comprised group 4, while groups 5 and 6 were dominated by quadrats in warm, semi-arid north-western parts of the study area. Group 7 was dominated by quadrats in semi-arid central and southern parts of the study area but included seven outlying quadrats from elsewhere. Group 8

Table 1 Two-way table showing quadrat groups and salticid species assemblages. Numbers within columns represent the number of species-quadrat group occurrences.

	QUADRAT GROUPS (number of quadrats)							
	1 (n=30)	2 (n=31)	3 (n=35)	4 (n=9)	5 (n=6)	6 (n=11)	7 (n=42)	8 (n=51)
ASSEMBLAGE 1 (22 spp.)	114	107	103	6	5	16	176	120
ASSEMBLAGE 2 (20 spp.)	17	18	8	15	5	7	9	3
ASSEMBLAGE 3 (6 spp.)	3	1	1	1	0	1	13	4
ASSEMBLAGE 4 (2 spp.)	1	2	2	0	0	0	0	0
ASSEMBLAGE 5 (23 spp.)	7	7	33	3	9	14	40	140
ASSEMBLAGE 6 (2 spp.)	1	0	0	1	0	0	2	0
ASSEMBLAGE 7 (2 spp.)	0	0	1	0	0	0	1	2

**Figure 3** Quadrats classified according to similarities in species composition. Dendrogram structure displayed to the 8-partition level. Classification includes quadrats with no overt salinity (SAL = 1 or 2) and saltflats (SAL = 4, landform = 2). See Table 1 for individual quadrat codes in each group. See Gibson *et al.* (2004) for detailed explanation of quadrat geomorphology.

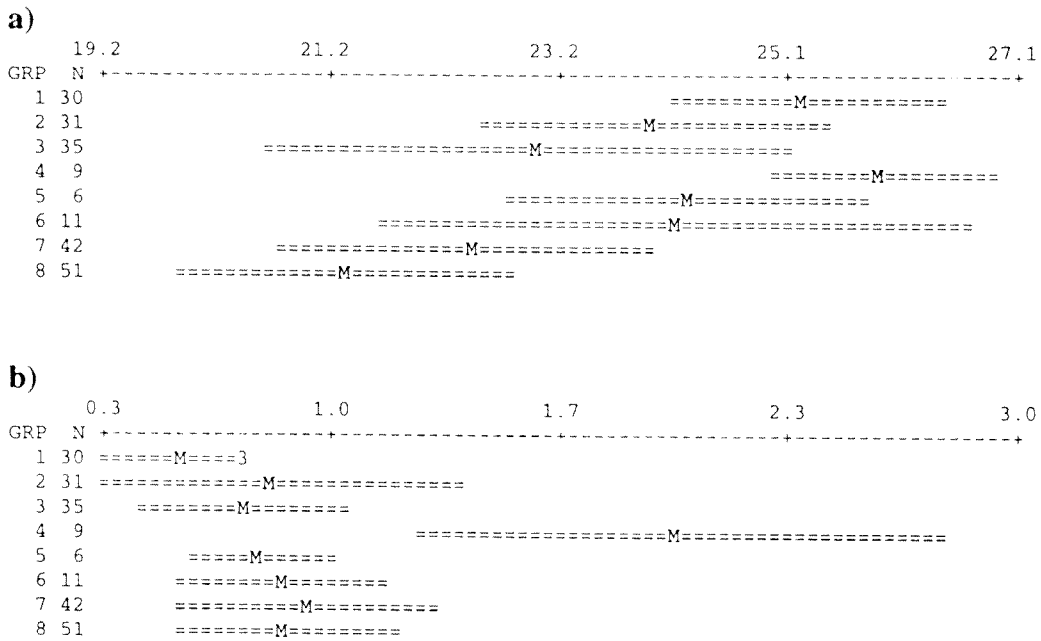


Figure 4 Average environmental attribute values for the quadrat groups defined in Figure 3. (a) Mean Temperature of the Warmest Quarter (°C; $H = 94.5$, $df = 7$, $P < 0.0001$); (b) Log Electrical Conductivity (mS/m; $H = 51$, $df = 7$, $P < 0.0001$). Bars indicate standard deviations about the mean (M); GRP = classification group number in Figure 3; N = number of quadrats in each classification group.

comprised quadrats along the cooler, mesic to semi-arid southern margin of the study area.

Differences in physical attributes of quadrats in the eight groups are summarised in Figure 4. The strongest differences between groups involved Mean Temperature of the Warmest Quarter (MTWrmQtr; $KW-H = 94.5$, $P < 0.0001$) and

Electrical Conductivity (logEC; $KW-H = 50.5$, $P < 0.0001$, Figure 5). Average annual Temperature and Leaf Litter Cover exhibited similar relationships to MTWrmQ. SAL, Salinity Type and pH varied among groups in the same way as logEC.

Physical attributes that emerged as most significant from the CAP analysis included Latitude

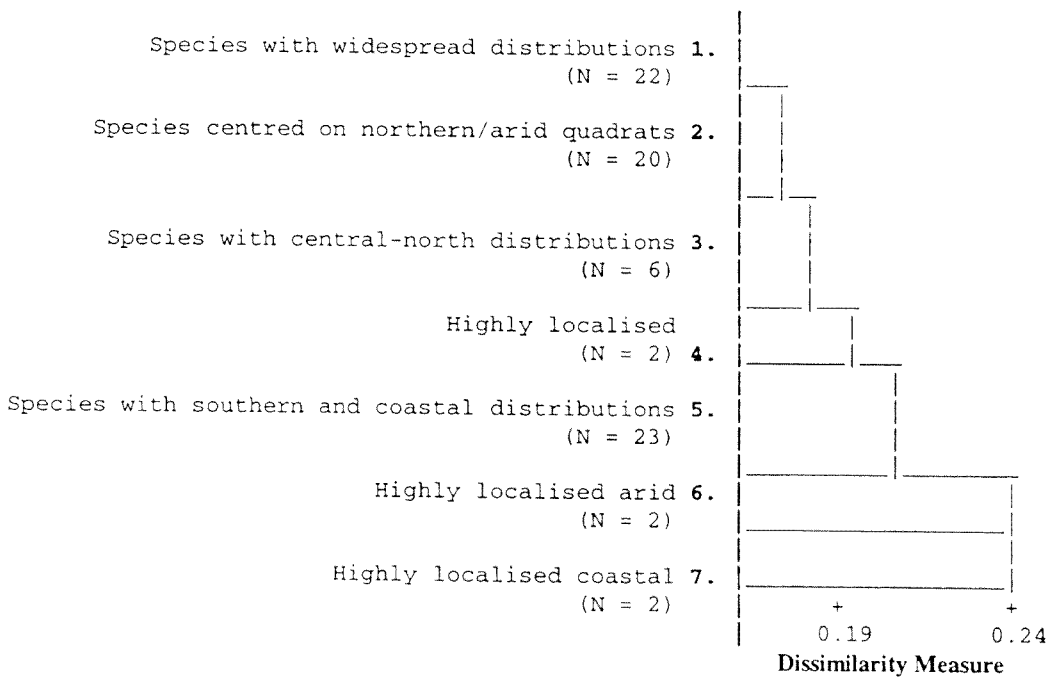


Figure 5 Species groups derived by classifying the salticid species according to their co-occurrences at the same quadrats. Dendrogram structure is displayed and characterised at the 7-cluster level. See text and Table 1 for details of each group. Species recorded from only a single quadrat are excluded.

Table 2 Two-way table showing survey area groups and salticid area species assemblages. Survey areas are printed vertically, and survey area groups are shown at the 10-group level; area species assemblages are listed at the 10-group level.

	1	2	3	4	5	6	7	8	9	10
	BMMW	DN	KM	QW	KW	DLPDG	SU	H	JNY	E
	ELOU	NO	LN	UH	NK	AKIUP	TN	Y	BRO	S
Species Group 1										
Genus 3 sp. 1			*		*				***	
<i>Breda jovialis</i>	*				*				**	
<i>Opisthoncus</i> sp. 1	*		*	*	**				**	
<i>Clynotis</i> sp. 2	**		*	**	**				***	
<i>Clynotis viduus</i>	**				*				**	
<i>Lycidas</i> sp. 8			**		*				*	
Genus 3 sp. 2	*	*	**		**					
Species Group 2										
<i>Zebraplatys fractivittata</i>	*		*	**						*
<i>Lycidas</i> sp. 16	* *		**	*	*	*		*	*	*
Genus 9 sp. 1	* **		*		*	*	*		*	*
<i>Grayenulla australensis</i>	****	**	**	**		*				*
Genus 5 sp. 1	****	**	**	*						
<i>Zebraplatys</i> sp. 1	***		**	*					***	
<i>Lycidas</i> sp. 19	****		*							
Genus 12 sp. 4	***	**				*				
<i>Lycidas</i> sp. 18	**	**								
Genus 13 sp. 1	* *	*		**		*				
<i>Hypoblemum</i> sp. 1	*		*	*						
<i>Holoplatys</i> sp. 2	*			*						
<i>Lycidas</i> sp. 6	* **			*						*
<i>Clynotis</i> sp. 3	* *			*						
Genus 10 sp. 1	*		*							
<i>Adoxotoma</i> sp. 1	**									
Species Group 3										
<i>Zenodorus</i> sp. 1			*					*		
Genus 6 sp. 1			*						*	
<i>Grayenulla nova</i>			**							
Genus 12 sp. 1	*			*						
<i>Lycidas</i> sp. 26	*		*							
Genus 3 sp. 4	*								*	
Species Group 4										
<i>Lycidas</i> sp. 1	****	**	**	**	**	*****	**	*	***	*
<i>Lycidas chrysomelas</i>	****	**	**	**	**	*****	**	*	***	*
Genus 2 sp. 1	* **	**	**	**	**	*****	**	*	**	*
Genus 1 sp. 1	****	**	**	**	*	*****	**	*	**	*
<i>Lycidas</i> sp. 3	****	**	**	**	**	* **	*	*	***	
<i>Lycidas</i> sp. 2	****	*	*			*****	**	*	***	
<i>Lycidas</i> sp. 4		**	**	**	**	**	*	*	****	*
Genus 1 sp. 3	** *	*	**	*		***		*	**	
Genus 1 sp. 2	****	**	*		*	* **		*		
<i>Paraplatoides</i> sp. 1	**	*		**		*	*	*	***	
<i>Maratus vespertilio</i>	*	*	*	*	*	*****	*		**	
<i>Lycidas</i> sp. 5	*		*			*****	**		***	*
<i>Margaromma</i> sp.1		*	*		**	*****		*	***	*
<i>Lycidas</i> sp. 17	** *				*	***	*		*	*
<i>Margaromma</i> sp.2		*	**	*	**	****				
<i>Clynotis</i> sp. 1			*	**		***			***	
<i>Lycidas</i> sp. 7				*		**		*	*	*
Species Group 5										
<i>Lycidas</i> sp. 12						*****	*	*	**	
<i>Lycidas michaelsoni</i>					*	*****	**		*	
<i>Sondra</i> sp. 1	*	*				****	**		**	
<i>Maratus pavonis</i>		*				***			*	
<i>Lycidas</i> sp. 22				*	*	***				

Table 2 (cont.)

	1	2	3	4	5	6	7	8	9	10
	BMMW	DN	KM	QW	KW	DLPDG	SU	H	JNY	E
	ELOU	NO	LN	UH	NK	AKIUP	TN	Y	BRO	S
<i>Opisthoncus</i> sp. 3	*					*	*			
<i>Adoxotoma chinopogon</i>		*				***				
Genus 1 sp. 7						**				
<i>Clynotis</i> sp. 9						**	**			
Genus 14 sp. 1						**	**			*
Genus 18 sp. 1		*				*	*	*		
<i>Clynotis</i> sp. 8						**	*			
<i>Lycidas</i> sp. 23						*	*			
Genus 17 sp. 1						*	*			*
Genus 12 sp. 2		*				*			*	
Genus 16 sp. 1						*			*	
Species Group 6 -----										
<i>Simaetha</i> sp. 1					*					
Genus 3 sp. 3		*			**					
<i>Bianor</i> sp. 1					*					
Species Group 7 -----										
<i>Opisthoncus</i> sp. 2			*			*				
<i>Clynotis</i> sp. 10						**				
<i>Cytaea</i> sp. 1					*	*				
<i>Holoplatys chudalupensis</i>					*	*				
Species Group 8 -----										
<i>Lycidas</i> sp. 13								*	*	
Genus 1 sp. 4						*		*	*	
<i>Lycidas</i> sp. 11					*	*		*	*	
Species Group 9 -----										
Genus 7 sp. 1									*	*
<i>Maratus mungaich</i>								*	*	
Species Group 10 -----										
<i>Clynotis</i> sp. 7			*			*				
Genus 1 sp. 5						*				
<i>Hypoblemum</i> sp. 2						**			*	

on axis 1 and Electrical Conductivity on axis 2. Latitude is strongly correlated with Mean Temperature of the Warmest Quarter (Kendall's Tau = 0.87, $P < 0.00001$). Thus, results from Kruskal-Wallis tests and CAP analysis were consistent.

Close examination of the species dendrogram (Figure 5), in conjunction with the two-way table (Table 1), revealed two types of species assemblage. At the seven-assemblage level in the dendrogram:

1. Assemblages 1, 2 and 5 comprised species with broad regional distributions related to ecological or biogeographical gradients. The species of assemblage 1 were usually widespread across the study area, but tended to be absent from saltflats and sub-coastal quadrats. Distributions of assemblage 2 species were centred on, but not limited to, northern arid quadrats. Species centred on southern and coastal quadrats (extending into quadrats of adjacent survey areas) formed assemblage 5.
2. Assemblages 3, 4, 6 and 7 comprised species

with geographical distributions that were strongly localised. Species were present at two, three, four or five quadrats; these quadrats were usually from the same or adjacent survey areas.

Broad biogeographic patterns

Ten groups were recognized in the survey area dendrogram (Table 2, Figure 6), although statistical analysis of differences in physical characteristics was undertaken only at the four-group level. Maximum Temperature of the Warmest Period (Figures 7 and 8) showed strongest differences between area groups.

Based on occurrence across survey areas, ten species assemblages were distinguished (Table 2, Figure 9) that reflected three types of distribution. Two of these were related to ecological or biogeographical gradients and one to highly localised patterns of occurrence of the component species:

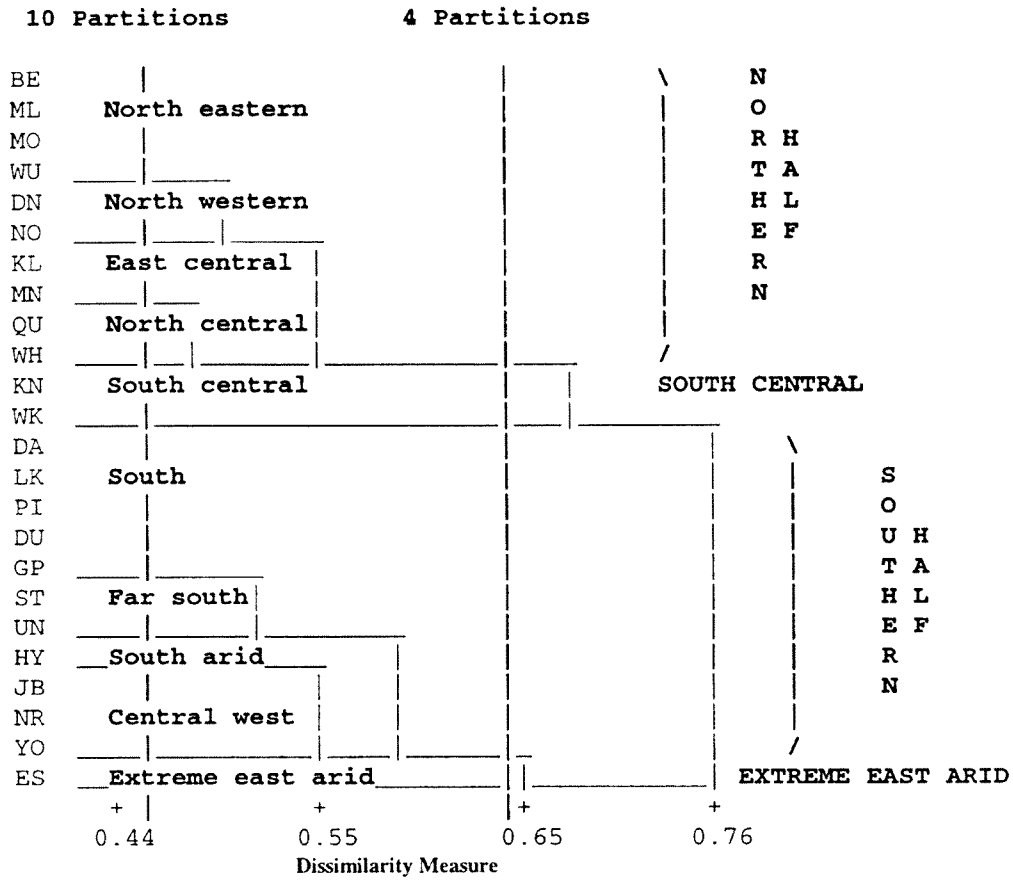


Figure 6 Survey areas classified according to similarities in species composition. Dendrogram structure displayed at the 4- and 10-group level. The 10-group level reflects localised differences, whereas the 4-partition level reflects regional climatic differences.

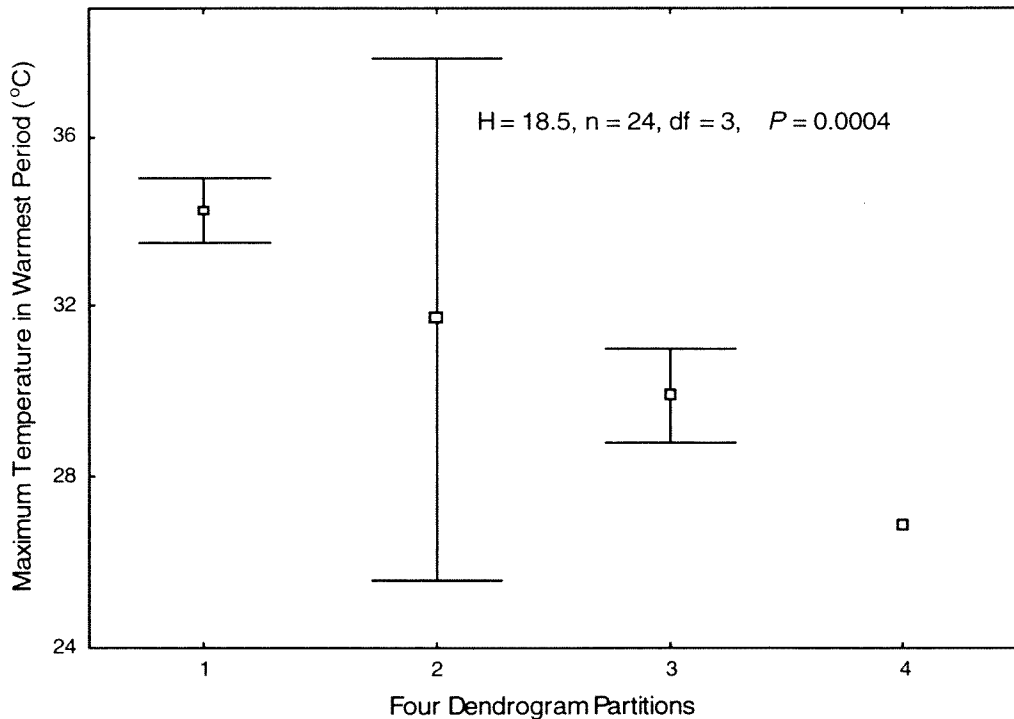


Figure 7 Statistical assessment of the four-group classification (Figure 6) according to the Maximum Temperature in the Warmest Period (°C) values for the quadrats comprising each survey area. Bars indicate 95% confidence intervals about the mean.

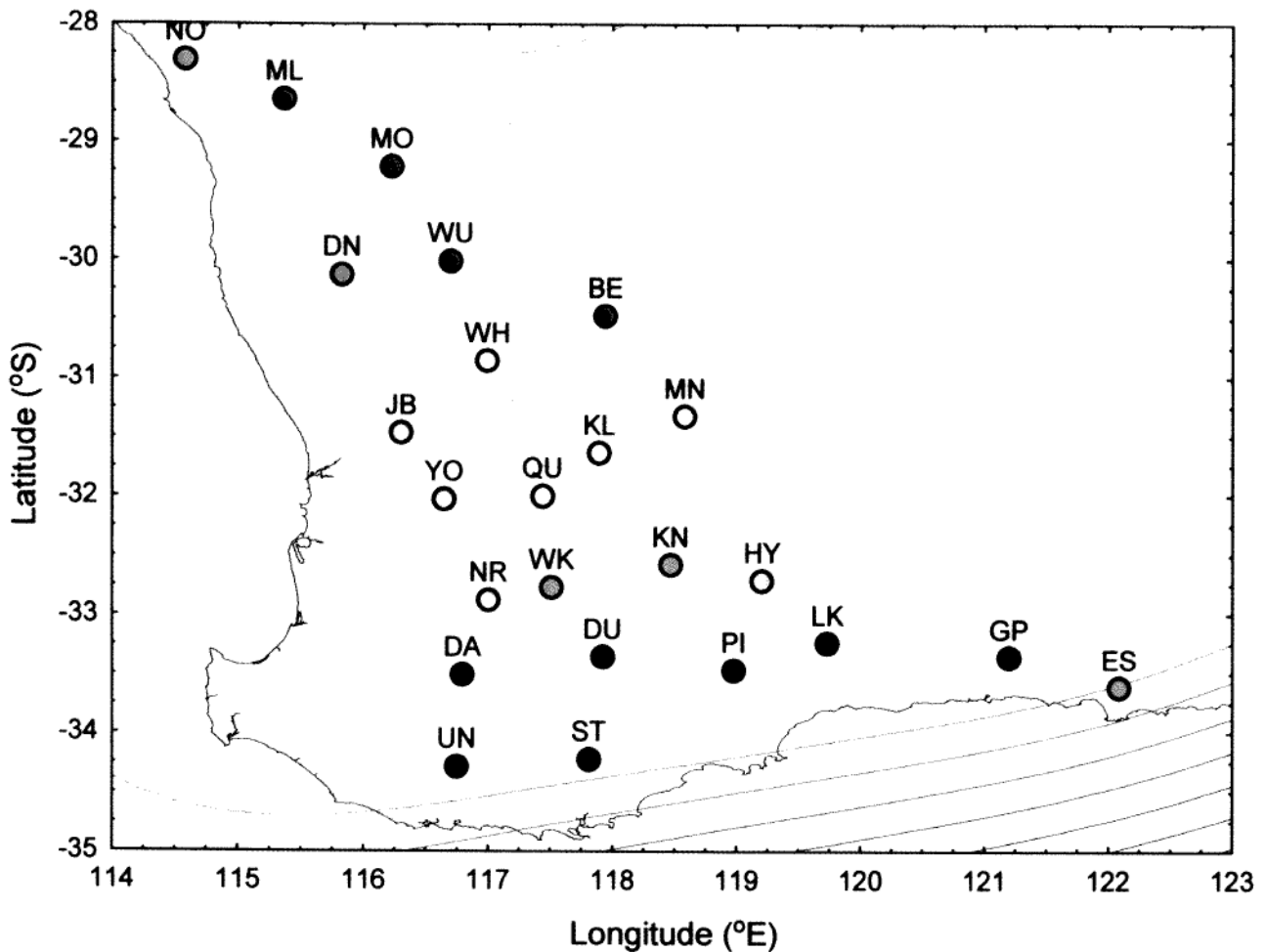


Figure 8 A diagrammatic representation of the classification dendrogram (Figure 6) and statistical analysis (Figure 7) overlain on the wheatbelt study area. The 24 survey areas are coloured according to the groupings at the 10-group level, illustrating their geographical differences. Survey area groups at the 4-group level are red-yellow colours - northern half, grey colour - South Central, blue-green colours - southern half, vivid green colour - extreme east arid. Maximum Temperature of the Warmest Period isotherms ($^{\circ}\text{C}$, coloured lines) are also shown.

1. Area assemblage 4 comprised species with widespread distributions across the survey areas.
2. Area assemblages 1, 2 and 5 consisted of species with regional distributions. Assemblage 1 species were limited to northern and north-central survey areas plus coastal areas and absent from high rainfall areas. Assemblage 2 species were centred on, but not limited to, northern survey areas. Finally, assemblage 5 species had southern and coastal survey area distributions, with some also present in adjacent northern survey areas.
3. Area assemblages 3 and 6–10 comprised species with strongly localised distributions. Species in assemblages 8 and 9 were confined to adjacent survey areas. Assemblage 3 species were mostly confined to adjacent areas but one species occurred in the outlying UN survey area.

DISCUSSION

Of the 41 salticid genera and 121 species identified during this survey, 87% could not be assigned to recognised taxa. This suggests that the wheatbelt study area possesses a rich and largely unknown salticid fauna. Comparable levels of salticid species richness were reported by Harvey *et al.* (2000) for a previous Western Australian survey in the southern Carnarvon Basin (39 genera and 58 species, of which 19 genera and 48 species, or 82% of the fauna, were undescribed). Currently, the undescribed taxon *Lycidas* sp. 1, and *Grayenulla australensis*, *Maratus vespertilio*, *Ocrisiona leucomis* and *Zebraplatys fractivittata* are known to occur in both the wheatbelt and Carnarvon survey areas. Thus, the combined salticid fauna from the two surveys, which sampled an area of approximately 325 000 km² or about 12% of the State, may exceed 170 species in 75 genera.

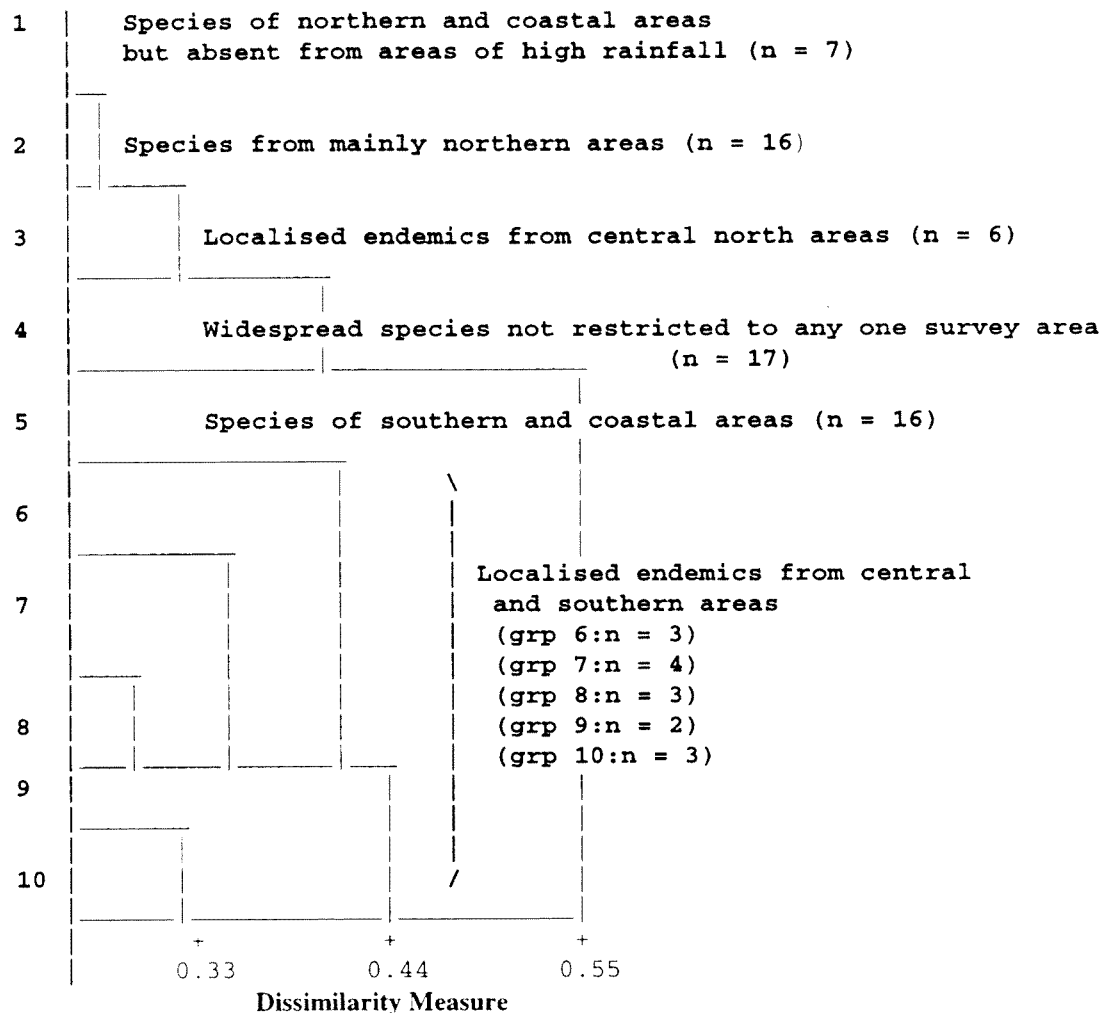


Figure 9 Species assemblages derived by classifying the salticid species according to their co-occurrences at the same survey areas. Dendrogram structure is displayed and characterised at the 10-assemblage level. See text for details of each survey area assemblage.

The number of new genera and species collected from this survey, the Carnarvon Basin (Harvey *et al.*, 2000), Kimberley rainforests (Main, 1991) and elsewhere in Western Australia (authors' unpublished data) make it likely that large numbers of salticids still await discovery, even in relatively well-known environments. Comprehensive taxonomic revisions are urgently required to determine the 'hotspots' of salticid diversity and the phylogenetic relationships between the many different forms of this diverse family.

Patterns in composition of salticid assemblages at quadrat scales were correlated with environmental gradients such as temperature, rainfall and salinity. Saltflats supported a distinctive assemblage, from which most of the widespread species were absent. An obvious northern assemblage was apparent that shared elements with the salticid fauna of the southern Carnarvon Basin. Geographical patterns in the total or overall spider fauna have been assessed for correlations with environmental gradients in

other surveys (e.g. Abensperg-Traun *et al.*, 1996; Harvey *et al.*, 2000). However, there is no information on environmental factors related to compositional patterns in salticids alone.

Patterns of salticid distribution at broader scales were most strongly correlated with maximum temperature in the hottest period (summer). A similar conclusion emerged from analysis of the entire non-arboreal araneomorph dataset from the study (Harvey *et al.*, 2004), although zodariids showed a distinctively different pattern (Durrant, 2004). In terms of nature conservation planning, salticid patterns cannot be used as a surrogate for zodariids.

The presence of many highly localised salticid species indicates an unexpectedly high level of local endemism. It is unlikely this result was a sampling artefact because species recorded only from small numbers of quadrats were consistently recorded from quadrats near each other. Thus, it appears that a powerful salticid speciation mechanism has

operated across south-west Western Australia, similar to that recognised by Hopper *et al.* (1996) and Main (1996) for other taxa. Salticids, particularly genera such as *Adoxotoma*, *Holoplatys*, *Ocrisiona*, *Paraplatoides* and *Zebraplatys*, are probably unable to balloon (Žabka, 1990, 2001), which is likely to have increased the frequency of populations becoming isolated and speciating.

The high proportion of singleton species in our dataset probably reflects the high levels of endemism but may also relate to the trapping methods we employed. For instance, a number of the new species encountered here belong to the crevice-dwelling genera *Adoxotoma*, *Holoplatys*, *Ocrisiona*, *Paraplatoides* and *Zebraplatys*, and are rarely encountered (or trapped) away from their crevice.

In summary, it appears that localised evolutionary processes associated with low mobility have resulted in the south-west Western Australian salticid fauna containing a high proportion of strongly localised endemic forms. Detailed comparisons of the salticid fauna with neighbouring areas, such as the southern Carnarvon Basin and Warren Bioregion (to the south), are required to determine phylogenetic relationships between taxa and to confirm the climatic scalars of species composition that have emerged from our analysis. Ecological and life history studies of species representing the various individual genera are required before the processes governing localised speciation will be fully understood.

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