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Patterns in the biodiversity of terrestrial environments in the southern Carnarvon Basin, Western Australia

N.L. McKenzie, G.J. Keighery, N. Gibson and J.K. Rolfe
Department of Conservation and Land Management, PO Box 51,
Wanneroo, Western Australia 6065, Australia

Abstract – Sixty-three quadrats each of 16 ha were chosen to represent the geographical extent and diversity of terrestrial environments in a 75 000 km^2 area of the Carnarvon Basin, Western Australia. A total of 626 plant and 456 animal species were recorded from the quadrats, an average of 120 (s.d. = 22.1) species per quadrat.

After species that occurred at only one quadrat and species for which the sampling methods were unreliable (e.g. snakes and raptors) were removed from the data-set, 730 species remained, an average of 108.6 per quadrat (s.d. = 20.1). These comprised 81 herpetofauna, 13 small ground mammals, 85 birds, 9 scorpions, 12 centipedes, 122 ground-dwelling spiders and 408 plants.

The data were compiled into a single matrix comprising the presence or absence of the 731 species at the quadrats. When the species were classified according to their co-occurrences, thirteen assemblages were distinguished. Each assemblage could be characterised in terms of the Australia-wide habitat preferences of its component species. Also, quadrat similarity matrices were generated for each of the seven types of organism sampled and 1000 random matrices. These were output as linear similarity vectors so that the differences in their biodiversity patterns could be quantified as a single matrix of correlation coefficients.

Analyses revealed that:

1. Geographical patterns in species composition derived from the combined matrix correlated with processes operating at both biogeographical and local (ecological) scales: the compositional structure of each assemblage was related to a different set of climatic plus soil and/or topographic attributes. Poisson error models with logarithmic links fitted the gradient in species richness of each assemblage across the study area. Similar environmental attributes emerged whether an assemblage's composition or its richness was analysed. Since these attribute-sets were also consistent with the assemblages' Australia-wide characterisations, they are unlikely to be artifacts of quadrat positioning or study area extent.
2. Each of the seven ecologically different types of organism had a distinct influence on the biodiversity model; cross-taxon congruence levels were low.

To be representative, a Carnarvon Basin reserve system should sample the geographical range of the various climatic, soil and topographic gradients identified by the analyses. It should also be designed using a biodiversity model that incorporates a wide range of organisms.

INTRODUCTION

In this paper we explore geographical patterns in the composition of communities in non-aquatic environments of the southern Carnarvon Basin (Figure 1). The only previous attempt to define patterns in the biota of the study area was by Beard (1976), who mapped vegetation units at a scale of 1 : 1 000 000 from base maps compiled at 1 : 250 000.

Our aims were to

- provide an overview of the composition and distribution of species assemblages, as components of communities,
- investigate the relationships between assemblage composition and measurable attributes of the study area's physical environment, to identify predictors of geographic patterns in species composition across the study area and
- examine levels of cross-taxon complimentarity (*sensu* Howard *et al.*, 1998) in the study area, as a potential issue in reserve selection (McKenzie *et al.*, 2000a).

We aimed to provide a regional context for conserving the study area's biodiversity by

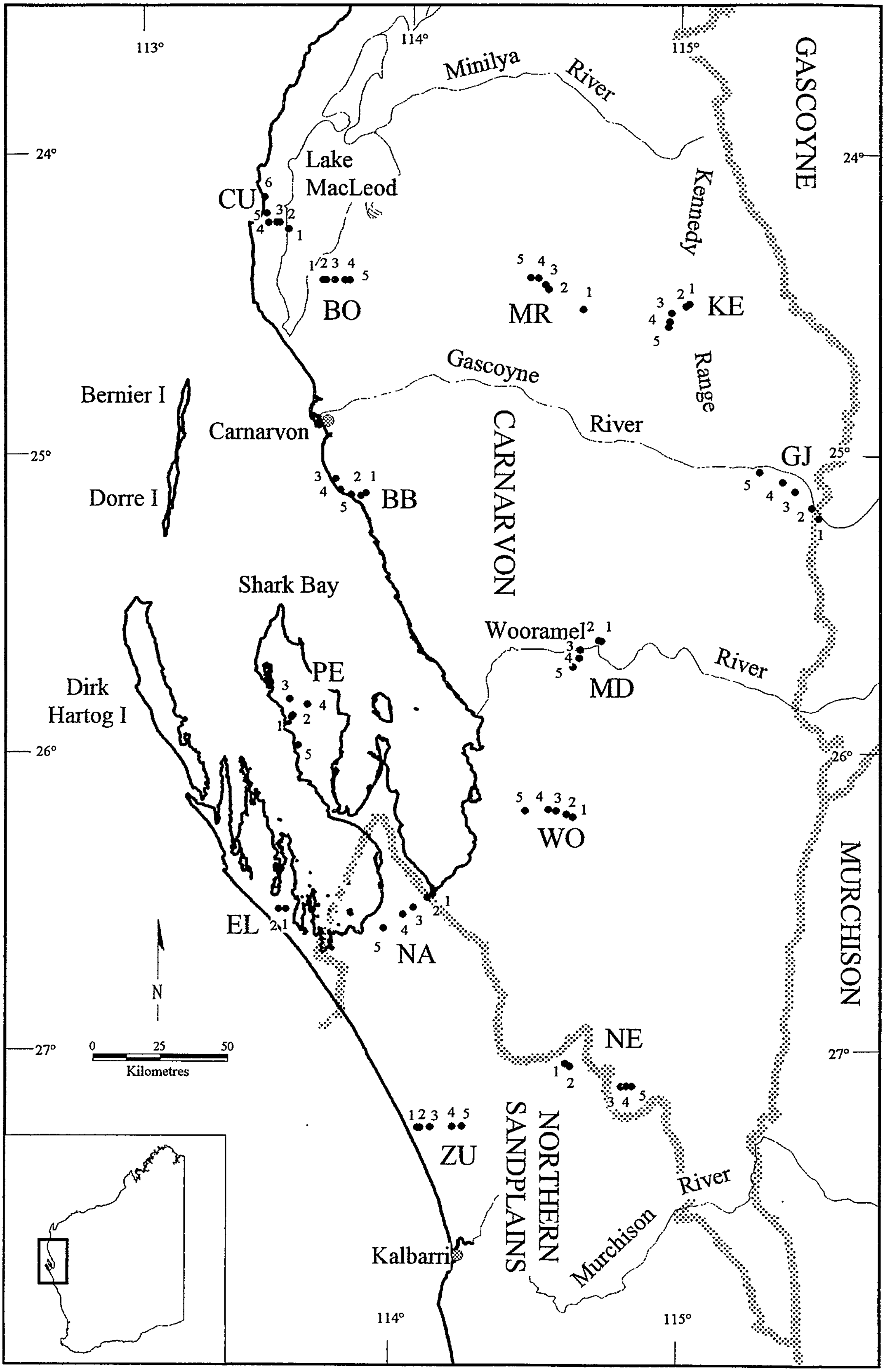

Figure 1 The Carnarvon Basin study area, showing the 13 survey areas (campsites) and individual quadrat positions. Precise quadrat co-ordinates are provided in Appendix A (this publication). The half-tone lines are the phytogeographic District boundaries of Beard (1980).

analysing data on seven ecologically distinct types of organisms from 63 quadrats,

- positioned to represent the diversity of the study area's physical environments across its geographical extent, and
- defined in terms of a wide array of measured physical attributes that were related to both regional and local scales.

Spatial patterns in biodiversity have usually been examined in terms of subjective categorisations based on vegetation structure or soil type, or from the perspective of a narrow range of organisms (e.g. plants or birds). We test the proposition that a more representative view of community patterns can be gained if a variety of ecologically distinct types of organism are sampled (Paine, 1980; Wiens, 1985; McKenzie *et al.*, 1991a, b).

METHODS

Study Area

The Carnarvon Basin study area covers 75 000 km^2 on Australia's western coast. It is centred on Shark Bay, and extends northwards from the Murchison River to the Minilya River, and eastwards to beyond Gascoyne Junction (Figure 1).

Its physical environments are detailed by Wyrwoll, Stoneman, Elliott and Sandercock (2000) and Wyrwoll, Courtney and Sandercocck (2000). Briefly, the region is a lowland characterised by gentle gradients on a basement of soft sediments. Under a variety of climates, interacting alluvial and aeolian processes have produced a complex landscape mosaic, that has been further modified by extensive coastal transgressions associated with sea-level changes. Today, the area south of Shark Bay has a semi-arid climate influenced by temperate weather systems (mainly winter rainfall). From Shark Bay northward, the climate is influenced by both tropical and temperate systems – semi-arid at the coast, but arid with locally unreliable rainfall further inland that falls in both summer and winter. In phytogeographic terms, the study area comprises the northern half of the Irwin District of the South-western Province, as well as the southern half of the Carnarvon District of the Eremean Province (Beard, 1980).

Extensive alluvial plains dominate the study area, although erosional uplands such as the Kennedy Range occur in its eastern parts. The plains are traversed from east to west by two large, ephemeral rivers lined with groves of River Gum (*Eucalyptus camaldulensis* and *E. victrix*): the Gascoyne and Wooramel. Low open woodlands of bowgada (*Acacia linophylla*) and snakewood (*A. xiphophylla*) over *Atriplex, Senna* and *Eremophila* shrubs and tussock grasses cover the plains, with *Acacia grasbyi* in areas where calcretes are exposed. Low red sand ridges scattered across the plains support shrubs over mainly hummock-grasses. In northern parts, the plains grade into red sand dune fields that support hummock-grass and mulga (*A. aneura*) communities reminiscent of Australia's 'red centre'. In the south the plains support woodlands of *Eucalyptus loxophleba* and *Callitris glaucophylla*, with mallee, *Banksia, Allocasuarina* and *Actinostrobus* scrubs and heaths on greyish and yellow sand dunes. A strip of limestone that follows the coast southwards from Shark Bay is partially mantled by pale yellow to grey sands supporting low proteaceous heaths with emergent thickets of *Banksia* and mallees such as *Eucalyptus erythrocorys*. White coastal sand dunes support *Spinifex longifolius* communities. Low-lying saline areas, such as the fringes of Lake MacLeod and the coastal flats, support samphire and saltbush communities. Descriptions of the vegetation in the study area are provided by Beard (1975, 1976), Payne *et al.* (1987), Gibson *et al.* (2000) and Keighery *et al.* (2000).

Sampling Strategy

Scale, complexity and patchiness need to be taken into account in sampling the biota of a study area to describe the diversity of its patterns (Braithwaite, 1984; Bowers, 1997).

A variety of factors can distort the results, including

- geographical and seasonal sampling bias (Braithwaite, 1984; Weins, 1985; Rosenzweig and Abramski, 1986),
- historic extinctions and introductions, and storage effects (Burbidge and McKenzie, 1989; Warner and Chesson, 1985),
- limitations in scale (Dale, 1983; Whitmore, 1984, p. 231; Bowers, 1997; MacNally and Quinn, 1997),
- inefficient sampling methods (Hobbs *et al.*, 1984; Rolfe and McKenzie, 2000), including the analytical implications of unreliable 'absence' data in the presence-absence matrix (Margules and Austin, 1994),
- the assumption that guilds follow taxonomic boundaries (Adams, 1985; Bowers, 1997; McKenzie and Rolfe, 1986),
- uneven taxonomic resolution (see McKenzie *et al.* 2000b), and
- strongly localised patterns of endemism (Solem and McKenzie, 1991).

Aspects of the survey design (details are provided in Keighery *et al.*, 2000; Harvey *et al.*, 2000; McKenzie *et al.* 2000b) offset some of these problems.

- The study area was large enough to encompass significant sections of both the geographical and environmental ranges of the species sampled (Austin and Heyligers, 1989).

- Sampling was carried out during an integrated programme; all quadrats were sampled in several seasons.
- The quadrat-size (16 ha for the zoological groups, and enclosing an 0.09 ha plant quadrat) was large enough to encompass the assemblages of the organisms being sampled considering their mobility, longevity and body-size in the context of their density, productivity and standing biomass in the study area. At the same time, the quadrats had to be small enough to allow the assumption that there was a reasonable level of internal homogeneity, and that there was syntopy between all biophysical attributes recorded within each quadrat (McKenzie *et al.*, 1991b).
- Environmental attributes that reflect processes operating at both regional scales and local scales were measured for each quadrat.
- Our quadrats were sampled for perennial and annual plants, birds, frogs and lizards, small ground mammals, ground-dwelling spiders, centipedes, and scorpions. Thus, wide ranges in mobility, longevity, daily energy and moisture requirement, nutritional role, biomass and reproductive strategy were represented in the data-base, and guilds were less likely to be fragmented or severed along taxonomic boundaries.
- Tested sampling methods were applied by experienced field survey ecologists, and species were only included in the analysis if they were reliably captured by the sampling methods (see Burbidge *et al.*, 2000, and Rolfe and McKenzie, 2000); thus the problems of unreliable 'absence' data in the presence-absence matrix were minimised.
- All specimen identifications were carried out by professional taxonomists familiar with the relevant group in Western Australia.

Quadrats were positioned throughout the geographical extent of the study area in a stratified random array derived from vegetation and surface lithology maps (Beard, 1976; Hocking *et al.*, 1987). They were placed in typical examples of each of the main lithological units that characterise the study area, and positioned in clusters that were reasonably evenly dispersed across the study area's areal extent. The relative number of quadrats within a surface unit was roughly proportional to the unit's aerial extent in the study area. Many quadrats were pseudo-replicated (locally as well as at distant points) to allow for the internal heterogeneity of the stratification units (hypothesised scalars) and to minimise any analytical circularity introduced by the stratification (Taylor and Friend, 1984; McKenzie *et al.*, 1989, 1991b).

Field Sampling

Quadrat locations and sampling procedures for the various taxa are provided elsewhere (Keighery *et al.*, 2000; Burbidge *et al.*, 2000; McKenzie *et al.*, 2000b; Harvey *et al.*, 2000). Briefly, species were sampled from 63 quadrats clustered in sets of two to six quadrats around each of 13 survey areas. Sampling was sparse. The study area encompassed 7.5 million hectares, and less than 1008 hectares was actually sampled (each quadrat was a releve' of 400 x 400 m = 16 hectares, and 63 quadrats x 16 ha = 1008 ha). Thus, less than 0.013% of study area was actually sampled for animals. Furthermore, only a 30 x 30 m area of each terrestrial quadrat was sampled for plants (0.0001% of the study area).

Analysis of Spatial Patterns in Species Assemblages

The survey design was based on quadrat sampling and 'assemblage-connectance' concepts (May, 1975). The analytical approach taken in this paper was based on the assumption that spatial distribution reflects an underlying correlation with environmental factors (Austin, 1991; Clarke, 1993). It is, however, an exploratory design. No experimental design has been implemented to confirm a null hypothesis (Austin and McKenzie, 1988), so alternative hypotheses are not excluded.

The input data was the "quadrat-x-species" matrix. We determined and analysed the presence and absence of species on the quadrats, rather than their relative abundance, because limitations in sampling techniques, aggravated by staff and time limitations, precluded reliable estimates of abundance (Austin, 1984; McKenzie *et al.*, 1991b).

We used cluster analysis (from PATN, Belbin, 1995) to expose patterns of species composition in the data matrices. The clustering techniques selected were described in McKenzie *et al.* (1991a). Briefly, the association measure "Two-step" (Belbin, 1980) was used to determine the quantitative relationship between each pair of species, and the Czekanowski measure (Czekanowski, 1932) was used to compare the quadrats according to their species similarities. For both measures of association, a modified version of "unweighted pair group arithmetic averaging" (UPGMA - Sneath and Sokal, 1973; Belbin, 1995) hierarchial clustering strategy was used, with the clustering parameter (Beta) set to -0.1.

A modification by Hubert and Arabie (1985) of the statistic by Rand (1971) was used to compare the classification partition structures derived from different data-sets [RIND module in PATN (Belbin, 1995)].

Further analysis was carried out in the following order:

1. The data matrix was partitioned into

Table 1 Vegetation attributes used to summarise the 'type' and structure (-stru) of the vegetation on the quadrats in ordinal terms.

Veg-stru	Veg-type
Grass and/or low shrubs = 1	Grass and/or low shrubs = 1
+ Shrubs to 1.5m high = 2	Shrubland = 2
+ tall shrubs (1.5 to 3m high)= 3	Tall Shrubland = 3
+ low trees and/or mallees = 4	Low Woodland: *Acacia* canopy = 4
+ trees > 8m high= 5	Woodland: mixed canopy = 5
–	Woodland: *Eucalyptus* canopy = 6

assemblages of species according to their co-occurrences at the same quadrats.

2. Each assemblage was characterised in terms of the known habitat preferences of its component species throughout their ranges elsewhere in Australia (Strahan, 1995; Wilson and Knowles, 1988; Ehmann, 1992; Tyler *et al.*, 1994; Jessop, 1981; Koch, 1981; Pizzey, 1980, as well as reviews in earlier papers in this volume).
3. Quadrats were classified according to similarities in the species composition (as above), to summarise each assemblage's pattern of occurrence across the study area in the form of a separate dendrogram (its compositional structure). Next, each dendrogram was analysed in terms of a set of attributes related to the physical environment of the quadrats (see Wyrwoll, Stoneman, Elliott and Sandercock (2000), Wyrwoll, Courtney and Sandercock (2000) and Appendix D, this publication). In this analysis, univariate data on aspects of the quadrats' physical environments were superimposed as a histogram on each dendrogram, attribute-by-attribute. This process allowed us to identify the physical attributes that most closely conformed with each dendrogram's partition structure, i.e. the pattern of its species-composition across the study area. The statistical significance of relationships was assessed using Kruskal-Wallis one way analysis of variance by ranks (the GSTA module in PATN - Belbin, 1995).
4. The generalised linear interactive modelling package GLIM (NAG, 1986; Nicholls, 1989) was used to model the relationships between the species richness of each assemblage and the physical attributes of the quadrats. Forward, stepwise regression models were fitted to each of the species-assemblages defined from the classification procedure, with quadrat species-richness as the dependent variable. The significance of the parameters in the regression equations was calculated using the Wald statistic, and is indicated by asterisks (* = significant at > 0.05, ** > 0.01, *** > 0.001 etc).

Eleven climatic attributes were derived for each quadrat using ANUCLIM (McMahon *et al.*, 1995). Soil and geomorphic attributes were also recorded from each quadrat (Wyrwoll, Stoneman, Elliott and Sandercock, 2000). The 17 soil chemical and texture values used herein were derived from sub-samples collected at a depth of 5–10 cm from 20–30 regularly dispersed points on each quadrat, then bulked (Appendix D). Two vegetation attributes were also generated: 'veg-type' and 'veg-stru' (defined in Table 1). Significant correlations between these

Table 2 Environmental attribute codes.

Code	Attribute	Code	Attribute
Pann	Annual average precipitation (mm)	Cl	Soil chloride (%)
Pcld	Coldest quarter precipitation (mm)	exNa	Exchangeable sodium (me%)
Pwet	Wettest quarter precipitation (mm)	EC	Electrical conductivity (mS/m)
Pwp	Wettest period precipitation (mm)	exMg	Exchangeable magnesium (me%)
Pwar	Warmest quarter precipitation (mm)	N	Total nitrogen (ppm)
Psea	Precipitation seasonality	exK	Exchangeable potassium (me%)
Tann	Annual average temperature (°C)	$K(HCO_3)$	Available potassium (ppm)
Twet	Wettest quarter mean temperature (°C)	P	Total phosphorus (ppm)
Tcld	Coldest quarter mean temperature (°C)	$P(HCO_3)$	Available phosphorus (ppm)
Twar	Warmest quarter mean temperature (°C)	$CaCO_3$	Calcium Carbonate (%)
Tdi	Temperature diurnal range (°C)	CEC	Cation exchange capacity (me%)
Tar	Temperature annual range (°C)	tx-shst	Soil textural shear strength (kPa)
Cst-dist	Distance to coast (km)	Stone	Amount of rock in soil profile
Alt	Altitude (m)	Sand	Percent sand
Lat	Latitude (°S)	gs-over	Over-bank stream flow
Long	Longitude (°E)	Veg-type	see Table 1.
		Veg-stru	see Table 1.

physical attributes were identified using Kendall's rank correlation coefficient (Kendall's tau). Physical attribute names and codes are listed in Table 2.

Influence of the Taxonomic Sub-sets on the Biodiversity Model

Our analytical strategy was similar to that used by Somerfield and Clarke (1995). Seven taxonomic sub-sets were represented in the community matrix: birds, small ground mammals, herpetofauna, ground-dwelling spiders, scorpions, centipedes and vascular plants. Analysis involved eight steps:

1. For each sub-set, and for the combined data-set, a dissimilarity matrix was derived by using the Czekanowski measure (Czekanowski, 1932, from the ASO module in Belbin, 1995) to compare quadrats in terms of their species composition.
2. Each dissimilarity matrix was output as a linear vector (Option 6 in the ASON module of PATN, Belbin, 1995).
3. Using Pearson Product-Moment Correlation, we calculated the correlation between each pair of vectors as a measure of congruence in their (spatial) biodiversity patterns. These correlation coefficients were compiled as a matrix of 'cross-taxon' congruence.
4. Next, the correlation matrix was converted to a dissimilarity matrix (1-coefficient), and Semi-strong Hybrid Scaling (SSH in Belbin, 1995) was used to reduce the dimensionality of this matrix, so that the relationships between the sub-set patterns and the combined pattern (the biodiversity model) could be displayed in three dimensions.
5. A 'minimum spanning tree' (MST in Belbin, 1995) was superimposed to indicate the nearest-neighbour linkages in the ordination space.
6. To provide some extrinsic measure of distance across the ordination space, 1000 uniform random matrices were generated and plotted in the same ordination space using the steps listed above.

RESULTS

Spatial Patterns in the Richness and Composition of Species Assemblages

A total of 626 plant and 456 animal species were recorded from the 63 quadrats, an average of 120 species per quadrat (s.d. = 22.1, n = 63; Table 3). The animals comprised 133 herpetofauna (12 frogs, 121 reptiles), 15 small ground mammals, 126 birds, 10 scorpions, 15 centipedes and 157 ground-dwelling spiders.

Quadrats on saline claypans (BB3, BO2, NA1, PE1, CU1) were poorest in species (average = 77 species, s.d. = 25, n = 5). Ignoring saline claypans, we also noted that

- quadrats that were being regularly grazed by stock, feral goats and/or rabbits at the time of our study were not significantly poorer in species than those that showed no sign of contemporary usage by these introduced herbivores (KE1-2, NA2-5, NE1, ZU1-5)(124.6±18.2, n = 46 versus 120.3 ± 15.8, n=12 respectively),
- even quadrats in overtly degraded condition, with sheet erosion and virtually no leaf litter or A1 soil-horizon remaining (BB1, BO5, GJ4-5, KE4, MD1,2,4,5, PE4 and WO1,4) retained only marginally lower richness overall (116.4±12.3, n=12 versus 125.6±18.5, n=46) and
- quadrats on deep red sands were the richest (131.5 ±16.6, n=20).

Using the entire 1082 species, the 63 quadrats were classified in terms of similarities in their species composition. After species that occurred at only one quadrat and species for which the sampling methods were unreliable (e.g. raptors and snakes, see Burbidge *et al.*, 2000 and McKenzie *et al.*, 2000b) were removed from the data-set, 730 species remained (an average of 108.6 per quadrat, s.d. = 20.1). These comprised 10 frogs, 71 lizards, 13 small ground mammals, 85 birds, 9 scorpions, 12 centipedes, 122 ground-dwelling spiders and 408 plants. Using this reduced matrix, the 63 quadrats

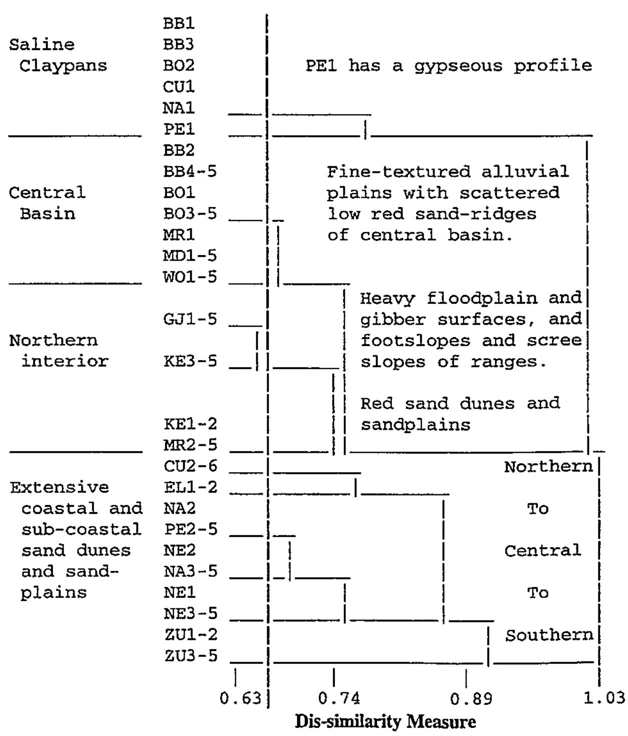

Figure 2 Quadrats classified according to their species composition using the 731 species data-set. Dendrogram structure to the 12-group level is displayed.

were again classified in terms of similarities in their species composition to yield a quadrat dendrogram that summarised geographical patterns of occurrence (Figure 2).

When the dendrogram partition structures derived from the 1082-species and the 730-species data-sets were compared using the modified RAND statistic (Table 4), the differences at the 12-group level were small (Hubert and Arabie RAND statistic = 0.96). Only two quadrats were assigned differently by the reduced data-set (CU1 and NA2).

The 730 species were classified according to similarities in their co-occurrences at the same quadrats. The 13 assemblages we defined are characterised in terms of the distributional characteristics and habitat preferences of their component species throughout their geographical ranges in Australia (Figure 3). Relevant annotations are on this dendrogram and additional notes are presented below.

Distributions Centred on the Arid Zone

Assemblage-1: Ubiquitous riverine species, such as River Gums. The dragon *Gemmatophora longirostris* also occurs in coastal dunes.

Assemblage-2: Species of fine-textured soils and associated lunettes. It comprises six species-subsets that formed distinct partitions at lower levels in the dendrogram:

2a. ubiquitous species;

2b. species of fine-textured riverine alluvia;

2c. ubiquitous non-saline species;

2d. species of saline playas or lunettes of playas, and of alluvial plains;

2e. species of semi-saline sandy lunettes in and around saline playas and claypans;

2f. species of sandy lunettes surrounded by extensive plains of fine-textured soils.

Unlike group 2d, species in '2e' and '2f' have localised occurrences in the study area.

Assemblage-3: Species of floodplains, footslopes and clayey interdune plains, i.e. of heavier soils than the species belonging to Assemblage-2. Some rock-outcrop species at ecotonal sites are included (e.g. *Sminthopsis longicaudata* and *Ptilotus polakii* were found at KE3 and GJ1 which straddled the lower slope and foot of scree slopes).

Assemblage-4: Specialists of deep red desert sand dunes and plains, including patches close to the coast. Some are centred on the Carnarvon Basin (e.g. *Verticordia forrestii*).

Table 3 Species richness per quadrat.

Campsite	Quadrat 1	2	3	4	5	6
BB	112	123	108	137	125	
BO	136	87	161	160	136	
CU	63	126	124	122	131	107
EL	98	101				
GJ	108	108	128	101	118	
KE	107	97	134	110	126	
MD	138	116	175	113	124	
MR	147	154	128	131	119	
NA	86	143	129	131	105	
NE	128	86	123	118	108	
PE	42	145	143	120	132	
WO	96	108	117	113	144	
ZU	103	131	137	104	129	

Ubiquitous Distributions

Assemblage-5: Species with distributions that cover arid, semi-arid and mesic regions, and which occur on all surfaces. Some even reach the mesic tropics (e.g. Black-faced Cuckoo-shrike, *Euphorbia australis* and *Cenchrus ciliaris*).

Semi-arid Distributions

Assemblage-6: Species with distributions centred on sand surfaces in the semi-arid.

Assemblage-7: Centred on semi-arid woodlands of (mainly) the temperate zone. Some extend into the arid zone in association with trees, such as along riverine fringes. Some birds reach the mesic tropics.

Widespread Saline and Calcareous Plain Species

Assemblage-8: Widespread claypan species, usually saline but also on chenopod plains with saltbush and/or bluebush. Some also occur in coastal areas adjacent to mangroves in Shark Bay. *Scaevola crassifolia* is an exception.

Coastal Sand Distributions

Assemblage-9: Specialists of coastal, semi-arid, sand surfaces in the temperate zone. Some are endemic to Edel Land.

Assemblage-10: Species of coastal, sub-tropical (northern), sand surfaces from Carnarvon to Exmouth (22°S, 114°E), except for *Triodia basedowei* which also occurs on red sand surfaces of inland Australia, and *T. pungens* of red sand surfaces in the Pilbara, Little Sandy Desert, Great Sandy Desert, southern Kimberley and elsewhere in northern Australia.

Distributions Centred on the Temperate Zone

Assemblage-11: Three species sub-sets formed discrete partitions at a lower level in the dendrogram:—

11a. Specialists of temperate (southern) coastal areas. Exceptions are *Solanum oldfieldii* which extends further inland, *Tiliqua rugosa* which is not reliably detected by our survey methods and therefore is a sampling artifact, and Thick-billed Grass-wren whose extant distribution is an extinction artifact.

11b. Temperate semi-arid species of sandy and

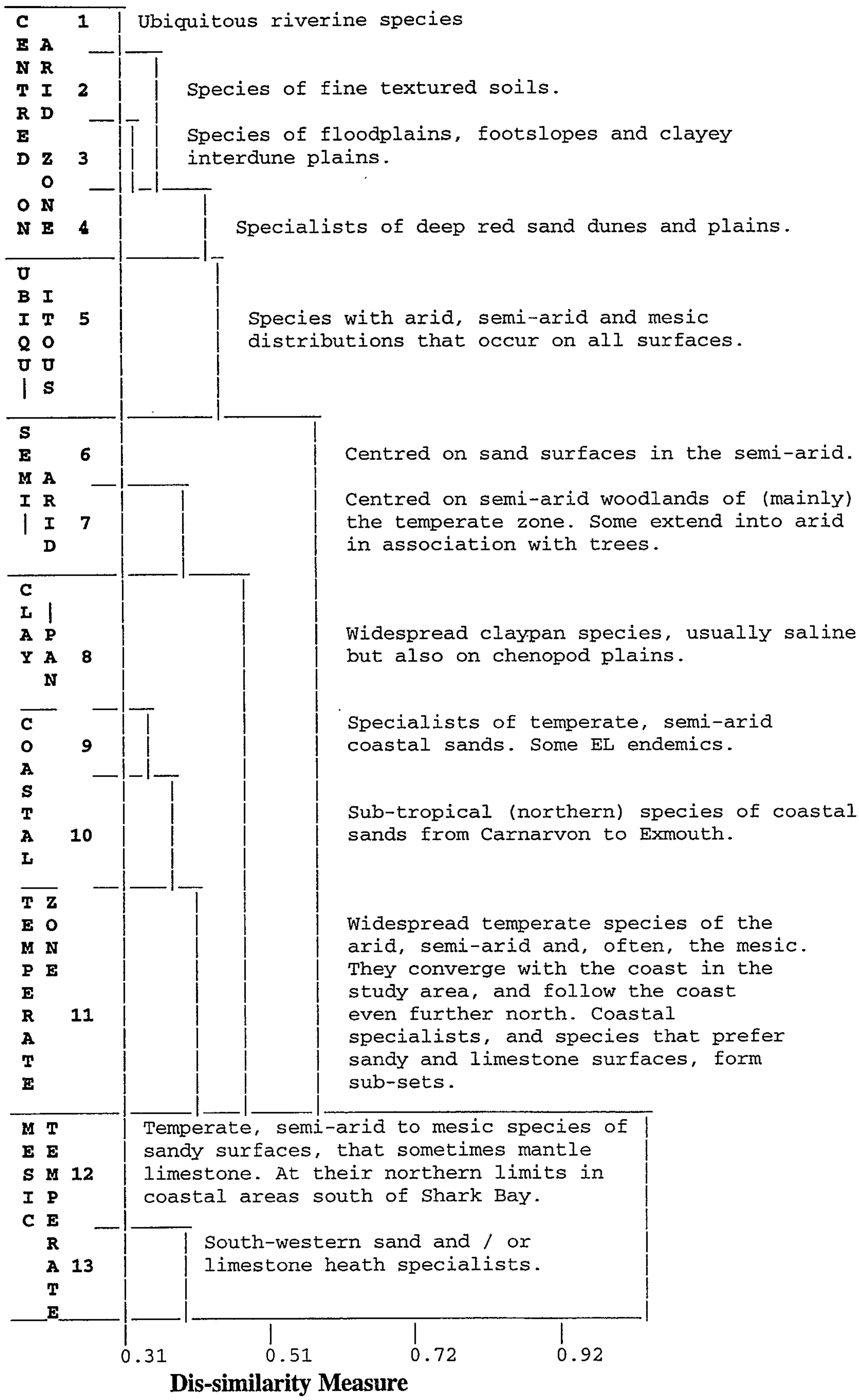

Figure 3 Species assemblages derived by classifying species according to their co-occurrences at the same quadrats. Dendrogram structure to the 13-group level is displayed. Assemblages are characterised in terms of the distributional characteristic and habitat preferences of their component species throughout their geographical ranges in Australia.

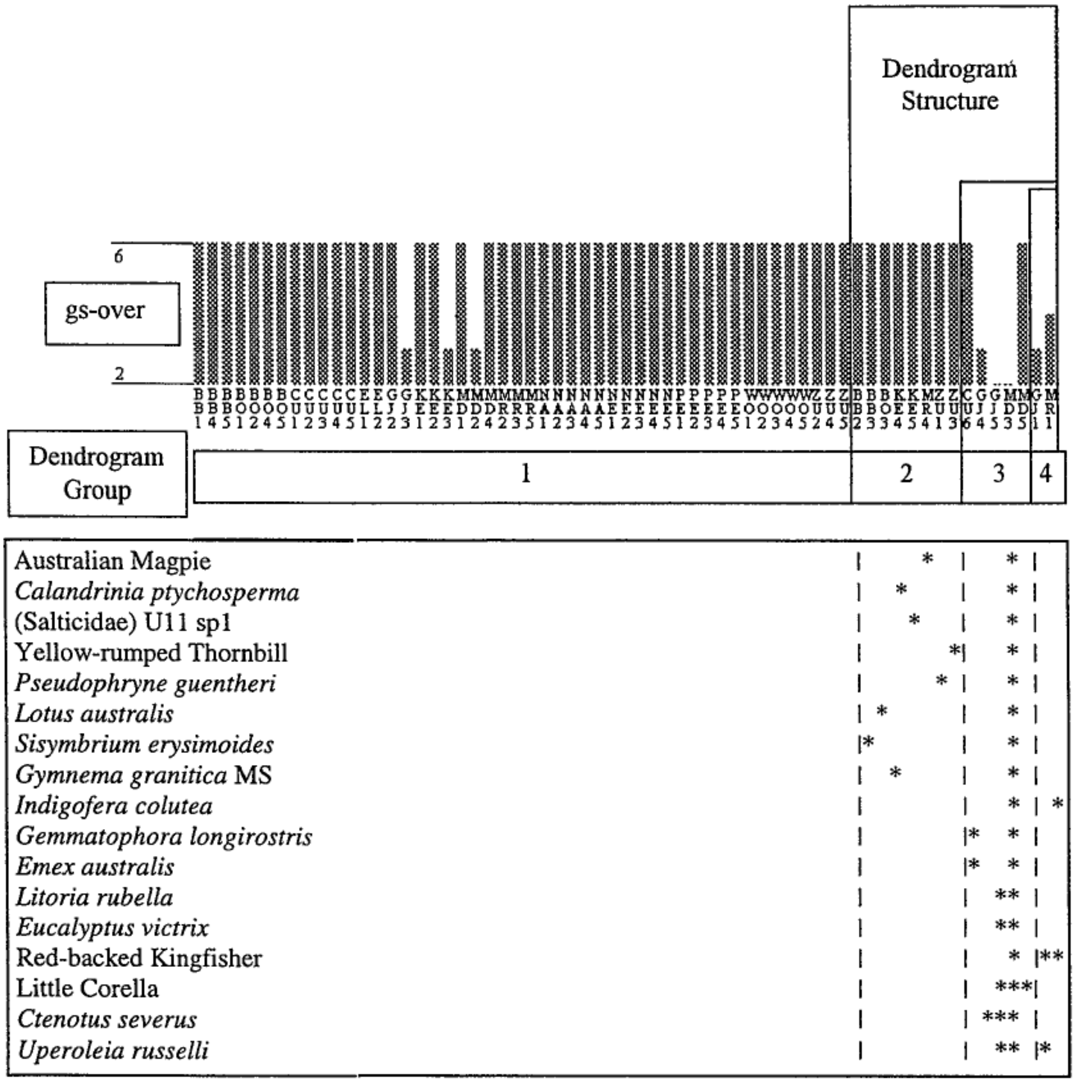

Figure 4 Attribute values for 'over-bank stream flow' (gs-over) superimposed as an histogram on the dendrogram structure derived from the classification of the 63 quadrats in terms of species belonging to assemblage-1. Quadrat codes are printed vertically. Values for gs-over ranged from 2 to 6 (see Wyrwoll, Courteney and Sandercock, 2000). The relevant re-ordered data matrix from Figure 12 is aligned beneath the histogram.

Table 4 Comparison between the quadrat classification partition derived from the 730 species data-set (Partition-1, see Figure 2) and the partition derived from the 1082 species data-set (Partition-2).

Partition-1	**Partition-2**											
	1	2	3	4	5	6	7	9	8	10	11	12
1	4	1	–	–	–	–	–	–	–	–	–	–
2	–	1	–	–	–	–	–	–	–	–	–	–
3	–	–	7	–	–	–	–	–	–	–	–	–
4	–	–	–	11	–	–	–	–	–	–	–	–
5	–	–	–	–	8	–	–	–	–	–	–	–
6	–	–	–	–	–	6	–	–	–	–	–	–
7	–	–	–	–	–	–	5	–	–	–	–	–
8	–	–	–	–	–	–	–	2	–	–	–	–
9	–	–	–	–	–	–	–	–	4	1	–	–
10	–	–	–	–	–	–	–	–	–	4	–	–
11	–	–	–	–	–	–	–	–	–	–	4	–
12	–	–	–	–	–	–	–	–	–	–	–	5

Hubert/Arabie RAND statistic = 0.96
Diagonal/total = 61/63= 0.97

Table 5 Relationship between environmental attributes and geographical patterns in assemblage richness and composition. Environmental attribute codes are explained in Table 2, and detailed in Wyrwoll, Courteney and Sandercock, 2000). In all cases, poisson error models with logarithmic links best fitted the richness gradients. 'Test' lists the quadrat/s to which the fitted model was sensitive, and whether or not the model estimates changed significantly after the quadrat's influence was suppressed (Yes/No). 'Group Level' indicates the level at which the relevant quadrat dendrogram was cut (the number of partitions defined).

Assemblage (from Fig. 3)	Richness Gradient Fitted Model: Ln(Richness) = (*<.05, **<.01 etc)	Test	Compositional Structure Group Level	Attributes	Kruskal -Wallis	Prob.
1	-2.3-15.5exNa+4.6exMg exNa and exMg = **** Scaled Deviance = 47, d.f.=60 Scaled Deviance of Null Model = 156	MD3, N	4	gs-overt†	17.9	0.0005
2	2.2-0.02Alt+0.004Alt^2-0.02Pwet+ 0.009P-0.04$CaCO_3$+0.24Tdi Alt, Alt^2, Pwet, P and $CaCO_3$ = ****; Tdi = ** Scaled Deviance = 132, d.f.=57 Scaled Deviance of Null Model = 683	CU6, N	3 5 8	Pwet P Tdi	32.3 25.1 36.1	<0.0001 <0.0001 <0.0001
3	-37.6+1.4Twar-8e^{-5}Pann^2+50.7N Twar, Pann^2 and N = **** Scaled Deviance = 67.1, d.f.=59 Scaled Deviance of Null Model = 576	CU1, N	6 6 6	Twar Pann N	42.0 33.8 4.1	<0.0001 <0.0001 0.5 NS
4	-19.6+0.06Pwar-0.007P+0.61Twar- 0.0055K(HCO_3) Pwar and Twar = ****; P and K(HCO_3) = ** Scaled Deviance 76.2, d.f.=58 Scaled Deviance of Null Model = 481	CU3, N	3 7 7	Pwar Twar K(HCO_3)	25.1 27.5 5.9	<0.0001 0.0001 0.43 NS
5	5.15-0.006Pwet-0.198exMg-0.002Alt- 0.006$CaCO_3$ Pwet, exMg, Alt and $CaCO_3$ = **** Scaled Deviance 94.5, d.f.=58 Scaled Deviance of Null Model = 347	PE1, N	6 6 11 11	Psea Alt exMg $CaCO_3$	43.9 26.3 29.5 37.9	<0.0001 0.0001 0.001 <0.0001
6	-0.55-9.07exK-0.216P(HCO_3)+0.117Psea- 0.277Pann exK, P(HCO_3), Psea and Pann = **** Scaled Deviance 88.3, d.f.=58 Scaled Deviance of Null Model = 373	NA4, N	4 4 9 9	exK Veg-type* P Psea	21.2 20.3 26.6 15.2	0.0001 0.0002 0.0008 0.055
7	-59.3-0.12P(HCO_3)+0.61Pcld-0.00094Pcld^2- 0.36Pwet+2.30Tann P(HCO_3), Pcld, Pcld^2, Pwet and Tann = **** Scaled Deviance 125.1, d.f.=57 Scaled Deviance of Null Model = 505	ZU1, N	6 6	Veg-type* Tcld	26.3 16.7	0.0001 0.005
8	-55.3+2.89 Tcld+0.98Cl+0.39Pwar- 0.00446Pwar^2+0.052$CaCO_3$ Tcld, Cl, Pwar^2 and $CaCO_3$ = ****, Pwar = *** Scaled Deviance 39.7, d.f.=57 Scaled Deviance of Null Model = 288	PE1, N	4 4 4 6 6	Cl P(HCO_3) Alt exMg $CaCO_3$	25.6 23.4 19.8 13.0 18.9	<0.0001 <0.0001 0.0002 0.024 0.002
9	-6.47+0.037$CaCO_3$+0.071Pwp $CaCO_3$ = ****, Pwp = ** Scaled Deviance = 30.1, d.f. = 60 Scaled Deviance of Null Model = 131	ZU2, N	2 4	Pwp $CaCO_3$	8.3 10.7	0.0041 0.0133
10	73.4-4.27Lat+0.27Pwp-0.15P(HCO_3)+ 0.71Tar Lat, Pwp and P(HCO_3) = ****, Tar = ** Scaled Deviance = 33.2, d.f. = 58 Scaled Deviance of Null Model = 278	CU5, N	7 7 7	Lat P(HCO_3) Tdi	20.5 10.6 16.2	0.002 0.10 NS 0.013
11	18440-323.2Long-0.24Tann^2-4.11exK+ 1.41Long^2-0.0088$CaCO_3$+9.80Tann+ 5.57exK^2-0.21exNa exK^2 and Tann = ***, all others = **** Scaled Deviance = 91.4, d.f. = 54 Scaled Deviance of Null Model = 828	PE1, N	8 8 8 6	Pcld Cst-dist exK exNa	37.9 38.1 40.2 17.1	<0.0001 <0.0001 <0.0001 0.0044
12	-24.6+0.027Pann+0.32Sand-0.78Tcld+ 0.051CEC^2 Pann and Sand = ****, Tcld = ***, CEC^2 = * Scaled Deviance = 54.7, d.f. = 58 Scaled Deviance of Null Model = 824	ZU5, N	5	Pcld	22.9	0.0001
13	Entire assemblage is either present or absent, so model will not converge.	—	2 2	Stone Pcld	9.5 5.7	0.002 0.017

† Ordinal data, not used in the GLM analysis.

limestone surfaces. They centre on the mid-latitude coast; many extend into semi-arid areas of the Coolgardie and Avon Bioregions, and further north along the coast than the species in Assemblage-11a.

11c. Widespread temperate species of arid, semi-arid and, often, mesic regions. They approach their northern limits at Shark Bay, where they converge with the coast and extend even further north because of coastal effects.

Distributions Centred on Mesic Regions of the Temperate Zone

Assemblage-12: Temperate, semi-arid to mesic species of sandy surfaces that sometimes mantle limestone. These are species of heath and scrubs, and are at their northern limits in coastal areas south of Shark Bay. The assemblage includes several specialists of deep sand surfaces that are centred on the strip from Geraldton (29°S 114° 30'E) to Shark Bay.

Assemblage-13: South-western heath specialists. This far north they need to be close to the coast. All of the plants are grasses or small heath plants; five of the 12 are restricted to coastal limestone surfaces. The others are found in sand- as well as limestone-heaths.

Species Richness and Composition in Relation to Quadrat Attributes

Several distinct step-wise structures dominate both the quadrat- and the species-dendrograms (Figures 2 and 3). Such structures would occur if the species-assemblages were responding to different gradients in the physical environment or differently to sub-sets of environmental gradients (McKenzie *et al.*, 1989, 1991a). To test this hypothesis, the 13 species-assemblages were treated as independent data-sets and analysed separately.

When the 63 quadrats were classified in terms of the species belonging to each of the 13 assemblages, each assemblage's pattern of occurrence across the study area was summarised in the form of a dendrogram (e.g. Figures 4 and 6). As described in 'Methods', univariate data on aspects of the quadrats' physical environments were superimposed as histograms on each dendrogram, attribute-by-attribute to identify the physical attributes that most closely conformed to the patterns in each assemblage's species-composition across the study area. As a parallel analysis, the package GLIM was used to model the pattern of each assemblage's species richness across the study area in terms of the physical attributes of the quadrats (see Methods).

The results of these analyses are summarised in Table 5, and are explained below. Correlations between relevant environmental attributes are summarised in Table 6.

- Assemblage-1's compositional structure showed a significant fit to the gradient in floodplain situations (over-bank stream flow, 'gs-over', see Wyrwoll, Stoneman, Elliott and Sandercock, 2000) (Figure 4). Although non-ratio data such as 'gs-over' were not included in the GLM analysis, the GLM richness model confirmed the compositional result because low soil sodium (exNa) and high magnesium (exMg) characterise the regularly washed soils that occur in drainage lines and associated floodplains (Table 5). The attibutes 'exMg' and 'gs-over' were intercorrelated in our study area (Table 6).

Table 6 Environmental attributes that showed the best fit to the group structure of the dendrogram derived by classifying the quadrats according to similarities in their composition. 'Group Level' indicates the level at which the relevant quadrat dendrogram was cut (the number of partitions). Tight inter-correlations with attributes in the richness models are listed in the final column.

Assemblage (from Figure 3)	Group Level	Attribute	Inter-correlations: Kendall's Tau (p.)
1	4	gs-over*	-0.33 with exMg (0.0016)
2	3	Pcld	0.95 with Pwet (<0.0001)
3	6	Pwet, Pcld	-0.84 with Twar (<0.0001), -0.87 with Twar (<0.0001)
4	3	Pwar	Attribute is in model
5	6	Psea	0.81 with Pwet (<0.0001)
6	4	$K(HCO_3)$	0.89 with exK (<0.0001)
7	6	Veg-type*, Twet	-,0.65 with Tann (<0.0001)
8	4	Cl	Attribute is in model
9	2	Long	-0.58 with $CaCO_3$ (<0.0001) -0.53 with Pwp (<0.0001)
10	7	Lat	Attribute is in model
11	8	$K(HCO_3)$	0.89 with exK (<0.0001)
12	5	$K(HCO_3)$, Pcld	-0.43 with Pann (<0.0001), 0.71 with Pann (<0.0001)
13	2	Stone	No model possible

* Ordinal data, not used in the GLM analysis.

- Assemblage-2's compositional structure (Figure 12) conformed with a precipitation gradient (low 'Pwet') across fine-textured lowland soils (high in phosphorus, potassium and soil shear strength, and at low altitude) (Figure 5a). Temperature diurnal range (Tdi) provided separation of a compositional variant of this assemblage that occurs on suitable sites near the coast. The same set of attributes (Altitude, 'Pwet', Phosphorus, and 'Tdi') were significant in the fitted richness model (Table 5), although soil calcium carbonate was also significant.
- Assemblage-3's compositional structure conformed to 'temperature in the warmest quarter' ('Twar') and, within this, with annual precipitation (Figure 5b) and soil total nitrogen (Table 5). These attributes also gave the best GLM model of the assemblage's species richness.
- Assemblage-4's compositional structure conformed with 'warmest quarter precipitation' ('Pwar'). Within that, high 'temperature in the warmest quarter' ('Twar'), with either low soil potassium ($KHCO_3$) or low soil phosphorus ($PHCO_3$), isolated the inland sandy quadrats where the compositionally diverse examples of this assemblage occurred (Figure 5c). The same attributes provided the best richness model.
- Assemblage-5: These species were mostly near-ubiquitous in the study area, although precipitation seasonality ('Psea') conformed to the assemblage's compositional structure (Figure 5d), with variants related to altitude ('Alt') and, at lower levels in the dendrogram, to soil calcium carbonate and soil magnesium. The tightest richness model used a similar set of attributes.
- Assemblage 6's compositional structure conformed with soil potassium ('exK') and 'veg-type'. Within that, low soil phosphorus (P), high precipitation seasonality and low soil shear strength distinguished the most compositionally diverse examples of this assemblage (group-5 from group-6) (Figure 5e). Groups-5 and 6 were also different in terms of soil cation exchange capacity ('CEC') and percentage clay. The richness model used the soil potassium and phosphorus, and the precipitation seasonality attributes (Table 5), although an alternative model used 'CEC' and 'precipitation in the warmest quarter' ('Pwar') instead of the seasonality attribute.
- Assemblage-7's compositional structure conformed with winter temperature ('Tcld'), with the most species-diverse examples at quadrats with cool winters, provided that they also had a *Eucalyptus* tree canopy (quadrats NA2, NE1-5 in Figure 6). If not, less than 10% of the assemblage's species were present. Hence the significance of 'Veg-type' (Table 5). The GLM model indicated that rich versions of this assemblage occurred in temperate, semi-arid sites, that were also low in soil phosphorus (Table 5).
- Assemblage-8's compositional structure conformed with altitude ('Alt'), soil salinity (e.g. 'Cl') and phosphorus ('$PHCO_3$'). The compositionally diverse sites were low in the landscape and had high phosphorus as well as either high soil chloride and/or high soil calcium carbonate levels; such sites were rich in magnesium ('exMg') (Figure 5f). Species richness was best predicted using soil chloride and calcium carbonate values in combination with temperature in the warmest quarter and precipitation in the warmest quarter. The temperature and precipitation attributes were an artifact because of the skewed occurrence of suitable environments in the study area; they were concentrated in northern near-coastal areas.
- Assemblage-9's compositional structure conformed with 'wettest period precipitation' ('Pwp') and longitude and, within these, with soil calcium carbonate (Figure 5g). Species richness was best predicted by GLM using the same precipitation and calcium attributes.
- Assemblage-10's compositional pattern conformed to Latitude, and within that, to soil phosphorus ($PHCO_3$) and 'temperature diurnal range' ('Tdi') (Figure 7). Rich assemblages occurred on the most northern quadrats, provided they were sands (i.e. soil phosphorus and potassium values were low), and had low 'annual temperature range' ('Tar') (Table 5). In the study area, low 'Tdi' and low 'Tar' are intercorrelated ($R^2 = 0.95$, $p. < 0.0001$) because they are coastal amelioration effects.
- Assemblage-11's gradient in composition conformed with high precipitation in the coldest quarter (Pcld: the wet winters of the temperate zone) and, within that, was influenced by distance from the coast ('cst-dist'), inter-correlated with longitude: $R^2 = 0.85$, $p. < 0.0001$), soil exchangeable potassium ('exK') and/or soil exchangeable sodium ('exNa') (Figures 8 and 5h). Similar attributes were identified from the GLM analysis: the rich assemblages occurred on low potassium soils near the coast (low longitude) (Table 5).
- Assemblage-12's compositional structure conformed with 'precipitation in the coldest quarter' ('Pcld') (Figure 9). The rich assemblages occurred in quadrats with highest annual rainfall ('Pann') and lowest winter temperatures ('Tcld'), although soil sandiness (% sand) and

Figure 5 Physical attributes that separated the quadrat-groups defined by an assemblage's dendrogram. The relevent data matrices are provided in Figure 12. N = number of quadrats in each classification group (GRP), "1==M==3" indicates one standard deviation either side of the mean (M), and * indicates that the mean and standard deviation points were too close to separate in the diagram. H = Kruskall-Wallis coefficient; df = degrees of freedom; p = probability).

a. Assemblage-2, partitioned at the 3-, 5- and 8-group levels in the classification structure.

Wet Quarter Precipitation (Pwet, mm) (3 groups: H = 32.3, df = 2, p = <0.0001).

```
       90           120            150           180   195
GRP N  +-------------+--------------+-------------+------+
1-3 38 1==========M========3
4-7 22                      1===========M==========3
  8  3                       1============M==============3
```

Total Phosphorus (P, ppm) (5 groups: H = 25.1 df = 4 p = <0.0001).

```
       22     100         200        300         400
GRP  N +--------+-----------+-----------+-----------+
1-2 28            1===M====3
  3 10   1====M===3
4-6 20  1==============M======================3
  7  2 13
  8  3  1=M=3
```

Temperature Diurnal Range (Tdi, °C) (8 groups: H = 36.1, df = 7, p = <0.0001).

```
       12.0              12.9             13.8             14.6        15.5
GRP N  +-----------------+-----------------+----------------+---------------+
1    6  1===M===3
2   22                                    1===============M==============3
3   10                          1==============M===============3
4   11     1==============M==============3
5    2       1====================M====================3
6    7                    1=========M=========3
7    2                                  1=M3
8    3                                1=======M=======3
```

Altitude (m) (8 groups: H = 20.7, df = 7, p = 0.004)

```
       1.0              88.3              175.5           263
GRP N  +-----------------+-----------------+-----------------+
1    6 1M3
2   22         1==============M==============3
3   10     1=======================M======================3
4   11 1===========M============3
5    2                1=============M============3
6    7         1=========M==========3
7    2                                1M3
8    3                1============M=============3
```

Soil Potassium ($K(HCO_3)$, ppm) (5 groups: H = 40.4, df = 4, p = <0.0001)

```
       12              174               336
GRP  N +-----------------+----------------+
1-2 28          1==========M==========3
  3 10  1==========M===================3
4-6 20  1==M===3
  7  2 13
  8  3  13
```

Soil Shear Strength (tx-shst, kPa) (5 groups: H = 32.5, df = 4, p = <0.0001)

```
       5           10           15          20        24
GRP  N +-------------+-----------+----------+---------+
1-2 28          1=================M=================3
  3 10  1========M========3
4-6 20 1==M==3
  7  2 1M3
  8  3   1====M=====3
```

Figure 5 (cont.)

b. Assemblage-3, partitioned at the 6-group level.

Warmest Quarter Mean Temperature (Twar, °C) (6 groups: H = 42.0, df = 5, p = <0.0001).

```
         27.4        28.0                    29.0                    30.0        30.6
GRP N  +-----------+--------------------+--------------------+-----------+
1    9                   1======M======3
2    6                    1================M=================3
3   11                                                          1====M===3
4    5                                 1============M============3
5    2              1M3
6   30  1==========M=========3
```

Annual Average Precipitation (Pann, mm) (6 groups: H = 33.8, df = 5, p = <0.0001).

```
         204              236               269              301
GRP N  +-----------------+-----------------+-----------------+
1    9   1=========M=========3
2    6     1======M======3
3   11  1======M=====3
4    5  L======M=======3
5    2                        1==M==3
6   30               1=================M=================3
```

c. Assemblage-4, partitioned at the 3- and 7-group levels.

Warmest Quarter Precipitation (Pwar, mm) (3 groups: H = 25.1, df = 2, p = <0.0001).

```
          29               44               59               74               88
GRP   N  +----------------+----------------+----------------+----------------+
1    28     1================M================3
2-5  25                1================M================3
6-7  10                                                  1=======M=======3
```

Warmest Quarter Temperature (Twar, °C) (7 groups: H = 27.5, df = 6, p = 0.0001).

```
         27.4        28.0              28.9              29.7              30.6
GRP N  +-----------+-----------------+-----------------+-----------------+
1   28  1===========M==========3
2   16             1====================M====================3
3    5   1====================M=====================3
4    2                                                           1M3
5    2                                      1============M=============3
6    4                     1M=3
7    6                                                  1====M====3
```

d. Assemblage-5, partitioned at the 6- level.

Precipitation Seasonality (Psea) (6 groups: H = 43.9, df = 5, p = <0.0001).

```
            70            78            87            95            103
GRP     N  +-------------+-------------+-------------+-------------+
1-3   16                           1======M=======3
4-7   36 1==========M==========3
 8     6                                             1==M==3
 9     2                                                       1M3
10     2                                                  1M3
11     1                                                *
```

Altitude (m) (6 groups: H = 26.3, df = 5, p = 0.0001).

```
            1        44               132              220
GRP     N  +--------+-----------------+-----------------+
1-3   16 1===M===3
4-7   36         1=================M================3
 8     6        1===========M==========3
 9     2             1==M===3
10     2                                  1=M3
11     1    *
```

e. Assemblage-6, partitioned at the 4- and 9-group levels.

Exchangeable Potassium (exK) (4 groups: H = 21.2, df = 3, p = 0.0001).

```
        0.02             0.32            0.62
GRP   N +-----------------+-----------------+
1    37    1=============M=============3
2-4  10  1========M=======3
5-6   9  1M3
7-9   7  1======M========3
```

Vegetation Type (Veg-type) (4 groups: H = 20.3, df = 3, P = 0.0002).

```
        1           2            3           4           5          6
GRP   N +-----------+------------+-----------+-----------+----------+
1    37     1============M==============3
2-4  10         1==========M===========3
5-6   9                                      1=========M=========3
7-9   7    1=========M=========3
```

Precipitation Seasonality (Psea) (9 groups: H = 15.2, df = 8, p = 0.055).

```
      70             78              86              95              103
GRP N +--------------+---------------+---------------+---------------+
1  37  1===================M=====================3
2   2                             1=M==3
3   4 1================M====================3
4   4                            1============M============3
5   4               1==========M=========3
6   5                                       1=========M========3
7   3                                      1============M============3
8   3      1==============M==============3
9   1      *
```

Total Phosphorus (P, ppm) (9 groups: H = 26.6, df = 8, P = 0.0008).

```
      22              172               322                476
GRP N +-----------------+-----------------+------------------+
1  37   1=============M============3
2   2    1========M========3
3   4  1===M===3
4   4   1=====M======3
5   4     1M3
6   5 1M3
7   3  1======================M=============================3
8   3  1=M==3
9   1                 *
```

Soil Shear Strength (tx-shst, kPa) (9 groups: H = 16.5, df = 8, p = 0.036).

```
      3.5             10.6              17.7                 30.0
GRP N +-----------------+-----------------+---------------------+-
1  37     1==============M==============3
2   2        1M3
3   4          1=========M=========3
4   4       1=======================M=======================3
5   4       1=M3
6   5 1==M==3
7   3       1==M=3
8   3      1=M=3
9   1                                                          *
```

Figure 5 (cont.)

f. Assemblage-8, partitioned at the 4- and 6-group levels.

Chloride (Cl, %) (4 groups: H = 25.6, df = 3, P = <0.0001).

```
        0                 0.64                    1.48
GRP N   +-----------------+-----------------------+
1-2 9   1===============M========================3
3-4 5   *
5   5   *
6  44   1M3
```

Soil Phosphorus (P(HCO₃), ppm) (4 groups: H = 23.4, df = 3, P = <0.0001).

```
        1                8                 15               22
GRP N   +----------------+-----------------+----------------+-
1-2 9                     1================M================3
3-4 5          1===M==3
5   5                     1============M============3
6  44    1=======M========3
```

Altitude (m) (4 groups: H = 19.8, df = 3, P = 0.0002).

```
        1                 88                 175
GRP N   +-----------------+-------------------+-----
1-2 9   1M=3
3-4 5    1===============M=================3
5   5            1===M==3
6  44          1=================M=================3
```

Electrical Conductivity (EC, mS/m) (6 groups: H = 21.0, df = 5, P = 0.0008).

```
       1.0              457                 913           1218
GRP N  +------------------+-------------------+-------------+
1    2 *3
2    7 1======================M===========================3
3    4 *
4    1 *
5    5 *
6   44 1M3
```

Soil Calcium Carbonate (CaCO₃ , %) (6 groups: H = 18.9, df = 5, P = 0.002).

```
       0              21               42               63               84
GRP N  +---------------+----------------+----------------+----------------+
1    2 1======M=====3
2    7 1==========M===========3
3    4 *3
4    1    *
5    5        1============================M===========================1
6   44 1M=3
```

Exchangeable Magnesium (exMg, me%) (6 groups: H = 13.0, df = 5, P = 0.024).

```
       0.04             1.2                  2.4                  3.8
GRP N  +------------------+-------------------+----------------------+
1    2     1==M==3
2    7          1========================M==========================3
3    4   1==M==3
4    1     *
5    5  1====M=====3
6   44 1=====M======3
```

g. Assemblage-9, partitioned at the 2- and 4-group levels.

Wet Period Precipitation (PwP, mm) (2 groups: H = 8.3, df = 1, p = 0.004).

```
          32              45              59              72
GRP  N  +---------------+---------------+---------------+--------
1   55       1================M================3
2-4  8                             L============M=============3
```

Soil Calcium Carbonate ($CaCO_3$, %) (4 groups: H = 10.7, df = 3, P = 0.01).

```
          0              21              42              63              84
GRP  N  +--------------+--------------+--------------+--------------+
1   55  1=M=====3
2    3  1===M====3
3    4                  1=====================M=================3
4    1    *
```

h. Assemblage-11, partitioned at the 8- and 6-group levels.

Cold Quarter Precipitation (Pcld, mm) (8 groups: H = 37.9, df = 7, p = <0.0001).

```
            69                101               133           165     181
GRP    N  +-----------------+---------------+-------------+-------+
  1  16                      1==========M==========3
  2  16                          1===============M=================3
  3   7      1=======M======3
  4   9    1=============M===========3
  5   7               1=M=3
6+7   5      1M3
  8   3    1=M=3
```

Coastal Distance (cst-dist, km) (8 groups: H = 38.1, df = 7, p = <0.0001).

```
          0.5             16              32              48              64
GRP  N  +--------------+--------------+--------------+--------------+
1   16  1=M3
2   16      1==============M===============3
3    7         1==================M====================3
4    9           1====================M=====================3
5    7                   1==============M============3
6+7  5                                         1======M======3
8    3                                           1=======M========3
```

Exchangeable Potassium (exK, me%) (8 groups: H = 40.2, df: 7, p = <0.0001).

```
            0.02            0.32              0.62        0.81
GRP    N  +-----------------+-----------------+-----------+
  1  16   1========M========3
  2  16  1=M3
  3   7             1==M===3
  4   9           1==================M=================3
  5   7            1========M=========3
6+7   5    1=========M==========3
  8   3           1====M====3
```

Exchangeable Sodium (exNa, me%) (6 groups: H = 17.1, df: 5, P.= 0.004).

```
            0.01           7.3              14.6
GRP    N  +----------------+-----------------+
1-2  32  *
  3   7  *
  4   9  1========M======================3
  5   7  *
6-7   5  *
  8   3  *
```

Table 7 Pearson correlation coefficents between the association matricies derived from each of the eight data-sets (the seven taxonomic sub-sets and the combined data.).

COMBINED							
BIRDS	0.81						
CENTIPEDES	0.35	0.17					
MAMMALS	0.50	0.33	0.11				
PLANTS	0.79	0.48	0.15	0.40			
REPTILES and FROGS	0.75	0.50	0.30	0.36	0.52		
SCORPIONS	0.46	0.38	0.18	0.22	0.27	0.32	
SPIDERS	0.71	0.42	0.30	0.34	0.45	0.53	0.30

'cation exchange capacity' ('CEC') modified the relationship (Table 5). 'Pann' and 'Pcld' are tightly intercorrelated ($R^2 = 0.71$, $p. < 0.0001$).

- Assemblage-13: comprises species that were only recorded in the study area at quadrats ZU1 and ZU2. These sites had the highest precipitation in the coldest quarter ('Pcld') of any quadrat sampled in the study area. They were also different from other southern sites by being on a coastal limestone ridge (hence the significance of 'Stone'), that was thinly mantled in sand (Figure 10). This assemblage was too localised for the richness model to converge.

Influence of the Taxonomic Sub-sets on the Biodiversity Model

The results of the sub-set comparison are presented in Table 7 and Figure 11. Figure 11 maps the position of each of the matrices in a three-dimensional ordination space defined in terms of the differences between their biodiversity patterns. Three features were noted:

1. The sub-sets were positioned all around the community matrix, so it would shift in 'biodiversity space' if any sub-set was eliminated.
2. The 'minimum spanning tree' linkages showed that the sub-sets were closer to the combined (community) matrix than to one another. We concluded that no sub-set provided a surrogate for another sub-set.
3. When 1000 randomly-generated matrices were added to the analyses, the cloud of random points was an average of 2.01 "nearest neighbour distance" units away from the community model, with 99% of these points between 1.92 and 2.13 units away. In comparison, the cluster of taxonomic sub-sets

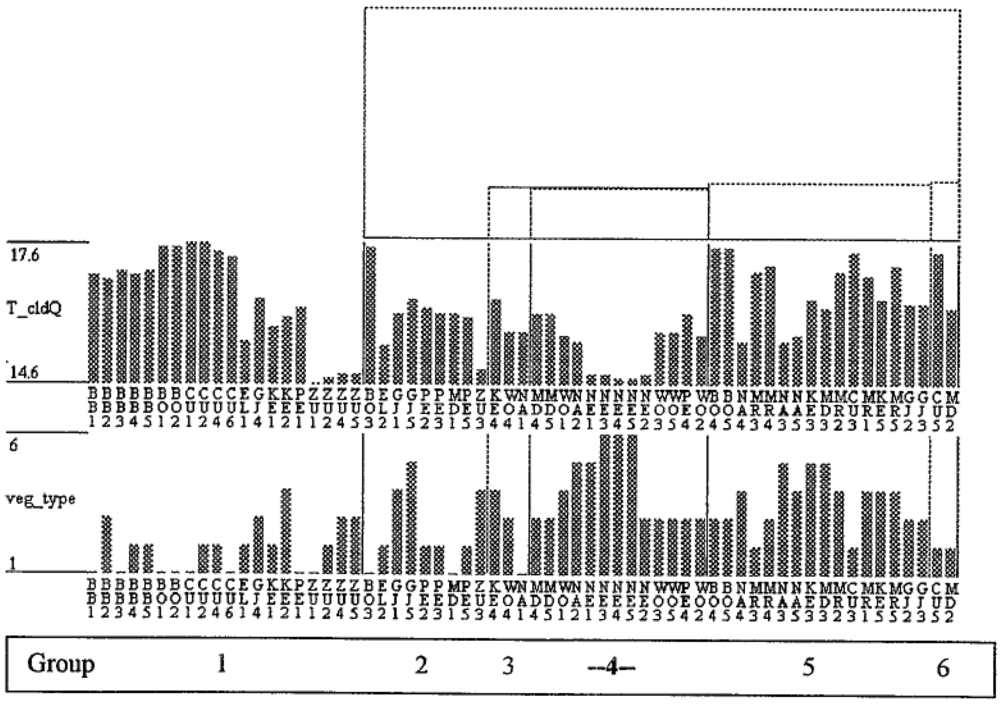

Figure 6 Attribute values for 'temperature in the coldest quarter' (Tcld) and 'vegetation type' (Veg-type) superimposed as histograms on the dendrogram structure derived from the classification of the 63 quadrats in terms of species belonging to assemblage-7. Quadrat codes are printed vertically. The relevant re-ordered data matrix is provided in Figure 12.

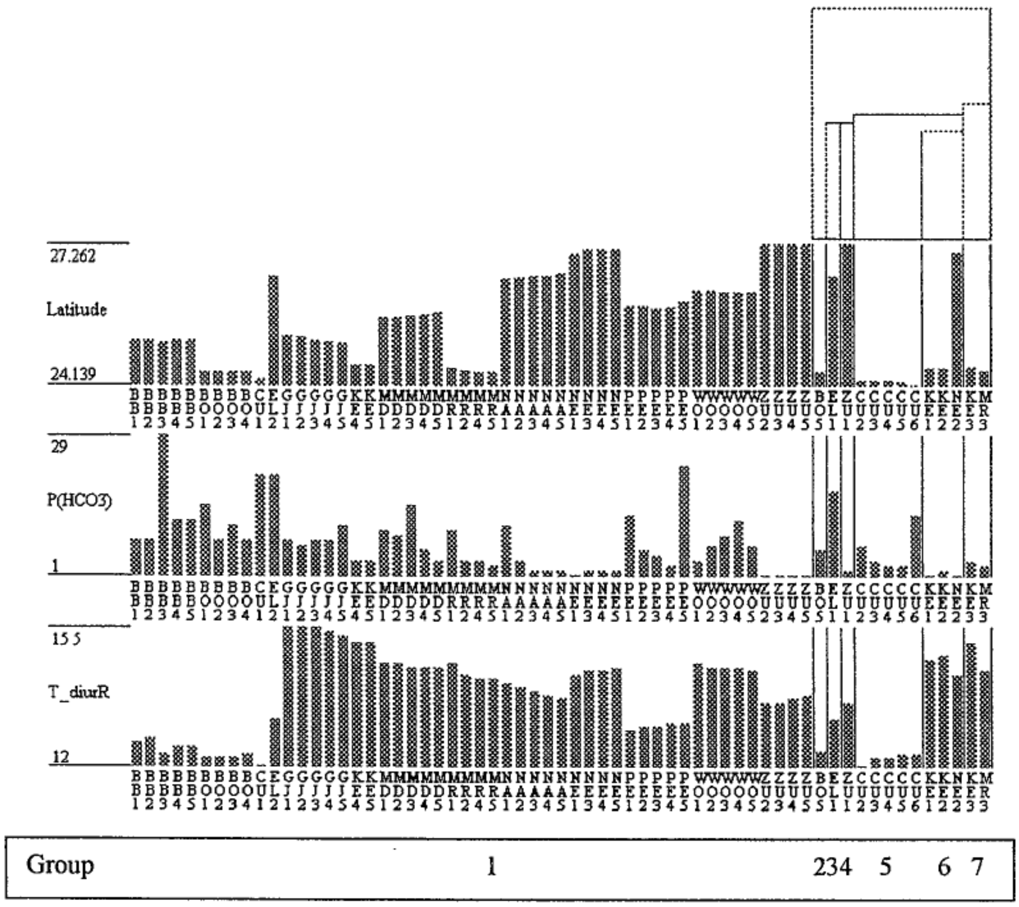

Figure 7 Attribute values for 'latitude', 'soil phosphorus' $P(HCO_3)$ and 'temperature diurnal range' (Tdi) superimposed as histograms on the dendrogram structure derived from the classification of the 63 quadrats in terms of species belonging to assemblage-10. Quadrat codes are printed vertically. The relevant re-ordered data matrix is provided in Figure 12.

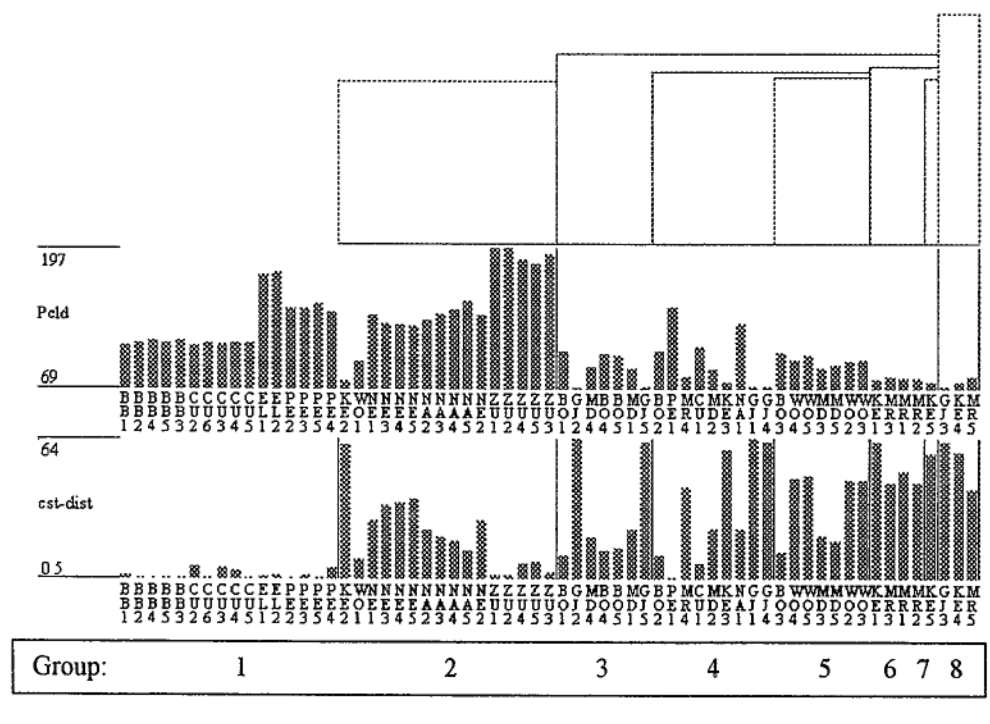

Figure 8 Attribute values for 'precipitation in the coldest quarter' (Pcld) and 'distance to coast' (cst-dist) superimposed as histograms on the dendrogram structure derived from the classification of the 63 quadrats in terms of species belonging to assemblage-11. Quadrat codes are printed vertically. The relevant re-ordered data matrix is provided in Figure 12.

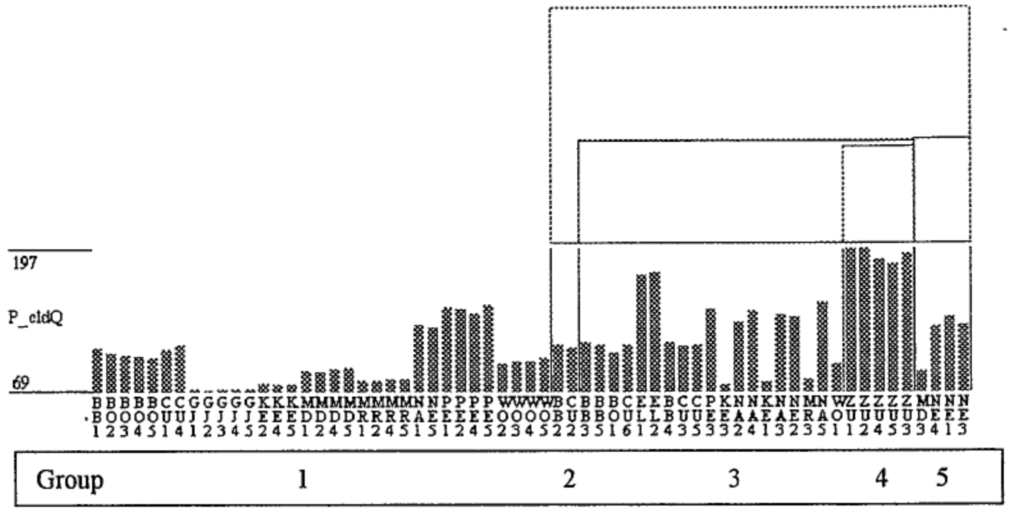

Figure 9 Attribute values for 'precipitation in the coldest quarter' (Pcld) superimposed as an histogram on the dendrogram structure derived from the classification of the 63 quadrats in terms of species belonging to assemblage-12. Quadrat codes are printed vertically. The relevant re-ordered data matrix is provided in Figure 12.

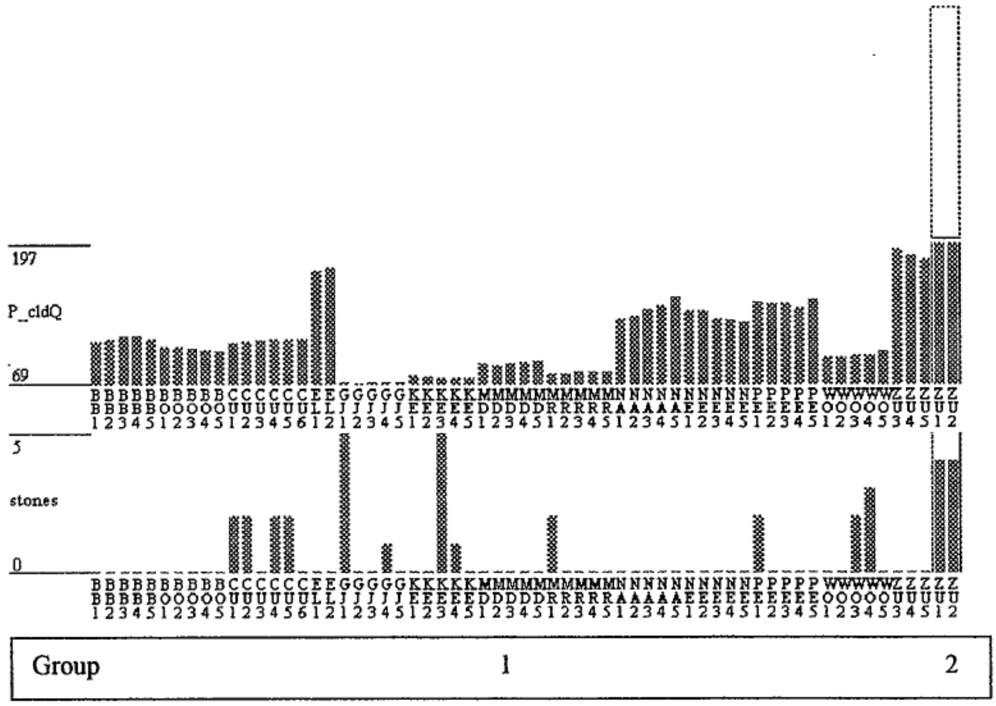

Figure 10 Attribute values for 'precipitation in the coldest quarter' (Pcld) and 'soil rockiness' (stones) superimposed as histograms on the dendrogram structure derived from the classification of the 63 quadrats in terms of species belonging to assemblage-13. Quadrat codes are printed vertically. The relevant re-ordered data matrix is provided in Figure 12.

had a radius that was 80% of this distance (1.6 units). Thus, the seven sub-sets were all well-separated from the community model, indicating that they had very different patterns of occurrence; none was its surrogate.

DISCUSSION

Species co-occurrence patterns in most of the southern Carnarvon Basin still approximate pre-European patterns because indigenous vegetations have not been cleared, known extinctions have been virtually confined to the relatively narrow mammalian component of the biota, and only a few of the introduced weeds are pervasive and/or allelopathic (e.g. *Cenchrus ciliaris*). Nevertheless, the dense populations of exotic herbivores have reduced the perennial vegetative cover and productivity of most surface-types, and changed the

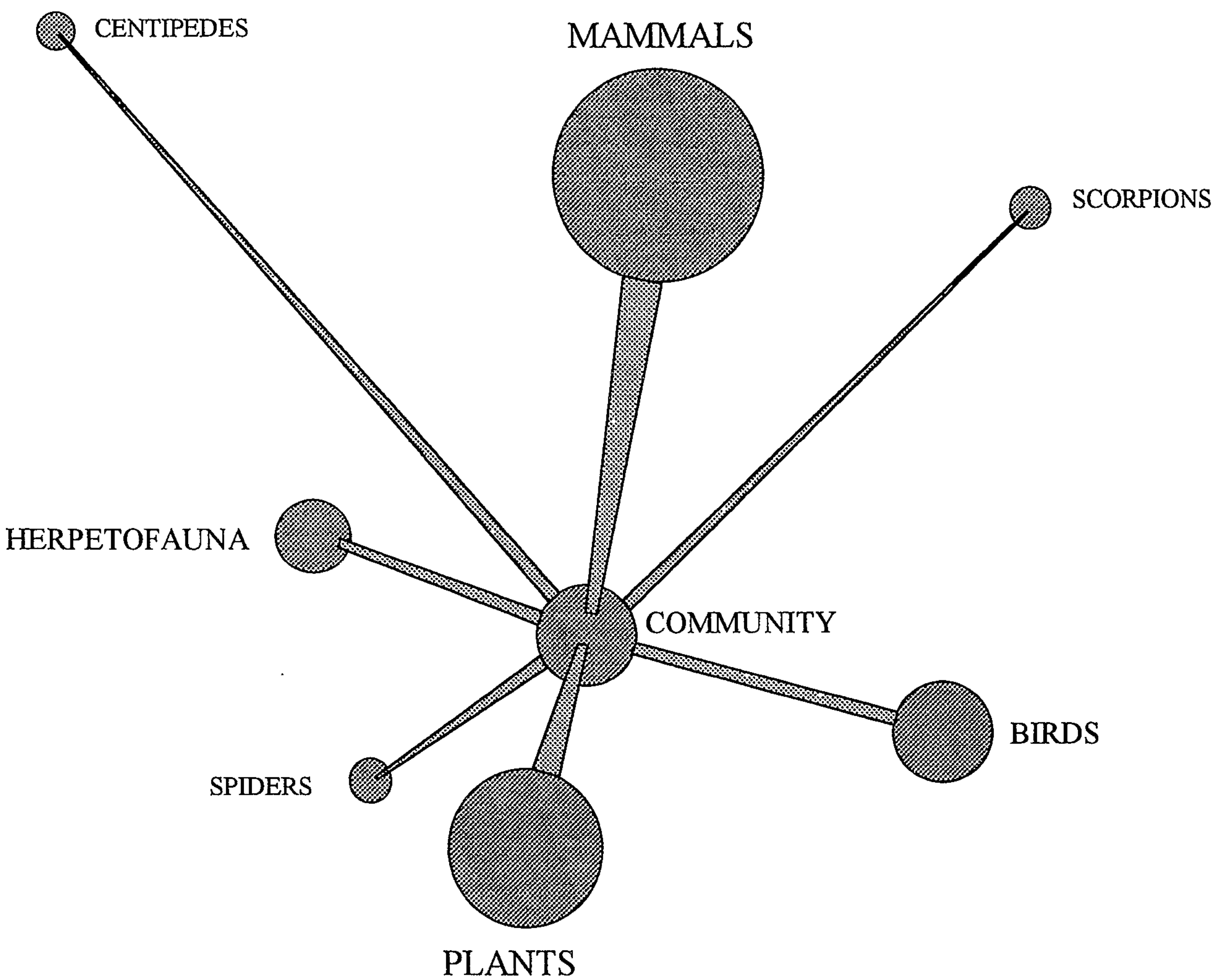

Figure 11 Comparison of the biodiversity patterns derived from the seven sub-sets sampled, and from the total data-set. A matrix of correlation coefficients was compiled from a pairwise comparison of the relevant quadrat similarity matrices. Results are displayed in three-dimensions using Semi-strong Hybrid Scaling (Belbin, 1991, stress = 0.13). Minimum Spanning Tree linkages (Belbin, 1995) are superimposed to indicate nearest neighbours in biodiversity space.

relative abundance of their plant species (Beard, 1976; Friedel and James, 1995; Landsberg *et al.*, 1997; Wyrwoll, Stoneman, Elliott and Sandercock, 2000).

When we compared the species richness of quadrats according to surface-type, the saline surfaces were the poorest regardless of their condition, and red sand surfaces were the richest. Red sands dominate Australia's arid zone, and their richness can be explained by an area effect (cf. Rosenzweig, 1992) in conjunction with their unsuitability for pastoral-use (Payne *et al.*, 1987). Yet our comparison also indicated that pastoral usage has not had a significant effect on the overall richness of indigenous species on the quadrats; even the most degraded quadrats had similar species richness to quadrats with little overt usage. While this result supports the view that pre-European co-occurrence patterns in species composition can be derived from our data-set, the similarity may be partly an artifact of our sampling regime. We positioned the quadrats in the least disturbed examples of each habitat-type that we could find because we aimed to provide the first quantitative biodiversity benchmark against which future changes in the compositional complexity of the region's indigenous ecosystems can be measured.

Several distinct stepwise structures dominated both the quadrat and the species classification dendrograms (Figures 2 and 3). In the context of our study, this would occur if the component species were responding to different environmental gradients and/or to the same gradients differently. On the reasoning that species which usually co-occur are more likely to be responding to the same environmental gradient/s than are species with different patterns of co-occurrence (see McKenzie *et al.*, 1989, pp. 255–6), we sought to untangle the biogeographical processes by treating the 13 species assemblages derived from the overall analysis as independent data-sets, and analysing them

Figure 12 Data matrices for each of the 13 assemblages defined from the species classification analysis (Figure 3). Quadrat codes are printed vertically. Quadrats have been re-ordered and clustered according to their species similarities within the relevant assemblage. A = frog, B = bird, C = centipede, PL = plant, SC = scorpion, SP = spider and R = lizard.

```
ASSEMBLAGE NUMBER                   CLASSIFICATION GROUP NUMBER (GRP in Fig. 5; Group in Figs 4, 6-10)

Assemblage-1                                               1                            2       3    4
                                    BBBBBBBCCCCCEEGGKKKMMMMMMNNNNNNNNNNPPPPPWWWWWZZZ|BBBKKMZZ|CGGMM|GM
                                    BBBOOOOUUUUULLJJEEEDDDRRRAAAAAEEEEEEEEEEOOOOOUUU|BBOEERUU|UJJDD|JR
                                    145124512345122312312423512345123451234512345245|23345413|64535|11

B  Australian Magpie                                                                |     *  |   * |
PL Calandrinia ptychosperma                                                         |   *    |   * |
SP (Salticicdae) U11 sp1                                                            |    *   |   * |
B  Yellow-rumped Thornbill                                                          |       *|   * |
A  Pseudophryne guentheri                                                           |      * |   * |
PL Lotus australis                                                                  | *      |   * |
PL Sisymbrium erysimoides                                                           |*       |   * |
PL Gymnema granitica MS                                                             |  *     |   * |
PL Indigofera colutea                                                               |        |   * | *
R  Amphibolurus longirostris                                                        |        |*  * |
PL Emex australis                                                                   |        |*  * |
A  Litoria rubella                                                                  |        |  ** |
PL Eucalyptus victrix                                                               |        |  ** |
B  Red-backed Kingfisher                                                            |        |   * |**
B  Little Corella                                                                   |        |  ***|
R  Ctenotus severus                                                                 |        | *** |
A  Uperoleia russelli                                                               |        |  ** |*

Assemblage-2                            1            2                 3          4       5    6     7  8
                                    BBBBBC|BBKKGKGGGGMMMMMMNWWWWW|CKPNNKMMMM|BBCCNZBPPCN|CN|EPEZNNP|ZZ|NNZ
                                    BOOOBU|OOEEJEJJJJDDDDDRAOOOOO|UEEAEERRRR|BBUUAUBEEUE|UE|LELUAEE|UU|AEU
                                    121331|4535142453451231145123|4115122543|24363152423|52|1523243|45|452

B  Black-faced Cuckoo-shrike           *  |**        *** *       |      ** *| *    *    |  |       |  |
B  Diamond Dove                        *  |******* *******       |      * **|          *|  |       |  |
PL Calandrinia sp. (GJK&NG1495)        *  |** *  *** ***     *   |      **  |           |  |       |  |
B  Mulga Parrot                           |**** *     *****  ****|    * *   |           |  |       |  |
PL Eremophila subfloccosa              *  |* ** *     *   *      |      **  |           |  |       |  |
PL Abutilon otocarpum                 *   |** *     *  * ** *    |      * * |           |  |       |  |
PL Phyllanthus maderaspatensis            |***      *    **      |      *** |**         |  |       |  |
PL Asphodelus fistulosus               *  |**        *****   *   |          |*          |  |       |  |
PL Chenopodium cristatum               *  |*   **   ** * **  *   |          |           |  |       |  |
PL Paspalidium basicladum                 |  ** *   *   * *      |*      *  | *         |  |       |  |
PL Ptilotus aervoides                     | * ***         *      |          |*     *    |  |       |  |
PL Cassia helmsii                         |** *******     *     *|      *   |          *|  |       |  |
SP Opopaea sp4                         ** |* **          *       |          |           |  |  **   |  |
B  Southern Whiteface                     |   * *****************|      ** *|*          |  |       |  |
R  Rhynchoedura ornata                    |      ********** ** * |    *  *  |           |  |       |  |
PL Ptilotus villosiflorus                 |     * **** ****      |      *   |* **       |  |       |  |
A  Neobatrachus wilsmorei                 |      ********    *   |          |**         |  |       |**|
PL Salsola kali                           |    * *  *  ***  **  *|          |** *  *    |  |***    |  |
PL Acacia victoriae                       | ** * **   ***   **   |          |           |  |       |  |
PL Tragus australianus                  * |  * * ****  ** *  *   |      *   |           |  |       |  |
PL Corchorus walcottii                  * |      **** **         |          |  **       |* |       |  |
PL Stenopetalum pedicellare           * * |       * **   **  *  *|          |*         *|  |  *    |  |
PL Triraphis mollis                    ** |      *** *** **     *|          |  *        |  |       |  |
PL Bulbostylis barbata                  * |   *    *     *       |      *** |**         |  |       |  |
SP Argiope protensa                     * |  **    *             |*** *     |***        |  |       |  |
C  Asanada spp                          * |      *    *       *  |     * ** |           |  |       |  |
B  Crimson Chat                       *  *|         * *** **     | *** *****|**         |  |       |  |
PL Dysphania rhadinostachya            *  |            * ***     |*     *** |           |* |* *    |  |
B  Little Button-quail                **  *|*              *      |***  ** **|      *    |  |       |  |
SP Neosparassus sp8                   *   |         *            | *   ***  |        *  |  |       |  |
PL Abutilon oxycarpum                   **|      *  *            |*         |           |  |       |  |
PL Eriachne dominii                     * |        *  *   *      |      *   |           |  |       |  |
PL Sida kingii                          * *|   *  *        *      |          |           |  |       |  |
PL Chthonocephalus spathulatus            |*     *   **  **  *  *|        * | *         |  |     * |  |
PL Parietaria debilis                     |*             **  *   |          |*          |  |* *  **|  |
B  White-backed Swallow                   |              *   * * |     **   |   **      |  |       |  |
SP Jotus sp1                              |*                 * * |        * | ** **     |  |       |  |
PL Rhodanthe charsleyae                 **|*  *     ***   * *****|          |           |  |    *  |  |
SP Forsterina sp3                      *  |    *  * *     * ** **|     **   |           |  |     * |  |
B  Hooded Robin                         **|    *      *    ******|          |*          |**|       |  |
PL Cuscuta epithymum                      |          *     * * **|          |      *    |  |  *    |  |
PL Gnephosis arachnoidea                  |              *** ** *|* *       |       *   |  |*      |  |
PL Lepidium rotundum                   ** |    *  *     *  ***   |          |           |  |***    |  |
PL Zygophyllum ovatum                     |             *   **  *|  *       |           |  |       |  |
PL Podolepis capillaris               *   |           * *    ****|          |        *  |  |       |  |
```

PL	*Tetragonia cristata*		* **					
R	*Egernia depressa*	*	* ***					
PL	*Schoenia cassiniana*	* *	* * *				**	
PL	*Acacia linophylla*		** * *** *					
PL	*Spartothamnella teucriiflora*		* * * ***					
PL	*Myriocephalus guerinae*	*	* * * **					
SP	*Grymeus* sp4		** *		**			
SP	*Paraplatoides?* sp1	*	** * ** *	*				
SP	Oonopidae Genus1 sp1	***	** *	*			*	
PL	*Tribulus forrestii*	* **	* *					
PL	*Convolvulus erubescens*	**	** **					
PL	*Heliotropium undulatum*	**	* * *		* *			
PL	*Hypochaeris glabra*	*	* * *		**		*	
PL	*Lotus cruentus*	***	*		** *			
PL	*Rhodanthe psammophila*	*	*		*** *			
R	*Diplodactylus conspicillatus*	* **	* * * *	**				
SP	*Lycosa* sp9	****	* * ***					
PL	*Cephalipterum drummondii*	***	**** *					
SP	*Lycosa* sp16	* *	* * ** *				*	
PL	*Calotis multicaulis*	****	* *******					
PL	*Senecio glossanthus*	** *	* * *					
SC	*Urodacus hoplurus*	* *	* ** * *					
PL	*Calotis hispidula*		* * * *					
PL	*Solanum cleistogamum*		* *			*		
PL	*Glycine canescens*	*	*		**			
PL	*Lepidium linifolium*	*	*				*	
PL	*Swainsona pterostylis*	****	*		*		*	
M	*Sminthopsis crassicaudata*	*** **	*	*				
PL	*Sclerolaena eurotioides*	*** *						
SP	(Lycosidae) Genus1 sp2	*****	* *	*				
SP	*Opisthoncus* sp1	******	*		*			
PL	*Atriplex vesicaria*	*** *	* *		*		*	
PL	*Maireana tomentosa*	* *	*				*	
SC	*Isometroides angusticaudis*	** *	*					
R	*Ctenophorus nuchalis*	* **	*** ** **	* *				*
PL	*Sclerolaena densiflora*	**	* ** * * **					
PL	*Pogonolepis muelleriana*	* *	* *					
PL	*Rhagodia drummondii*		*		*		*	
PL	*Boerhavia gardneri*		** * ** *		*			
PL	*Hakea preissii*		* ** **					
R	*Diplodactylus klugei*	*	** * **					
SP	*Lycosa* sp3	*	* * **** *					
M	*Antechinomys laniger*	*	* *					
PL	*Maireana carnosa*		* * *					
PL	*Trianthema triquetra*		* ***					
PL	*Rhodanthe citrina*		* **		*			
PL	*Eremophila crenulata* MS		**					
PL	*Tribulus cistoides*		**					
PL	*Sclerolaena recurvicuspis*	*	** * * *					
PL	*Brachyscome ciliaris*	*	** * *					
PL	*Portulaca oleracea*	*	***					
PL	*Amaranthus mitchellii*	*	***		**			
PL	*Commicarpus australis*	*	***		* * **			
PL	*Enteropogon acicularis*		* ** * **					
PL	*Eremophila latrobei*		* **					
PL	*Atriplex lindleyi inflata*	*	*					
PL	*Eremophila clarkei*		* *					
PL	*Eremophila leucophylla*		**					
PL	*Ptilotus grandiflorus*		***					
PL	*Acacia grasbyi*		** *					
PL	*Sarcostemma viminale*		**					
PL	*Cassia* sp.		* **					
PL	*Thysanotus speckii*		***	*				
PL	*Atriplex semilunaris*		* **					
PL	*Sisymbrium irio*		* **					
C	*Cormocephalus strigosus*		****	*				
PL	*Leichardtia australis*		**				*	
PL	*Rhagodia eremaea*		** *					
PL	*Senecio gregorii*		**					
A	*Neobatrachus sutor*		* *		*			
PL	*Lobelia winfridae*		* *					
SP	*Hypoblemum* sp1		** *			*		
SP	*Lampona cylindrata*		*		*			
B	Rainbow Bee-eater		* * *		**			
SP	(Desidae) Genus2 sp1		* *		*			
SP	*Grymeus* sp2		* * *		*			
PL	*Adriana tomentosa*		*	*	**			
PL	*Trichodesma zeylanicum*		* * *	*	**			
PL	*Lawrencia densiflora*	*	*		*			
PL	*Wahlenbergia tumidifructa*	*	* *					
SP	*Gamasomorpha* sp2	**	*		**			

Figure 12 (cont.)

```
SP Neosparassus sp9                 *   |                      |          |           |  |*      |  |
SP (Stiphidiidae) Genus1 sp1        *   |                      |     *    |           |  |**     |  |
PL Dactyloctenium radulans          *   |        *             |          |           |  |       |  |
PL Eragrostis basedowii             *   |        *             |          |           |  |       |  |
PL Tribulus terrestris              *   |      *               |          |           |  |       |  |
R  Tiliqua occipitalis              **  |                      |          |           |  |       |  |
PL Calandrinia eremaea              **  |                      |          |          *|  |       |  |
PL Rhodanthe chlorocephala          *   |*                     |          |           |  |       |  |
PL Maireana trichoptera           **    |                 *    |          |       *   |  |       |  |
PL Angianthus tomentosus           * * *|                 *    |          |           |  |       |  |
PL Lawrencia spicata               * *  |                *     |          |           |  |       |  |
R  Ctenotus mimetes                  *  |                  *   |          |           |  |       |  |
PL Maireana georgei               *  *  |                      |          |           |  |       |  |
PL Zygophyllum kochii                ** |                      |          |           |  |       |  |
SP Maratus vespertilio               *  |                      |    *     |           |  |       |  |
PL Acanthocarpus verticillatus       *  |                      |          | *         |  |       |  |
```

Assemblage-3

```
                                       1         2          3          4     5              6
                                   BCBWWBCWM|BMNWKM|GGGGGMMKKKM|KMMMW|NP|BBBBBBCCCCEEMNNNNNNNNPPPPZZZZZ
                                   BUOOOBUOD|BDAOER|JJJJJRREEER|EDRDO|EE|BBOOOOUUUULLDAAAAEEEEEEEEUUUUU
                                   162543135|511224|12354253451|14331|53|241345234512223451234124512345
                                            |      |           |     |  |
B  Chestnut-breasted Quailthrush            |      |       * **|     |  |
R  Lerista muelleri(d)                      |    * |       *** |     |  |
PL Enneapogon caerulescens              *   |      |*      ****|     |  |
SP Miurga sp3                           *   |      |       ****|     |  |
PL Acacia xiphophylla                 *     |      |       ** *|     |  |
PL Haloragis trigonocarpa                   |      |*      * **|   * |  |
R  Ctenotus uber                            |   *  |*      *** |     |  |
PL Sauropus crassifolius                    |      |       **  |     |  |
SP Cytaea sp1                           *   |      |       **  |     |  |
PL Sida corrugata                          *|      |       *   |     |  |
PL Stenopetalum sphaerocarpum521            |      |           |     |  |
M  Sminthopsis macroura            * *******|      |       ****|     |  |
SP Lycosa sp18                     ******   |      |*   *  ** *|     |  |
PL Ptilotus exaltatus                **     |      |*      *   |     |  |
B  Slaty-backed Thornbill                   |      |        ** |     |  |
PL Goodenia tenuiloba                       | *    |         * |     |  |
B  Little Woodswallow                       |      |*       *  |     |  |
M  Sminthopsis longicaudata                 |      |*      *   |     |  |
PL Cassia sturtii                           |      |*  **  *   |     |  |
PL Ptilotus polakii                         |      |    *  *   |     |  |
PL Hibiscus burtonii                       *|      |      *    |     |  |
PL Indigofera monophylla                    |      | *     *  *|     |  |
PL Streptoglossa liatroides                 |      |  **   *   |     |  |
B  Grey-crowned Babbler                     |      |* *    *** |   * |  |
PL Ptilotus helipteroides                   |      |*** ** ****|     |  |
PL Tribulus astrocarpus                     |      |* ****  ***|     |  |
B  Cockatiel                                |  *   | **  *  ***|   * |  |
PL Acacia aneura                            |      | **  ***** |  *  |  |
C  Ethmostigmus pachysoma                   |    **| *** *** * |     |  |
B  Torresian Crow                           |      |*****  * * |     |  |
PL Tripogon loliiformis                     |      |*******  * |     |  |
PL Eriachne pulchella                       |      | ** * ** * | *   |  |
PL Goodenia havilandii                      |      | ** *  **  |     |**|
SP Pediana tenuis                      *    |*     | ***     **|     |  |
SP Lycosa sp19                         *    |      |* ** *    *|     |  |
PL Eriachne helmsii                         |    * |  *       *|     |  |
PL Yakirra australiensis                    |      |  *      * |     |  |
PL Cleome viscosa                           |      | *        *|     |  |
PL Lepidium oxytrichum                      |      |    *     *|     |  |
PL Eriachne aristidea                       |      | ****      |**** |  |
R  Lerista gascoynensis                     |      |*****      | *  *|  |
R  Lerista muelleri(a)                      |      |*****      |     |  |
A  Cyclorana maini                          |      |*****      |   * |  |
A  Limnodynastes spenceri                   |      |*****      |   * |  |
SP (Stiphidiidae) Genus3 sp1                |      |*** *      |     |  |
PL Panicum effusum                          |      |   **      |     |  |
PL Sida aff. intricata                      |      |  * *      |     |  |
A  Neobatrachus fulvus                      |      | ***       |     |  |
A  Neobatrachus aquilonius                  |      | * *       |     |  |
PL Marsdenia viridiflora                    |      | **        |     |  |
```

Assemblage-4

```
                                                 1                        2            3    4  5   6     7
                                   BBBBBCCEEMMNNNNNNPPPWWWZZZZZ|BMBBBNNPWBGKKMGM|KPWNN|GG|GM|CCCC|KKMMMM
                                   BBBOOUULLDDAEEEEEEEEOOOUUUUU|BDOBOAAEOOJEERJD|EEOAA|JJ|JD|UUUU|EERRRR
                                   1231216123411234513434512345|4155323524245132|32145|14|55|2345|122543
                                                               |                |     |  |  |    |
B  Black Honeyeater                                            |     *          |     |  |  |    |*
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```
SP (Salticidae) U17 sp1             |                | *   |  |  |    |*
PL Acacia murrayana                 |  *             |     |  |  |    |*
PL Brachychiton gregorii            |     *          |     |  |  |    |**
M  Dasykaluta rosamondiae           |                |*    |  |  |    |**
B  Rufous-crowned Emu-wren          |                |     |  |  |    |**
R  Ctenotus saxatilis               |                |     |  |  |    |**
R  Diporiphora winneckei            |                |     |  |  |    |**
R  Notoscincus ornatus ornatus      |                |     |  |  |    |**
PL Plectrachne schinzii             |                |*    |  |  |    | *
SP Holoplatys planissima gp         |                |***  |  |  |    | *
B  Bourke's Parrot                  |            **  |     |  |  |    |     *
PL Waitzia acuminata                |             *  |     |  |  |    |  *  *
PL Hibiscus coatesii                |         **     |     |  |  |    |  * **
PL Pityrodia paniculata             |  *             |     |  |  |    |     *
PL Psammagrostis wiseana            | *              |     |  |  |    |     *
PL Indigofera occidentalis MS       |*               |     |  |  |    |     *
PL Grevillea stenobotrya            |                |    *|  |  |    |     *
PL Corynotheca pungens              | **             |     |  |  |    |     *
PL Tephrosia gardneri (GJK&NG1074)  |**              |     |  |  |    |     *
R  Ctenophorus femoralis            |                |     |  |  |    |*    *
PL Verticordia forrestii            |      *         |     |  |  |    |*    *
R  Diplodactylus stenodactylus      |             *  |     |**|  |    |  ***
PL Eriachne avenacea                |             *  |     |  |**|    |  ***
PL Maireana planifolia              |         * * ** |     |  |  |    |  ***
PL Thyridolepis mitchelliana        |           **   |     |  |  |    |  * *
PL Acacia anastema                  |             *  |     |  |  |    |  ***
SP (Stiphidiidae) Ge2 sp1           |       *        |     |  |  |    |   **
SP Clynotis? albobarbatus           |                | * **|  |  |    |   **
PL Eriachne benthamii               |    *           |     |  |  |    |    *
PL Gyrostemon ramulosus             |        *       |     |  |  |    |    *
SP (Salticidae) U16 sp2             |   *            |     |  |  |    |    *
SP Neosparassus sp7                 |                |    *|  |  |    |    *
PL Chorizema racemosum              |    *           |     |  |  |    | *  *
PL Menkea villosula                 |            *   |     |  |  |    |* **
R  Ctenotus calurus                 |                |     |  |  |    |**** *
R  Ctenotus hanloniB                |                |*    |  |  |    |******
R  Ctenophorus rubensB              |          *     |     |  |  |    |******
R  Ctenotus pantherinus             |                |     |  |  |*   |******
R  Ctenotus iapetus                 |                |     |  |  |****|******
M  Sminthopsis youngsoni            |                |     |  |  |****|******
R  Eremiascincus fasciolatus        | *            **|     |  |  |    |*   **
PL Pityrodia loxocarpa              |**              |     |  |  |    |*   **
R  Ctenophorus clayi                |                |     |  |  |    |* * **
R  Ctenotus rufescens               |                |     |  |  |    |*  ***
R  Menetia surda cresswelli         |                |     |  |  |    |*   **
R  Ctenotus piankai                 |                |     |  |  |    |   ***
PL Plectrachne rigidissima          |                |     |  |  |    |  * **
R  Menetia greyii(c)                |                |     |  |  |    |  ****
PL Eremophila setacea MS            |  *             |     |  |  |    |   ***
PL Sida rohlenae                    |                |     |  |  |    |    **
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Assemblage-5

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                                       1        2 3          4          5     6       7        8    9 10 11
                                 BBBBBCCCCPPPC|B|CN|BBBBPMMMMMNMWWWWW|NNNNN|GGGGG|KKKKKMMMM|NNNZZZ|EE|ZZ|P
                                 BBBBBUUUUEEEU|O|UA|OOOOEDDDRDADOOOOO|EEEEE|JJJJJ|EEEEERRRR|AAAUUU|LL|UU|E
                                 1324523452536|2|11|13454124132521354|15342|12543|123452534|354345|12|12|1

B  Australian Ringneck                        | |  |  ** *** *** *   |*****| ****| *****  *|* ** *|  |  |
B  Grey Butcherbird                           | |  |  ** ******* ****| ****|*    |*********|* ****|**| *|
B  Spiny-cheeked Honeyeater        ***        | | *| *** ************|*****|*** *|*********|**** *|* |**|
SC Urodacus hartmeyeri             *    ***  *| |  | *** ** * ** * * |*****| * **|*** *****|*** **|  |  |
B  Common Bronzewing                         * | | *|  ***  **** **** |*****|* *  |   ******|******|  | *|
B  Rufous Whistler                   *  *       | | *|    *************|*****|  *  |* ****** |****  |  |  |
B  Grey Shrike-thrush              * * **       | | *| ***** ****** ***|*****|     | ********|******|  |  |
B  Grey Fantail                      ****       | |  |   * *   ********|*****|     |  * *    |***** |  |  |
B  Broad-tailed Thornbill            * *    *   | |  |  * *     * **** |*****|     |  ****   |******|  |  |
SP Forsterina sp1                           *   |*|  |*  ****   * *****|*****|     |   **  **|**  * |**|**|
SP Opopaea sp2                           *   ** |*|  |  *    *   * *  *|**** |*   *|  ** *  *|*  ** |  | *|
SP Lycosa sp17                     *     **     | |  |*  *       *** * |**** |    *|*       *| *    |  | *|
SC Urodacus armatus                **           | | *|   ** *   *    * |  * *|*  * |  * ** * |    **|  |  |
B  Splendid Fairy-wren                          | | *|     *** ********|*****|  *  |    *    |      |  |  |
R  Ctenophorus scutulatus                       | |  | ** ****  **  ** |*****|     |         |      |  |  |
R  Lerista connivens                  *      *  | |  | *  *   **   ****|*****|     |         | *    |  |  |
R  Heteronotia binoei                        *  *|*|  |****  ** *   ****|**** |**   |         |  *   |  |  |
R  Lerista muelleri(b)             *            |*|  |********** ******|**** |     |     ** *|   *  |  |  |
SP Lycosa sp2                           *       | |  | ** *  ** *******|* ***| *   |     *** |      |  |  |
PL Waitzia nitida                    *  *  *    |*|  |  * *  *   ***   |**** | *   |      *  |      |  |  |
SP Ocrisiona leucocomis                    * *  | |  |   **  **  *    *|  ** | *   |    *    |  *   |  |  |
SP Lycosa bicolor                               |*|  | *  * * *  ****  | *   |     |      *  |  *   |  |  |
B  Willie Wagtail                  * **** *  ** | |  |   **** ** ******|** **|*   *|*** *****|******|  |  |*
B  Variegated Fairy-wren           *************| | *| ****************|**   |*    |****** **|***   |**|  |
B  White-browed Babbler            ********** * | |**| ****************|*****|  *  |  *******|******|  |  |
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Figure 12 (cont.)

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B  Crested Bellbird                 * ***********| |**| ****************|*****|*****| ********|***** |* | |
R  Gehyra variegata                 *********  **| |  | * **************|*****|*****|**** ****|******|* | |
B  Singing Honeyeater               *************| |**|******** ********|*****|*** *|***** * *|******|**|*|
C  Cormocephalus turneri            ****** * ****|*|**|***** ***********|*****|*****|*********|***** |  |**|
C  Scolopendra morsitans            *************|*|**|****************|*****|*****|*********|******|  |**|
SP Grayenulla australensis          ** * ** *****|*|  |****************|*****|*****| ********|******|  |**|
C  Ethmostigmus rubripes            * ***********|*|* |*********   *  ***|*****|*****|* * *****|******|**|**|*
SP Myrmopopaea spp                  ***** *******|*| *|***** ***** ***|**** |*  **|** ******|******| *|**|
C  Scolopendra laeta                *************| | *|***** **********|*****|     |***  ****|******|**|**|
M  Pseudomys hermannsburgensis      ** **********|*|**|** * ** ***** ***|**** |* ***|**** ** *|* *  *| *| |*
B  Western Wedgebill                *************| |**|****************|     |    *|  *** *  |***   | *| |
B  Little Crow                      *************|*|**|************* ***|*  * |   * |  * ** * |***   | *| |*
PL Calandrinia polyandra            * ***** **** |*|* |********  *******|* *  |     |    *****|****  |**| |
R  Nephrurus levis                  *************| |  | ******  ****    |*   *|*** *|*    ****|***  *|**| |
M  Notomys alexis                   * ***********|*|  |****** ** * ***  |*** *| ** *|** ******|***** |  | |
SP (Lycosidae) Genus2 sp2           * * ******** |*| *| ***** ******** *|  *  | ****|* *   ***|*** *  |  | |*
B  Crested Pigeon                   *************| |**|****************|     |*****|    **** |   *** |  | |
B  Zebra Finch                      *************|*|**|********** ***   |     | ****|*********| **    |  | |
B  Tree Martin                      * ********  *| | *|     * * ***  ** |*** *|*  **|**      *|** *   |  |*|*
C  Allothereua spp                   **** *** ***|*|**|*       ********|     |* ***|*********|*  *   |**|**|*
B  Horsfield's Bronze Cuckoo        *****    *** | |**| * **       *** | ** * |     |* * **  *|     **|* |* |
R  Pogona minor                     *************|*|  |** ****   *** ** |  ** |     |  *** ***|*** **|* |**|
SP Miturga sp2                      ** ******** *| |  |**         * ***|*   *|     | * * ****|***  * |  | |
B  Pied Honeyeater                  ** *** * *** | | *| *  *   * **   * |     |    *|**   ****|***  *|  | |
C  Geophilida spp                    * *** **    |*| |*****    *     *|*  * |**   |* ****   | ****  |* |**|
SC Lychas sp3                        ****** * * *| | *| ***     ** *   |*  **|**   |  *     *|***  * |  | *|
B  Black-eared Cuckoo                 ** ***     | |  |  **   ****     |* *  |*** *|*********|   *** |  | |
B  Budgerigar                       *****        | |  |  ** * *** *    | *   |*   *|*********| *     |  | |
B  White-winged Triller             *   *  **    | | *|  **   ***    **| *   |*    |  *  ****|*   *  |  | |
B  Black-faced Woodswallow          *      **   *| |  |  ** ** *    ***|  * *| * **|**** ****|    ** |  | *|
PL Aristida holathera                      **  * | |  |* ******* **  ***|*    |*****|*********|       |  | |
SP Opopaea sp1                             * *  *| |  |*** *        **  |     | ****|*********|   **  |  | |
SP (Salticidae) U05 sp1                 * **   * | |  |*****   *  *  **  |     | ** *|* * *** *|* *  * |  | *|
B  Pied Butcherbird                   *******    | |* | **  *** ***  *  |   *  |*****| *  *****|     * |  | *|
PL Euphorbia drummondii              * ** ** ****| |  |   * * ****      |     |*** *|*   * ***|       |**| |
PL Solanum lasiophyllum                * ** *****|*| |  *** * **    *   *|     |*****|*********|*      | *| |
PL Eragrostis lanipes                  * ** *    | |  | ***             |     |** **|* ***** *|       |  | |
PL Murchisonia volubilis              **   * **  | |  |  ** * **       *|     |  *  |  *  *  * | *     |  | |
PL Cassia chatelainiana                  * **  * | |  |  ** **         *|  *  |     |* **   * |       |  | |
SP Zebraplatys keyserlingi          ****  **** * |*| |****      ********|  *  |**** | **  *** |       |  | *|
SP Miturga sp1                      *** *    *   | |  |*****  ***** *  *|  *  |* * *|  *****  |       |  | |
B  Redthroat                        ****** **    | |**|**** ************|*** *|*****|  **** **|***    |  | |
R  Lerista uniduo                   **** **      | |  |****************|**   |*****|     ****|*      |  | |
SP Lycosa sp5                       **** *       |*| *|********* *******|    *| *** |*********|       |  | |
R  Lerista macropisthopus           *****    *** | |  |****** **********|*****|  *  |**** ****|       |  | |
R  Diplodactylus squarrosus         *** *        |*|* |**** ***** ** ***|  *  | *** |    **   | *     |  | |
PL Ptilotus polystachyus             ** *        | |  | ***************|     | * **|*   *****|***    |  | |
R  Menetia greyii(a)                * ***       *| |  |  **   ***** *** |*   *|*** *|  * *    |* *    |  | |
SP Bianor sp2                       ** **        |*| |**** *  *    *   |**   |* ** |  *****  |       |  | |
PL Ptilotus gaudichaudii            *    *    ** |*| |**     ** * * ***|  * * |*****|   ****  |       |**| |
PL Ptilotus obovatus                     *** ****|*| |*** ** ** *******|  *** |*****|  **  *  |   *   |  | |
PL Chenopodium gaudichaudianum         *         | |  |*********   * ***|     |****|*  *     |   **  |* | |
B  Chestnut-rumped Thornbill                     | | *|  * ************|*****|*****|*********|**     |  | |
B  Galah                              ****       | | *|     * **********|* * *|*****|  *******|   *   |  | |
B  Red-capped Robin                   * *        | |  | *   ************|**** |*****|* **** **|       |  | |
SC Lychas sp1                       ** *        *| | *|**  *  ** *******|**** |**** |  ***** *|  *    |  | |
C  Arthrorhabdus paucispinus        **     *     | |  |*     *   ******|***  |*    |  ********|       |  | |
R  Ctenotus schomburgkii            *    *    *  | |  |     ****  *** **|**** |*****|         |       |  | |
R  Ctenophorus reticulatus          *            |*| |***  ****      **|   *  | ****|  ***  * |       |  | |*
PL Eragrostis dielsii               **       **  |*|**|*    *****    *  |     | *** |  ****  *|       |  | |
SP Lycosa sp4                       **       *** |*|**| * ** *  * ** ** |**  *|  * *|   * *   |  *    |  | |*
PL Crassula colorata                *   *    **  | |**|* * *   **  *****| ***  |     |    *    |    *  |**| |
PL Brachyscome iberidifolia                *  ** | |  |* * * **  ***   *| ***  |     |  *** *  |       |**| |
PL Erodium cygnorum                  **  ******* | |* | ***  ** ********|****  |     |   **    |   *   |**| |
PL Pimelea microcephala                  ** *****| |  | *** *   ** *   *|***  |  *  |  *      |   *   |**| |
PL Goodenia berardiana                   *  ** * | |  |    ******* *    |     |     |    **   |       |**| |
PL Rhagodia latifolia                 **  *  **  | |  |      *****      |**** |*    |         |  **   |* | |
PL Acacia sclerosperma                ***        | |  |***  *  **  * * *|     | **  |  *      |       |  | |
PL Tetragonia diptera                 * *        |*| *|**  ******* * ***|     |  *  |    *    |***    |  | |
PL Acacia tetragonophylla             * *******  | |  |*******  **** ***|     | ****|  **    *|       |  | |
SC Lychas sp2                          ********  | |  |*********  ** * *|  ** |***  | *     * |  *    |  | |
PL Enchylaena tomentosa              ** *  ***** | |  |**** **  ** * ***|     |     |  **     |       |  | |
PL Paractaenum novae-hollandiae      ***** **   *| |  |**** * * ** * ** |     | **  | *    ** |       | *| |
C  Ethmostigmus curtipes             ** ******** | |  | ***       *     |   ** |     |***  ** *|***    | *| |
PL Sida calyxhymenia                 ** ******** | |  |*  **      * **  |  *  |    *|  **  *  |*      | *| |
PL Stylobasium spathulatum               ** ***  | |  |  *     ** ***   |     |     |   **    |****   |  | |
R  Moloch horridus                    *      **  | |  |***        *     |  *  |     |     *   |* *  * |  | |*
B  Masked Woodswallow                        *** | | *|  *  *   ** *    |     |    *|  * * **|***    |  | |*
SP Lycosa s11                                *** | |  | * * ***   *     |  ***|     | *  * ***|***  * |  | |
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B White-fronted Honeyeater	* **		*	* **	* *	*	** ****	******			
SP (Lycosidae) Genus2 sp1	* ***		*	**** *	* *		**	*** **	*		
SP *Grymeus* sp6	*			*** * *			*	*** *		*	
SP *Gamasomorpha* sp1	* * **			*			**	** **			
SP *Lycosa* sp13	*			***** * *** *	*	*		****		*	
SP *Grymeus* sp1	* *			***** * *****	*	*	*	**** *		**	
SP *Lycidas* sp2	*** **			***** * **	*		* **	* *			
SP *Lycosa* sp8	* *			***** * **	*	**		* *			
SP (Salticidae) U02 sp1	** *			***** * *	*	*		*			
PL *Triglochin calcitrapum*	* *	*	*	* *** ** *				*			*
SP (Salticidae) U04 sp1	** ** **	*	*	*** * *	**			*			
PL *Eremophila maitlandii*	* *			** * ***			*				
PL *Rhyncharrhena linearis*	* **			** * **	*						
PL *Porana sericea*	* *			* * * * *							
SP *Heteropoda kalbarri*	* *			* ** * * *				*			
PL *Chthonocephalus tomentellus*	* *			*** * **			**				
R *Strophurus strophurus*	****** ****		*	** * * *		* **	** **	***			*
B White-winged Fairy-wren	*************	*	**	** * **		***	* ****	* *	**	**	*
SC *Isometroides vescus*	***** **** *	*	*	**** * *	*	*	*	* * *	**		
SP *Opopaea* sp3	***** ** **	*		** *			* * *				
PL *Cenchrus ciliaris*	** ** ** *	*		*** * ** *		****	* *				
PL *Euphorbia boophthona*	***********	*		**** *** * *		****	* * * *		*		
PL *Nicotiana occidentalis*	* *** *** *	*		*** ** * *	*	*	*		**		
SP *Wandella* sp5	* ***	*		**** * *		** **	**		*		
PL *Brachyscome cheilocarpa*	* * ** *	*	*	* * * *		* *					
SP *Lycosa* sp20	* *** **			** * *			* *				
SP *Bianor* sp1	* *		*	***			**	*			
PL *Euphorbia australis*	* * * *			*** * *			*				
PL *Heterodendrum oleifolium*	* **			** * * *							

Assemblage-6

	1	2	3	4	5	6	7	8	9
	BBBBBBBCCCEGGGGGKKKMMMMMMMNPPPPWWWWWZ	BN	KMMZ	BPBZ	NNNN	NNNNZ	CZE	CCK	M
	BBBBOOOUUULJJJJJEEEDDDDDRRAEEEEEOOOOOU	BE	ERRU	OEOU	AEEE	AAEAU	UUL	UUE	R
	1345245146212345345123453511245123452	22	2245	1334	2345	34153	211	351	1
B Brown-headed Honeyeater					****	****			
B Grey-fronted Honeyeater					**	**			
PL *Bursaria occidentalis*					***	**			
PL *Plectrachne bromoides*						**	**		
R *Ctenotus alleni*		*			*	***			
PL *Acacia longispinea*						***			
PL *Tricoryne* aff. *corynothecoides*						***			
B Malleefowl						** *			
PL *Eucalyptus eudesmioides*						*** *			
PL *Lamarchea hakeifolia* var. *brevi*					*	***			
PL *Stenanthemum complicatum*				*		***			
PL *Pityrodia verbascina*		*				* *			
R *Ctenophorus maculatus maculatus*			*	*		* **			
PL *Calothamnus borealis*				*		* *		***	
PL *Grevillea eriostachya*		*	* **			*			
SP *Isopedella saundersi*			**			*			
SP *Lycosa* sp23		**				*			
SP *Badumna insignis*						*		*	*
SP *Neosparassus* sp4				**		*			
SP (Salticidae) *U05 sp2*				***		*			
PL *Acacia subrigida*						**			
PL *Lasiopetalum oppositifolium*						**			
PL *Melaleuca aff. quadrifidus*						**			
PL *Eremophila occidens* MS						* *			
PL *Wurmbea cernua*						* *			
B Fan-tailed Cuckoo						* *			
PL *Halgania cyanea*						*		*	
SP *Lycosa forresti*						*	*		
R *Lerista kendricki*					*	* **			
PL *Baeckea* sp. Nanga (ASG11346)					*	* *			
PL *Acacia latipes*						* *			
SP (Salticidae) *U12 sp1*			*		*	* *			
PL *Acacia spathulifolia*						* *	*	**	
PL *Lechenaultia linarioides*		*				*			
PL *Alyxia buxifolia*						*	*		
PL *Melaleuca aff leiopyxis*			*			**			
SP *Gmogala* sp2		*				**			
PL *Allocasuarina acutivalvis*		*	*	*		*			
SP (Salticidae)(Unidentati_*14) sp1*							**		

Assemblage-7

	1	2	3	4	5	6
	BBBBBBBCCCCEGKKPZZZZ	BEGGPPMPZ	KWN	MMWNNNNNNNWWPW	BBNMMNNKMMCMKMGG	CM
	BBBBBOOUUUULJEEEUUUU	OLJJEEDEU	EOA	DDOAEEEEEEOOEO	OOARRAAEDRURERJJ	UD
	12345121246141211245	321523153	441	4512134523542	4543435332315523	52
B Chestnut Quail-thrush				*******		

Figure 12 (cont.)

PL	*Solanum orbiculatum*	*****		* *** *		
PL	*Acacia coolgardiensis effusa*			* * *** ***	*	
PL	*Leucochrysum fitzgibbonii*			**** *** *		
B	Yellow-throated Miner			***	**** ** * * *	
PL	*Calandrinia lehmannii*			** ** *** *		
PL	*Uldinia ceratocarpa*			*** * **	* *	
B	Mistletoebird		*	** **	***	
PL	*Marsdenia australis*	***		* ** *	*	
B	Weebill	*		******	* * **	
PL	*Monachather paradoxus*			******	* * ****	
PL	*Chthonocephalus pseudevax*	*		* **	*	
PL	*Wurmbea densiflora*		*	* *****		
PL	*Thysanotus manglesianus*	* *		***** *		
B	Red-tailed Black Cockatoo	**		****		
PL	*Goodenia occidentalis*			* ****	*	
PL	*Trachymene cyanopetala*			* **	*	
PL	*Eucalyptus mannensis*			* ***	*	
PL	*Calandrinia corrigioloides*	*		** ***		
PL	*Ptilotus drummondii*		*	***	*	
SP	*Lycidas* sp5			* **		
PL	*Synaptantha tillaeacea*		*	* *		
PL	*Gnephosis tenuissima*			* *		**
PL	*Brunonia australis*			* * *	* *	
SP	*Myrmarachne* sp1			*	*	
PL	*Velleia hispida*			*	*	
SP	*Lycosa* sp15			** ***	*	
PL	*Actinobole uliginosum*	**		** *		
SP	*Zebraplatys* sp3		*	*		
PL	*Plantago* aff. *hispidula*			* **		
PL	*Grevillea paradoxa*			* *		
PL	*Podolepis canescens*	*** *		* * *		
PL	*Acacia roycei*			*****		
PL	*Gnephosis eriocephala*			** *		
PL	*Poranthera microphylla*			**		
SP	(Salticidae) *U13 sp1*			**		
PL	*Centrolepis drummondiana*			* *		
PL	*Comesperma integerrimum*			* *		
PL	*Callitris glaucophylla*			***		
PL	*Gilberta tenuifolia*			***		
PL	*Trachymene ornata*			* ***		
PL	*Lysiana casuarinae*			* *		
B	Golden Whistler	*		** *		
B	Western Gerygone	*		** **	*** *	
PL	*Lawrencella davenportii*			** ** *	**	
R	*Diplodactylus pulcher*(a)			** * **	****** * **	
B	Varied Sittella		**	*	**	
SP	(Salticidae) *U16 sp1*			*	****	
PL	*Eremophila oldfieldii*			**		
PL	*Ptilotus stirlingii*			* *		

Assemblage-8

		1	2	3	4	5	6
		BP	BBBBCPN	BKWC	P	CMECE	BBBBCCGGGGGKKKKMMMMMMMMMNNNNNNNNNPPWWWWZZZZZ
		BE	BBBOUEA	BEOU	E	UDLUL	OOOOUUJJJJJEEEEDDDDRRRRRAAAAEEEEEEEEOOOOUUUUU
		15	3542111	2412	3	33162	13454512345123512451234523451234524234512345
B	Brown Songlark	*	*			*	
B	White-fronted Chat		* *	*			
SP	*Hadrotarsus* sp1		**				
PL	*Scaevola crassifolia*		*			*	
PL	*Frankenia pauciflora*		* *			***	
PL	*Zygophyllum ammophilum*		*			*****	
PL	*Rhodanthe humboldtiana*					**	
PL	*Acacia ramulosa*			* *			
PL	*Alectryon oleifolius*			**			
SP	Genus3 sp1			* *			
SP	*Opisthoncus* sp2	**	* *				
PL	*Carpobrotus dioica* MS	*	*				
PL	*Rhodanthe stricta*	*	*				
PL	*Didymanthus roei*		* * *				
PL	*Cyperus bulbosus*		* *			*	
PL	*Millotia myosotidifolia*		*		*	*	
B	Orange Chat		** *				
PL	*Atriplex paludosa moquiniana*		**	*			
B	Samphire Thornbill		**				
B	Yellow White-eye		***	*			
PL	*Frankenia* aff. *pauciflora*	*	*				
PL	*Triglochin centrocarpum*	*	*				
PL	*Eragrostis pergracilis*		***				
PL	*Podolepis gardneri*		***				

PL *Gunniopsis septifraga*	**			
PL *Lawrencia viridigrisea*	**			
SP (Desidae) Genus5 sp1	**			
PL *Zygophyllum compressum*	* *			
PL *Halosarcia halocnemoides*	* **			
PL *Sondottia glabrata*	* ***			
PL *Swainsona kingii*	* *			
PL *Halosarcia indica*	* * *			
SP (Salticidae) U03 sp1	** ***			

Assemblage-9

	1	2	3	4
	BBBBBBBBBBCCGGGGGKKKKKMMMMMMMMMMMNNNNNNNNNNPPPPPWWWWWZZZZ	CCC	CZEE	N
	BBBBBOOOOOUUJJJJJEEEEEDDDDDRRRRRAAAAAEEEEEEEEEEEOOOOOUUUU	UUU	UULL	A
	12345123451212345123451234512345134512345123451234513 45	345	6212	2
R *Tympanocryptis parviceps*			****	
PL *Acanthocarpus robustus*			***	
PL *Podotheca gnaphalioides*			**	*
PL *Stipa crinita*		*	**	
PL *Waitzia suaveolens*		***	**	
PL *Lepidium puberulum*			**	
PL *Olearia aff axillaris*			**	
PL *Poa drummondiana*			**	
PL *Triglochin trichophorum*			**	

Assemblage-10

	1	2	3	4	5	6	7
	BBBBBBBBBCEGGGGGKKMMMMMMMMMNNNNNNNNNNPPPPPWWWWWZZZZ	B	E	Z	CCCCC	KKN	KM
	BBBBBOOOOULJJJJJEEDDDDDRRRRAAAAAEEEEEEEEEEOOOOOUUUU	O	L	U	UUUUU	EEE	ER
	12345123412123454512345124512345134512345123452345	5	1	1	23456	122	33
R *Ctenotus hanloni*(a)					****		
PL *Triodia pungens*					****		
PL *Brachysema macrocarpum*			*		* **		
PL *Daviesia hakeoides*					* *		
PL *Haloragis gossei*					***		
SP *Fissarena sp1*		*			**		
PL *Acacia coriacea coriacea*					*** *		
PL *Scaevola sericophylla*					***	* *	
PL *Triodia basedowii*					****	**	
SP *Grayenulla* sp2					*****	*	
R *Menetia greyii*(b)					****		
PL *Dampiera incana*				*	***		
SP *Simaethula* sp1					**		
R *Strophurus rankini*					* *		
PL *Stackhousia muricata*					*		*
PL *Acacia chartacea*					**		
PL *Diplopeltis intermedia*					**		
PL *Goodenia triodiophila*					**		
PL *Scaevola thesioides*					**		
PL *Olearia dampieri dampieri* MS					*		**

Assemblage-11

	1	2	3	4	5	6	7	8
	BBBBBCCCCCEEPPPP	KWNNNNNNNNNZZZZZ	BGMBBMG	BPMCMKNGG	BWWMMWW	KMMM	K	GKM
	BBBBBUUUUULLEEEE	EOEEEEAAAAEUUUUU	OJDOODJ	OERUDEAJJ	OOODDOO	ERRR	E	JER
	1245326345122354	2113452345212453	1244515	214123114	3453523	1312	5	345
B Laughing Turtle-Dove	* *							
SP *Lycosa mainae*	* *							
PL *Beyeria cinerea*	* *							
PL *Eremophila glabra*	*** *							
PL *Danthonia caespitosa*	**							
SP *Neosparassus* sp6	**							
PL *Solanum oldfieldii*	**	*						
SP *Wandella* sp2	** *	*						
B Thick-billed Grasswren	****				*			
R *Tiliqua rugosa*	****				*			
SP *Lycosa* sp6	****	*						
R *Lerista varia*	* ****	*						
R *Lerista praepedita*(b)	** * ****				*			
PL *Calandrinia liniflora*	*	*			*			
SP *Wandella* sp1	* *	**						
PL *Daucus glochidiatus*	* * * *	*			*			
SP *Deinopis* sp1	* * *		* *					
PL *Eragrostis barrelieri*	* *							
PL *Wurmbea inframediana*	** *	*						
PL *Erodium cicutarium*	** *							
PL *Triodia plurinervata*	* * *							
SP *Matilda* sp1	* * *							
PL *Urospermum picroides*	* *							
PL *Atriplex cinerea*	* *							
SP *Wandella* sp4	** **							

Figure 12 (cont.)

PL	*Cryptandra leuophracta*	*	*					
SP	(Salticidae) U07 sp1	*	*					
SP	*Gmogala* sp1	* *	*				*	
B	Yellow Robin	*	* *					
PL	*Jasminum calcarium*		*	*			*	
B	Australian Pipit	***** *** *	*	* *	** ** ***	*		
R	*Ctenophorus maculatus badius*	** ******** *	* *	**	**			
R	*Lerista planiventralis plan.*	*** *** *					**	
B	Grey-breasted White-eye	****** ***	*					
PL	*Senecio lautus*	*** * *		*				
SP	*Grymeus* sp5	* * *	*		*		*	
SP	(Desidae) Genus1 sp1	* ****	*			*		
SP	*Lycosa* sp22	***** *						
PL	*Indigofera brevidens*	* *** *				*		
PL	*Zygophyllum eremaeum*	* * *				*		
SP	*Neosparassus* sp2	* * *			*			
PL	*Dysphania plantaginella*	* *			*			
SP	*Wandella* sp3	* * *			*			
PL	*Stipa nitida*	* * *			*	*		
PL	*Lobelia heterophylla*	*** *	*	**				
PL	*Anthobolus foveolatus*	* *						
PL	*Exocarpos sparteus*	*		*				
PL	*Hibiscus sturtii*	*				*		
PL	*Rostraria pumila*	** ** *********	*	* *	* * **	****.		
PL	*Sonchus oleraceus*	*** * * ****		* *	*	* *		
PL	*Scaevola spinescens*	* * *** *		****	*	*		
PL	*Scaevola tomentosa*	* * *** *****	*	***		* *	*	
PL	*Zygophyllum fruticulosum*	* * ****		******				
PL	*Brassica tournefortii*	*** *** *****	** *		*	*		
PL	*Threlkeldia diffusa*	** *** ******	*	*	*	*		
PL	*Ptilotus divaricatus*	* * ** * ***	**			*** **		
PL	*Rhagodia preissii*	** ** ****	*			*** *		
B	Rufous Fieldwren	**************	****		* *			
R	*Lerista elegans*	**** **********	* * ** *				***	
R	*Morethia lineoocellata*	** ********	** *** *		***			
R	*Lerista lineopunctulata*(a)	**** **** ****	* *** ** *					
SP	*Lycosa* sp7	**** * * ***	* * ****	*			**	
SP	*Lycosa* sp1	**** ***** **	*					
PL	*Bromus arenarius*	* ** * **				*		
R	*Diplodactylus ornatus*	* ** ***	* *					
PL	*Brachyscome latisquamea*	** ******		*		*		
PL	*Exocarpos aphyllus*	* * *******						
PL	*Melaleuca cardiophylla*	* ******	*					
PL	*Thryptomene baeckeacea*	********	** *					
PL	*Sclerolaena diacantha*	* ** *** *			***			
B	Welcome Swallow	* ***** *	***		* *			
SP	(Lycosidae) Genus1 sp1	* ***** *	****					
SP	*Lycosa sp21*	* ***	* *					
R	*Ctenotus fallens*	** ** *	*** * *					
R	*Diplodactylus alboguttatus*	* * *****	*** ** *					
SP	(Salticidae) *U01 sp1*	*** **** *	* * * *					
PL	*Acacia ligulata*	* **			*		**	
PL	*Trichanthodium skirrophorum*	****				* *		
PL	*Podotheca angustifolia*	* **** *	*					
PL	*Trachymene elachocarpa*	* * *	*					
PL	*Olearia axillaris*	* * *	* *					
B	White-browed Scrubwren	**** **** *	***** ****		*			
M	*Sminthopsis dolichura*	******	***************		*			
SP	*Lycosa* sp12	** ****	*** ******		*			
R	*Menetia 'amaura'*	** * ** *	**** *** **					
C	*Cormocephalus aurantiipes*	************	****************		***	* *	*	
SP	*Lycosa* sp14	* ** ** ***	* **** ** **	*	*	* *		
SP	*Lycosa* sp10	** * *	* *** *****	***			*	
R	*Lerista praepedita*(a)	* *****	* **********					
PL	*Dianella revoluta*	**	* ****** * *					
PL	*Stipa elegantissima*	** *	****** *			**		
SP	*Lycidas* sp1	*	* *** ** ** *			*		*
PL	*Mirbelia ramulosa*	* *	* * ** *	*				
SP	*Nicodamus mainae*	* *** *	* ** ***		*			
PL	*Acacia rostellifera*	* * * *	*** * *					
R	*Cyclodomorphus celatus*	* *	*** * *					
B	Southern Scrub-robin	** *	***** **					
PL	*Acanthocarpus* aff. *robustus*	***	* ** ***					
PL	*Thysanotus patersonii*	* ***	* * * ** *					
SP	*Lycidas* sp3	* * *	** * *					
R	*Menetia surda* subsp. indet.	* *	* * ****					
SC	*Urodacus* sp1	*	** * ***					
R	*Lerista planiventralis decora*	**	***					
R	*Crenadactylus* aff. *ocellatus*	*	* **** *					
M	*Sminthopsis hirtipes*		* **** *			***		

Assemblage-12

		1	2		3																			4					5			
		BBBBBCCGGGGGKKKMMMMMMMMNNPPPPWWWW	B	C	B	B	B	C	E	E	B	C	C	P	K	N	N	K	N	M	N	M	W	Z	Z	Z	Z	Z	M	N	N	N
		BOOOOUUJJJJJEEEDDDDRRRRAEEEEEOOOO	B	U	B	B	O	U	L	L	B	U	U	E	E	A	A	E	A	E	R	A	O	U	U	U	U	U	D	E	E	E
		123451412345245124512451512452345	2	2	3	5	1	6	1	2	4	3	5	3	3	2	4	1	3	2	3	5	1	1	2	4	5	3	3	4	1	3
B	Australian Raven																						*	*	*	*	*	*	*	*	
SP	*Uliodon tarantulinus*					*		*										*	*						*	*	*	*				
B	Brown Honeyeater														*		*		*						*	*	*					
PL	*Calytrix brevifolia*																	*	*		*	*			*	*	*					
PL	*Ecdeiocolea monostachya*																							*	*	*	*				*	*
SP	*Forsterina* sp2																*					*	*	*	*	*	*					
A	*Arenophryne rotunda*								*															*	*	*	*	*				
M	*Pseudomys albocinereus*								*	*														*	*	*	*	*				
R	*Diplodactylus spinigerus spinig.*								*	*														*	*	*		*				
PL	*Hibbertia conspicua*																*		*					*	*		*	*				
PL	*Persoonia acicularis*															*	*							*	*		*	*				
SP	*Margaromma* sp1											*												*	*		*	*				
SP	Miturga agelenina				*	*																			*		*	*				
PL	*Melaleuca* aff. *nesophila*															*	*							*								
SP	(Salticidae) *U09 sp1*						*	*		*							*							*	*							
B	Pallid Cuckoo		*	*																					*			*				
PL	*Banksia ashbyi*																	*	*	*					*							
PL	*Banksia sceptrum*																		*	*					*							
PL	*Geleznowia verrucosa*																		*					*	*							
SP	*Grymeus* sp3													*										*	*							
PL	*Loxocarya aspera* MS								*															*	*			*				
PL	*Melaleuca acerosa*																							*	*			*				
PL	*Grevillea annulifera*																	*							*							
PL	*Plectrachne danthonioides*																					*			*							
PL	*Scholtzia* sp. Folly Hill										*														*							
PL	*Hibbertia racemosa*																								*			*				
PL	*Hibbertia subvaginata*																								*			*				
PL	*Opercularia spermacocea*																*							*			*					
PL	*Melaleuca conothamnoides*																							*			*					
PL	*Melaleuca scabra*																							*			*					
PL	*Mesomelaena preissii*																							*			*					
R	*Cryptoblepharus carnabyi*																										*	*				
R	*Ctenotus australis*																										*	*				
PL	*Conostylis stylidioides*																										*	*				
PL	*Hibbertia pungens*																										*	*				
B	Tawny-crowned Honeyeater																							*	*	*	*					
PL	*Calothamnus blepharospermus*																							*	*	*	*					
PL	*Eremaea ebracteata*																							*	*	*	*					
PL	*Stylidium macrocarpum*																							*	*	*	*					
PL	*Stylidium repens*																							*	*	*	*					
PL	*Lysinema ciliatum*																							*	*		*					
PL	*Neurachne alopecuroidea*																							*	*		*					
PL	*Petrophile brevifolia*																							*	*		*					
PL	*Schoenus clandestinus*																							*	*		*					
PL	*Boronia coerulescens*																								*		*					
PL	*Brachysema aphyllum*																								*		*					
PL	*Monotaxis lurida*																								*		*					
PL	*Petrophile semifurcata*																								*		*					
PL	*Scaevola canescens*																								*		*					
PL	*Acacia cavealis* MS																								*	*						
PL	*Drosera stolonif. stolonifera*																								*	*						
PL	*Conospermum microflorum*																								*	*	*	*				
PL	*Lepidobolus preissianus*																								*	*	*	*				
B	Blue-breasted Fairy-wren																								*	*	*	*				
PL	*Phymatocarpus porphyrocephalus*																								*	*	*	*				
PL	*Drosera stolonifera humilis*																							*	*	*	*	*				
PL	*Malleostemon* sp. Cooloomia																								*	*		*				
PL	*Mesomelaena pseudostygia*																								*	*		*				
PL	*Leucopogon cordifolius*																							*	*	*						
PL	*Cassytha aurea*												*											*	*	*						
SP	*Neosparassus* sp3																							*		*						
PL	*Acacia blakelyi*																									*	*					
PL	*Actinostrobus arenarius*																									*	*					
PL	*Allocasuarina campestris*																									*	*					
PL	*Calytrix strigosa*																									*	*					
PL	*Leucopogon cucullatus*																									*	*					
PL	*Lyperanthus nigricans*																									*	*					
PL	*Tetraria microcarpa*																									*	*					
PL	*Thryptomene denticulata*																									*	*					

Figure 12 (cont.)

```
Assemblage-13                                         1                                          2
               BBBBBBBBBBCCCCCCEEGGGGGKKKKKMMMMMMMMMMNNNNNNNNNNPPPPPWWWWWZZZ|ZZ
               BBBBBOOOOOUUUUUULLJJJJEEEEEDDDDRRRRAAAAAEEEEEEEEEEOOOOOUUU|UU
               1234512345123456121234512345123451234512345123451234512345345|12
                                                                            |
M  Tarsipes rostratus                                                       |**
M  Sminthopsis granulipes                                                   |**
PL Amphipogon turbinatus                                                    |**
PL Boronia purdieana                                                        |**
PL Cassytha racemosa                                                        |**
PL Conostylis aculeata                                                      |**
PL Dryandra borealis borealis                                               |**
PL Gompholobium tomentosum                                                  |**
PL Grevillea preissii                                                       |**
PL Hibbertia spicata spicata                                                |**
PL Patersonia occidentalis                                                  |**
PL Pimelea leucantha                                                        |**
PL Pityrodia oldfieldii                                                     |**
PL Stylidium elongatum                                                      |**
```

separately (cf. McKenzie *et al.*, 1989, 1991a; McKenzie and Belbin, 1991).

As expected, we found that geographical patterns in the occurrence of the various assemblages were related to different sets of environmental attributes. Even so, some attibutes were significant for several assemblages (e.g. precipitation, and soil potassium and phosphorus). Potassium, for instance, is readily leached from soil profiles by rainfall or flood water and provides a sensitive measure of fertility (T. Stoneman, personal communication). As linear predictors, however, attributes such as soil potassium are of little practical value for unsampled sites because data on soil chemistry is only available at a few points in the study area. The tight correlation of soil potassium, 'percent sand' and 'percent silt' with soil shear strength despite six (10%) missing values in the shear strength data, suggests that it should be a useful surrogate for field work (Kendall's tau = 0.45 to 0.48 ***).

The analyses exposed strong relationships between compositional patterns and environmental attributes for all assemblages. In all 13 cases, both the compositional and richness relationships that emerged from the analysis (Table 5) were consistent with the Australia-wide distributional and habitat characterisations summarised in Figure 3. Thus, the attribute-sets are unlikely to be artifacts of the quadrat positioning or of the relatively small size of the study area in relation to the size of the geographical ranges of most of the species (see Blackburn and Gaston, 1998).

The geographical pattern in the species richness of each assemblage fitted a Poisson error model, with logarithmic links (Crawley, 1993; Nicholls, 1989), and usually involved the same (or a very similar) set of environmental parameters as did the corresponding compositional analysis (Table 5). Within each assemblage, richness provided a reasonable surrogate for composition because regionally-nested patterns in species composition (cf. Patterson and Brown, 1991; Wright *et al.*, 1998) are visible in each assemblage (see Figure 12). This would be expected in re-ordered matrices, where species have been clustered according to their co-occurrences. That they are not cleanly defined is due, in part at least, to localised patterns in allopatry and sampling errors (e.g. see Rolfe and McKenzie, 2000). Further, well-defined nested patterns in species composition would not be expected for assemblages where richness and composition are influenced by the interaction of several divergent environmental gradient vectors, and a variety of different trophic levels and guilds are represented (Brown, 1995).

In general, climatic as well as soil and/or geographical attributes were required to explain the observed pattern of occurrence of each assemblage across the study area. Thus, patterns in the species composition of the Carnarvon Basin assemblages were being influenced by environmental processes operating at two geographical scales. At the biogeographical scale, patterns were related to the differences between the Eremean and South-western biotas, and corresponding to the study area's arid-to-mesic and tropical-to-temperate climatic gradients, but mitigated by coastal effects in northern parts of the study area. At the local scale, patterns were related to topographic, vegetation and/or soil attributes. Previous studies have shown that scale is important in determining which environmental attributes emerge as significant correlates with compositional patterns (Dale, 1983; Whitmore; 1984, Bowers, 1997). Regional studies have usually linked compositional patterns to climatic and/or geological categories (Ashton, 1976; McKenzie *et al.*, 1987b, 1991a, 1992, 1994; McKenzie and Rolfe, 1995), whereas the importance of topographic setting and lithology have emerged from more geographically restricted studies (Whitmore, 1984).

In our study area, the overt patterns of compositional variation that are usually referred to as patchiness or regional heterogeneity (Weiher and Keddy, 1995) could be explained numerically in terms of attributes of the physical environment. Thus, our results are consistent with the landscape paradigm proposed by Pastor *et al.* (1997), that spatial heterogeneity (patchiness) is a template to which organisms respond as well as an "emergent feature of their collective responses".

While axes of habitat heterogeneity can be separate or totally coupled and confounded by species responses to the heterogeneity (Bowers, 1997), the question of scaling adds further to the complexity of landscape ecology (Bowers, 1997; MacNally and Quinn, 1997). To expose these patterns for reserve system design and other aspects of wildlife management, we need to measure attributes of the environment that reflect processes at scales that fit the organisms' responses. For instance, a particular response-scale was significant in determining assemblage composition in the region's insectivorous bat guild (McKenzie and Muir, 2000). To explain the biodiversity patterns defined herein, we had to invoke a much wider range of attributes at a greater range of scales. Furthermore, localised patterns of allopatry among closely related species belonging to the more diverse genera, and unevenness in taxonomic discrimination within different taxa, were additional sources of variation (Aplin *et al.*, in press; McKenzie *et al.*, 2000b). In combination with contemporary theory, our results indicate that the Carnarvon Basin reserve system will need to sample the geographical extent of the various climatic and soil gradients identified by the analyses, if evolutionary processes are to be protected therein.

Another issue of immediate concern is the premise that a particular sub-set of the biota, such as the flora, can be used as a reliable surrogate for spatial patterns in biodiversity. The question of whether spatial patterns in the biota coincide across different phylogenetic groups, termed congruence, has usually been addressed in terms of patterns in species richness (e.g. Howard *et al.*, 1998) rather than composition. As with richness, available compositional studies have usually shown that different types of organisms show different geographical patterns of occurrence (e.g. Yen, 1987; Solem and McKenzie, 1991; Ferrier and Watson, 1996; Michaels and Mendel, 1998; but also see Oliver *et al.*, 1997). Our comparison of compositional patterns in seven types of organism shows that each contributed significant amounts of information to our description of the biodiversity pattern. While our result should be treated with caution (because our approach is exploratory rather than experimental), it is not surprising for several reasons.

- The substantial physiological differences between plants and animals, homeotherms and heterotherms, etc, imply very different responses to environmental gradients.
- Guild boundaries do not necessairily conform to taxonomic boundaries (Adams, 1985). For instance, small co-occurring predators such as dasyurids, birds, spiders, scorpions, centipedes, bats, reptiles and frogs partition similar food resource axes, and show patterns of species replacement in geographical space.
- The diversity of prey species at sites is influenced by predation (e.g. Spiller and Schoener, 1998).

Pimm and Lawton (1998) point out, "*... we still do not have a theoretical understanding of why the geographical patterns of hotspots, rarity, and complementarity are so different among taxa. Although at large scales distinct biogeographic realms are apparent, within these, nature apparently plays dice with distributions.*" In identifying aspects of pattern and complexity in biodiversity, macroecological studies such as ours are a first step towards a rigorous understanding of the mechanisms that cause the patterns (Brown, 1995; Blackburn and Gaston, 1998).

We conclude that reserve selection procedures which are based on only one or two types of organism will produce distorted outcomes, although cross-taxon congruence in between-site complementarity (Howard *et al.*, 1998) is likely to offset this problem at biogeographical scales. The distortion is likely to operate at local scales, affecting the representativeness rather than comprehensiveness (*sensu* Woinarski and Norton, 1993) of reserve systems.

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