Terrestrial flora and vegetation of the Western Australian wheatbelt

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Abstract – Six hundred and eighty-two quadrats were located across the Western Australian wheatbelt and adjacent regions to cover as much of the geographical, edaphic and geomorphological variation of the terrestrial plant communities as possible. The study area covered 230,000 km^2 or 70% of the South West Botanical Province, one of the world's 25 biodiversity hotspots. It included all or part of the six biogeographical regions centred on the wheatbelt. The native vegetation in the study area is highly fragmented with 74% having been cleared for agriculture. Clearing has not been uniform; more extensive areas of bushland remain along the southern and western margins.

A total of 2609 taxa of vascular plants in 103 families was recorded from the quadrats. The species frequency pattern followed a lognormal distribution. At a scale of 400 m^2, there was little difference in species richness between woodland, mallee and shrubland formations but those on duplex soils had lower species richness than those on deep sand, laterite and granite soils.

Over 60% of taxa were recorded in fewer than five quadrats. These uncommon taxa were not randomly distributed but concentrated at the periphery of the study area, particularly in the west and south. At least eight previously unrecognized taxa were collected for the first time. Further collections of 15 taxa listed as Declared Rare under the Wildlife Conservation Act, and 161 taxa on the Department of Conservation and Land Management's priority flora list were made.

There was little congruence in phytogeographic patterning between lifeforms or taxonomic levels. This implies that analyses of only some components of the flora, or analyses at higher taxonomic levels will not elucidate the full phytogeographic pattern. Phytogeographic patterning in the quadrat classification, which included the 1022 most common species, was strongly related to climatic gradients and edaphic factors.

Twenty-six assemblages were defined from the species classification, four were later combined with the total number of assemblages analyzed reduced to 23. Of these 20 formed natural groups that were consistent with the known distribution and habitat preferences of the component taxa. Species richness in these assemblages was modeled as a surrogate for composition using climatic and soil parameters. Explanatory power of the models ranged from 43.2 to 84.2%.

The present biogeographical regions and subregions defined for the study area received little support from the analyses of either the quadrat classification or the assemblage patterning. Available structural vegetation mapping also showed little correlation with composition. Species patterning across the study area was primarily gradational along a northeast-southwest rainfall gradient and a north-south temperature gradient, as well as a widespread diffuse pattern associated with specific granite and saline associations.

INTRODUCTION

The old subdued landscapes of the South West Botanical Province (SWBP) belie a subtlety and richness in flora and vegetation that is rivaled by few other places on earth (Hopper *et al.*, 1996). Australia is recognized as one of the 12 megadiverse countries with a rich biota and high levels of endemism (Common and Norton, 1992; Mummery and Hardy, 1994), and the SWBP has been recognized as one of the 25 biodiversity hotspots under significant threat (Myers *et al.*, 1990) with a high concentration of endemic species and extensive clearing of the original vegetation.

The landscapes of the SWBP have developed on the Archaean granitic basement rocks of the Yilgarn Craton which have undergone little mountain building since the Permian glaciations. This area has largely been above sea level since that time, and
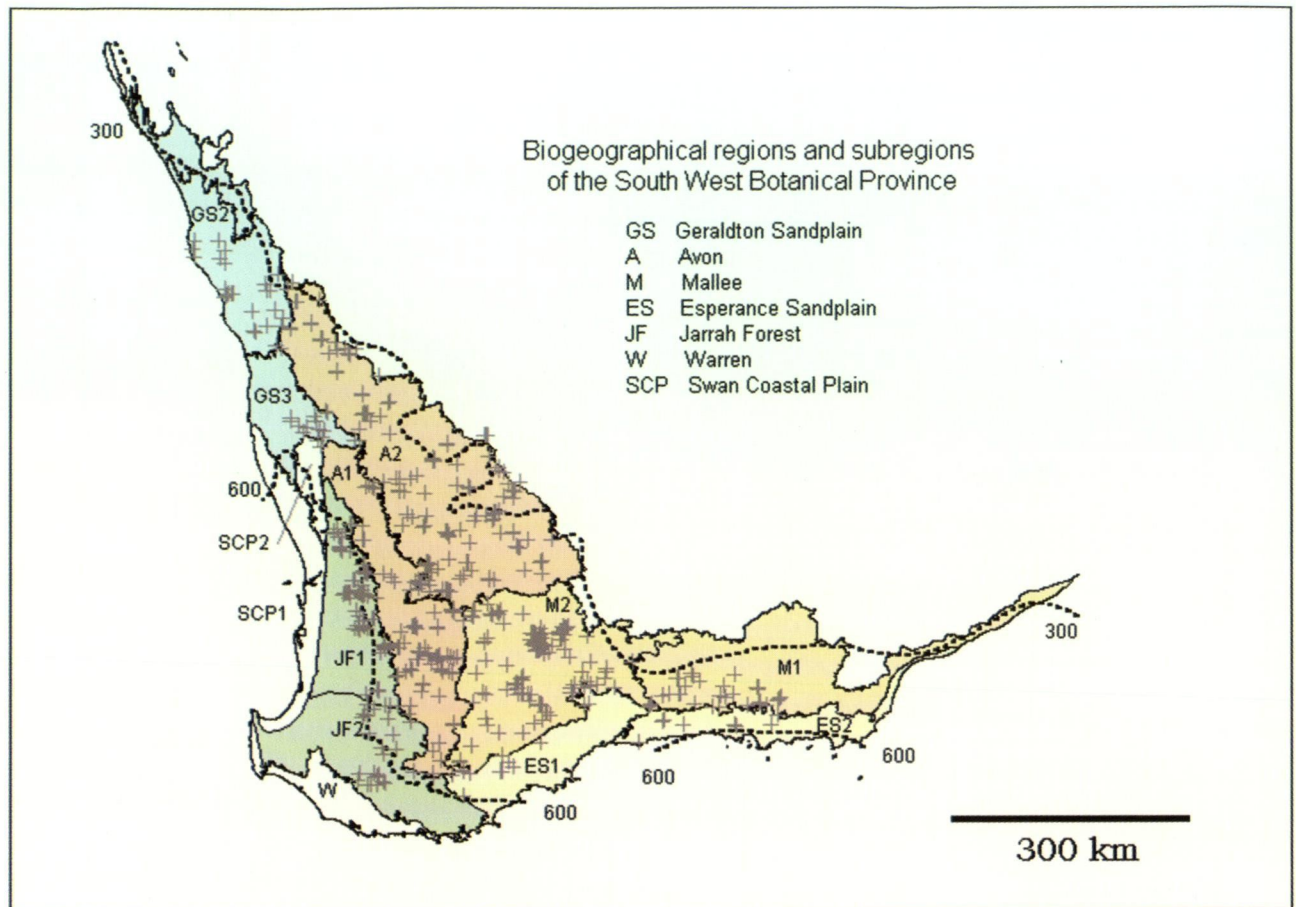
Figure 1 Map of the South West Botanical Province showing currently recognized biogeographic regions and subregions. The 682 quadrats are shown by crosses, most fall between the 300 and 600 mm rainfall isohytes. The quadrats were distributed over 230,000 km².

as a result, has undergone an extended period of weathering. The resulting subdued landscape of the Darling Plateau is mantled by Tertiary-Quaternary laterites and sandplains on the upland, and duplex soils in the broad valleys. The drainage systems to the west of the Meckering line have been rejuvenated due to minor recent uplift along the western edge of the plateau, while to the east drainage is sluggish, largely consisting of series of salt lakes following the Tertiary paleodrainage lines (Mulcahy, 1967; McArthur, 1993; Beard, 1999, 2000). The Yilgarn Craton is flanked to the west and south by sedimentary basins that presently form narrow coastal plains.

The first detailed descriptions of the vegetation of south-west Australia were provided by Diels (1906) in his seminal work *"Die Pflanzenwelt von West Australien südlich des Wendekreises"* where the origins of the different elements of the flora were described and a vegetation classification, a vegetation map and a phytogeographic interpretation developed (Beard, 2001a, b). Diel's concept of a mediterranean South West Botanical Province that abuts the arid Eremaean Province was further refined by Gardner and Bennetts (1956), and

subsequently by Beard (1980), based on extensive structural vegetation mapping. A series of botanical districts and subdistricts were defined within the SWBP (Beard 1980) and these have subsequently been further modified (Beard, 1990; Thackway and Creswell, 1995; Environment Australia, 2000). Currently there are seven IBRA (Interim Bioregionalization of Australia) bioregions recognized in the SWBP (Figure 1; Environment Australia 2000).

A simpler system has been used by Hopper (1979) who recognized three zones in the south west, the high rainfall zone (800–1500 mm annual rainfall), the transitional rainfall zone (300–800 mm) and the arid zone (< 300 mm). The high rainfall zone (HRZ) essentially equates to the western Jarrah Forest, the Warren and the southern Swan Coastal Plain bioregions. The transitional rainfall zone (TRZ) as originally defined included most of the remainder of the SWBP and small parts of the goldfield's woodlands (Coolgardie bioregion). The arid zone included the remainder of the Coolgardie bioregion and the southern Eremaean (Beard 1990).

Neither the IBRA or Hopper regionalizations has been subject to detailed floristic analysis, although

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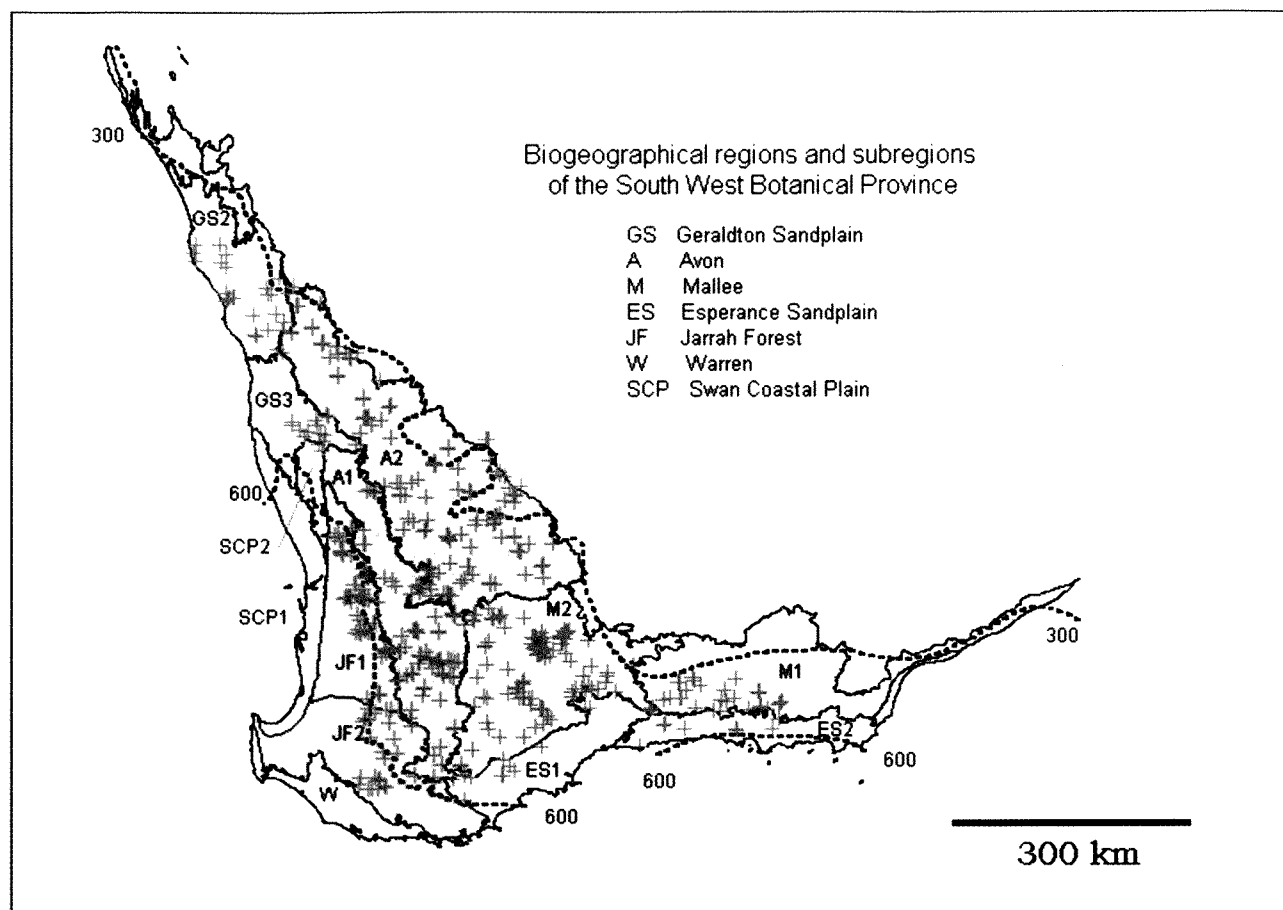Neither the IBRA or Hopper regionalizations has been subject to detailed floristic analysis, although

Table 1   The current biogeographical regions and subregions (IBRA, Environment Australia 2000) in the South West Botanical Province by total area, area of remaining vegetation and percentage clearance (Shepherd *et al.* 2002). Area in km².

IBRA Region	Sub-region Code	Sub-region Area	Sub-region Vegetation Area	% cleared
Avon Wheatbelt	AW1	65,660.2	13,074.9	80.1
	AW2	30,129.8	2,679.3	91.1
Esperance Sandplains	ESP1	19,039.5	9,649.7	49.3
	ESP2	16,065.2	7,878.5	51.0
Geraldton Sandplains	GS1	9,283.0	9,009.4	2.9
	GS2	22,420.3	8,807.1	60.7
	GS3	13,589.2	5,503.3	59.5
Jarrah Forest	JF1	22,559.0	13,735.3	39.1
	JF2	31,601.2	16,838.7	46.7
Mallee	MAL1	40,814.3	32,168.5	21.2
	MAL2	47,639.6	15,169.3	68.2
Swan Coastal Plain	SWA1	4,478.6	1,255.5	72.0
	SWA2	13,339.0	5,585.2	58.1
Warren	W	10,276.4	6,735.2	34.5
Total		346,895.4	148,090.0	57.3

information is available for some genera (Speck, 1958; Gill *et al.*, 1985; Morrison, 1987; Hnatiuk and Maslin, 1988; Taylor and Hopper, 1988; George, 1991; Lamont and Connell, 1996; Gibson *et al.*, 1997; Hopper and Brown, 2001) and some families (Speck, 1958; Keighery, 1996; Gibson *et al.*, 1997).

Since European settlement in 1829 over 151,000 km² of native vegetation in south-west Australia has been cleared for winter cereal crop and pasture production (Shepherd *et al.*, 2002). Clearing has been most extensive between the 250 and 600 mm rainfall isohyets (Table 1), and primarily affects the Avon Wheatbelt and Esperance Sandplains IBRA bioregions, and subregions in the Geraldton

Sandplains (subregions 2 and 3), and the Mallee (subregion 2). The wheatbelt largely falls within the TRZ of Hopper (1979). Overall 57.3 % of the SWBP has been cleared, with clearance within some individual subregions greater than 90% (Table 1).

As a result, the remnant vegetation of the wheatbelt consists of highly fragmented patches of varying size within a matrix of agricultural farmland (Table 2). For example, the 612 nature reserves in the Department of Conservation and Land Management's (CALM) Wheatbelt Region have a median size of 116 ha, while the median size of more than 5000 other government reserves is < 4 ha. Clearance was initally biased toward the more

Table 2   Reserves in CALM's Wheatbelt region (centred on the Avon bioregion) by number and area (total, minimum, maximum, average and median). Wheatbelt Region covers 13.1 million ha (R. Wilson, Information Management Branch, CALM, pers. comm.). Areas given in ha.

	Number	Total area	Minimum area	Maximum area	Average area	Median area
CALM Reserves						
Conservation Park	1	257.7				
National Park	2	55,352.6	1,292.0	54,060.6		
Nature Reserve	612	1,070,909.8	0.5	311,719.9	1,749.9	116.0
5h Reserves	3	72.6	8.2	43.7	24.2	20.7
State Forest	3	28,367.0	4,065.7	20,186.0	9,455.7	4,115.3
CALM Reserves Total	*621*	*1,154,959.7*				
Non-CALM Reserves						
Crown Reserves vested in Local Government	1,957	52,105.9	< 0.1	4,367.0	26.6	2.5
Other Crown Reserves	942	69,011.7	< 0.1	3,450.2	73.6	4.1
Unvested Crown Reserve	2,146	168,541.4	< 0.1	35,730.2	78.5	2.4
Non CALM Reserves Total	*5,045*	*289,659.0*				
Total	*5,666*	*1,444,618.7*				

productive soil types, in the broad valleys, but later included the sandy soils on uplands as trace element problems were overcome (Main, 1993).

The introduction of rabbits and dryland salinity have also had a major impact on the remaining remnant vegetation of the wheatbelt. Dryland salinity has resulted from changes in water balance brought about by the clearance of the native perennial vegetation, and is having a major adverse impact on the remnant vegetation of the broad valleys and saline drainage systems (Mann, 1907; Wood, 1924; George et al., 1995). George et al. (1995) suggests that these impacts will not be restricted to remnants of the valleys but, depending on local hydrology, also affect some upland areas.

Hopper (1992) estimated that there are 8000 plant species in SWBP with at least 75% endemic to the province. More recent work has suggested that this figure is too high at the specific level (Beard et al., 2000) but is likely to be a reasonable estimate when subspecies and varieties are included. Beard et al. (2000) reported 5710 species in the SWBP of which 3000 (52.5%) were endemic to the Province. Their figure did not include any of the more than 700 taxa still awaiting formal description (Paczkowska and Chapman, 2000). Many of these undescribed taxa occur in, or are restricted to, the SWBP.

Given the extent of vegetation clearing and associated impacts of fragmentation and salinity on wheatbelt plant diversity, it is not suprising that the majority of extinct vascular plant taxa (11 of 15) and the majority of threatened vascular plant taxa (214 of 351, listed as Declared Rare Flora under the WA Wildlife Conservation Act) occur in CALM's Mid-West, Wheatbelt and South Coast Regions (Atkins 2003) that cover most of the cleared cropping lands. In addition to these threatened taxa CALM maintains a priority list of taxa of conservation concern, 1068 (51%) of the 2101 plant taxa on this list are recorded from these three Regions (Atkins, 2003).

The only regional overview of the vegetation across the entire SWBP is that provided by Beard's structural vegetation mapping at 1:250000 (see Beard, 1981 and references therein). Beard used structure and dominance to map the vegetation. In associated publications, he amalgamated recurring catenary sequences of soil and vegetation into vegetation systems, that reflect the consistent pattern of vegetation change in relation to underlying geomorphology. Of the vegetation formations of the SWBP, reviews are only available for the species-rich shrublands (George et al., 1979; Lamont et al., 1984; Hopkins and Griffin, 1984; Brown, 1989) and the eucalypt woodlands (Yates and Hobbs, 1997; Yates et al., 1999). Brown's (1989) survey was based on detailed quadrat sampling of 20 laterite uplands across the central wheatbelt allowing detail description of compositional patterns.

Havel (2000) mapped the majority of the IBRA Jarrah Forest and Warren bioregions adopting a similar approach to Beard's. Here, the recurring patterns of vegetation types across closely related landforms were grouped into vegetation complexes. Havel (2000) notes that, as with his previous work in the Jarrah Forest (Havel, 1975a, b; Heddle et al., 1980) and the Swan Coastal Plain (Havel, 1968; Heddle et al., 1980), the vegetation overstorey is largely invariant with a significant changeover of understorey species across different landforms. He termed the patterning in vegetation in the forest regions as a "lumpy continuum" primarily determined by climate and landform.

Neither Beard's or Havel's maps have been subject to detailed floristic analysis to assess congruence with compositional gradients, although available quadrat-based datasets were used by Havel in the definition of vegetation complexes, and validation with individual species predictions has been attempted. Gibson et al. (1994) report poor correspondence between a 43-group floristic classification based on 509 fully enumerated quadrats and the vegetation complex mapping available for the Swan Coastal Plain (Heddle et al., 1980).

While mapping at a finer scale than Beard's 1:250000 maps is available for many individual reserves across the wheatbelt (Muir, 1977 and other reports in the series; many unpublished consultants' reports held in CALM library; Gibson and Keighery, 2000; Keighery et al., 2002) there is little consistency between methodologies and generally little correlation has been found between structural groups and floristic composition across the SWBP (Havel, 1975a; Loneragan, 1978; Hnatiuk and Hopkins, 1981).

To address the lack of consistent fine-scale vegetation maps across the wheatbelt, Hobbs et al. (1989) attempted to use "landsat" data to derive fine scale structural mapping for several reserves in the Kellerberrin area. This proved unsuccessful except for very broad units. More recently, attempts have been made to model vegetation distributions (structural units) using generalized additive models (GAM) based on climatic parameters and fine scale digital terrain surfaces (Dirnböck et al., 2002). While explaining significant amounts of variance, these models were not able to effectively predict vegetation pattern at a fine scale.

From 1997 to 2000 a regional biodiversity survey centred on the wheatbelt was undertaken to identify priority areas where attempts will be made to protect all components of the biota from salinization. The results of this biodiversity survey are reported elsewhere (McKenzie et al., 2004; Walshe et al., 2004). An expanded quadrat-based vegetation survey was carried out in parallel, and

the results of the terrestrial component of that survey are reported here.

We were interested in seven primary questions:

1) Can species assemblages, rather than vegetation structural units, be modeled in terms of geographical, climatic and soil variables across the wheatbelt?

2) What are the primary environmental correlates with the quadrat classification across the study area?

3) How well does the quadrat classification correlate with Beard's 1:250000 mapping units?

4) Can pattern of occurrence in species assemblages or quadrat groups be related to the current IBRA biogeographical regionalizations of the study area?

5) Given that regional quadrat-based surveys are expensive, how comparable are analyses at different taxonomic resolution in recovering vegetation patterning?

6) Similarly, how comparable are analyses of different plant lifeform groups in recovering vegetation pattern?

7) Finally, given the high percentage of uncommon taxa in the dataset, what patterning is apparent in these taxa?

METHODS

Study area

The wheatbelt study area comprises all or part of 6 IBRA bioregions (Thackway and Creswell 1995, Figure 1): the entire Avon Wheatbelt bioregion, and parts of the Mallee, Geraldton Sandplains, Jarrah Forest, Esperance Sandplains and Swan Coastal Plain bioregions. Most of the study area lies between the 300 and 600 mm isohyets, but some sampling was undertaken in the higher rainfall areas on the south-western boundary and in more arid areas on the eastern boundary (Figure 1). The study area extends from Mt Ney northeast of Esperance to the southern boundary of Kalbarri National Park and covers 230 000 km^2 or 70% of the SWBP. Some 74% of the native vegetation in the study area has been cleared for agriculture and what remains is highly fragmented (R. Wilson, Information Management Branch, CALM, pers. comm.). All of the study area experiences a Mediterranean climate.

To examine the patterning of the flora and vegetation 1511 quadrats were established. At 304 of these quadrats, reptiles, spiders, small mammals, and scorpions were also sampled (see McKenzie *et al.* 2004). Six hundred and eighty-two quadrats sampled the terrestrial vegetation and 829 quadrats sampled the wetlands and their associated surrounding vegetation (i.e. low rises, and seasonally inundated and/or waterlogged flats

adjacent to the wetlands). The division between the terrestrial and wetland datasets is necessarily somewhat arbitrary. Of the 682 terrestrial quadrats, 10 fell in Hopper's (1979) HRZ, 650 in the TRZ, and the remaining 22 occurred along the western edge of the Arid Zone.

This paper reports on the biogeographical patterning of the terrestrial vegetation and flora, Lyons *et al.* (2004) reports on the patterning of the wetland vegetation and flora. Quadrats on granite substrates (including granite pools) were included in the terrestrial dataset.

Field sampling and physical attributes

Quadrats were arrayed across the landscape to cover as completely as possible the geographical and geomorphological patterning of the landscape. Sampling was constrained by both agriculture clearance and access. Quadrats were established between October 1997 and September 2000. Sampling was undertaken in spring when annuals and herbaceous perennials were likely to be most conspicuous and when most taxa were flowering. At each site, overstorey species were recorded in a 20 m x 20 m quadrat, and all other vascular plants were recorded in a nested 10 m x 10 m subplot. Most sites were visited on two occasions in different years, except those in Esperance and Grass Patch areas (where quadrats were scored once in spring of 2000), and where flooding precluded access to the sites on the second visit.

Seven areas were sampled at higher density to allow examination of pattern at a finer scale, these results will be reported elsewhere (Birdwhistle Nature Reserve, Boolanelling Nature Reserve, Dragon Rocks Nature Reserve, Charles Gardner Nature Reserve, Corrigin town site, Lake Hurlstone Nature Reserve - Mattiske Consulting Pty Ltd (1999); and Wandoo Conservation Park – Ecologia (1994)).

A structural vegetation description, and information on soil type and depth to impeding layer, were recorded at each quadrat. Soil types were categorized as granite (derived from granites or fine textured gradational soils of the valley floors), duplex (occurring on valley floor and erosional slopes below the duricrust), siltstone (sandy soils developed on Permian sediments in the north of the study area), laterite (duricrust pavement and shallow sands on massive laterites or lateritic gravel), and deep sands. Soils depth was coded into 9 classes from 1 (< 10 cm) to 9 (> 80 cm).

A stratified bulked soil sample from the top 10 cm was collected from the 10 m x 10 m subplot at 681 of the 682 quadrats, and soil mechanical and macro-nutrient analyses were undertaken (Appendix 1; for methods see McArthur 1991). Climate parameters for each site were estimated

from the climate modelling program ANUCLIM (Houlder *et al.*, 1999; Appendix 2).

Attributes available for each quadrat were latitude, longitude, elevation, broad soil type (4 classes), soil depth class (9 classes), 15 soil chemical and texture values from the bulked soil sample and 17 climatic estimates from ANUCLIM. Significant correlations between these attributes were identified using Spearman rank correlation coefficients, and one from each pair of highly intercorrelated attributes was deleted. The attribute names and codes that are referred to in Results and Discussion are listed in Table 3.

All quadrats were photographed and their position taken with a GPS unit accurate to better than 30 m horizontally. Nomenclature generally follows Paczkowska and Chapman (2000); voucher specimens are lodged in the Western Australian Herbarium.

Congruence between taxonomic levels

In order to determine how taxonomic resolution affected the recovery of vegetation patterning, a series of analyses were undertaken at different taxonomic levels following the methods of Somerfield and Clarke (1995) and Olsgard *et al.* (1997, 1998). An analysis was undertaken of the full species presence/absence data matrix, then these

Table 3   List of environmental attributes used in the analyses.

EC	Electrical conductivity (mS m⁻¹)
pH	pH
OrgC	Organic carbon (%)
NTOT	Total nitrogen (ppm)
PTOT	Total phosphorus (ppm)
Pav	Available (HCO_3) phosphorus (ppm)
Kav	Available (HCO_3) potassium (ppm)
Mg	Exchangeable magnesium (me%)
Ca	Exchangeable calcium (me%)
Na	Exchangeable sodium (me%)
Clay	Percent clay
Silt	Percent silt
Sand	Percent sand
Long	Longitude (°E)
Elev	Altitude above sea level (m)
MTAnn	Annual mean temperature (°C)
Isoth	Isothermality
MnTCP	Minimum temperature coldest period (°C)
T_AR	Annual temperature range (°C)
MTWetQ	Mean temperature wettest quarter (°C)
MTDQ	Mean temperature driest quarter (°C)
MTClQ	Mean temperature coldest quarter (°C)
Pann	Annual mean precipitation (mm)
PWetP	Wettest period precipitation (mm)
PSeas	Precipitation seasonality
PWrQ	Warmest quarter precipitation (mm)
Stype	Soil type (major soil types)
Sdep	Soil depth class

data were sequentially amalgamated at genus, family, order and class levels, with number of taxa at each level (untransformed) used to generate the association matrix.

The association matrices were derived by using the Bray-Curtis measure (PRIMER v 5.2.8, Clarke and Gorley, 2001) at each level of the taxonomic hierarchy. Spearman ranked correlation coefficients were then calculated between each pair of matrices. These correlation coefficients were compiled as a matrix (2STAGE in Clarke and Gorley, 2001) and used as a measure of 'cross-taxonomic' congruence in the spatial patterning of quadrats at different taxonomic levels. The correlation matrix was converted to a dissimilarity matrix (1 – coefficient), and multidimensional scaling ordination (MDS in Clarke and Gorley, 2001) was used to reduce the dimensionality of this matrix, so that the relationships between the different levels of taxonomic resolution could be displayed in two dimensions. In such an ordination each point represents an association matrix and the (non-metric) distance between indicates the rank level of similarity between the matrices.

An additional association matrix was derived from a randomized data matrix where the original species richness per quadrat was retained. This was included to allow contrasts between correlation coefficients derived from the different taxonomic associations matrices with that derived from a random association matrix.

Congruence between lifeforms

An analysis of congruence in patterns of distribution between different lifeforms was undertaken using similar methods to those outlined above. Four broad lifeform sub-sets were represented in the full matrix: trees, mallets and mallees; perennial excluding geophytes; perennials including geophytes; and annuals. For each four subsets, the complete data matrix and a random matrix (with the same species richness characteristics), an association matrix was derived by using the Bray-Curtis measure to compare quadrats in terms of their composition. The analysis was restricted to the 492 quadrats which were represented by at least one member of each lifeform group. Spearman ranked correlation coefficients were then calculated between each pair of matrices and the subsequent analysis was then essentially the same as outlined above for congruence between taxonomic levels.

Patterning in the distribution of uncommon taxa

Preliminary analysis showed that 807 taxa (30.9% of total) were recorded from only one quadrat and a further 780 taxa (29.9% of total) were recorded from fewer than five quadrats. Thus 60.8% of taxa

were individually recorded from < 1% of the 682 quadrats. The composition of these uncommon taxa was compared with the total species pool of 2609 taxa in terms of taxonomic affinity and lifeform spectrum using a Chi-square analysis (Statsoft, 2001).

Comparisons were also undertaken using methods outlined above (2STAGE, Clarke and Gorley, 2001) between association matrices derived from (a) the full data matrix and those derived from (b) taxa occurring in two or more quadrats, (c) taxa occurring in five or more quadrats and (d) a randomized full data matrix where original species richness per quadrat was retained. Finally, the spatial distribution of these 1587 uncommon taxa was investigated by mapping their richness per quadrat across the study area.

Quadrat analysis

Quadrats were classified according to similarities in species composition (presence/absence data) using the Bray-Curtis coefficient and unweighted pair-group mean average fusion method (UPGMA module in PATN, beta value - 0.1, Belbin, 1995; Sneath and Sokal, 1973). As the primary aim was to gain an understanding of landscape-scale patterning, the analysis was restricted to 1022 taxa that occurred in at least five of the 682 quadrats. A modification by Hubert and Arabie (1985) of the Rand statistic (Rand, 1971) was used to assess the influence of uncommon taxa on classification partition structures (RIND in PATN, Belbin, 1995). Methods of Dufrene and Legendre (1997) were used to determine the best indicator species for each level in the classification, defined as an INDVAL value of 25% or greater (PC-ORD v4.24, McCune and Mefford 1999). Classification results were presented at the 25 group level.

Quadrats were ordinated using the semi-strong hybrid method (SSH in PATN, cut level 0.9), correlations with environmental vectors were determined by principal axis correlation analysis (PCC in PATN, also known as rotational correlation analysis) and significance tested by Monte-Carlo simulation (MCAO in PATN, Belbin 1995).

Patterns in species composition

Cluster analysis was used to depict similarities in species occurrence (based on quadrat presence/absence data) using the two-step association coefficient (Belbin, 1980). UPGMA hierarchial clustering strategy was used with a beta value set to -0.1 (Belbin, 1995). Further analysis was carried out in the following order:
1) The data matrix was partitioned into assemblages of species according to their co-occurrences at the same quadrats.
2) Each plant assemblage was characterized in terms of the known habitat preferences of its component species throughout their ranges elsewhere in Australia (Muir, 1977; Jessop, 1981; Beard, 1981; Anon., 1984; Gibson *et al.*, 1997; Gibson and Lyons, 1998a, b; 2001a, b; Anon., 1999; Keighery *et al.*, 2000; Paczkowska and Chapman, 2000).
3) The species-quadrat matrix of each assemblage was assessed for nestedness (Atmar and Patterson, 1993).
4) The relationship between composition and species richness was examined by plotting richness against a 1D ordination for each assemblage (SSH in PATN, cut level 0.2, Belbin, 1995). This allowed an assessment of whether the species richness pattern of an assemblage was a useful surrogate for its composition.
5) The generalized linear interactive modeling package GLIM (NAG 1986, Nicholls 1989) was used to model the relationships between the species richness of each assemblage and a set of attributes related to edaphic and climatic factors (see Appendices 1 and 2). 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. Poisson distributions were assumed and logit link functions were used. The significance of the parameters in the regression equations was calculated using the Wald statistic.

Geographical patterns in plant biodiversity

If species richness provides a good surrogate for composition in the species assemblages, and most of the scaled deviance in the richness gradients can be explained in terms of climatic or other measured environmental attributes, then these gradients provide perspectives on the phytogeography within the study area (McKenzie *et al.*, 1989, 1991, 2000, 2004). These gradients were displayed as a series of dot plots, where dot diameter was proportional to assemblage richness, and were overlaid onto the currently recognized IBRA bioregions and subregions (Thackway and Creswell, 1995; Environment Australia, 2000).

As a second approach to assessing phytogeographical patterns within the study area, we classified the 682 quadrats in terms of their relative weighting for the various species assemblages identified from the quadrat classification analysis (described above), and compared the results with the existing bioregions and subregions. For this analysis, species assemblages were weighted equally by using the proportion of an assemblage's maximum species richness recorded at each quadrat as input data.

RESULTS

Flora

A total of 2609 taxa of vascular plants in 103 families were recorded from the 682 quadrats (Appendix 3). These comprised 14 ferns or fern allies, 8 gymnosperms, 1 cycad and 2586 flowering plants (of which 132 were naturalized aliens).

Over 60% of these taxa occurred in less than five of the 682 quadrats and two species (the perennial native grass, *Neurachne alopecuroidea*, and a weedy annual herb *Hypochaeris glabra*) occurred in more than half the quadrats. The frequency of occurrence of the 2609 taxa approximates a lognormal distribution (shape 1.2725, threshold −2.3174, scale 5.6795, Figure 2).

The largest families were the Myrtaceae (407 taxa, 15.6% of the flora), Proteaceae (288, 11.0%), Papilionaceae (180, 6.9%), Asteraceae (143, 5.5%), Mimosaceae (138, 5.3%), Cyperaceae (121, 4.6%), Orchidaceae (109, 4.2%), Epacridaceae (93, 3.7%), Poaceae (89, 3.4%), and Stylidiaceae (69, 2.6 %). Together these 10 families comprised 62.7% of the total flora.

Of the remaining 93 families, only 13 contained more than 20 taxa. These were Goodeniaceae (with 57 taxa), Anthericaceae (51), Rutaceae (45), Dilleniaceae (44), Rhamnaceae (43), Haemodoraceae (43), Restionaceae (38), Chenopodiaceae (36), Droseraceae (34), Apiaceae (33), Dasypogonaceae (32), Lamiaceae (25), and Euphorbiaceae (22). These 13 families combined contributed a further 19.3% of the total flora.

Twenty-one genera were represented by more than 20 taxa. These were *Acacia* (138 taxa), *Eucalyptus* (108), *Melaleuca* (107), *Stylidium* (63), *Hakea* (55), *Leucopogon* (54), *Schoenus* (53), *Grevillea* (46), *Dryandra* (45), *Hibbertia* (44), *Caladenia* (41), *Daviesia* (37), *Lepidosperma* (34), *Drosera* (34), *Petrophile* (30), *Banksia* (30), *Verticordia* (29), *Conostylis* (28), *Baeckea* (28), *Synaphea* (24), and *Austrostipa* (21), representing 40.2% of the taxa encountered.

Twenty-one lifeforms were represented across the 2609 taxa (Table 4). The most common lifeforms encountered were shrubs (52.1% of taxa), annual herbs (13.5%), perennial herbs (10.8%), geophytes (6.9%) and perennial sedges (4.2%).

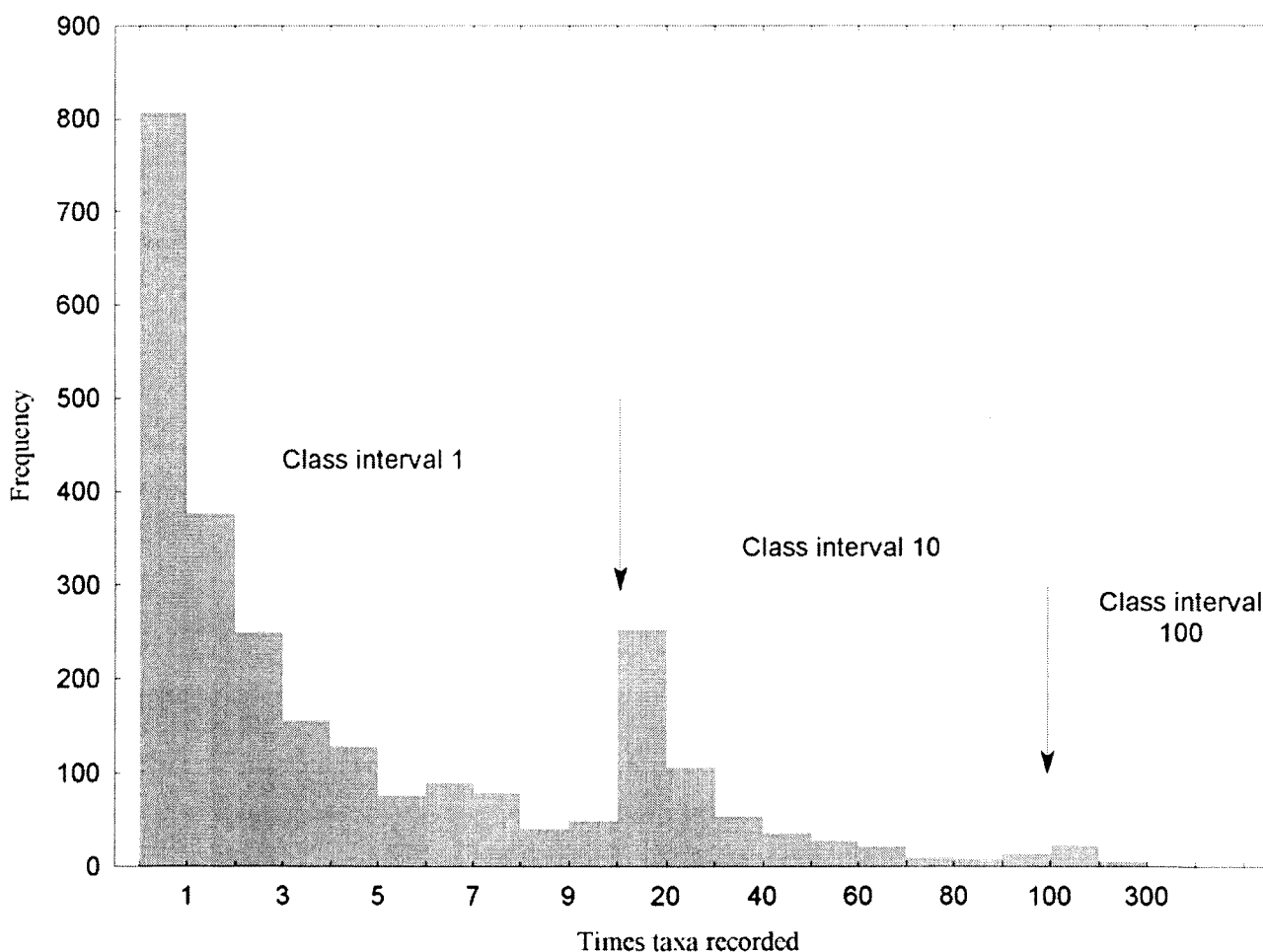Of the 2609 taxa recorded, 15 taxa are currently listed by CALM as Declared Rare Flora and may be

Figure 2 Frequency distribution of the 2609 taxa recorded from the 682 quadrats. Note three different class intervals used. Just over 60% of taxa were recorded from fewer than five quadrats.

Table 4 Percentage of taxa in each of 21 lifeform groups for the total flora, for taxa known from only 1 quadrat, and for taxa known from < 5 quadrats. Chi-square tests between uncommon groups and total flora showed no significant difference ($P > 0.05$).

Lifeform	All 2609 taxa	807 taxa recorded from 1 quadrat	1587 taxa recorded from < 5 quadrats
Fern allies	0.1	0.1	0.1
Fern	0.5	0.6	0.4
Arborescent monocot	0.3	0.2	0.3
Cycad	0.0	0.0	0.0
Annual grass	1.5	1.0	0.8
Annual sedge	0.7	0.4	0.6
Annual herb	13.5	10.8	10.5
Parasitic annual herb	0.3	0.1	0.1
Geophyte	6.9	5.0	6.0
Perennial climber	0.6	0.4	0.5
Perennial grass	1.9	1.2	1.4
Perennial restiad	1.4	1.1	1.4
Perennial sedge	4.2	3.3	3.8
Perennial herb	10.8	10.2	10.1
Parasitic perennial herb	0.1	0.1	0.1
Shrub	52.1	61.7	59.7
Parasitic shrub	0.1	0.1	0.1
Mallee	2.8	2.7	2.6
Mallet	0.2	0.1	0.2
Small tree	0.6	0.2	0.3
Tree	1.2	0.5	0.8

regarded as threatened in international terms. A further 175 taxa are listed as being of conservation significance (Atkins 2003).

Eight taxa were collected for the first time by the survey: *Brachyloma* sp. (GJK and NG 5870); *Conostephium* sp. (GJK and NG 5871); *Melaleuca* sp. Dongolocking (GJK and NG 2896); *Philotheca* sp. (GJK and NG 6804), *Schoenus* sp. Toodyay (GJK and NG 2918); *Stenanthemum* sp. Burma Road (GJK and NG 2904); *Tribonanthes* sp. Lake Muir (GJK and NG 2134); and *Trymalium monospermum*. Several other apparently new taxa were collected but these require further work to clarify their taxonomic status. Further collections were made of other recently recognized taxa from the wheatbelt (e.g. *Acacia* aff. *tetanophylla* (B.R.Maslin 6309), *Austrodanthonia* sp. Goomalling (Wildflower Society OAKP10 63)) (Appendix 3).

In the 682 quadrats, 132 introduced taxa were recorded, representing 5% of the total number of taxa encountered. This may be an underestimate of weed occurrence in the study area as quadrats were deliberately placed in the least disturbed sites available where weed were least likely to occur. The proportion of weeds recorded in the entire Western

Australian flora is ca. 9% (Keighery, 1995; Paczkowska and Chapman, 2000). The families with the largest number of introduced taxa were Poaceae (34 taxa), Asteraceae (15), Papilionaceae (14), Caryophyllaceae (10), Iridaceae (6), Brassicaceae (6), Scrophulariaceae (5), Geraniaceae (5), Aizoaceae (4), and Polygonaceae (4), with these 10 families representing 78% of the recorded introduced taxa. The genus *Trifolium* recorded the highest number of weeds (nine taxa). Most of the weeds (107 of 132 taxa) were annuals.

Each of the four main soil types showed a similar range in species richness and a similar pattern in distribution across the rainfall gradient (Figure 3). However, mean richness for quadrats on deep sand, laterite and granite soils was significantly higher (43.3–44.7 taxa/quadrat) than for quadrats on duplex soils (average 33.7 taxa/quadrat, Table 5).

Species richness in the 23 richest families was significantly different between the four major soil types with the single exception of the Mimosaceae (Table 5). Eleven families showed highest richness on the deep sand and laterite soils, two families were most common on laterite and granite soils and a further two families were common on all soil types except the duplex soils. Seven families showed clear preference for a single soil type; four were richest on granite soils (Asteraceae, Orchidaceae, Poaceae and Apiaceae), the Chenopodiaceae were richest on duplex soils, the Restionaceae on deep sands, and the Rhamnaceae on laterite soils (Table 5).

In the 23 richest families, species richness was positively correlated with estimated annual rainfall in 17 families, negatively correlated with rainfall in two families (Asteraceae and Chenopodiaceae) and not correlated with rainfall in five families (Myrtaceae, Mimosaceae, Poaceae, Rutaceae, and Lamiaceae, Table 6).

Similarly, species richness in the five most diverse lifeform classes and the tree, mallet and mallee classes were correlated with estimated annual rainfall. Six of the eight lifeforms considered were positively correlated with estimated annual rainfall, while annual herbs and mallees showed a negative correlation (Table 7). Species richness in 17 of 19 lifeform classes was also significantly different between the four major soil types. Annual herbs, annual grasses, annual sedges, geophytes and perennial grasses were richest on granite soils. Mallees and mallets were richest on laterite and duplex soils. Arborescent monocots, perennial herbs, perennial sedges and shrubs were richest on laterite and deep sand soils. Perennial restiads were richest on deep sand soils, while trees were fewest on laterite soils (Table 8).

No significant difference was found between mean species richness of the three major structural formations sampled (woodland, mallee and
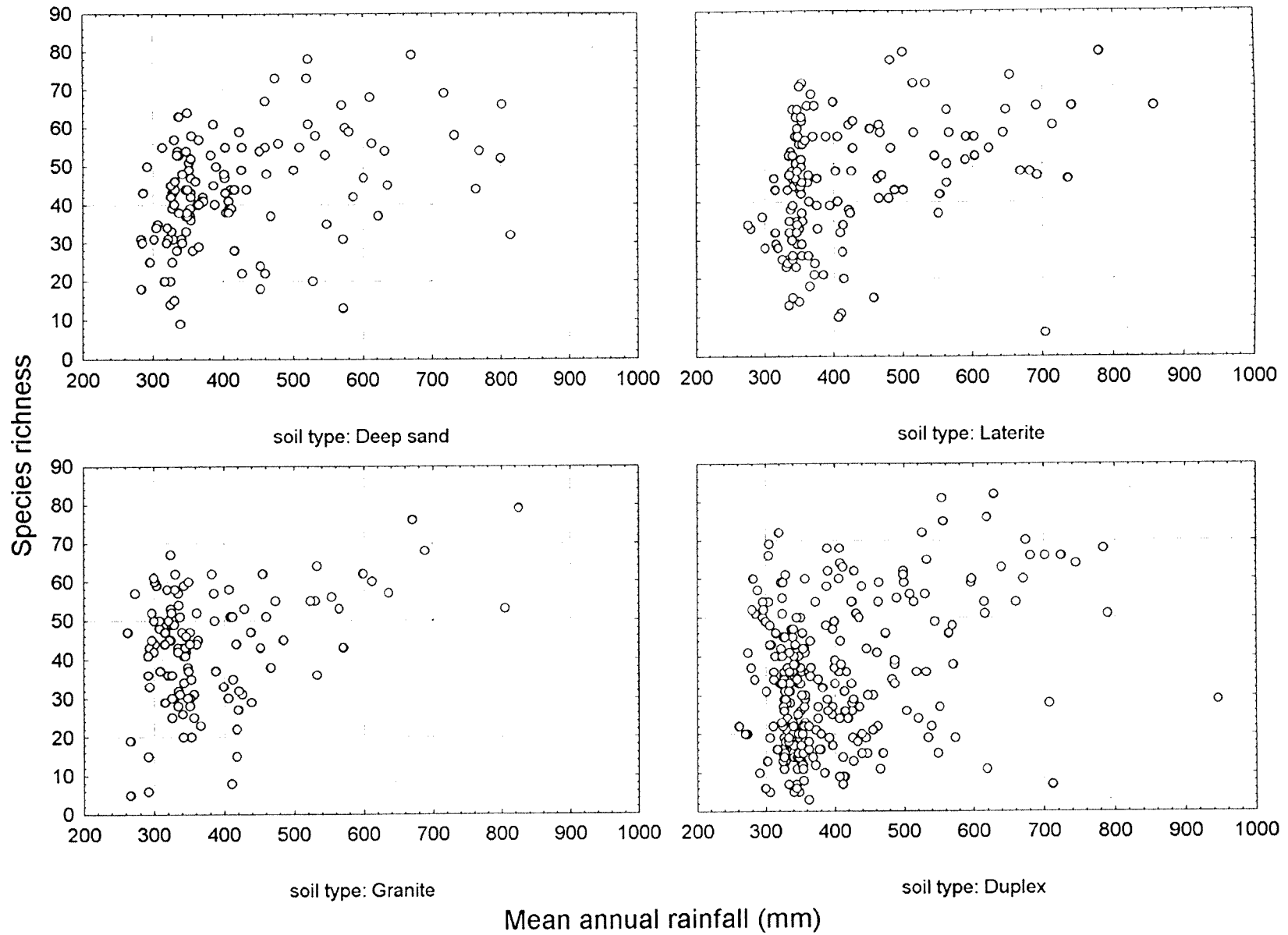
Figure 3 Species richness pattern on the four major soil types and rainfall. While range in richness was similar on all soil types, mean richness on duplex soils was significantly lower.

Table 5 Species richness patterns in the 23 richest families in relation to major soil types. Significant difference (*P*) in mean species richness between major soil groups tested by Kruskal–Wallis 1-way analysis of variance. Siltstone soils were not considered as only 6 quadrats occurred on this type. (sd = standard deviation, ns = *P* > 0.05).

	Deep sand		Laterite		Granite		Duplex		*P*	% total
	mean	sd	mean	sd	mean	sd	mean	sd		flora
Myrtaceae	5.2	3.4	6.1	3.4	1.7	1.6	3.3	2.5	< 0.0001	15.6
Proteaceae	4.0	3.8	5.5	4.3	0.6	1.1	0.7	1.3	< 0.0001	11.0
Papilionaceae	1.8	1.9	2.2	2.2	0.8	1.2	1.0	1.4	< 0.0001	6.9
Asteraceae	4.9	4.3	2.9	3.2	9.1	5.1	6.0	5.4	< 0.0001	5.5
Mimosaceae	0.8	1.0	1.0	1.1	1.0	1.1	1.0	1.0	ns	5.3
Cyperaceae	2.9	2.0	3.2	2.1	1.4	1.3	1.0	1.5	< 0.0001	4.6
Orchidaceae	1.4	1.5	1.5	1.6	1.9	1.8	1.3	1.7	0.0044	4.2
Epacridaceae	1.1	1.3	1.5	1.4	0.2	0.5	0.3	0.8	< 0.0001	3.7
Poaceae	3.5	2.4	2.6	2.0	5.6	2.5	4.4	2.9	< 0.0001	3.4
Stylidiaceae	1.4	1.3	1.7	1.4	0.9	1.3	0.5	1.0	< 0.0001	2.6
Goodeniaceae	0.7	0.9	1.1	1.1	1.3	1.3	0.7	1.1	< 0.0001	2.1
Anthericaceae	1.5	1.3	1.8	1.6	2.0	1.7	1.2	1.4	< 0.0001	1.9
Rutaceae	0.5	0.7	0.5	0.7	0.0	0.2	0.2	0.5	< 0.0001	1.7
Dilleniaceae	0.9	1.0	1.2	1.0	0.2	0.6	0.3	0.6	< 0.0001	1.6
Haemodoraceae	0.9	1.2	0.8	0.9	0.2	0.5	0.2	0.7	< 0.0001	1.6
Rhamnaceae	0.2	0.6	0.6	0.8	0.2	0.5	0.2	0.5	< 0.0001	1.6
Chenopodiaceae	0.2	0.7	0.0	0.0	0.4	1.2	1.1	1.8	< 0.0001	1.4
Restionaceae	1.6	1.3	0.9	1.0	0.3	0.6	0.3	0.8	< 0.0001	1.4
Apiaceae	1.1	1.1	1.0	1.2	2.2	1.5	1.4	1.5	< 0.0001	1.3
Droseraceae	1.3	1.2	1.4	1.0	1.4	1.4	0.5	1.0	< 0.0001	1.3
Dasypogonaceae	0.9	1.1	1.0	1.2	0.3	0.5	0.5	0.7	< 0.0001	1.2
Lamiaceae	0.2	0.5	0.2	0.4	0.0	0.2	0.1	0.3	0.0068	1.0
Euphorbiaceae	0.4	0.6	0.5	0.7	0.4	0.5	0.1	0.4	< 0.0001	0.8
Total richness	43.6	14.0	44.7	15.6	43.3	14.1	33.7	17.70	<0.0001	81.7
No. of quadrats	130		144		118		284			

Table 6 Spearman rank correlations between family richness (number of taxa per quadrat) and estimated annual rainfall for 682 quadrats. (*P* = significance level, ns = *P* > 0.05).

Family	Spearman rank correlation	*P*	% total flora
Myrtaceae	0.01	ns	15.6
Proteaceae	0.32	< 0.0001	11.0
Papilionaceae	0.49	< 0.0001	6.9
Asteraceae	-0.21	< 0.0001	5.5
Mimosaceae	-0.05	ns	5.3
Cyperaceae	0.43	< 0.0001	4.6
Orchidaceae	0.28	< 0.0001	4.2
Epacridaceae	0.33	< 0.0001	3.7
Poaceae	0.03	ns	3.4
Stylidiaceae	0.44	< 0.0001	2.6
Goodeniaceae	0.05	ns	2.1
Anthericaceae	0.30	< 0.0001	1.9
Rutaceae	-0.02	ns	1.7
Dilleniaceae	0.41	< 0.0001	1.6
Haemodoraceae	0.45	< 0.0001	1.6
Rhamnaceae	0.08	< 0.05	1.6
Chenopodiaceae	-0.41	< 0.0001	1.4
Restionaceae	0.43	< 0.0001	1.4
Apiaceae	0.09	< 0.05	1.3
Droseraceae	0.20	< 0.0001	1.3
Dasypogonaceae	0.35	< 0.0001	1.2
Lamiaceae	0.06	ns	1.0
Euphorbiaceae	0.16	< 0.0001	0.8
Total richness	0.28	< 0.0001	81.7

Table 7 Spearman rank correlations between species richness of the major lifeform class (number per quadrat) and estimated annual rainfall for the 682 quadrats. (*P* = significance level).

Major lifeform	Spearman rank correlation	*P*	% total flora
Annual herb	-0.12	< 0.01	13.5
Geophyte	0.34	< 0.0001	6.9
Perennial herb	0.44	< 0.0001	10.8
Perennial sedge	0.42	< 0.0001	4.2
Shrub	0.14	< 0.001	52.1
Mallee	-0.18	< 0.0001	2.8
Mallet	0.09	< 0.05	0.2
Tree	0.17	< 0.0001	1.8

shrubland) nor was the soil type x formation interaction significant, there was a significant soil type effect (*P* < 0.0001, two-way ANOVA of 656 quadrats with the eight herbland quadrats and six siltstone quadrats excluded, Table 9). Richness in eucalypt woodland quadrats was largely composed of annuals while richness in the *Banksia* woodlands and the shrublands largely comprised shrubs. Quadrats sampling the mallee association had a variable understory primarily determined by soil type, annuals dominating on duplex soils and shrubs on laterite and deep sand soils.

Table 8 Patterns in species richness within lifeforms in relation to major soil types. Significance difference (P) in mean species richness between major soil groups for each lifeform tested by Kruskal–Wallis 1-way analysis of variance. Siltstone soils were not considered as only 6 quadrats occurred on this type. (sd = standard deviation, ns = P > 0.05).

Lifeform	Deep sand		Laterite		Granite		Duplex		P
	mean	sd.	mean	sd.	mean	sd.	mean	sd.	
Fern & fern allies	0.0	0.21	0.0	0.22	0.7	0.85	0.1	0.34	< 0.0001
Arborescent monocot	0.2	0.42	0.3	0.52	0.1	0.24	0.1	0.26	<0.0001
Cycad	0.0	0.21	0.1	0.24	0.0	0.18	0.0	0.13	ns
Annual grass	0.8	1.10	0.4	0.81	2.1	1.57	1.5	1.77	<0.0001
Annual sedge	0.3	0.52	0.3	0.52	0.8	0.93	0.3	0.80	<0.0001
Annual herb	8.9	7.12	5.8	5.86	19.0	8.91	11.2	10.10	<0.0001
Parasitic annual herb	0.4	0.58	0.4	0.57	0.1	0.30	0.1	0.32	<0.0001
Geophyte	3.4	2.57	3.8	2.78	5.3	3.57	3.5	3.89	<0.0001
Perennial climber	0.2	0.53	0.2	0.40	0.3	0.52	0.2	0.46	ns
Perennial grass	2.6	1.58	2.1	1.41	3.1	1.69	2.6	1.64	<0.0001
Perennial restiad	1.6	1.30	0.9	0.94	0.3	0.55	0.3	0.77	<0.0001
Perennial sedge	2.8	1.96	3.0	2.15	0.8	1.09	0.8	1.22	<0.0001
Perennial herb	5.2	3.73	5.6	4.60	3.7	2.56	2.9	3.16	<0.0001
Parasitic perennial herb	0.0	0.09	0.0	0.00	0.1	0.22	0.0	0.12	<0.01
Shrub	15.5	9.05	20.4	9.84	5.6	5.30	7.8	5.42	<0.0001
Parasitic shrub	0.0	0.09	0.0	0.08	0.0	0.00	0.0	0.08	ns
Mallee	0.4	0.75	0.7	1.07	0.2	0.53	0.8	1.27	<0.0001
Mallet	0.0	0.00	0.1	0.39	0.0	0.00	0.1	0.29	<0.001
Trees	1.2	1.13	0.7	0.91	1.2	1.07	1.3	0.97	<0.0001
Total richness	43.6		44.7		43.3		33.7		
No. of quadrats	130		144		118		284		

Given the different sampling effort between the different associations and soil types it is difficult to draw many inferences from the patterns in the total number of species encountered. Total number of taxa recorded was highest in the woodlands with similar numbers from shrublands and mallees, however the woodlands were sampled more intensively than the other formations (Table 9). Among soil types, duplex soils recorded the highest number of taxa, but again they were sampled more intensively than the other major soil types. The relatively low number of taxa recorded from granite soils reflects the lower sampling effort (Table 9).

Congruence between taxonomic levels

The species presence/absence matrix contained 2609 taxa grouped into 489 genera, 103 families, 51 orders and 9 classes. The changes in the number of taxonomic units between adjacent levels showed a reduction to c. 20% except for the change from families to orders that only showed a 50% reduction.

The ordination derived from the correlation between the association matrices showed marked changes between the association matrix derived from species presence/absence data and the three matrices derived from the abundance values for

Table 9 Differences in mean species richness by major soil type and structural formations. Note six quadrats on siltstone soil type excluded, several forest quadrats have been included in woodland formation, standard deviation given in parentheses.

	Granite	Duplex	Laterite	Deep Sand	No. of quadrats	Total taxa
Herbland	19.5 (10.0)				8	79
Shrubland	42.7 (10.1)	36.3 (15.4)	44.8 (11.6)	42.7 (13.1)	139	1359
Mallee	42.6 (9.6)	29.2 (12.3)	43.0 (14.8)	41.4 (12.7)	150	1415
Woodland	46.2 (13.9)	34.8 (19.0)	46.5 (20.5)	45.5 (15.1)	379	1739
No. of quadrats	118	284	144	130		
Total taxa	914	1440	1352	1395		

Stress : 0

Class (r = 0.687)
△

Order (r = 0.849)
△
△
Family (r = 0.866)

△
Genus (r = 0.898)

Random (r = 0.557)
△

Species △
(presence/absence)
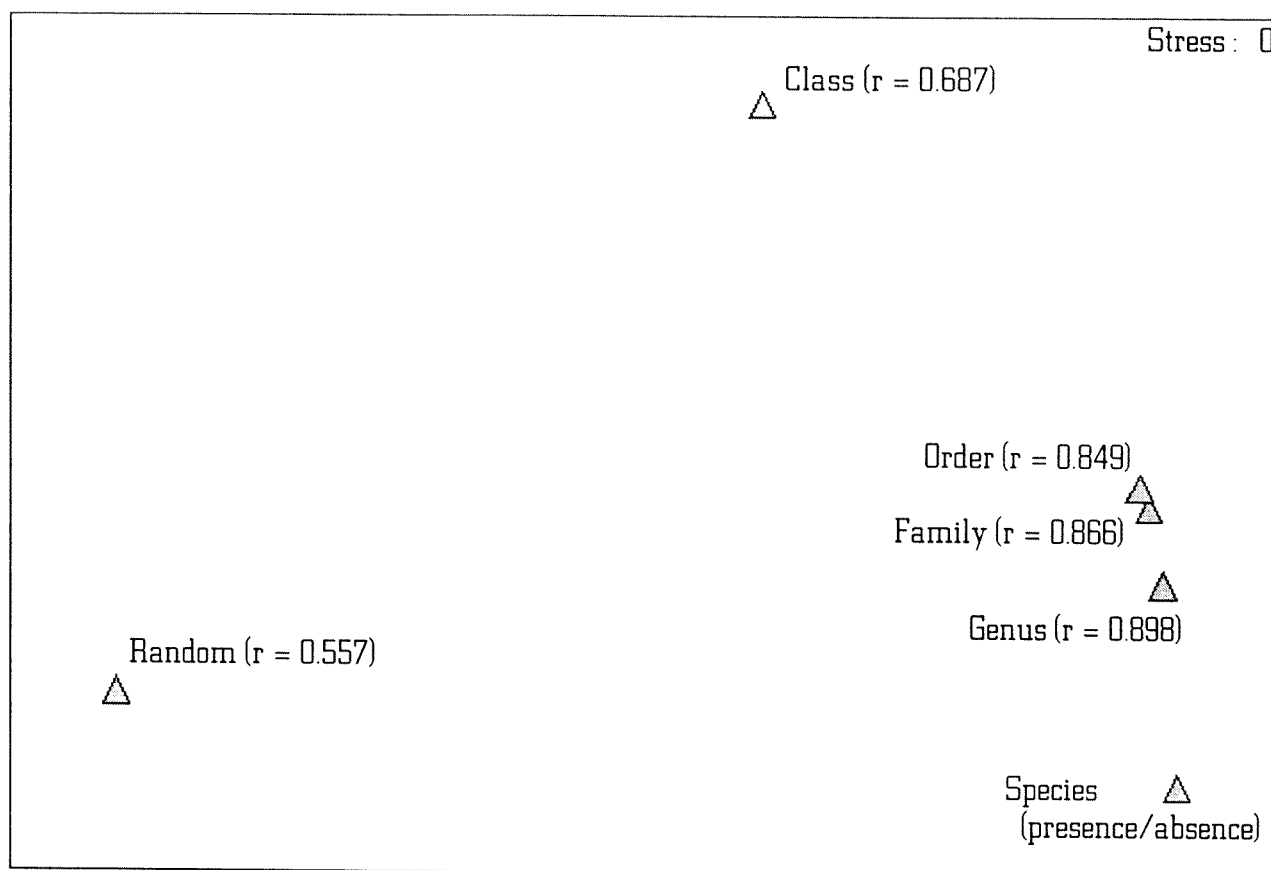
Figure 4   Comparison of floristic patterning of four higher taxonomic ranks (untransformed abundances) with the taxon presence/ absence dataset from 682 quadrats. A matrix of correlation coefficients was compiled based on pairwise comparison of individual association matrices of each taxonomic rank. Also included was a random matrix with the same distributional properties as the original presence / absence matrix. Results are displayed as a two dimensional non-metric multidimensional scaling ordination, stress was zero.

genera, families and orders that were generally similar to each other. This was followed by another large change to the matrix derived from class abundance data (Figure 4). All matrices showed a more or less similar distance to the random matrix with the distance between the class abundance matrix and the full presence/absence matrix c. 75% of this distance. The same general pattern was found when the abundance matrices were first subjected to a square root transformation to downweight the importance of the taxonomic groups with high abundances.

Congruence between lifeforms

Congruence between broad lifeform classes was examined in 492 quadrats in which at least one representative of each class occurred. Most of the quadrats excluded were shrublands that lacked an overstorey component. Species were not distributed evenly between the major lifeform classes. Of the 1511 taxa analysed annuals were represented by 293 taxa, perennials (excluding geophytes) by 1002, geophytes by 127, and trees, mallees and mallets by

89 taxa. (Taxa recorded from only a single quadrat were not considered.)

The ordination derived from the correlation between the association matrices showed that the total matrix (containing all lifeform classes) was more similar to each of the subsets than any subset was to any other subset except for the two perennial subsets. The exclusion of geophytes had little influence of the position of the perennial subset in ordination space (Figure 5). All matrices were well separated from the random matrix. The tree matrix was least similar of the subsets to the full matrix at a distance of c. 62% of the full matrix to random matrix distance.

Patterning in the distribution of uncommon taxa

As outlined above, of the 2609 taxa recorded in the 682 quadrats, 807 taxa (30.9% of total) were recorded from only one quadrat and a further 780 taxa (29.9% of total) were recorded from fewer than five quadrats. The composition of these 1587 uncommon taxa was analysed by lifeforms (Table 4) and taxonomic ranks (Table 10). Chi-square tests
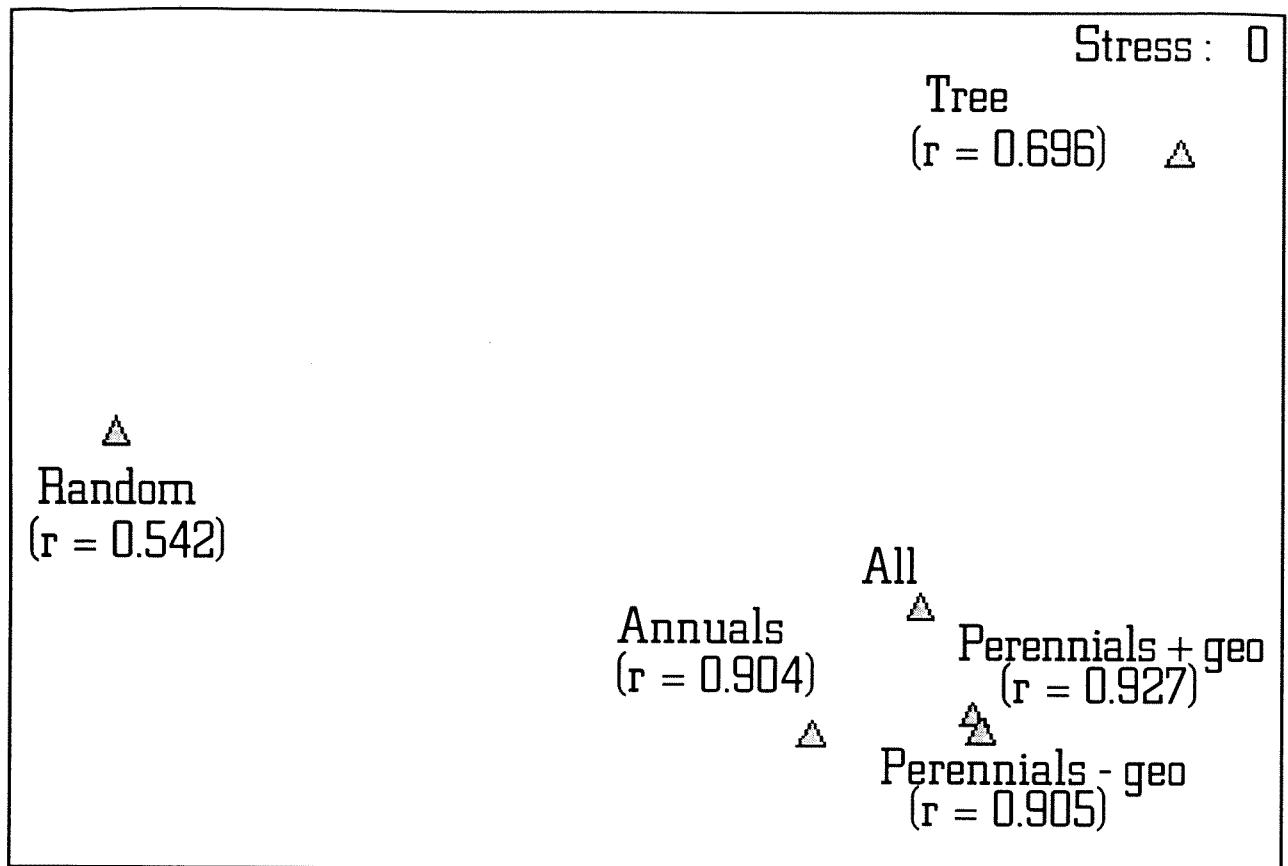
Figure 5 Comparison of floristic patterning of four broad lifeform categories (untransformed abundances) with total dataset from 492 quadrats which had at least one member of each lifeform group present. A matrix of correlation coefficients was compiled based on pair wise comparison of individual association matrices. Also included was a random matrix with the same distributional properties as the original dataset. Results are displayed as a two dimensional non-metric multidimensional scaling ordination, stress was zero.

between the uncommon groups and the total flora showed no significant difference in either taxonomic makeup or lifeform spectrum.

The Spearman rank correlations between the association matrices derived from the full presence/absence dataset (2609 taxa x 682 quadrats) and the two datasets with uncommon taxa removed (taxa only recorded in a single quadrat removed – 1802 taxa x 682 quadrats; and taxa recorded in less than five quadrats removed – 1022 taxa x 682 quadrats) were high (Table 11). Even with 60.8% of the species removed, the correlation coefficient with the full dataset was 0.999. The correlation coefficient between a random matrix and all three datasets was similar at about 0.56.

If the distribution of the uncommon taxa was randomly spread across the study area then the richness per quadrat for this group should follow a

Table 10 Percentage of the total flora, taxa known from only 1 quadrat and taxa known from < 5 quadrats in the richest 23 families. Chi-square tests between uncommon groups and total flora showed no significant difference ($P > 0.05$).

Family	All 2609 taxa	807 taxa recorded from 1 quadrat	1587 taxa recorded from < 5 quadrats
Myrtaceae	15.6	15.1	16.6
Proteaceae	11.0	11.9	12.1
Papilionaceae	6.9	8.8	7.9
Asteraceae	5.5	4.3	4.0
Mimosaceae	5.3	7.8	6.4
Cyperaceae	4.6	3.6	4.2
Orchidaceae	4.2	3.7	4.0
Epacridaceae	3.6	5.5	4.3
Poaceae	3.4	2.2	2.3
Stylidiaceae	2.6	2.9	2.5
Goodeniaceae	2.2	1.7	2.1
Anthericaceae	2.0	1.1	1.4
Rutaceae	1.7	2.9	2.0
Dilleniaceae	1.7	1.0	1.3
Rhamnaceae	1.6	1.4	1.8
Haemodoraceae	1.6	2.0	2.0
Restionaceae	1.5	1.1	1.4
Chenopodiaceae	1.4	1.5	1.6
Droseraceae	1.3	1.2	1.0
Apiaceae	1.3	0.9	0.7
Dasypogonaceae	1.2	0.5	0.9
Lamiaceae	1.0	1.9	1.3
Euphorbiaceae	0.8	1.2	1.0

Table 11 Spearman rank correlation coefficients between the association matrices derived from the 682 quadrats and (a) the full 2609 taxa, (b) the 1802 taxa occurring in ≥ 2 quadrats, (c) the 1022 taxa occurring in ≥ 5 quadrats, and (d) a randomized matrix with same species richness distribution as the full matrix.

	2609 taxa	1802 taxa	1022 taxa
2609 taxa			
1802 taxa	0.9999		
1022 taxa	0.9990	0.9993	
random matrix	0.5572	0.5571	0.5576

Poisson distribution. The species richness of these 1587 uncommon taxa showed a skewed Poisson distribution (Chi-square 949.3, df = 9, $P < 0.00001$) with higher than expected occurrences at a frequency of less than two taxa per quadrat; lower than expected occurrences at frequencies of between three and eight taxa per quadrat; and much higher than expected occurrences at frequencies of more than eight taxa per quadrat (Figure 6).

Quadrats with higher than expected numbers of these uncommon taxa were concentrated along the edges of the study area (Figure 7).

Quadrat analysis

A 25 group classification of both the full dataset (2609 taxa x 682 quadrats, Appendix 4) and a dataset which did not include taxa recorded from less than five quadrats (1022 taxa x 682 quadrats) was undertaken. Comparison of the partition structure shows a high degree of similarity (80% agreement in quadrat allocation) between the two classifications, with a modified Rand statistic of 0.622 (Table 12).

Partition comparisons were undertaken between the smaller dataset (with 25 partitions) and a varying number of partitions in the full dataset (from 21 to 40 groups). The modified Rand statistic was generally stable between 0.615 to 0.630 over the range of 25 to 36 groups in the full dataset (Figure 8), indicating that the 25 group partition structure in both datasets gave near optimal matching. Agreement in allocation of quadrats was optimal at the 25 group partition structure in both datasets. Inspection of the classifications showed that the
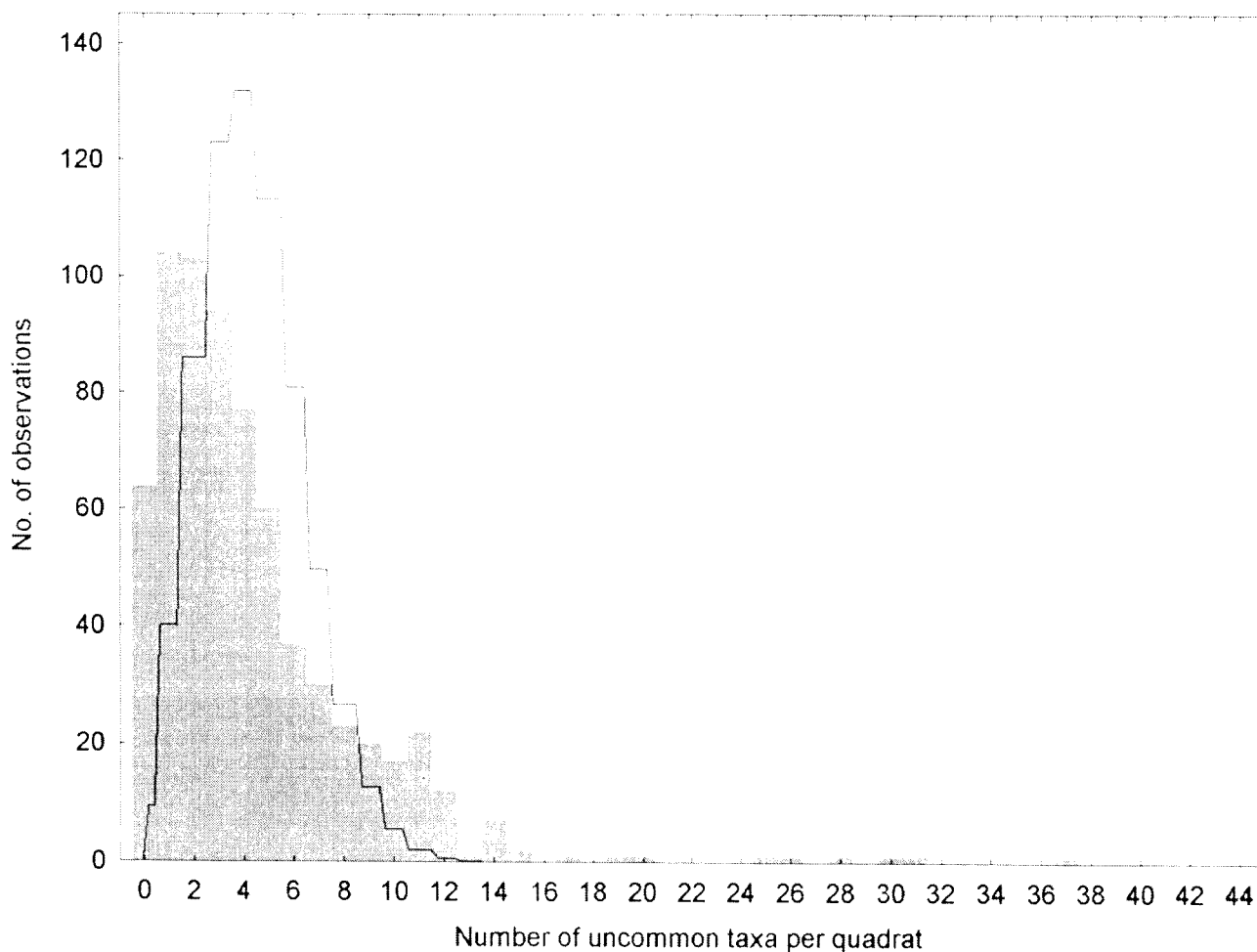
Figure 6 Comparison of the distribution of uncommon taxa (those that occurred at less than five quadrats) with the Poisson distribution expected if uncommon taxa had equal chance of occurring at the 682 quadrats. Solid line – Poisson distribution; bars – actual distribution of the uncommon taxa.
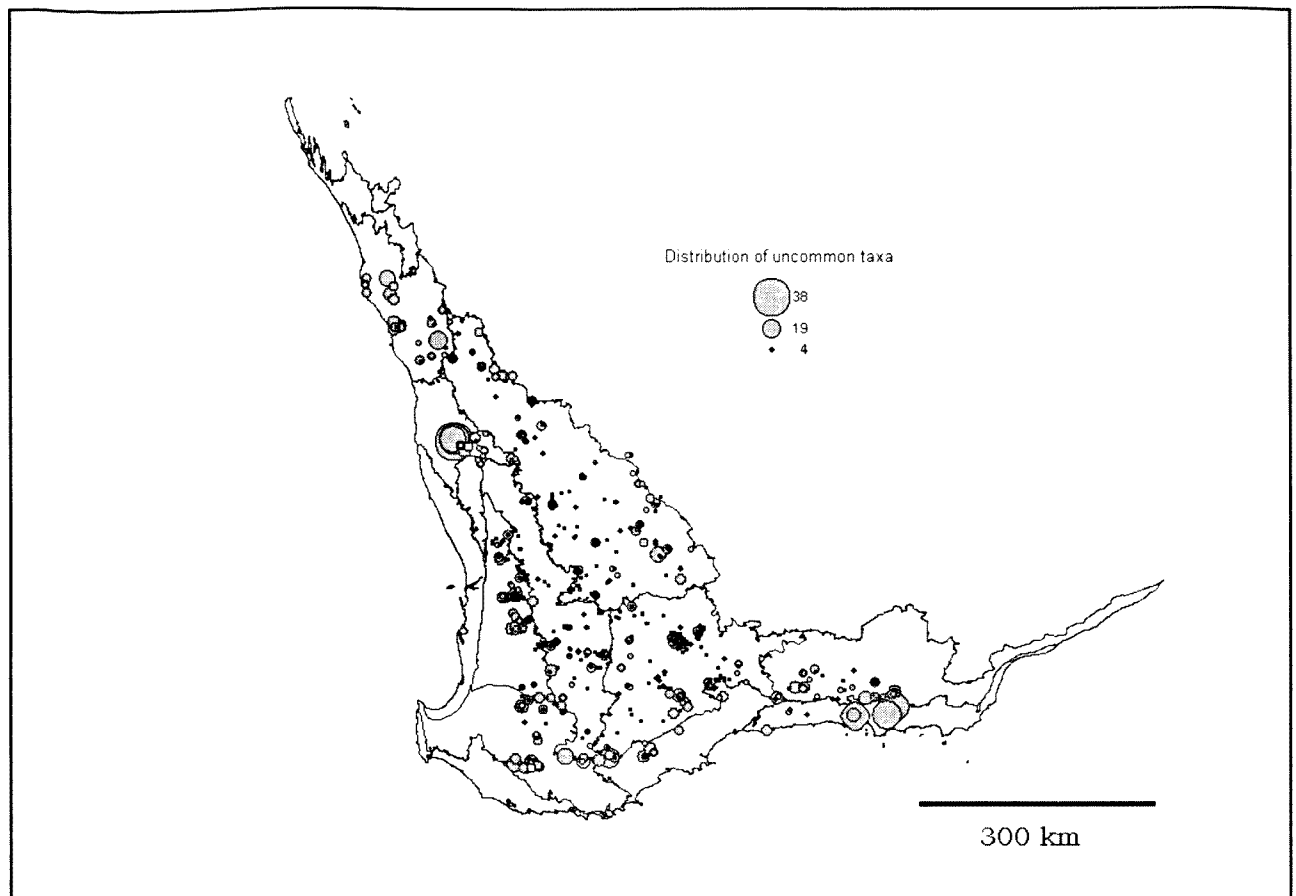
Figure 7 Geographical spread of the uncommon taxa (those that occurred at less than five quadrats). Diameter of dots reflects the number of uncommon taxa recorded at individual quadrats. Highest numbers were concentrated along the southern and western boundaries of the study area.

reduced dataset (1022 taxa x 682 quadrats) more clearly showed the major regional trends and it is the results from this analysis that are presented below.

The 25 groups classification showed significant geographical partitioning across the study area (Table 13). The 25 groups formed eight broad regional and edaphic classes (Tables 13, 14 and 15; Figure 9). These are described below in terms of distribution in IBRA regions and subregions, soil preference and typical taxa:

Northern woodland and mallee quadrats
1. This group represented herb-rich woodlands and mallees predominately of granite and duplex soils occurring in the drier northern part of the study area almost entirely restricted to the Avon 1 and Geraldton Sandplains 2 subregions. *Waitzia acuminata* and *Velleia cycnopotamica* were typical species of these quadrats.
2. Group 2 comprised herb-rich woodlands generally on duplex soils dominated by *Eucalyptus loxophleba* or *E. salmonophloia*, with a wider distribution than group 1 extending into Avon 2 and Geraldton Sandplains 3 subregions. The soils were generally higher in available P

and K and had a higher levels of soil Ca than those of group 1.

Central and southern woodland and mallee quadrats
3. A small group of predominately species-poor quadrats (mean 10.1 taxa/quadrat) from large lake dunes, generally dominated by eucalypts. Species richness was low, with soil that had high levels of available K and Ca, high electrical conductivity (mean 160.4 mS m^{-1}), and a high pH (mean 7.5). Most quadrats of this type were located in the Mallee 1 and 2 subregions. *Threlkeldia diffusa* and *Rhagodia drummondii* were typical species of these quadrats.
4. These quadrats had soils with the highest Ca levels (mean 12.4 me%) and high pH (mean 7.8) variously dominated by *Eucalyptus longicornis*, *E. kondininensis* or *E. salmonophloia* almost exclusively recorded from duplex soils. Less species-rich than the northern woodlands (groups 1 and 2) and generally lacking many of the herbs. Chenopods were a common component of the understory with *Sclerolaena diacantha* and *Atriplex vesicaria* the most typical species of these quadrats. This group was generally restricted to the Mallee 2

Table 12 Comparison between the quadrat classification partition structure derived from the complete 2609 taxa dataset (full dataset) and the partition structure derived from the 1022 taxa dataset (dataset with taxa occurring in ≥ 5 quadrats).

Dataset with taxa occurring in ≥ 5 quadrats

Full dataset	1	12	9	25	10	11	2	5	6	3	4	7	8	13	14	15	17	16	20	21	22	24	23	18	19
1	46						10																		
2	3	68					14																		
3			6																						
4				2																					
5					24	1	1	8	1	1			1		5							1			
6						21																			
7							41				1														
8							6	29																	
9	3						3	1	21													1			
10										8															
11							1				19														
12		11		2								45	8												
13													12												
14														19	3										
15													3	6	38	1	3								
16																8									
17														4	1		23	1							
18														2				24							
19																			18						
20																			2	27					
21						1															16	1	3		
22																						4			
23																					1		5		
24							1	1					1	6	1							1		12	
25							5	3																	12

Hubert/Arabie modification of Rand's statistic = 0.6220
Percentage of total on diagonal = 80.4%

subregion but extended west into the Avon 2 subregion with one quadrat into Avon 1 subregion.

5. Quadrats from group 5 predominately occurred on duplex soils with moderate to high Ca levels, generally dominated by woodlands of *Eucalyptus salmonophloia, E. longicornis, E. occidentalis* or *E. astringens*. Widespread, occurring from Jarrah Forest 2 through Avon 2, Avon 1, Mallee 2 subregions and into Mallee 1 subregion. Soils of this group showed lower available P and K than groups 3 and 4, and generally lacked the chenopod understorey of group 4.

6. These quadrats occurred in mallees and woodlands mostly on duplex soils in the Mallee 2 subregion extending into the Avon 2 and the Avon 1 subregions. Eucalypt dominance was variable but *Eucalyptus calycogona* was the most typical. The soils had the lowest Ca and total N levels, and lowest available P and K levels of the central and southern woodland and mallee quadrats.

Mesic quadrats

7. Quadrats in this group occurred in the wettest part of the study area and were generally dominated by *Eucalyptus marginata, E. calophylla,* or *E. wandoo*. Soil type was variable with quadrats recorded from granite, duplex laterite and deep sand soils. These quadrats had the highest species richness (mean 52.3 taxa) of any group. Many of the taxa recorded were restricted to the wetter southwest corner of the study area. Organic carbon in soil samples was high (mean 4%) compared to all other groups, except group 19. Quadrats were almost totally confined to Jarrah Forest bioregion.

8. Quadrats in group 8 were dominated by eucalypt or *Banksia* woodlands and were largely restricted to deep sands and laterites of the wetter southwest corner of the study area. Consequently, soil nutrients (especially P) were generally lower than those recorded in group 7. Many of the taxa recorded were restricted to sands in higher rainfall areas (*Lyginia barbata* and *Hypolaena exsulca* being the most typical). The quadrats in this group were more widely dispersed than those of group 7, with occasional occurrences in the Avon 2 subregion, and the Geraldton and Esperance Sandplains bioregions.
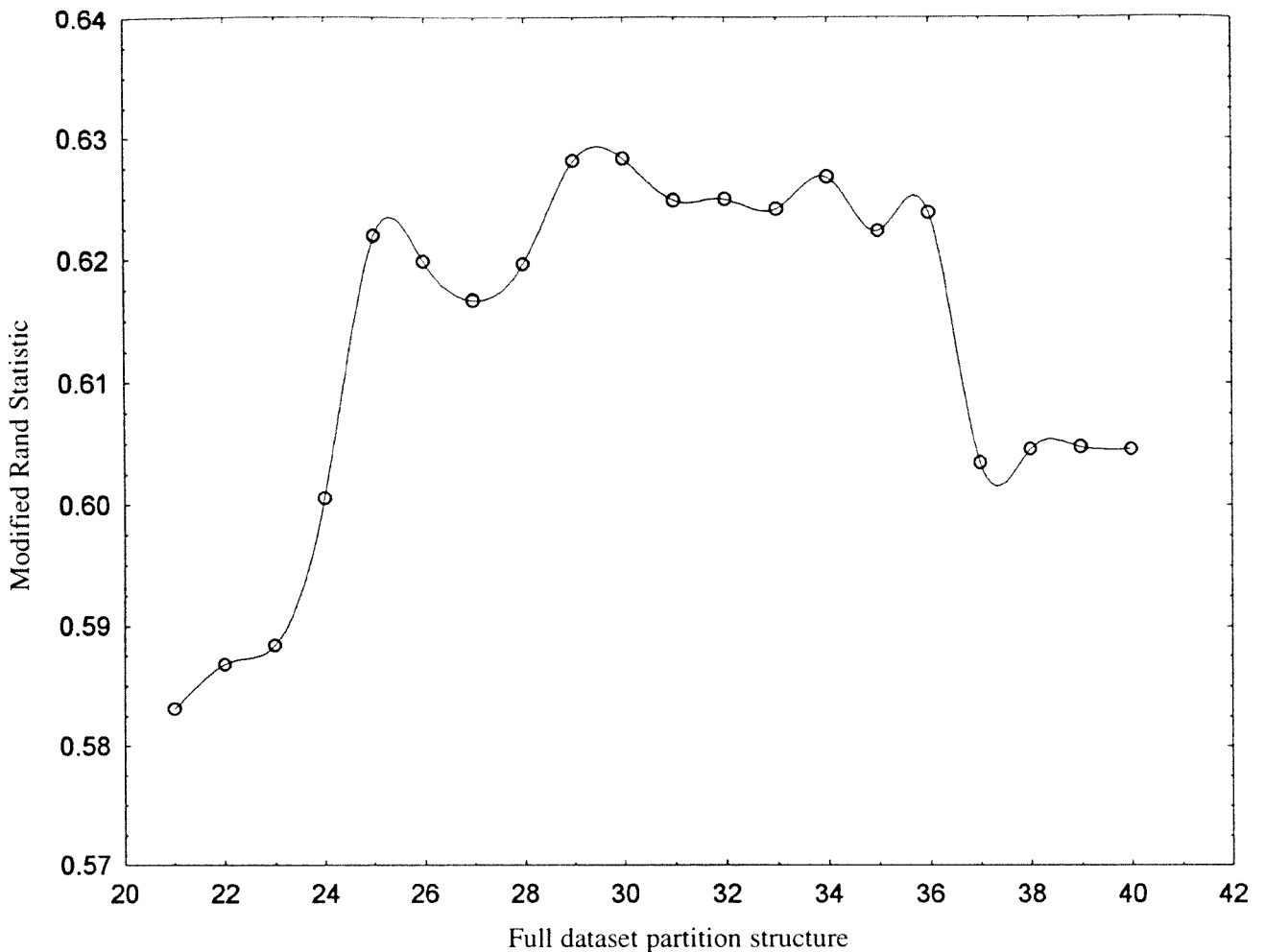
Figure 8   Relationship of the modified Rand statistic to the partition structure in the full dataset, when the number of partitions in the reduced dataset was held at 25. Below 25 partitions and above 36 partitions in the full dataset there was a rapid degrading of the relationship.

Seasonal wet flats and granite quadrats

9. A small group of species poor quadrats (mean 8.8 taxa/quadrat), comprising the salt affected flats from the Jarrah Forest bioregion on duplex soils, formed group 9. In addition, one quadrat occurred in a *Melaleuca* woodland on a laterite soil that had been modified by deposition of fine material from upslope sheet erosion, and another quadrat was a species poor granite pool from the eastern edge of the study area that shared weedy species with the saline affected flats. Mean soil electrical conductivity was the highest recorded (359 mS m^{-1}) as was exchangeable Na (2.3 me%). The most typical species of these quadrats were *Centrolepis polygyna, Juncus bufonius* and *Cotula coronopifolia*, the last two taxa being alien species.

10. Quadrats of group 10 were centred on the Avon 2 subregion and also extended west into the Jarrah Forest bioregion and east into Mallee bioregion. This group occurred at disturbed sites (either salt-affected or weed-invaded) but still retained moderate levels of species richness (mean 30.8 taxa/quadrat). Typical species of these quadrats were the weeds, *Briza minor* and *Ehrharta longiflora*. Most quadrats occurred on duplex soils on flats, but also included some granite soils and a number of breakaways. Vegetation was generally woodlands or mallees dominated by *Acacia acuminata, Allocasuarina huegeliana* or eucalypt species. Soils showed elevated levels of electrical conductivity (mean 77.4 mS m^{-1}) and exchangeable Na (mean 1.6 me%), P levels were similar to other woodland quadrat groups while N and K levels were somewhat higher.

11. Group 11 was largely comprised of quadrats in shrublands, and herblands developed on the shallow soils of granite rocks; it also included quadrats sampling shallow granite pools. Soils had the highest mean total P (234.4 ppm) and available P (13.7 ppm) indicating the younger soil age. These granite shrubland and herbland quadrats were widespread across the study area

```
1  ───────
2  ─────────┤──────────────────┐        Northern mostly granite and duplex soils
                               │        herb-rich Eucalyptus or Acacia dominated.
3  ─────                       │
4  ───┤                        │
5  ───┤            ┤           │
6  ──┤──────────────┤──────────┤──────── Eucalypt woodlands and mallees
                               │         of duplex soils occurring in
                               │         the Avon & Mallee bioregions.
7  ──                          │
8  ─┤─────────────────────     High rainfall sites on duplex, laterite and
                               │  deep sands generally dominated by eucalypts.
9  ──────────┐                 │
10 ──────────┤──               │
11 ──────────┤────────         │
12 ───────────────────┤────────┤────────────┤──── Seasonal wet flats
                                              │    and granites.
13 ───────────┐                               │
14 ───────────┤  ┤                            │
15 ───────┤─┤─┤                               │
16 ──────────┤──────────── Shrublands, mallee shrublands and woodlands on
            │             deep sand or laterite of the western wheatbelt.
17 ──────┐                                    │
18 ──┤────────                                │
19 ──────────────┤────────┤──── Shrublands and mallee shrublands on laterite
                         │     and mallets & breakways on duplex soils of the
                         │     central wheatbelt.
20 ─                                          │
21 ┤──────────────────────┤──────────── Shrublands and mallee
                         │              shrublands on deep sand or
                         │              laterite of eastern
                         │              wheatbelt.
22 ─                                          │
23 ┤────────                                  │
24 ──────────┤──────                          │
25 ──────────────────┤────────┤──────────────┤──────┤ Species-poor quadrats
                                                      of eastern wheatbelt
                                                      +/- confined to duplex
                                                      soils & deep sands.

  │       │       │       │       │       │
 1.04    1.14    1.23    1.33    1.42    1.52
            Dissimilarity measure
```

Figure 9 Annotated dendrogram showing both the 8 (solid line) and 25 group classification of the 682 quadrats based on species composition of 1022 taxa occurring in five or more quadrats.

being recorded from the Avon, Geraldton Sandplains and Mallee bioregions and the Esperance Sandplains 2 subregion. Mean species richness was 33 taxa/quadrat and the most typical species included the herbs *Siloxerus multiflorus, Quinetia urvillei* and *Centrolepis polygyna.*

12. These species rich woodland quadrats (mean 48.3 taxa/quadrat) on granite or duplex soils were generally dominated by *Eucalyptus loxophleba, Allocasuarina huegeliana, Acacia acuminata* or *Eucalyptus wandoo.* They generally occurred in the Avon bioregion and the Jarrah Forest 1, and Mallee 2 subregions but also extended farther north and east. Typical species included *Podolepis lessonii, Borya sphaerocephala* and *Gonocarpus nodulosus.*

Western sand and laterite quadrats

13. Quadrats of group 13 were concentrated in the Avon 2 subregion but also extended into the Jarrah Forest bioregion and the Mallee 2 subregion. These quadrats almost exclusively occurred on laterite or deep sand, and the vegetation was generally shrubland or mallee shrubland but also included *Banksia* and eucalypt woodlands. Typical species included *Leptospermum erubescens, Banksia sphaerocarpa, Dryandra armata, Xanthorrhoea drummondii* and *Conostylis setigera.* Mean species richness was high (42.4 taxa/quadrat) and soil nutrient levels were much lower than quadrat groups 1 to 12.

14. More widespread than group 13, this group was well represented in the Avon bioregion, and the Geraldton Sandplains 2 and Mallee 2 subregions as well as extending into the Jarrah Forest bioregion and further north. Soil nutrients were poorer than quadrats in group 13, and again predominantly occurred on deep sand and laterite soils. Species richness was

Table 13 Distribution of 682 quadrats in the 25 group classification subdivided into biogeographic regions and subregions. (Other = biogeographic regions on eastern margin of study area; n = number of quadrats.)

	Jarrah Forest		Avon		Geraldton Sadplains		Swan Coastal Plain	Mallee		Esperance Sandplains		Other	n
	JF1	JF2	A1	A2	GS2	GS3	SCP2	M2	M1	ES1	ES2		
Group													
1	–	–	40	1	7	–	–	–	–	–	–	4	52
2	–	–	53	12	2	2	–	4	–	–	–	3	76
3	–	–	1	–	1	–	–	4	3	–	–	–	9
4	–	–	5	1	–	–	–	14	–	–	–	–	20
5	–	2	6	16	–	1	–	16	3	–	–	–	44
6	–	–	7	7	–	–	–	13	–	–	–	–	27
7	29	15	–	1	–	–	–	–	–	–	–	–	45
8	14	5	–	2	–	1	1	–	–	1	–	–	24
9	3	2	–	–	–	–	–	–	–	–	–	1	6
10	1	5	1	10	–	–	–	2	–	7	–	–	26
11	–	–	5	2	1	3	–	5	3	–	1	2	22
12	23	1	10	24	6	1	–	12	–	2	–	–	79
13	4	1	–	18	–	–	–	2	–	–	–	–	25
14	2	1	10	17	10	2	1	9	1	–	–	–	53
15	–	–	1	–	2	7	–	–	–	–	–	–	10
16	–	–	14	12	–	–	–	5	–	–	–	–	31
17	–	–	9	6	–	–	–	10	4	–	–	–	29
18	–	–	–	–	–	–	–	12	–	–	–	–	12
19	1	–	1	8	–	–	–	2	–	–	–	–	12
20	–	–	–	–	–	–	–	4	4	5	6	–	19
21	–	–	–	2	–	–	–	24	–	1	–	–	27
22	–	–	–	–	–	–	–	8	7	2	–	–	17
23	–	–	–	–	–	–	–	–	6	–	2	–	8
24	–	–	–	–	–	–	–	5	2	–	–	–	7
25	–	–	–	–	–	–	–	–	–	–	–	2	2

high (mean 40.1 taxa/quadrat) but dominance was variable, generally dominated either by eucalypt or *Banksia* species, but also occasionally by *Allocasuarina huegeliana*.

15. Group 15 were largely restricted to the Geraldton Sandplains bioregion, occurring solely on deep sands that represented the most deficient soils of the western deep sand and laterite quadrats. Typical species included *Drosera stolonifera, Xylomelum angustifolium, Ecdeiocolea monostachya, Banksia prionotes* and *Verticordia densiflora*. Mean species richness was 33.1 taxa/quadrat.

16. These quadrats were largely restricted to the Avon bioregion extending into the Mallee 2 subregion. Again occurring largely on deep sands or laterite soils. The vegetation was usually shrublands dominated by *Allocasuarina campestris* or open shrub mallees dominated by *Eucalyptus macrocarpa*. Typical species included *Allocasuarina campestris, Baeckea crispiflora, Melaleuca leptospermoides* and *Lepidobolus chaetocephalus*. Mean species richness was 40.7 taxa/quadrat. Soil nutrient levels were low and generally intermediate between those of quadrat groups 14 and 15 except for available K

(mean 66.6 ppm) which was higher than for either of those groups.

Central sand and laterite quadrats

17. Restricted to the Avon and Mallee bioregions these quadrats largely occurred on laterite or deep sands where they were variously dominated by eucalypt mallees, *Allocasuarina acutivalvis, A. campestris* or *Callitris* spp. Mean species richness (25.1 taxa/quadrat) was lower that quadrat groups 13 to 16. While the soils were nutrient impoverished they had higher levels of soil Ca (mean 2.3 me%) and available K (mean 111.3 ppm) than present in the western sand and laterite groups.

18. Only occurring in the Mallee 2 subregion on laterite or duplex soils these quadrats were dominated by various eucalypt mallees. The most typical species of this group were the *Melaleuca uncinata* complex, *Eucalyptus phaenophylla* subsp. *phaenophylla* and *Trymalium elachophyllum*. Species richness was similar to quadrat group 17 (mean 22.5 taxa/quadrat).

19. This small group of quadrats generally occurred on breakaways or in mallet stands on laterites. They were typically species poor (mean 11.1
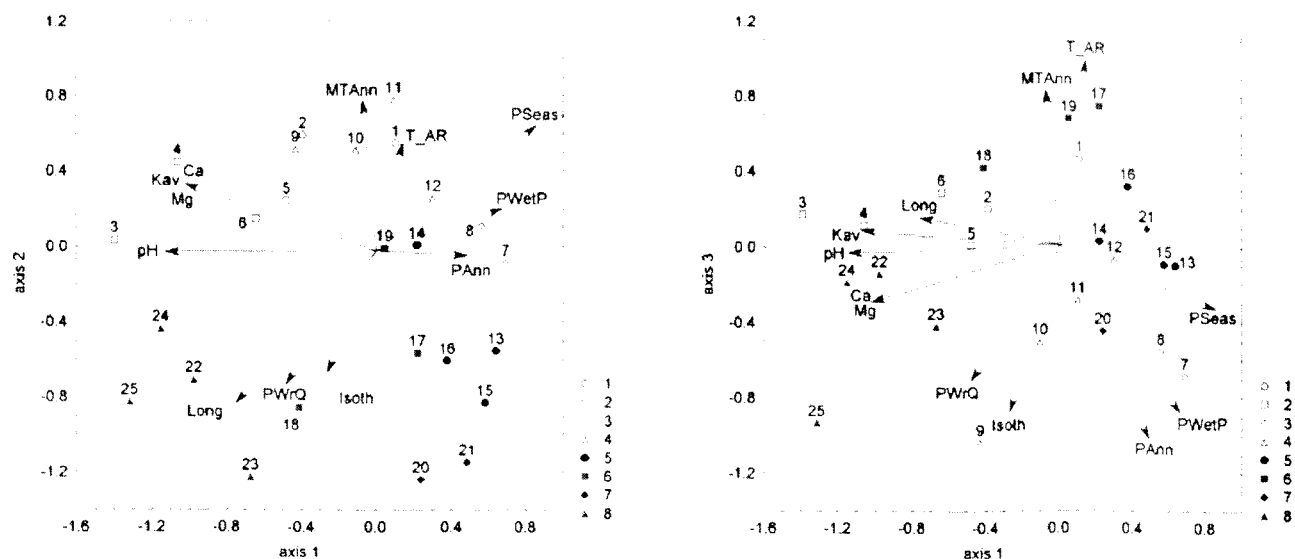
Figure 10 Ordination showing the group means for of the 25 quadrat groups classification (numbered), and the relationship to higher eight group classification shown as symbols. Principal axis correlations with the environmental attributes (r > 0.45) shown as vectors in the same ordination space. All correlations significant at $P < 0.001$, attribute codes as in Table 3. (a) Axis 1 vs 2, (b) Axis 1 vs 3.

taxa/quadrat) and were generally dominated by *Eucalyptus astringens* subsp. *astringens*. Soils had elevated electrical conductivity (mean 36.6 mS m⁻¹), total P (101.8 ppm), available K (240.7 ppm) and exchangable cations, probably as a result of the active erosion of the laterite cap and the exposed clays.

Eastern sand and laterite quadrats

20. Quadrats in this group were confined to the Mallee and Esperance Sandplains bioregions generally dominated by eucalypt mallees of which *Eucalyptus pleurocarpa* was the most common. Occasionally, *Banksia speciosa* formed the dominant canopy species. All but one quadrat occurred either on laterite or deep sand. Typical species for this group included *Lysinema ciliatum, Mesomelaena stygia, Allocasuarina thuyoides* and *Hakea corymbosa*. Soils were very nutrient deficient with mean total P values of 16.6 ppm.

21. Almost 90% of quadrats of group 21 were restricted to Mallee 2 subregion with a small number occurring in the adjacent Avon 2 and Esperance Sandplains 1 subregions. Most quadrats occurred on laterite soils supporting mallee shrublands or shrublands dominated by a large number of taxa. The most typical species of this group were *Conostylis argentea, Baeckea preissiana, Hakea cygna* and *Isopogon teretifolius*. These quadrats had higher mean species richness (43.3 taxa/quadrat) than the previous group and occurred on slightly more fertile soils.

Species poor duplex and granite soil quadrats

22. Confined to the Mallee bioregion and Esperance Sandplains 1 subregion this group of quadrats was largely restricted to duplex soils that supported eucalypt woodlands or mallee shrublands. Mean species richness was low (13.5 taxa/quadrat) and few taxa except for *Melaleuca cucullata* could be considered typical. Soil Ca levels were elevated with a mean of 4.6 me%.

23. These quadrats supported eucalypt woodlands or mallee shrublands in the Mallee 1 and Esperance Sandplains 2 subregions. All the quadrats occurred on duplex soils or sand dunes surrounding lakes. Typical species occurring in these quadrats included *Eucalyptus kessellii, E. incrassata, Astartea ambigua* and *Lepidosperma* sp. A2. Mean species richness was 17.1 taxa/quadrat.

24. These species-poor eucalypt woodlands and mallee quadrats on duplex soils were restricted to the Mallee bioregion. Mean species richness was low at 6.3 taxa/quadrat. The soils were near neutral with elevated electrical conductivity (87.4 mS m⁻¹) similar to other woodland quadrats on duplex soils. Typical species of these quadrats included *Eucalyptus salubris,* and two subspecies of *Melaleuca pauperiflora.*

25. The final group comprised two quadrats from granite pools on the eastern edge of the study area. Dominated by annuals the quadrats shared *Glossostigma drummondii* and *Crassula natans.* Mean species richness was 3 taxa/quadrat. Soil nutrient levels were high.

Table 14 Means and standard errors (se) of soil parameters, selected climatic estimates and species richness (after removal of taxa occurring in < 5 quadrats) of the 25 group classification (codes as in Table 3). Kruskal–Wallis ANOVA indicates significant differences between group means for all parameters at $P < 0.001$. Soil parameters were not available for one quadrat in group 11.

Group		1	2	3	4	5	6	7	8	9	10	11
EC	mean	8.44	16.24	160.44	60.34	21.63	19.00	6.88	4.21	358.93	77.44	17.39
	se	2.55	4.21	70.40	23.86	3.60	3.86	0.55	0.44	249.63	20.10	5.51
pH	mean	5.91	6.56	7.54	7.75	6.35	6.49	6.02	5.80	5.67	6.05	5.85
	se	0.06	0.07	0.28	0.13	0.07	0.13	0.04	0.07	0.34	0.12	0.13
OrgC	mean	0.94	1.36	1.90	2.30	2.77	1.97	4.00	1.66	2.87	2.93	1.22
	se	0.08	0.08	0.39	0.22	0.30	0.20	0.32	0.33	0.61	0.33	0.10
NTOT	mean	0.05	0.08	0.12	0.15	0.11	0.08	0.13	0.05	0.12	0.15	0.09
	se	0.00	0.01	0.03	0.02	0.01	0.01	0.01	0.01	0.02	0.02	0.01
PTOT	mean	71.63	95.34	115.56	115.35	101.57	60.07	91.80	31.92	118.17	103.46	234.43
	se	6.02	6.39	38.66	10.98	10.78	3.78	7.16	7.42	21.40	12.39	78.33
Pav	mean	1.68	4.43	5.89	6.50	5.47	2.62	3.69	2.02	4.00	4.36	13.69
	se	0.17	0.48	1.41	0.76	0.78	0.33	0.39	0.31	0.63	0.65	5.53
Kav	mean	112.69	212.14	415.00	568.50	232.39	159.00	110.44	40.04	94.83	195.08	114.62
	se	8.78	18.30	130.92	40.32	23.27	16.36	8.32	7.67	14.62	29.03	14.21
Mg	mean	0.60	1.90	3.21	4.23	3.12	3.30	1.46	0.59	5.36	4.35	0.70
	se	0.09	0.17	1.09	0.38	0.32	0.37	0.12	0.11	1.81	0.77	0.11
Ca	mean	1.62	4.52	8.91	12.41	6.35	4.14	5.74	2.88	1.83	5.75	1.43
	se	0.15	0.39	1.66	1.14	0.56	0.55	0.47	0.48	0.73	0.80	0.16
Na	mean	0.16	0.29	1.15	1.13	0.64	0.62	0.22	0.10	2.27	1.63	0.48
	se	0.03	0.03	0.40	0.23	0.10	0.10	0.03	0.02	0.68	0.32	0.08
Clay	mean	3.46	3.80	2.84	3.39	4.30	5.45	2.86	1.74	5.54	4.49	2.79
	se	0.23	0.29	0.50	0.36	0.59	0.64	0.36	0.67	1.39	0.88	0.44
Silt	mean	3.44	3.61	2.82	4.51	2.83	3.31	3.16	1.69	4.86	3.85	3.61
	se	0.16	0.15	0.61	0.39	0.21	0.23	0.15	0.31	0.73	0.40	0.43
Sand	mean	93.10	92.59	94.33	92.09	92.97	91.24	93.99	96.56	89.61	91.77	93.61
	se	0.31	0.38	0.70	0.52	0.57	0.77	0.39	0.93	1.15	1.06	0.81
Long	mean	116.89	117.34	119.25	118.75	118.35	118.29	116.60	116.62	116.64	117.63	118.27
	se	0.16	0.11	0.72	0.21	0.20	0.14	0.04	0.09	0.10	0.13	0.49
MTAnn	mean	18.48	17.75	16.71	16.84	15.92	16.38	15.55	16.07	16.18	15.43	17.03
	se	0.12	0.12	0.41	0.20	0.11	0.13	0.13	0.21	0.77	0.14	0.31
Isoth	mean	0.48	0.49	0.52	0.50	0.51	0.50	0.51	0.51	0.51	0.52	0.51
	se	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
T_AR	mean	29.33	28.65	25.58	27.45	26.15	27.60	25.16	25.98	25.88	24.04	26.88
	se	0.11	0.11	0.61	0.35	0.28	0.23	0.28	0.40	1.22	0.52	0.56
Pann	mean	315.02	328.87	338.33	324.40	380.05	347.63	669.87	570.92	572.33	452.96	368.23
	se	3.30	3.95	11.49	4.77	6.93	4.42	15.51	17.92	63.00	18.76	14.11
PWetP	mean	58.44	59.82	51.67	50.60	61.66	57.59	127.51	108.92	104.00	72.31	61.86
	se	1.25	1.14	7.25	1.40	1.88	1.31	3.73	3.99	11.94	3.83	4.60
Pseas	mean	63.88	63.55	44.44	49.45	55.23	56.67	76.78	75.96	71.33	57.08	55.36
	se	1.23	0.98	7.46	2.18	1.97	1.56	1.42	2.01	3.75	2.39	4.10
PWrQ	mean	40.69	38.14	47.22	43.55	44.30	41.07	45.49	42.50	46.50	47.88	46.82
	se	0.68	0.38	2.47	1.16	1.19	0.87	1.37	1.59	3.84	2.16	2.17
Species	mean	35.65	41.97	10.11	19.35	23.41	20.59	52.29	44.42	8.83	30.81	32.95
richness	se	1.76	1.32	1.21	1.69	1.32	1.58	1.79	3.07	1.87	2.38	2.07
Number quadrats		52	76	9	20	44	27	45	24	6	26	22

The 3D quadrat ordination (stress = 0.24) showed strong linear correlations with all environmental parameters ($P < 0.001$, Table 16). Strongest correlations were with rainfall (mean annual rainfall and rainfall of wettest period), annual temperature range (at 90° to the rainfall vector), longitude and the soil parameters, available K, exchangeable Mg and pH (all strongly divergent from the rainfall vector, Figure 10). The plot of the first and second axes show the groups typical of sand or laterite soils (quadrat groups 7, 8, 13 to 17, 19 to 21) concentrated in the lower right quadrant, with a strong longitude gradient toward the lower left corner and a strong pH gradient more or less parallel to axis 1. The gradient in annual rainfall can be seen in the axis 1 vs axis 3 plot with rainfall

12	13	14	15	16	17	18	19	20	21	22	23	24	25
7.10	7.28	4.89	3.20	2.58	5.79	9.00	36.58	4.68	7.07	19.31	9.44	87.43	18.13
0.45	0.99	0.46	0.63	0.21	1.06	2.29	8.27	1.06	1.94	3.56	2.20	49.89	10.68
5.97	5.78	5.88	6.01	5.90	5.96	6.35	5.93	5.92	6.04	6.98	6.89	6.91	5.35
0.04	0.05	0.06	0.05	0.05	0.08	0.08	0.10	0.06	0.05	0.18	0.40	0.26	0.75
1.89	1.78	1.21	0.52	0.73	1.40	1.41	5.59	0.86	0.75	1.67	1.44	2.25	0.77
0.12	0.16	0.18	0.04	0.05	0.13	0.16	0.69	0.13	0.05	0.12	0.23	0.18	0.21
0.09	0.07	0.05	0.02	0.03	0.06	0.05	0.17	0.03	0.03	0.06	0.05	0.10	0.08
0.01	0.01	0.01	0.00	0.00	0.01	0.01	0.02	0.01	0.00	0.00	0.01	0.01	0.03
68.53	52.04	33.94	14.00	29.35	44.55	40.33	101.83	16.58	20.59	40.47	23.13	74.00	235.00
3.09	5.66	2.71	2.62	2.24	4.14	4.91	11.79	3.91	1.23	3.71	6.70	16.73	55.00
2.43	1.74	1.27	0.38	0.81	1.11	1.63	4.45	1.24	0.67	2.28	1.70	3.43	10.50
0.21	0.26	0.16	0.18	0.17	0.20	0.26	0.79	0.21	0.15	0.48	0.46	0.61	5.50
127.75	89.68	62.30	22.40	66.61	111.34	130.17	240.67	50.89	84.56	188.00	121.38	371.43	140.00
6.57	10.40	8.75	4.89	6.34	8.36	22.17	32.34	7.28	7.70	19.93	28.69	39.67	20.00
0.95	0.62	0.41	0.14	0.36	0.94	1.07	3.48	0.48	0.48	2.55	1.19	6.30	0.54
0.08	0.08	0.06	0.03	0.04	0.18	0.23	0.59	0.15	0.05	0.25	0.26	0.79	0.23
3.36	1.95	1.86	0.75	1.11	2.29	3.58	7.71	1.02	1.12	4.63	4.45	7.09	0.73
0.25	0.26	0.28	0.09	0.16	0.32	0.56	1.47	0.11	0.12	0.46	1.85	1.40	0.48
0.20	0.18	0.13	0.06	0.04	0.16	0.26	1.42	0.12	0.12	0.37	0.24	1.68	0.49
0.02	0.03	0.02	0.02	0.01	0.03	0.07	0.34	0.05	0.03	0.05	0.05	0.71	0.04
3.15	3.37	2.52	2.14	2.83	3.80	3.25	4.69	2.59	3.18	4.45	2.72	5.82	5.45
0.20	0.44	0.21	0.26	0.14	0.56	0.22	0.59	0.42	0.33	1.30	0.43	2.37	0.25
3.58	2.45	1.95	1.23	2.17	3.26	3.08	2.67	2.17	2.20	3.26	2.11	4.45	4.50
0.17	0.25	0.16	0.13	0.10	0.20	0.27	0.38	0.32	0.15	0.26	0.47	0.59	0.20
93.26	94.18	95.52	96.63	95.00	92.94	93.67	92.64	95.24	94.62	92.29	95.16	89.73	90.05
0.27	0.44	0.32	0.27	0.17	0.58	0.40	0.73	0.65	0.38	1.31	0.70	2.23	0.45
117.22	117.34	117.18	115.92	117.95	118.77	119.06	117.55	120.52	119.03	120.35	121.71	119.81	117.67
0.13	0.09	0.20	0.36	0.11	0.26	0.08	0.22	0.34	0.09	0.34	0.24	0.40	0.88
16.30	15.42	17.05	18.28	16.53	16.50	15.83	15.94	15.59	15.75	15.60	15.88	15.80	18.70
0.12	0.05	0.18	0.22	0.08	0.15	0.07	0.23	0.10	0.06	0.10	0.11	0.10	0.70
0.50	0.50	0.50	0.51	0.50	0.50	0.51	0.50	0.54	0.51	0.53	0.55	0.53	0.48
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
26.59	26.32	26.95	28.38	27.99	27.33	26.51	27.00	21.99	26.05	23.12	21.93	24.74	30.15
0.19	0.14	0.23	0.31	0.12	0.39	0.30	0.19	0.32	0.27	0.27	0.25	0.33	0.45
447.09	447.52	378.47	421.90	346.45	346.55	347.50	410.42	442.53	351.19	383.65	451.00	341.43	279.00
11.38	13.99	7.12	24.65	1.58	5.89	1.99	17.20	18.01	3.20	11.62	13.70	5.00	13.00
83.05	80.84	70.60	88.80	60.45	54.69	52.25	73.17	58.11	52.19	48.82	56.63	46.43	47.50
2.91	3.49	2.53	6.39	0.94	1.20	0.76	4.54	3.13	0.89	1.57	2.31	2.18	5.50
68.65	67.04	67.21	78.80	61.77	52.66	46.92	65.33	39.68	46.44	36.76	39.13	38.71	56.00
1.60	1.58	2.07	3.17	1.46	2.06	1.40	2.71	1.71	1.23	1.31	1.14	3.36	6.00
39.97	40.08	38.87	42.90	37.39	44.03	47.00	39.50	61.79	47.37	56.82	67.50	50.29	38.50
0.68	0.52	0.85	0.81	0.88	1.55	1.02	0.99	1.63	0.82	1.75	0.63	1.49	0.50
48.30	42.36	40.70	33.10	40.71	25.10	22.50	11.17	34.63	43.33	13.47	17.13	6.29	3.00
1.31	1.72	1.58	3.02	1.94	1.37	1.32	0.91	2.00	1.68	0.77	1.94	1.43	1.00
79	25	53	10	31	29	12	12	19	27	17	8	7	2

increasing toward the lower right corner of the plot.

Patterns in species composition

The 1022 taxa that occurred in five or more quadrats were partitioned into 26 assemblages based on similarity of occurrence in the 682 quadrats (Figure 11). Three small assemblages (assemblages 18, 19 and 20) were considered not to have been well sampled and were amalgamated with a larger assemblage (assemblage 21) with similar habitat preferences. The resulting 23 assemblages were characterized in terms of the distributional characteristics and habitat preferences of their component species throughout their geographical ranges, and are described below:

Table 15 Percentage of occurrence of taxa in quadrat groups. Only includes those taxa with INDVAL value of > 25% (method of Dufrene and Legendre 1997). These taxa are regarded as the best indicator species for each level in the quadrat classification. Division level in classification indicated by binary code on right margin and shading. Note an individual taxon may be good indicator species for more than one level in the classification.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	level
Waitzia acuminata	92	49	11	5	14	11	–	8	–	4	5	35	8	38	–	26	3	–	–	–	4	–	–	–	–	0000
Velleia cycnopotamica	73	30	–	5	–	4	–	–	–	4	27	29	4	11	–	3	–	–	–	–	–	–	–	–	–	0000
Lawrencella rosea	67	33	–	–	–	4	2	13	–	8	–	30	–	8	–	–	3	–	–	–	–	–	–	–	–	0000
Cheilanthes austrotenuifolia	54	11	–	–	–	–	–	–	–	4	23	22	–	2	–	–	3	–	–	–	–	–	–	–	–	0000
Plantago aff. *hispidula*	8	47	–	10	–	11	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	0001
Calotis hispidula	8	58	–	25	5	22	–	–	–	4	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	0001
Trachymene cyanopetala	77	74	11	–	11	30	2	4	–	–	–	47	–	32	10	26	7	–	17	–	–	–	–	–	–	000
Erodium cygnorum	38	51	–	–	–	–	–	–	–	–	5	14	–	4	–	–	–	–	–	–	–	–	–	–	–	000
Waitzia acuminata	92	49	11	5	14	11	–	8	–	4	5	35	8	38	–	26	3	–	–	–	4	–	–	–	–	000
Goodenia berardiana	42	49	–	–	–	11	–	–	–	–	9	18	–	9	–	13	–	–	–	–	–	–	–	–	–	000
Velleia cycnopotamica	73	30	–	5	–	4	–	–	–	4	27	29	4	11	–	3	–	–	–	–	–	–	–	–	–	000
Chthonocephalus pseudevax	33	26	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	000
Enchylaena tomentosa	13	67	67	70	9	15	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	000
Arctotheca calendula	42	67	–	5	14	11	9	21	17	15	32	33	8	26	–	3	7	–	–	–	4	–	–	–	–	000
Hyalosperma glutinosum	17	41	–	–	–	7	2	–	–	–	5	4	–	–	–	–	–	–	–	–	–	–	–	–	–	000
Plantago aff. *hispidula*	8	47	–	10	–	11	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	000
Calotis hispidula	8	58	–	25	5	22	–	–	–	4	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	000
Threlkeldia diffusa	–	5	67	5	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	00100
Carpobrotus modestus	–	–	44	–	14	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–	6	–	–	–	00100
Rhagodia drummondii	6	59	78	50	14	4	–	4	–	8	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	00100
Asteridea athrixioides	–	5	–	50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	00101
Atriplex vesicaria	–	17	11	65	5	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	00101
Sclerolaena diacantha	–	53	–	80	5	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	00101
Lycium australe	–	5	11	50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	00101
Eucalyptus longicornis	–	4	–	50	20	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	00101
Zygophyllum ovatum	–	4	–	30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	00101
Atriplex vesicaria	–	17	11	65	5	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0010
Enchylaena tomentosa	13	67	67	70	9	15	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0010
Lycium australe	–	5	11	50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0010
Asteridea athrixioides	–	5	–	50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0010
Sclerolaena diacantha	–	53	–	80	5	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	0010
Rhagodia drummondii	6	59	78	50	14	4	–	4	–	8	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	0010
Eucalyptus calycogona	–	1	–	–	2	33	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	00111
Enchylaena tomentosa	13	67	67	70	9	15	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	00
Austrostipa elegantissima	44	92	–	80	75	74	4	–	–	62	–	66	8	72	10	55	17	8	8	–	–	6	–	14	–	00
Crassula colorata	33	80	11	25	32	56	2	29	–	15	73	19	16	36	10	6	10	–	–	–	–	–	–	–	–	00
Trachymene cyanopetala	77	74	11	–	11	30	2	4	–	–	–	47	–	32	10	26	7	–	17	–	–	–	–	–	–	00
Rhagodia drummondii	6	59	78	50	14	4	–	4	–	8	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	00
Eucalyptus salmonophloia	–	37	–	25	57	26	–	–	–	–	–	1	–	–	–	–	–	–	8	–	–	–	–	14	–	00
Lechenaultia biloba	–	–	–	–	–	–	53	–	–	–	–	1	8	2	–	–	–	–	–	–	–	–	–	–	–	0100

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Sample codes (column headers, left to right): 0100 (×13), 0101 (×6), 010 (×26), 011000 (×2)

Species		
Bossiaea ornata	40	—
Trichocline spathulata	42	—
Dampiera alata	40	—
Tetraria octandra	67	21
Eucalyptus marginata	56	38
Dryandra lindleyana	56	21
Hibbertia commutata	53	13
Astroloma pallidum	53	13
Gompholobium marginatum	49	13
Lagenophora huegelii	69	42
Desmocladus fasciculatus	58	33
Lysinia barbata	2	58
Hypolaena exsulca	13	58
Phlebocarya ciliata	—	29
Hibbertia subvaginata	9	38
Hovea trisperma	9	38
Schoenus curvifolius	2	46
Eucalyptus marginata	56	38
Tetraria octandra	67	21
Desmocladus fasciculatus	58	33
Xanthorrhoea preissii	51	50
Dryandra lindleyana	56	21
Lagenophora huegelii	69	42
Eucalyptus calophylla	47	33
Lomandra hermaphrodita	38	38
Astroloma pallidum	53	13
Hibbertia hypericoides	47	29
Bossiaea eriocarpa	33	58
Lechenaultia biloba	53	—
Trachymene pilosa	56	88
Conostylis setigera	40	50
Hibbertia commutata	53	13
Gompholobium marginatum	49	13
Macrozamia riedlei	33	25
Lepidosperma leptostachyum	53	17
Dampiera linearis	42	17
Hakea lissocarpha	62	8
Hypolaena exsulca	13	58
Xanthosia huegelii	24	42
Lomandra caespitosa	33	25
Trichocline spathulata	42	—
Bossiaea ornata	40	—
Acacia pulchella	31	29
Stylidium calcaratum	42	29
Centrolepis polygyna	—	4
Juncus bufonius	—	4

Table 15 (cont.)

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	level
Cotula coronopifolia	–	–	–	–	–	–	–	–	50	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	011000
Ehrharta longiflora	13	17	–	–	16	4	–	–	–	58	5	10	–	9	–	–	–	–	–	–	–	–	–	–	–	011001
Briza minor	–	3	–	–	5	–	31	–	17	69	23	27	–	–	–	–	–	–	–	–	–	–	–	–	–	011001
Siloxerus multiflorus	6	–	–	–	–	–	2	–	17	8	68	24	–	–	–	–	–	–	–	–	–	–	–	–	–	01101
Centrolepis polygyna	2	–	–	–	–	–	–	4	100	31	64	3	–	–	–	–	–	–	–	–	–	–	–	–	–	01101
Quinetia urvillei	12	7	–	–	5	–	4	29	17	4	68	28	4	8	10	–	–	–	–	–	–	–	–	–	–	01101
Centrolepis pilosa	2	1	–	–	2	–	–	29	–	4	45	13	4	9	–	–	–	–	–	–	–	–	–	–	–	01101
Crassula exserta	2	3	–	5	14	7	–	4	–	19	45	–	–	–	–	–	3	–	–	–	–	–	–	–	–	01101
Centrolepis polygyna	2	–	–	–	–	–	–	4	100	31	64	3	–	–	–	–	–	–	–	–	–	–	–	–	–	0110
Briza minor	–	3	–	–	5	–	31	–	17	69	23	27	–	–	–	–	–	–	–	–	–	–	–	–	–	01100
Podolepis lessonii	23	32	–	–	9	7	7	–	–	4	27	66	4	4	–	3	–	–	–	–	–	–	–	–	–	0111
Borya sphaerocephala	13	7	–	–	2	–	13	17	–	15	18	61	–	8	–	16	–	–	–	–	4	–	–	–	–	0111
Gonocarpus nodulosus	29	5	–	–	–	–	2	–	–	19	36	52	–	6	10	–	3	–	–	–	–	–	–	–	–	0111
Gonocarpus nodulosus	29	5	–	–	–	–	2	–	–	19	36	52	–	6	10	–	3	–	–	–	–	–	–	–	–	011
Parentucellia latifolia	8	11	–	–	–	–	18	17	–	35	50	54	–	11	–	–	–	–	–	–	–	–	–	–	–	011
Hypochaeris glabra	88	72	–	25	55	33	62	83	33	81	100	90	48	92	20	23	21	8	8	–	4	12	–	–	–	011
Ursinia anthemoides	35	37	–	–	50	15	4	50	–	58	59	70	4	68	10	23	3	–	–	–	4	–	–	–	–	011
Podolepis lessonii	23	32	–	–	9	7	7	–	–	4	27	66	4	4	–	3	–	–	–	–	–	–	–	–	–	011
Anagallis arvensis	6	9	–	–	16	–	11	8	–	62	23	43	–	11	–	–	–	–	–	–	–	–	–	–	–	011
Borya sphaerocephala	13	7	–	–	2	–	13	17	–	15	18	61	–	8	–	16	–	–	–	–	4	–	–	–	–	011
Drosera glanduligera	31	7	–	–	–	4	16	17	–	12	64	54	8	8	–	6	24	–	–	–	4	–	–	–	–	011
Aira caryophyllea	37	32	–	30	32	15	60	58	–	58	68	73	28	38	10	13	–	–	–	–	–	–	–	–	–	011
Siloxerus multiflorus	6	–	–	–	–	–	2	–	17	8	68	24	–	–	–	–	–	–	–	–	–	–	–	–	–	011
Aira caryophyllea	37	32	–	30	32	15	60	58	–	58	68	73	28	38	10	13	–	–	–	–	–	–	–	–	–	01
Hypochaeris glabra	88	72	–	25	55	33	62	83	33	81	100	90	48	92	20	23	21	8	8	–	4	12	–	–	–	01
Lagenophora huegelii	–	3	–	5	7	–	69	42	–	19	–	37	4	–	–	–	–	–	–	–	–	–	–	–	–	01
Trachymene pilosa	2	13	–	–	25	11	56	88	–	19	41	54	32	43	10	3	–	–	17	–	–	–	–	–	–	01
Parentucellia latifolia	8	11	–	–	–	–	18	17	–	35	50	54	–	11	–	–	–	–	–	–	–	–	–	–	–	01
Hydrocotyle callicarpa	15	1	11	–	2	–	49	21	–	–	18	54	8	2	–	13	3	–	8	–	–	–	–	–	–	01
Eucalyptus wandoo	–	3	–	–	30	–	53	8	33	19	–	49	16	–	–	3	–	–	–	–	–	–	–	–	–	01
Briza minor	–	3	–	–	5	–	31	–	17	69	23	27	–	–	–	–	–	–	–	–	–	–	–	–	–	01
Briza maxima	15	12	–	–	7	–	20	38	17	50	18	42	–	6	–	–	–	–	–	–	–	–	–	–	–	01
Hypochaeris glabra	88	72	–	25	55	33	62	83	33	81	100	90	48	92	20	23	21	8	8	–	4	12	–	–	–	0
Vulpia sp.	56	61	11	35	39	59	27	71	33	27	100	58	16	66	10	19	10	–	25	–	–	6	13	–	–	0
Austrostipa elegantissima	44	92	–	80	75	74	4	–	–	62	–	66	8	72	10	55	17	8	8	–	–	6	–	14	–	0
Aira caryophyllea	37	32	–	30	32	15	60	58	–	58	68	73	28	38	10	13	–	–	–	–	–	–	–	–	–	0
Ursinia anthemoides	35	37	–	–	50	15	4	50	–	58	59	70	4	68	10	23	3	–	–	–	4	–	–	–	–	0
Trachymene cyanopetala	77	74	11	–	11	30	2	4	–	–	–	47	–	32	10	26	7	–	17	–	–	–	–	–	–	0
Neurachne alopecuroidea	17	22	–	–	34	15	82	42	–	42	5	87	92	81	50	97	52	75	–	74	100	24	38	–	–	1
Lepidobolus chaetocephalus	4	4	–	–	–	–	2	8	–	4	–	11	44	38	50	68	–	–	–	–	16	70	–	–	–	1
Drosera macrantha	33	5	–	–	2	–	36	29	–	4	9	41	68	40	10	68	83	–	–	–	16	52	–	–	–	1

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Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Code
Mesomelaena preissii	4	5	–	–	–	–	2	–	–	–	–	3	40	47	50	55	–	–	–	5	48	–	–	–	1
Amphipogon turbinatus	–	1	–	–	2	–	9	46	–	4	–	3	40	32	30	23	3	–	–	89	74	–	–	–	1
Neurachne alopecuroidea	17	22	–	34	15	82	42	–	42	5	87	92	81	50	97	52	75	–	74	100	24	38	–	–	10
Lepidobolus chaetocephalus	4	4	–	–	–	2	8	–	4	–	11	44	38	50	68	–	–	–	16	70	–	–	–	–	10
Drosera macrantha	33	5	–	2	–	36	29	–	4	9	41	68	40	10	68	83	–	–	16	52	–	–	–	–	10
Mesomelaena preissii	4	5	–	–	–	–	2	–	–	–	–	3	40	47	50	55	–	–	–	5	48	–	–	–	10
Amphipogon turbinatus	–	1	–	–	2	–	9	46	–	4	–	3	40	32	30	23	3	–	–	89	74	–	–	–	10
Mesomelaena preissii	4	5	–	–	–	–	2	–	–	–	–	3	40	47	50	55	–	–	–	5	48	–	–	–	1000
Banksia sphaerocarpa	–	–	–	–	–	–	–	–	–	–	–	64	2	–	16	–	–	–	5	33	–	–	–	–	100000
Dryandra nivea subsp. *nivea*	–	–	–	–	–	–	2	4	–	–	–	44	–	10	–	–	–	–	5	4	–	–	–	–	100000
Xanthorrhoea drummondii	–	–	–	–	–	–	2	–	–	–	3	48	6	–	6	–	–	–	–	–	–	–	–	–	100000
Eucalyptus drummondii	–	–	–	–	–	–	–	–	–	–	–	32	–	–	–	–	–	–	–	–	–	–	–	–	100000
Chamaexeros serra	–	–	–	–	–	–	7	–	–	–	1	52	2	–	3	–	–	8	16	19	–	–	–	–	100000
Leptospermum erubescens	–	–	–	–	2	–	11	8	–	–	19	72	28	30	10	14	33	–	11	15	–	–	–	–	100000
Melaleuca subtrigona	–	–	–	–	2	–	–	4	–	–	–	48	8	10	16	3	–	–	11	7	–	–	–	–	100000
Dryandra armata	–	–	–	–	–	–	13	–	–	–	–	52	8	–	6	–	–	8	37	7	–	–	–	–	100000
Hakea lehmanniana	–	–	–	–	–	–	–	–	–	–	–	32	–	–	–	–	–	–	5	11	–	–	–	–	100000
Conostylis setigera	–	–	–	–	–	–	40	50	–	8	–	5	60	9	10	10	–	–	16	4	–	–	–	–	100000
Schoenus latitans	–	1	–	–	–	–	–	–	–	–	–	–	4	50	3	–	–	–	–	–	–	–	–	–	1000011
Dampiera spicigera	–	–	–	–	–	–	–	4	–	–	–	–	–	40	–	–	–	–	–	–	–	–	–	–	1000011
Jacksonia floribunda	–	–	–	–	–	–	–	4	–	–	–	–	–	40	–	–	–	–	–	–	–	–	–	–	1000011
Pileanthus peduncularis	2	–	–	–	–	–	–	–	–	–	–	–	–	40	–	–	–	–	–	–	–	–	–	–	1000011
Dryandra shuttleworthiana	–	–	–	–	–	–	–	–	–	–	–	–	2	40	–	–	–	–	–	–	–	–	–	–	1000011
Verticordia densiflora	–	–	–	–	–	–	–	17	–	–	1	–	6	50	–	–	–	–	11	–	–	–	–	–	1000011
Calytrix flavescens	–	–	–	–	–	–	–	8	–	–	–	–	2	40	–	–	–	–	–	–	–	–	–	–	1000011
Mesomelaena pseudostygia	–	–	–	–	–	–	–	–	–	–	–	–	6	40	–	–	–	–	–	–	–	–	–	–	1000011
Calytrix strigosa	–	–	–	–	–	–	–	–	–	–	–	–	6	40	–	–	–	–	–	–	–	–	–	–	1000011
Drosera stolonifera	4	1	–	–	–	–	24	17	–	–	18	5	–	19	70	3	–	8	–	–	–	–	–	–	1000011
Ecdeiocolea monostachya	15	1	–	–	–	–	–	–	–	–	–	1	–	23	60	3	3	–	–	–	–	–	–	–	1000011
Beaufortia elegans	–	–	–	–	–	–	–	4	–	–	–	–	–	2	40	–	3	–	5	–	–	–	–	–	1000011
Synaphea spinulosa ssp. *spinulosa*	–	–	–	–	–	–	–	4	–	–	–	1	–	2	40	3	–	–	5	4	–	–	–	–	1000011
Xylomelum angustifolium	–	1	–	–	–	–	–	–	–	–	–	–	–	11	40	–	–	–	–	–	–	–	–	–	1000011
Melaleuca trichophylla	–	–	–	–	–	–	–	–	–	–	–	3	–	–	30	–	–	–	–	–	–	–	–	–	1000011
Hibbertia acerosa	–	–	–	–	–	–	–	–	–	–	–	–	–	2	30	–	–	–	5	–	–	–	–	–	1000011
Banksia prionotes	–	–	–	–	–	–	–	–	–	–	–	–	–	19	40	–	–	–	–	4	–	–	–	–	1000011
Triodia danthonioides	–	–	–	–	–	–	–	–	–	–	–	–	–	6	30	–	–	–	–	–	–	–	–	–	1000011
Melaleuca leptospermoides	–	–	–	–	–	–	–	–	–	–	–	–	–	21	–	71	3	–	–	4	–	–	–	–	10001
Psammomoya choretroides	2	–	–	–	–	–	–	–	–	–	–	–	–	13	–	58	7	–	–	30	–	–	–	–	10001
Allocasuarina campestris	29	–	–	–	2	–	–	–	–	–	5	18	–	25	20	81	52	–	11	22	–	–	–	–	10001
Baeckea crispiflora	2	–	–	5	–	–	–	4	–	–	5	28	13	10	71	31	17	–	–	30	–	–	–	–	10001
Hakea incrassata	–	–	–	–	–	4	4	–	–	–	1	36	13	10	61	7	–	–	–	30	–	–	–	–	10001
Verticordia chrysantha	2	1	–	–	–	–	–	–	–	–	5	–	9	–	68	34	8	–	11	48	–	–	–	–	10001
Hibbertia exasperata	2	–	–	–	–	–	2	–	–	–	–	32	13	–	58	14	42	–	–	33	–	–	–	–	10001
Comesperma scoparium	2	–	–	–	–	–	–	–	–	–	–	1	–	25	20	42	–	–	–	11	–	–	–	–	10001

Table 15 (cont.)

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	level
Lepidobolus chaetocephalus	4	4	–	–	–	–	2	8	–	4	–	11	44	38	50	68	–	–	–	16	70	–	–	–	–	10001
Phebalium tuberculosum	10	1	–	–	2	–	–	–	–	–	–	1	–	15	–	6	38	58	–	–	4	18	–	–	–	10010
Allocasuarina acutivalvis	19	–	–	–	–	4	–	–	–	–	–	–	–	6	–	6	59	25	8	–	33	–	–	–	–	10010
Hakea scoparia subsp. *scoparia*	4	–	–	–	–	–	–	–	–	–	–	3	–	2	–	26	45	17	–	–	7	–	–	–	–	10010
Micromyrtus obovata	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	3	38	–	–	–	4	–	–	–	–	100100
Trymalium elachophyllum	–	–	11	–	–	4	–	–	–	–	–	–	–	–	–	–	–	50	–	–	–	6	–	–	–	100101
Eucalyptus phaenophylla subsp. *phaenophylla*	–	–	–	–	2	7	–	–	–	–	–	1	–	–	–	–	7	50	–	5	–	6	–	–	–	100101
Melaleuca uncinata group	15	4	11	–	14	41	–	–	–	8	–	13	4	13	–	10	38	100	33	–	15	6	–	–	–	100101
Cryptandra minutifolia subsp. *minutifolia*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3	42	–	–	–	–	–	–	–	100101
Platysace maxwellii	–	–	–	–	–	4	–	–	–	–	–	4	–	–	–	3	–	42	–	–	7	–	–	–	–	100101
Melaleuca spicigera	2	1	–	–	–	7	–	–	–	–	–	–	–	–	–	3	3	42	8	–	–	–	–	–	–	100101
Melaleuca laxiflora	4	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	7	42	8	–	–	–	–	–	–	100101
Eucalyptus astringens subsp. *astringens*	–	–	–	–	14	4	–	–	–	4	–	–	–	–	–	–	–	–	83	–	–	–	–	–	–	10011
Amphipogon turbinatus	–	1	–	–	2	–	9	46	–	4	–	3	40	32	30	23	3	–	–	89	74	–	–	–	–	101
Lysinema ciliatum	–	–	–	–	–	–	–	8	–	–	–	–	8	9	–	16	3	–	–	68	52	–	–	–	–	101
Hibbertia gracilipes	2	–	–	–	–	4	2	–	–	–	–	–	8	2	–	3	7	–	–	68	63	12	50	–	–	101
Conostylis argentea	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	6	–	–	–	11	74	–	–	–	–	101
Hakea cygna	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	10	–	–	–	21	56	–	–	–	–	101
Baeckea preissiana	–	–	–	–	–	–	–	4	–	–	–	1	40	13	–	16	3	–	–	21	70	–	–	–	–	101
Beaufortia micrantha	2	–	–	–	–	–	–	–	–	–	–	–	12	8	10	23	7	–	–	32	56	–	–	–	–	101
Isopogon buxifolius	–	–	–	–	–	4	–	–	–	4	–	1	4	4	–	6	3	8	–	37	52	–	25	–	–	101
Banksia violacea	–	–	–	–	–	–	–	–	–	–	–	–	12	2	–	–	–	–	–	16	52	–	–	–	–	101
Eucalyptus pleurocarpa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	63	15	–	–	–	–	101
Isopogon teretifolius	–	–	–	–	–	–	–	–	–	–	–	–	36	–	–	–	3	–	–	11	56	–	–	–	–	101
Mesomelaena stygia	–	–	–	–	–	–	4	–	–	–	–	–	4	2	–	10	–	–	–	63	11	–	–	–	–	101
Chamelaucium naviculum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–	–	5	44	–	–	–	–	101
Hakea corymbosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	53	7	–	–	–	–	101
Lomandra mucronata	2	1	–	–	2	–	–	–	–	–	–	1	12	2	–	–	3	17	–	32	33	–	13	–	–	101
Eucalyptus pleurocarpa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	63	15	–	–	–	–	1010
Hakea corymbosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	53	7	–	–	–	–	1010
Mesomelaena stygia	–	–	–	–	–	–	4	–	–	–	–	–	4	2	–	10	–	–	–	63	11	–	–	–	–	1010
Allocasuarina thuyoides	4	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	3	–	–	53	7	–	–	–	–	1010
Agonis spathulata var. *spathulata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	42	7	–	–	–	–	1010
Darwinia vestita	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	–	–	–	–	–	1010
Schoenus obtusifolius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	4	–	–	–	–	1010
Lysinema ciliatum	–	–	–	–	–	–	–	8	–	–	–	–	8	9	–	16	3	–	–	68	52	–	–	–	–	1010
Anarthria humilis	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–	–	32	–	–	–	–	–	1010

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Species																									
Isopogon polycephalus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26	–	–	–	–	1010
Conostylis argentea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	6	–	11	74	–	–	–	1011
Banksia violacea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	2	–	–	16	52	–	–	–	1011
Chamelaucium naviculum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–	5	44	–	–	–	1011
Hakea cygna	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	10	21	56	–	–	–	1011
Isopogon teretifolius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	36	–	–	3	11	56	–	–	–	1011
Baeckea preissiana	–	–	–	–	–	–	–	4	–	–	–	–	–	–	1	40	13	16	3	21	70	–	–	–	1011
Chamaexeros fimbriata	8	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	19	–	–	44	–	–	–	1011
Dryandra ferruginea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	3	3	–	33	–	–	–	1011
Astartea ambigua	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	5	–	53	88	–	11
Melaleuca undulata	2	–	–	–	2	19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	53	38	14	11
Melaleuca societatis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	29	50	–	11
Astartea ambigua	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	5	–	53	88	–	110
Melaleuca undulata	2	–	–	–	2	19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	53	38	14	110
Melaleuca societatis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	29	50	–	110
Astartea ambigua	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	5	–	53	88	–	1100
Melaleuca societatis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	29	50	–	1100
Melaleuca undulata	2	–	–	–	2	19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	53	38	14	1100
Grevillea oligantha	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	24	38	–	1100
Melaleuca cucullata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	35	–	14	11000
Eucalyptus kessellii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	6	63	–	11001
Astartea ambigua	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	5	–	53	88	–	11001
Phymatocarpus maxwellii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	50	–	11001
Melaleuca subfalcata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	6	50	–	11001
Banksia media	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26	4	–	50	–	11001
Gahnia ancistrophylla	–	–	–	5	7	–	–	–	8	–	1	–	–	–	–	–	–	–	7	21	–	12	63	–	11001
Melaleuca glaberrima	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	3	5	–	–	38	–	11001
Melaleuca societatis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	29	50	–	11001
Boronia albiflora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	4	–	38	–	11001
Eucalyptus incrassata	–	–	–	–	–	4	–	–	–	–	–	4	2	–	–	–	–	8	8	21	–	–	50	–	11001
Lepidosperma sp. A2	–	1	–	5	5	–	–	–	–	4	–	4	8	6	–	3	3	25	8	21	4	–	63	–	11001
Eucalyptus uncinata	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	3	11	–	6	38	–	11001
Eucalyptus salubris	–	20	–	15	7	15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	57	–	1101
Melaleuca pauperiflora subsp. pauperiflora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	43	–	1101
Melaleuca pauperiflora subsp. fastigiata	–	5	22	5	–	7	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	43	–	1101
Glossostigma drummondii	–	–	–	–	–	–	–	–	–	–	36	–	–	–	–	–	–	–	–	–	–	–	–	100	111
Crassula natans	–	–	–	–	–	–	–	–	–	–	45	–	–	–	–	–	–	–	–	–	–	–	–	100	111
Isoetes caroli	–	–	–	–	–	–	–	–	–	–	18	–	–	–	–	–	–	–	–	–	–	–	–	50	111
Agrostis avenacea	–	–	–	–	2	4	–	–	17	15	18	4	–	–	–	3	–	–	–	–	–	–	–	50	111

Table 16 Correlation of environmental parameters with quadrat ordination scores. Codes as given in Table 3. Significance tested by Monte-Carlo simulation, all with $P < 0.001$.

Environmental parameter	Correlation with ordination
PAnn	0.7199
PWetP	0.6860
Kav	0.6014
T_AR	0.5811
Long	0.5790
Mg	0.5697
pH	0.5655
PSeas	0.5599
Isoth	0.5555
Ca	0.4878
MTAnn	0.4548
PWrQ	0.4522
NTOT	0.4376
Elev	0.4256
MTDQ	0.4111
PTOT	0.4081
Na	0.4051
Silt	0.3667
Pav	0.3381
MTWetQ	0.3294
Sand	0.3134
EC	0.2944
OrgC	0.2694
MnTCP	0.2625
MTClQ	0.2427
Clay	0.2035

Assemblages centred on duplex and granite soils

1. The taxa of assemblage 1 are widespread across the Avon and Coolgardie bioregions with some of the annual and shrub components extending into *Acacia* shrublands of the Eremaean. It is overwhelmingly composed of annual herbs and geophytes. The species are more abundant on the more fertile duplex and granite soils; they generally do not occur in wetlands or the highest rainfall areas of the SWBP. Typical species include the canopy species *Eucalyptus loxophleba* subsp. *loxophleba, Acacia acuminata, E. capillosa* subsp. *capillosa* and *Santalum acuminatum* and numerous annual herbs that are common in *Eucalyptus loxophleba* woodlands (e.g. *Waitzia acuminata, Rhodanthe laevis, Hyalospermum demissum*).

2. Taxa predominantly of the eucalypt mallee shrublands and *Acacia* shrublands of the Geraldton Sandplains, Yalgoo and Avon bioregions, extending south into the Coolgardie bioregion constitute assemblage 2. They generally occur on sandy loams and sand derived from granitic or lateritic surfaces but also includes taxa that can occur on the fine textured soils of the broad valley units. Typical species include *Acacia coolgardiensis* subsp. *coolgardiensis, A. stereophylla* subsp. *stereophylla, Eucalyptus loxophleba* subsp. *lissophloia, E. eudesmioides, Spartochloa scirpoidea* and *Triodia longipalea*.
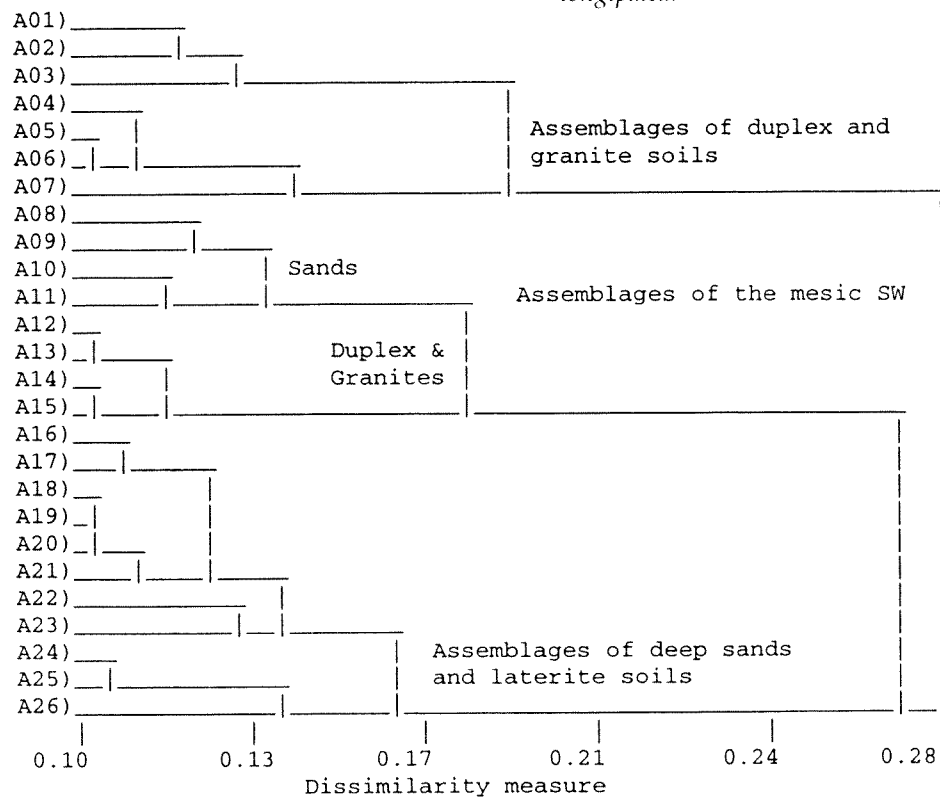
Figure 11 Annotated dendrogram showing 26 group classification of the 1022 taxa (occurring in ≥ 5 quadrats) based on similarity in occurrence at 682 quadrats. The three group level broadly corresponds edaphic and rainfall groupings.

3. Semi-arid and arid woodland species of the duplex soils of broad valley floors in the Coolgardie bioregion, the southern part of the Yalgoo, the eastern part of the Avon and the northern part of the Mallee bioregions form assemblage 3. It also includes woodland species of calcareous soils. Canopy species include *Eucalyptus salmonophloia*, *E. longicornis*, *E. yilgarnensis*, *E. salubris*, and the shrubs *Acacia erinacea*, *Olearia muelleri*, *Enchylaena tomentosa*, *Rhagodia drummondii* and *Sclerolaena diacantha*. Typical herbs include *Velleia rosea*, *Myriocephalus guerinae* and *Ptilotus exaltatus*. This assemblage faces significant risk from dryland salinity.

4. Assemblage 4 consists of taxa occurring on sand and sandy gravels or sand over laterite, largely restricted to the Yalgoo and the Coolgardie bioregions and the eastern part of the Avon bioregion, but also extending into the northern part of the Mallee bioregion. Typical taxa include *Allocasuarina acutivalvis*, *A. corniculata*, *Eucalyptus burracoppinensis*, *E. phaenophylla* subsp. *phaenophylla*, *Grevillea paradoxa*, *Hakea subsulcata*, *Callitris tuberculata*, *C. verrucosa* and the cushion sedge *Schoenus calcatus*.

5. The composition of assemblage 5 is variable, made up of taxa typical of breakaways and/or heavy duplex soils but also including some taxa more common on sandy soils. Most taxa occur from the boundary of the Jarrah Forest and Avon bioregions extending eastward into the Mallee bioregion. Typical taxa of breakways and duplex soils include *Eucalyptus astringens* subsp. *astringens*, *E. capillosa* subsp. *polyclada*, *Gastrolobium parvifolium*, *Nemcia tricuspidata*, and the orchid *Oligochaetochilus sargentii*. Atypical taxa of this assemblage include *Carpobrotus modestus* and **Asparagus asparagoides* (weed) that are more common on sand and extend onto the sandy soils of the Swan Coastal Plain and Esperance Sandplains bioregions.

6. Woodland and mallee species of the Avon, Mallee and Coolgardie bioregions, occurring on duplex soil associated with uplands and side slopes comprise assemblage 6. Typical eucalypts include *E. platypus*, *E. flocktoniae*, *E. phenax*, *E. calycogona*, *E. conglobata* and *E. eremophila*. The assemblage also includes some species common on low lake dunes sands adjacent to salt lakes (e.g. *E. spathulata*, *E. kondininensis*). Other typical species include *Melaleuca teuthidoides*, *Melaleuca acuminata*, *M. adnata*, *Zygophyllum ovatum* and *Westringia rigida*. This assemblage faces significant risk from dryland salinity in specific topographical positions.

7. Assemblage 7 is made up of wetland taxa occurring mostly on granite or duplex soils but also on sands, and includes both freshwater (*Glossostigma drummondii*) and saline (*Halosarcia leptospermoides*) taxa. A heterogeneous assemblage drawing taxa from a limited number of granite pools and saline affected valley floor woodlands sampled.

Assemblages centred on mesic south west

8. Taxa of *Eucalyptus marginata–E. calophylla* (Jarrah–Marri) woodlands of the SWBP comprise assemblage 8. Taxa of this assemblage occur on both sands and laterites but are restricted to the high rainfall areas of the Jarrah Forest, Swan Coastal Plain, Warren bioregions, and the western part of the Avon. In addition to the eucalypts other typical taxa include *Banksia grandis*, *Anigozanthos manglesii*, *Bossiaea ornata* and *Lechenaultia biloba*.

9. Assemblage 9 comprises taxa of seasonally wet duplex soils of the high rainfall zone centred on the Jarrah Forest bioregion. Similar distribution to assemblage 8 but more typical of fine textured soils which are often seasonally wet. A small assemblage with taxa such as *Trymalium ledifolium*, *Hakea undulata*, *Diuris longifolia* and *Eryngium pinnatifidum* being typical.

10. Assemblage 10 includes taxa occurring on the sands of high rainfall areas, generally seasonally inundated, whose distribution is centred on the Jarrah Forest and Warren bioregions, extending into the Swan Coastal Plain and western edge of the Avon bioregion. This assemblage was only partially sampled in the current survey. Typical species include *Melaleuca preissiana*, *Cyathochaeta avenacea*, *Bossiaea linophylla*, *Melaleuca thymoides* and *Eucalyptus decipiens*.

11. *Banksia* woodland taxa centred on the deep Tertiary or Quaternary sands in the Jarrah Forest and Swan Coastal Plain bioregions form assemblage 11; these taxa can also extend into the Avon and north to the Geraldton Sandplains bioregion. Typical taxa are *Banksia attenuata*, *Adenanthos cygnorum*, *Hypolaena exsulca*, *Jacksonia furcellata*, *Hibbertia subvaginata*, *Calothamnus sanguineus*, and *Anigozanthos humilis*.

12. Taxa primarily of granite aprons and seasonally inundated clay flats comprise assemblage 12. Some of the taxa can also occur on sands. In this assemblage herbs and geophytes predominate, with distributions centred on the Jarrah Forest and Avon bioregions but also extending onto the Swan Coastal Plain bioregion and east into the wetter parts of the Mallee bioregion. Typical taxa include *Allocasuarina huegeliana*, *Eucalyptus occidentalis*, *Stypandra glauca*, *Borya laciniata*, *B. sphaerocephala*, *Siloxerus multiflorus*, *Aphelia cyperoides*, *Waitzia suaveolens*, *Caesia micrantha*, *Sowerbaea laxiflora* and *Centrolepis drummondii*.

13. Assemblage 13 is comprised of taxa typical of *Eucalyptus wandoo* (Wandoo) woodlands on duplex soils, some taxa in this assemblage are also common on sandy soils. The distribution patterns of taxa in this assemblage are similar to assemblage 12, being centred on the eastern edge of the Jarrah Forest bioregion. Characteristic taxa include *Eucalyptus wandoo, Chamaescilla versicolor, Hyalosperma cotula, Hibbertia commutata, Bossiaea eriocarpa, Diuris corymbosa, Desmocladus asper* and *Craspedia variabilis.* This assemblage faces some risk from dryland salinity in susceptible landscape positions.

14. Species of seasonally wet clay flats (duplex soils) centred on the Jarrah Forest and Swan Coastal Plain bioregions extending into the Warren and wetter parts of the Avon bioregion make up assemblage 14. Some taxa can extend into water-gaining sites on the Geraldton Sandplains and Esperance Sandplains bioregions. This assemblage was only partially sampled in this dataset. Generally claypans quadrats form part of the wetland dataset (see Lyons *et al.,* 2004). Typical taxa include *Tribonanthes longipetala, Chorizandra enodis, Utricularia multifida, Aphelia drummondii* and *Philydrella pygmaea.*

15. Small diverse group of taxa of well drained fine textured and sandy soils make up assemblage 15. Thirty percent of taxa in this assemblage are weeds (indicated by *). The distribution patterns of the taxa are generally centred on the Jarrah Forest and Avon bioregions but some taxa occur more widely across the SWBP. An atypical taxon in this assemblage is *Rostraria pumila* whose distribution is centred on the Eremaean. This assemblage was not well sampled. Taxa include *Moraea flaccida, *Rostraria pumila, Pelargonium havlasae* and *Hibbertia rupicola.*

Assemblages centred on deep sands or laterite soils.

16. Taxa of assemblage 16 are typical of lateritic shrublands that can also occur on deeper sands. Distributions are centred on the Geraldton Sandplains and the western Avon and adjacent bioregions. Some taxa extend into the Mallee and Esperance Sandplains bioregions. Typical taxa include *Hakea gilbertii, Laxmannia omnifertilis, Dryandra cynaroides, Eucalyptus drummondii, D. nivea* subsp. *nivea* and *Xanthorrhoea drummondii.*

17. Small group of taxa of lateritic and duplex soils form assemblage 17. Distributions are centred on the eastern part of the Jarrah Forest and western part of the Avon bioregions but there is little congruence between the distributions of individual taxa.

Some taxa extend into the southwest corner and one extends to the Esperance Sandplains bioregion, others are restricted to the Geraldton Sandplains, Avon and the northern part of the Jarrah Forest bioregions. This assemblage was not well sampled in the current survey. Typical taxa include *Eucalyptus falcata, E. accedens, Astroloma drummondii, Gahnia australis, Dryandra squarrosa* subsp. *squarrosa* and *Gastrolobium microcarpum.*

18_21.The 20 taxa that form the next three small assemblages (18–20) were generally represented only in a few quadrats. These assemblages are not considered to be well sampled in the current survey. They represent taxa of sand or lateritic shrublands and woodlands with distributions centred on the southern parts of the Jarrah Forest and Avon bioregions, and extending into the Warren, Mallee and Esperance Sandplains bioregions. These patterns were a subset of those in assemblage 21 with which they were amalgamated. Taxa in assemblage 21 are generally widespread across the entire SWBP, with distributions centred on sandy and lateritic soils but also occurring on granite and duplex soil types. Typical taxa include *Neurachne alopecuroidea, Drosera macrantha, Conostylis setigera, Opercularia vaginata, Eriochilus dilatatus* and *Leptospermum erubescens.* A recognizable subset of this assemblage occurs on similar substrates but with distributions centred further to the west (e.g. *Schoenus clandestinus, Stylidium diuroides*).

22. Taxa of assemblage 22 are typical of sands over laterite occurring widely across the SWBP and often the adjacent Eremaean. This assemblage is largely absent from the Jarrah Forest and the Warren bioregions and the southern parts of the Swan Coastal Plain bioregion. Some taxa also occur on sandy granitic substrates. Typical taxa include *Allocasuarina campestris, Astroloma serratifolium, Dampiera lavandulacea, Melaleuca leptospermoides, Borya constricta,* and the *Amphipogon strictus* complex. A subset of taxa in this assemblage have more restricted distributions in Geraldton Sandplains and parts of the Avon bioregions (*Eucalyptus macrocarpa*) or Esperance Sandplains and parts of the Mallee bioregions (*Verticordia brownii*) on the same substrate types.

23. Assemblage 23 is made up of sandplain or *Banksia* woodland taxa common on deep sands and/or sands with laterite at depth. Distributions are centred on the Geraldton Sandplains bioregion, extending into Avon, the northern parts of the Swan Coastal Plain and Mallee bioregions, occasionally also occurring further south. Typical taxa include *Banksia*

prionotes, Actinostrobus arenarius, Ecdeiocolea monostachya, Alexgeorgea nitens and *Austrostipa macalpinei.*

24. Taxa of assemblage 24 are typical of lateritic shrublands, with distributions largely southern and centred in the Mallee and Esperance Sandplains, and the southern parts of the Avon bioregions, with some taxa extending into adjacent regions. Typical taxa include *Grevillea cagiana, Petrophile merrallii, Banksia violacea, Melaleuca pungens, Lysinema ciliatum, Isopogon buxifolius, Hibbertia gracilipes* and *Hakea cygna.* Of these, *Lysinema ciliatum* is unusual in being widespread across the SWBP.

25. Taxa of assemblage 25 occur on sandplains, with widespread distributions, but generally not occurring in the eastern part of the Avon, the northern part of the Mallee or the wettest areas of the Jarrah Forest and Warren bioregions. Typical taxa include *Dryandra armata, Allocasuarina thuyoides, A. humilis, A. microstachya, Amphipogon turbinatus, Lepidobolus chaetocephalus, Mesomelaena preissii, Baeckea preissiana* and *Banksia sphaerocarpa.*

26. Assemblage 26 comprise taxa of sandplain of deep sands and sands over lateritic gravels. Distribution are primarily centred on the sandplains of the southern part of the Mallee and Esperance Sandplains bioregions, but also extend into southern Avon and Jarrah Forest bioregions. Typical taxa include *Agonis spathulata* subsp. *spathulata, Argentipallium niveum, Banksia media, Eucalyptus pleurocarpa* and *Hakea pandanicarpa. Anarthria humilis* has a somewhat different distribution occurring in both the Esperance Sandplains and Geraldton Sandplains bioregions.

Environmental domains of the species assemblages

The relationship between assemblage richness and compositional gradients was examined by plotting assemblage richness against 1D ordination score (SSH, Belbin 1995, cut level 0.2) for each of the 23 assemblages (assemblages 18 to 21 were combined, see above). Species richness for individual assemblages generally had a unimodal distribution in relation to the primary compositional gradient, with 16 of the 23 assemblages showing a unimodal response to the primary compositional gradient, a further two showing a bimodal responses while the remaining five showed no clear relationship (Table 17). Most of the species assemblages (15 of the 23) were significantly nested as defined by Atmar and Patterson's (1993) temperature calculator (Table 17). Such patterns would be expected if the species assemblages were responding to different gradients in the physical environment or differently to subsets

of environmental gradients (McKenzie *et al.,* 1989, 1991a, 2000b). To test this hypothesis, the 23 species assemblages were treated as independent datasets and analyzed separately.

Generalized linear models (GLM) were used to generate species richness models for each assemblage in terms of the physical attributes of the quadrats assuming poisson error models with logarithmic links. Twenty-one of the 23 models showed moderate or good fits when cumulative poisson probability curves were constructed. The two assemblages that gave poor fits were assemblages 5 and 15. Models explained between 43.2% to 84.2% of the total scaled deviance (Table 17).

Sixteen of the 23 assemblages showed good correlation between the model terms and the characterization based on wider known distributions and habitat preferences of the component species (see above), a further four assemblages were somewhat consistent, and the last three assemblages showed no correlation (Table 17).

Geographical patterns in plant biodiversity

Geographic patterns in assemblage occurrence were examined in two ways. Initially dot plots of species richness were produced for each assemblage and the boundaries of the IBRA regions and subregions were overlaid onto these maps (Figure 12). The diameter of the dots is proportional to the maximal species richness in each assemblage. Inspection of these maps shows a poor correlation between the IBRA regions or subregions and the geographical extent of the assemblages. Of the 23 assemblages, assemblage 3 is largely restricted to the Avon 1 subregion, assemblage 10 to the Jarrah Forest 2 subregion, assemblages 8, 9 and 14 to the Jarrah Forest bioregion, and assemblages 6 and 24 to the Mallee bioregion. None of these assemblage patterns exactly coincides with the IBRA boundaries.

Many other patterns are seen in the remaining 16 assemblages, including assemblages that are widespread (e.g. assemblages 1, 18_21), assemblages that occur along the eastern boundary of the study area and cross a number of regions and subregions (e.g. assemblages 2, 4, 22), or assemblages that straddle current IBRA boundaries (e.g. assemblages 17, 26). The Jarrah Forest bioregion is the only IBRA bioregion partially supported by assemblage phytogeography, however six assemblages cross the Jarrah Forest-Avon boundary (e.g. assemblages 11, 12, 13, 15, 17, 18_21).

The second method of examining congruence between patterns of assemblage occurrence and biogeographic regions and subregions was to classify all 682 quadrats in terms of their weighting

Table 17 A summary of the assemblage composition in terms of total richness and number of quadrats at which the assemblage was present, degree of nestedness (measured by the Temperature statistic following methods of Atmar and Patterson, 1993) and significance (P, tested by Monte-Carlo simulation), compositional relationship between richness and compositional gradient assessed from a plot of richness against 1D ordination (SSH in PATN, cut level 0.2, Belbin 1995), percentage scaled deviance of null model explained by GLM equation, assessment of fit of species richness data to Poisson distribution, assessment of the congruence of the GLM parameters with the know distribution and habitat preference of the each assemblage's component species. GLM modeling were based on all 682 quadrats sampled. ns = $P > 0.05$.

	Species richness of assemblage	No. of quadrats present	Temperature	Temperature P	Richness-compositional relationship based on 1D ordination	Scaled deviance explained by GLM model (%)	Poisson fit model of GLM model	Consistent with known distribution and habitat
A1	110	606	9.11	<0.0001	unimodal	43.2	Good	yes
A2	43	201	15.48	ns	unimodal	44.5	Good	yes
A3	89	272	9.07	<0.0001	unimodal	65.8	Good	yes
A4	63	248	11.3	<0.0001	unimodal	51.3	Good	yes
A5	31	227	15.66	ns	no relationship	25.8	Poor	no
A6	47	194	11.71	<0.0001	unimodal	56	Good	yes
A7	36	123	16.79	<0.0001	unimodal	47.8	Moderate	somewhat
A8	73	169	10.48	<0.0001	unimodal	84.2	Moderate	yes
A9	23	84	27.67	ns	no relationship	61.2	Moderate	somewhat
A10	19	60	29.33	ns	unimodal	74	Moderate	somewhat
A11	30	137	20.62	<0.0001	unimodal	68.4	Good	yes
A12	52	411	16.03	<0.0001	unimodal	52	Moderate	yes
A13	38	386	11.06	<0.0001	unimodal	64.6	Good	yes
A14	19	78	30.98	ns	no relationship	53.9	Moderate	somewhat
A15	17	86	33.51	ns	no relationship	17.3	Poor	no
A16	21	90	26.64	<0.05	unimodal	55	Moderate	yes
A17	13	59	46.94	ns	no relationship	47.8	Moderate	no
A18_21	51	460	6.15	<0.0001	bimodal	55.6	Moderate	yes
A22	50	351	6.92	<0.0001	unimodal	49.1	Good	yes
A23	34	120	13.95	<0.0001	weak bimodal	70.5	Moderate	yes
A24	46	157	14.02	<0.0001	unimodal	72.4	Moderate	yes
A25	77	339	13.71	<0.0001	unimodal	70.1	Good	yes
A26	40	101	22.57	ns	unimodal	72.4	Good	yes
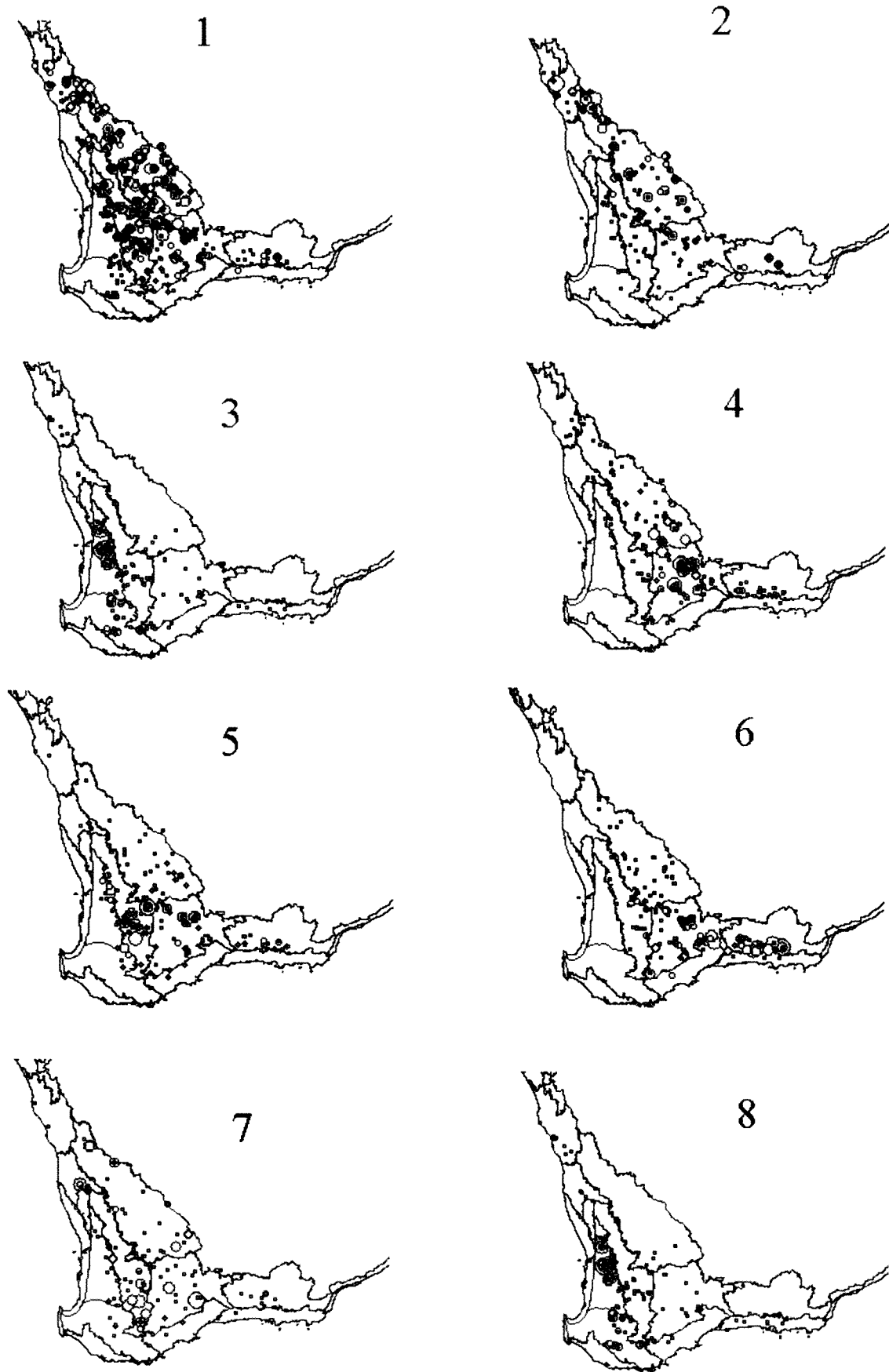
Figure 12   Assemblage richness maps showing currently recognized biogeographical regions and subregions. Dot diameter represents proportion of the maximum number of taxa of an assemblage recorded in a quadrat. Where no taxon of an assemblage occurs at a quadrat, no dot was plotted.
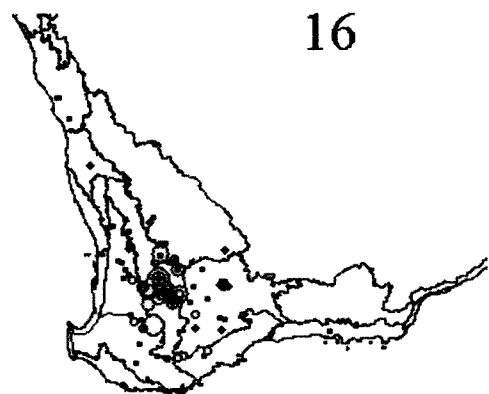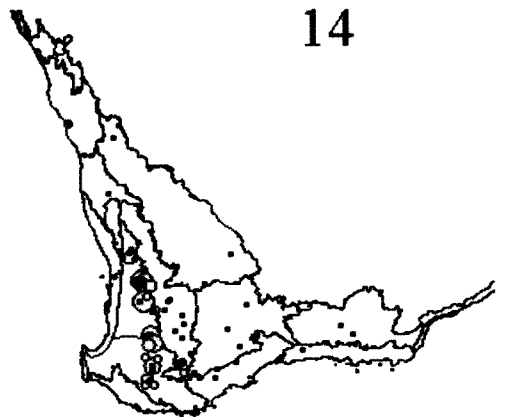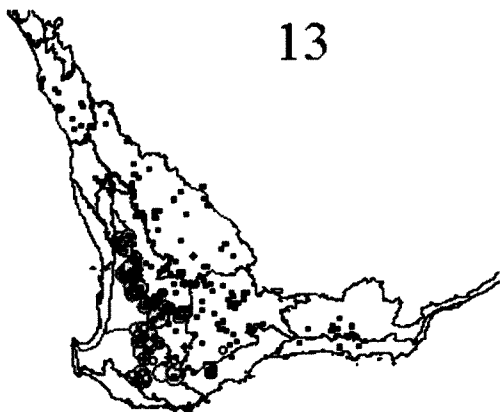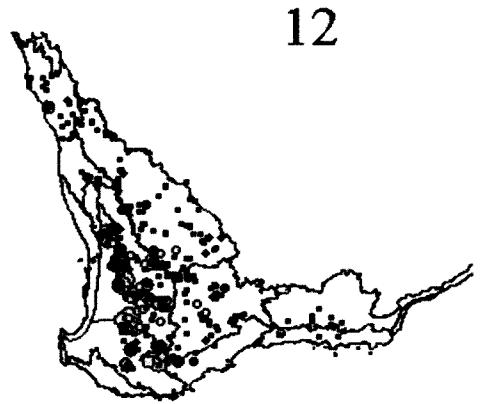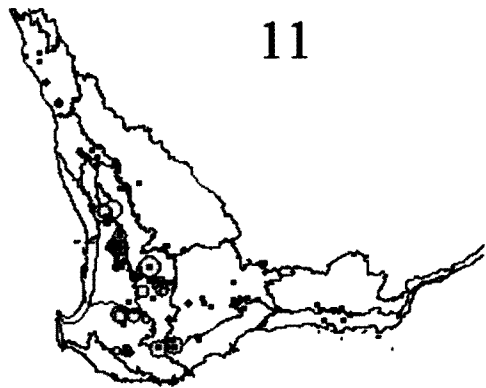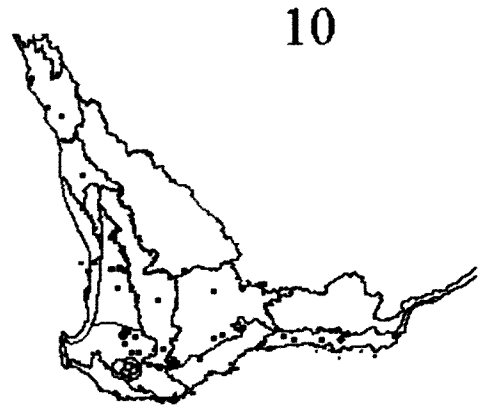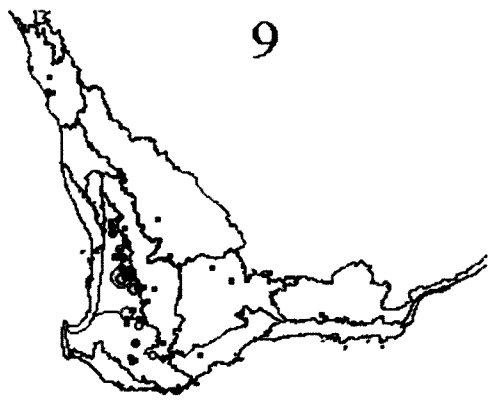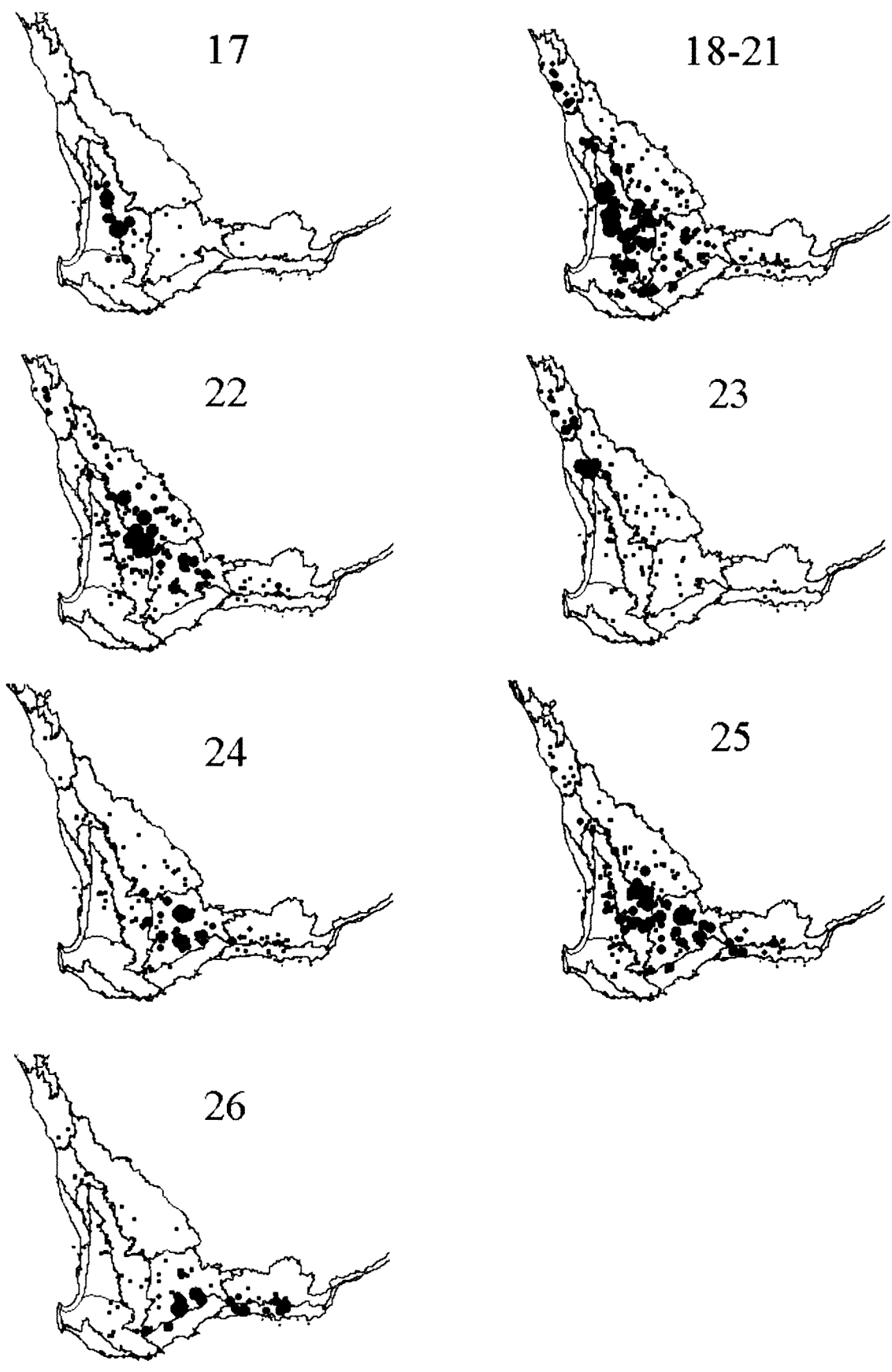
Figure 12   (cont.)

Figure 12   (cont.)

Table 18   GLM models of 23 assemblages, parameters codes as in Table 3, superscript indicates a squared term. All terms significant at $P < 0.05$, calculated using Ward's statistic (except the intercept in model for assemblage 15).

A1 =   -386.6-0.3627*STYPE+0.09615* STYPE^2+0.1234* CA-0.01062* CA^2+6.711* LONG-0.02928* LONG^2+0.01652* PWETP-0.00016* PWETP^2+0.1927* MTDQ

A2 =   -37.29+0.0472* STYPE^2+0.03078* PTOT-0.00011* PTOT^2-0.5131* MG+3.795* MTANN-0.09811* MTANN^2-0.3058* PAV

A3 =   -43.04+0.896* STYPE-0.1075* STYPE^2+3.97*PH-0.2642* PH^2+0.4854* MG-0.03741* MG^2+3.047* MTANN-0.07438* MTANN^2-0.00892* PANN

A4 =   -20.68+1.408* STYPE-0.3118* STYPE^2-0.07239* MG^2+05907* PANN-6.88E-05* PANN^2-0.00085* PSEAS^2+0.3993* T_AR

A5 =   -92.43+0.219* STYPE+0.455* ORGC+10.33* MTANN-0.3155* MTANN^2+0.03383* PANN-4.08E-05* PANN^2-9.301* NTOT

A6 =   -121.5+2.882* STYPE-0.4589* STYPE^2+7.868*PH-0.5306* PH^2+5.245* MTDQ-0.1285* MTDQ^2+0.1568* PWETP-0.00151* PWETP^2+0.2696*LONG

A7 =   -14.38+0.5992* STYPE+0.009067*PTOT-4.18E-06* PTOT^2+2.166*NA-0.3037* NA^2+0.0454* PANN-4.23E-05* PANN^2-0.8036* ORGC

A8 =   -13.45+0.5369* STYPE-0.1446* STYPE^2+0.3513* CA-0.01961* CA^2+0.04214* PANN-2.74E-05* PANN^2-0.00025* PWRQ^2-0.4281* MG

A9 =   12.5-0.01743* SDEP^2-0.00103* LONG^2-2.324* MTWETQ+0.09227* MTWETQ^2+0.05012* PANN-3.74E-05* PANN^2-0.0275*EC

A10 = 64.18-0.0001* EC^2-8.574* MTANN+0.2271* MTANN^2+0.09944* MNTCP^2+0.03293* PANN-2.24E-05* PANN^2-0.01314*PTOT

A11 = -9.202-1.446* STYPE+0.1781* STYPE^2-0.01171* KAV+0.03096* PANN-2.30E-05* PANN^2+0.3694* PWRQ-0.00419* PWRQ^2-0.2017* T_AR

A12 = -973+0.07686* STYPE^2-0.3522* MG+0.02234* MG^2+16.68* LONG-0.07169* LONG^2+0.02276* PANN-1.91E-05* PANN^2-0.09738* T_AR

A13 = -652.2+0.02369* STYPE^2+11.24* LONG-0.04868* LONG^2-0.00756* MTANN^2+0.02385* PANN-1.75E-05* PANN^2-0.01672* EC

A14 = 42.64+1.899* STYPE-0.2232* STYPE^2-0.9751* ORGC-7.221* MTANN+0.2074* MTANN^2+0.05221* PANN-3.97E-05* PANN^2+14.82* NTOT

A15 = 14.95+47.32* NTOT-133.1* NTOT^2-0.00131* LONG^2-0.3381* MTANN+0.02327* PANN-2.35E-05* PANN^2-0.5733* ORGC

A16 = 140.5+2.352* STYPE-0.5126* STYPE^2-0.5516* CA+0.02198* CA^2-1.513* LONG+6.51* MTANN-0.2507* MTANN^2-0.0097* PANN

A17 = -11.42+2.018* ORGC-0.119* ORGC^2-0.5951* MG+0.1895* PWETP-0.00098* PWETP^2-19.53* NTOT

A18_21 = 878.6+0.3706* STYPE-0.08026* STYPE^2-0.5714* MG-15.23* LONG+0.06253* LONG^2+6.249* MTANN-0.2007* MTANN^2+0.08549* SILT

A22 = -71.13-0.5953* MG+8.95* MTANN-0.2692* MTANN^2-0.06348* PWETP+0.000654* PSEAS^2-0.00569* PTOT

A23 = 36.99-0.3158* STYPE-0.02513* PTOT-0.5757* LONG+5.396* MTCLQ-0.2239* MTCLQ^2-1.133* MG

A24 = 56.11+1.847* STYPE-0.4272* STYPE^2-0.6116* CA+0.02719* CA^2-8.854* MTCLQ+0.3615* MTCLQ^2-0.04542* PSEAS-0.03201* PTOT

A25 = -63.48+0.9217* STYPE-0.2363* STYPE^2+7.055* PH-0.551* PH^2-0.504* CA+0.02452*CA^2+5.597* MTANN-0.1798* MTANN^2-0.5496* MG

A26 = -42.93+1.181* STYPE-0.255* STYPE^2-0.693* CA+2.968* T_AR-0.06414* T_AR^2+0.2827* PWRQ-0.00188* PWRQ^2-0.9719* NA

Note, to obtain robust models, some quadrats were dropped from some models: A2, 1 quadrat excluded; A11, 2 quadrats excluded; A16, 3 quadrats excluded; A23, 2 quadrats excluded

of the 20 ecological meaningful assemblages discussed above. (A second analysis was undertaken including assemblages 5, 15 and 17 with essentially similar results). The analysis was undertaken at the 6 and 11 group level corresponding to the number of biogeographic regions and subregions currently recognized in the study area (Figure 13, Table 19).

Little correlation was found between the phytogeographic pattern emerging from the classificatory groups at either the 6 or 11 group level and the biogeographic regions or subregions. Only group 5 (of the 11 group classification) was largely restricted to a single IBRA region (Jarrah Forest, Table 19). What was apparent was a strong northeast–southwest (rainfall, distance from the coast) gradient, second north–south (temperature) gradient and one widespread group that represented predominance of the granite herbland/ saline flat assemblage (i.e. distinct seasonally wet or

Table 19 Classification of 682 quadrats in terms of their weighting of the 20 most robust assemblages compared with the current IBRA bioregions (6 group level) and subregions (11 group level). JF–Jarrah Forest; A–Avon Wheatbelt; GS–Geraldton Sandplains; SCP–Swan Coastal Plain; M–Mallee; ES–Esperance Sandplains; Other–IBRA regions on eastern margin of study area.

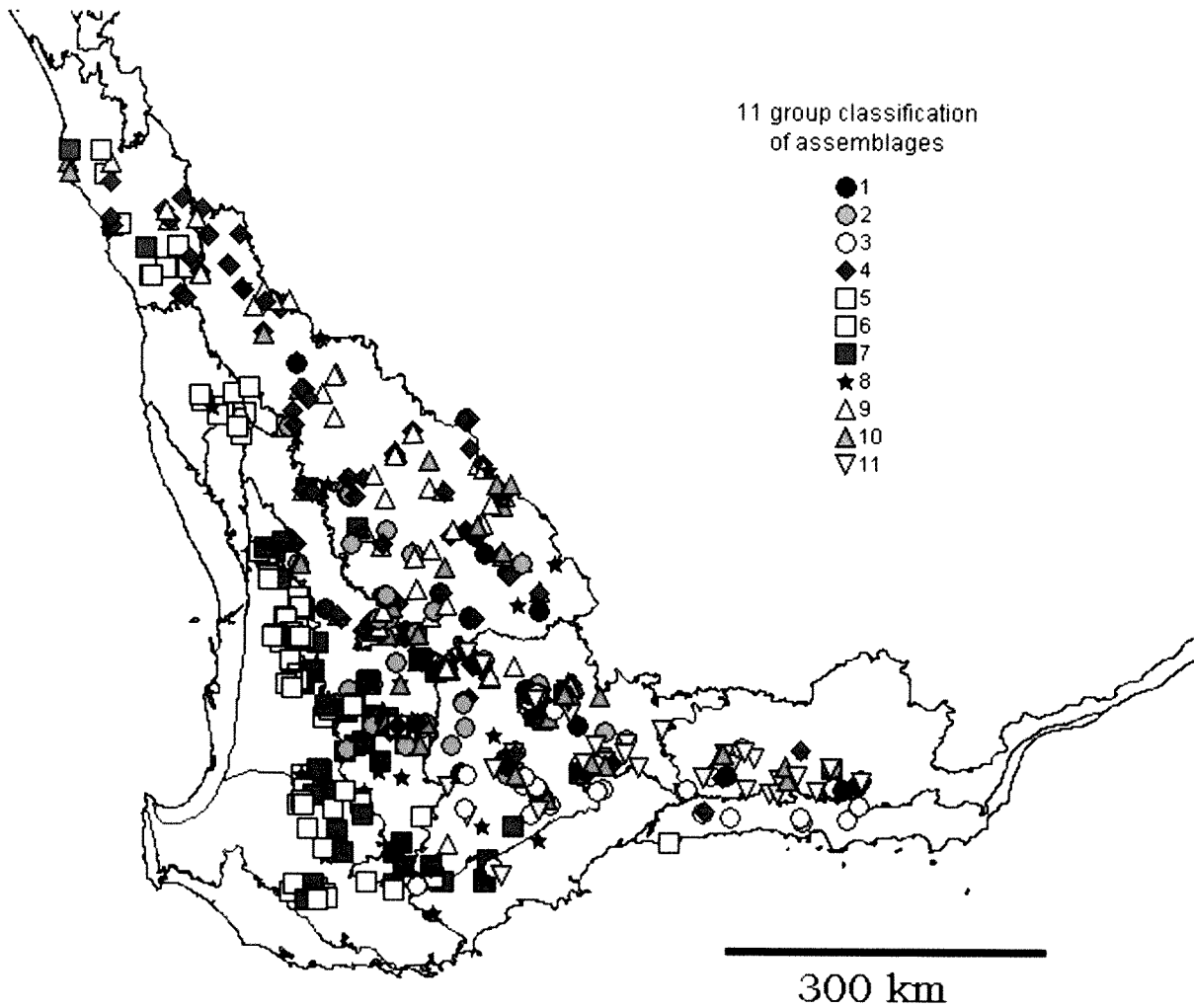| 6 group	11 group	JF1	JF2	A1	A2	GS2	GS3	SCP2	M2	M1	ES1	ES2	Other
1	1	–	–	11	6	–	–	–	29	5	–	–	1
1	2	1	–	23	37	–	2	–	10	2	–	–	–
1	3	–	–	1	2	–	–	–	25	3	6	6	–
2	4	–	–	52	22	10	–	–	14	3	–	1	3
3	5	33	17	–	2	–	–	–	–	–	–	–	–
3	6	14	6	1	7	9	10	2	–	–	1	1	–
3	7	26	7	6	32	4	–	–	8	1	5	–	–
4	8	3	2	6	7	–	3	–	3	1	4	–	5
5	9	–	–	43	2	3	2	–	10	–	–	–	2
5	10	–	–	20	17	3	–	–	27	5	–	–	1
6	11	–	–	–	5	–	–	–	25	13	2	1	–

Figure 13 Distribution of the 11 group classification of the weighted occurrence of the 20 ecological meaningful assemblages. Richness data were range standardized for each assemblage so that all assemblages made equal contribution to classification. Three patterns are seen, a NE–SW gradient, a N–S gradient and one widespread group (group 8).

Table 20 Comparison of the 25 group quadrat classification with Beard's 1:250000 structure and dominance vegetation mapping. Last row shows number of quadrats in each of the 25 quadrat groups. Key below gives codes to Beard's vegetation types.

Beard's vegetation unit	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Sheoak woodlands																									
SW1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Jarrah–Marri forest & woodlands																									
JM1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
JM2	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
JM3	–	–	–	–	–	–	1	–	–	2	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
JM4	–	–	–	–	–	–	5	1	–	–	–	3	1	–	–	–	–	–	–	–	–	–	–	–	–
JM5	–	–	–	–	–	–	18	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
JM6	–	–	–	–	–	–	1	3	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
JM7	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
JM8	–	–	–	–	–	–	3	3	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
JM9	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
JM10	–	–	–	–	1	–	6	9	2	3	–	10	2	–	–	–	–	–	1	–	–	–	–	–	–
Salmon Gum woodlands																									
SG1	–	–	1	–	3	2	–	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	–	–
SG2	–	5	–	2	–	1	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	1
SG3	–	1	2	7	3	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	1	1	–	3	–
SG4	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SG5	–	1	–	2	–	3	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–
SG6	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SG7	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
SG8	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	1	–	–
SG9	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Wandoo woodlands																									
WW1	–	–	–	–	2	–	–	1	–	–	–	2	–	–	–	–	–	–	1	–	–	–	–	–	–
WW2	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
WW3	–	–	–	–	–	–	3	1	–	–	–	2	2	1	–	–	–	–	–	–	–	–	–	–	–
WW4	–	–	–	–	1	–	1	–	–	3	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
WW5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
WW6	2	8	–	–	–	2	–	–	–	–	–	2	–	6	–	1	2	–	–	–	–	–	–	–	–
WW7	–	–	–	–	5	1	–	–	–	3	–	8	12	3	–	–	–	–	6	–	–	–	–	–	–
Yate woodlands																									
YW1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
YW2	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
YW3	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
YW4	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–

York Gum woodlands

YO1	1	4	–	1	2	–	1	–	–	–	–	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–
YO2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
YO3	2	2	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
YO4	–	4	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–
YO5	–	2	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–
YO6	–	5	–	1	9	2	–	–	–	2	1	3	2	1	–	1	–	–	–	–	–	–	–	–	–	–
YO7	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
YO8	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Banksia woodlands & shrublands

BW1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
BW2	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BW3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–
BW4	1	2	–	–	1	–	–	–	–	–	3	2	–	6	3	7	2	–	–	–	–	–	–	–	–	–

Acacia forest & shrublands

AC1	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
AC2	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC3	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC4	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC5	8	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
AC6	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC7	8	1	–	–	–	2	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–	–	–	–	–
AC8	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC9	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC10	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC11	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC12	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC13	–	–	–	–	–	–	–	–	–	–	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
AC14	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC15	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–
AC16	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AC17	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Mallee woodland & shrublands

M1	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
M2	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
M3	7	5	–	1	–	2	–	–	–	1	–	1	–	3	–	–	1	–	1	–	–	–	–	–	–	–
M4	–	–	–	1	3	5	–	–	–	–	1	3	–	2	–	4	5	7	2	1	12	3	2	–	–	–
M5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	1	2	–	–
M6	–	–	–	–	–	–	–	–	–	2	1	–	1	–	–	4	1	–	2	–	5	–	2	–	–	–
M7	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–
M8	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	3	2	–
M9	–	–	–	–	–	2	–	–	–	–	–	1	–	1	–	–	2	1	–	–	–	1	–	–	–	–
M10	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
M11	–	–	–	–	–	–	–	–	–	3	1	1	–	–	–	–	–	–	–	–	7	2	1	1	–	–
M12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–

Table 20   (cont.)

Beard's vegetation unit	25 quadrat groups																								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
Tammar shrublands																									
T1	4	1	1	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T2	–	1	–	–	2	1	–	–	–	–	–	4	–	1	–	9	–	–	–	–	–	–	–	–	–
Low shrublands																									
LS1	–	–	–	–	1	1	–	–	–	–	–	4	3	–	–	–	–	–	–	–	–	–	–	–	–
LS2	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
LS3	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
LS4	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
LS5	–	–	–	–	3	–	–	–	–	–	–	–	1	1	–	–	1	–	–	–	5	–	–	–	–
LS6	–	–	–	–	–	1	–	–	–	–	–	2	–	2	–	6	1	–	1	–	–	–	–	–	–
LS7	–	–	–	–	–	–	–	–	–	–	–	3	–	3	1	–	–	–	–	–	–	–	–	–	–
LS8	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3	–	–	–	–	–	–	–	–	–	–
LS9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
LS10	–	2	–	–	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	–	3	–	–	–
LS11	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
LS12	–	4	–	–	–	–	–	–	–	–	–	–	–	2	–	1	–	–	–	–	–	–	–	2	–
LS13	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Teatree shrublands																									
TT1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TT2	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
TT3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Melaleuca woodland & shrublands																									
ME1	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ME2	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
ME3	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Saline units																									
SA1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SA2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SA3	–	1	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
SA4	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
SA5	–	2	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SA6	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bare areas																									
B1	3	1	–	–	1	–	1	–	1	–	3	6	–	1	–	1	1	1	–	–	–	–	–	–	1
B2	–	1	1	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Quadrat group total	52	76	9	20	44	27	45	24	6	26	22	79	25	53	10	31	29	12	12	19	25	19	8	7	

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Sheoak woodlands:-SW1, Low woodland - *Allocasuarina huegeliana* & York gum; **Jarrah–Marri forest & woodlands**:-JM1, Medium forest - jarrah & marri on laterite with blackbutt (*E. patens*) in valleys, swampy bottomlands with bullich (*E. megacarpa*) & *Agonis flexuosa* ; JM2, Medium forest - jarrah & marri on laterite with wandoo in valleys, sandy swamps with teatree & *Banksia*; JM3, Medium forest - jarrah & wandoo (*E. wandoo*); JM4, Medium forest - jarrah, marri & wandoo; JM5, Medium forest - jarrah-marri; JM6, Medium open woodland - wandoo; JM7, Medium woodland - jarrah (south coast); JM8, Medium woodland - jarrah, marri & wandoo; JM9, Medium woodland - jarrah, wandoo & powderbark; JM10, Medium woodland - marri & wandoo; **Salmon Gum woodlands**:-SG1, Medium woodland - salmon gum; SG2, Medium woodland - salmon gum & gimlet; SG3, Medium woodland - salmon gum & morrel; SG4, Mosaic: Medium woodland - salmon gum & gimlet / Shrublands - mallee scrub, redwood & black marlock (*E. redunca*); SG5, Mosaic: Medium woodland - salmon gum / Shrublands - mallee scrub, redwood & black marlock (*E. redunca*); SG6, Mosaic: Medium sparse woodland - salmon gum & yorrell / Succulent steppe - saltbush & samphire; SG7, Mosaic: Medium woodland - salmon gum & morrel/ /Shrublands - mallee scrub, redwood; SG8, Mosaic: Medium woodland - salmon gum & red mallee / Shrublands - mallee scrub *Eucalyptus eremophila*; SG9, Mosaic: Shrublands - Medium woodland - salmon gum & gimlet / York gum & *Eucalyptus sheathiana* mallee scrub; **Wandoo woodlands**:-WW1, Medium woodland - wandoo; WW2, Medium woodland - wandoo & mallet; WW3, Medium woodland - wandoo & powderbark (*E. accedens*); WW4, Medium woodland - wandoo & yate; WW5, Medium woodland - wandoo, yate & river gum; WW6, Medium woodland - wandoo, York gum, salmon gum, morrel & gimlet; WW7, Medium woodland - powderbark & mallet; Yate woodlands:-YW1, Medium woodland - yate; YW2, Medium woodland - yate & paperbark (*Melaleuca* spp); YW3, Medium woodland - yate (*E. occidentalis*); YW4, Mosaic: Medium woodland - yate / Shrublands - mallee scrub, black marlock; **York Gum woodlands**:-YO1, Medium woodland - York gum; YO2, Medium woodland - York gum & river gum; YO3, Medium woodland - York gum & salmon gum; YO4, Medium woodland - York gum (*E. loxophleba*) & wandoo; YO5, Medium woodland - York gum, salmon gum & gimlet; YO6, Medium woodland - York gum, wandoo & salmon gum (*E. salmonophloia*); YO7, Mosaic: Medium woodland - York gum & salmon gum / Shrublands - mallee scrub *Eucalyptus eremophila* & black marlock; YO8, Mosaic: Medium woodland - York gum /Shrublands - *Allocasuarina campestris* thicket; **Banksia woodlands & shrublands**:-BW1, Low woodland - *Banksia*; BW2, Low woodland - *Banksia prionotes*; BW3, Shrublands - *Banksia* scrub-heath on sandplain in the Esperence Plains Region; BW4, Shrublands - scrub-heath on yellow sandplain *Banksia-Xylomelum* alliance in the Geraldton Sandplain & Avon-Wheatbelt Regions; **Acacia forest & shrublands**:-AC1, Low forest - *Acacia rostellifera*; AC2, Shrublands - Mixed acacia thicket on sandplain; AC3, Shrublands - *Acacia ligulata & Melaueca uncinata* dominated thicket on dark brown loamy soil; AC4, Shrublands - *Acacia neurophylla*; AC5, Shrublands - *Acacia neurophylla, A. beauverdiana & A. resinomarginea* thicket; AC6, Shrublands - acacia scrub, various species; AC7, Shrublands - acacia, casuarina & melaleuca thicket; AC8, Shrublands - bowgada & jam scrub; AC9, Shrublands - bowgada & jam scrub with scattered *Allocasuarina huegeliana* & York gum; AC10, Shrublands - bowgada scrub with scattered eucalypts & cypress pine; AC11, Shrublands - jam & *Acacia rostellifera* (+hakea) scrub with scattered York gum; AC12, Shrublands - jam scrub with scattered *Allocasuarina huegeliana* & York gum; AC13, Shrublands - jam scrub with scattered York gum; AC14, Shrublands - thicket, acacia & *Allocasuarina campestris*; AC15, Shrublands - thicket, *Acacia-Casuarina* alliance species; AC16, Shrublands - thicket, Jam & *Allocasuarina huegeliana*; AC17, Mosaic: Shrublands - jam scrub with scattered York gum in the valleys / *Allocasuarina campestris* thicket; **Mallee woodland & shrublands**:-M1, Medium woodland - merrit (*E. flocktoniae*) & red mallee (*E. oleosa*); M2, Shrublands - mallee & acacia scrub on south coastal dunes; M3, Shrublands - mallee & casuarina thicket; M4, Shrublands - mallee scrub, black marlock; M5, Shrublands - mallee scrub, black marlock & Forrest's marlock; M6, Shrublands - mallee scrub, Eucalyptus eremophila; M7, Shrublands - mallee scrub, Eucalyptus eremophila & black marlock (*E. redunca*); M8, Shrublands - mallee scrub, Eucalyptus eremophila & Forrest's marlock (*E. forrestiana*); M9, Shrublands - mallee scrub, redwood & black marlock; M10, Shrublands - mallee-heath (Stirling Range); M11, Shrublands - tallerack mallee-heath; M12, Mosaic: Shrublands - mallee scrub, black marlock / Shrublands - tallerack mallee-heath; **Tammar shrublands**:-T1, Shrublands - Allocasuarina campestris thicket; T2, Shrublands - Allocasuarina campestris thicket with scattered wandoo; **Low shrublands**:-LS1, Shrublands - *Dryandra* heath; LS2, Shrublands - mixed heath; LS3, Shrublands - mixed thicket (*Melaleuca & Hakea*); LS4, Shrublands - scrub-heath; LS5, Shrublands - scrub-heath in the Mallee Region; LS6, Shrublands - scrub-heath in the south-east Avon-Wheatbelt Region; LS7, Shrublands - scrub-heath on coastal association, yellow sandplain; LS8, Shrublands - scrub-heath on lateritic sandplain in the central Geraldton Sandplain Region; LS9, Shrublands - scrub-heath on lateritic sandplain in the southern Geraldton Sandplain Region; LS10, Shrublands - scrub-heath on sandplain; LS11, Mosaic: Shrublands - Hakea scrub-heath / Shrublands - *Dryandra* heath; LS12, Mosaic: Shrublands - scrub-heath (SE Avon)/ Shrublands - *Allocasuarina campestris* thicket; LS13, Mosaic: Shrublands - scrub-heath on deep sandy flats / Shrublands - thicket, *Acacia-Casuarina* alliance; **Teatree shrublands**:-TT1, Shrublands - tea-tree scrub; TT2, Shrublands - tea-tree thicket with scattered wandoo & yate; TT3, Shrublands - York gum & *Eucalyptus sheathiana* mallee scrub; **Melaleuca woodland & shrublands**:-ME1, Low woodland - paperbark (*Melaleuca* sp.); ME2, Shrublands - *Melaleuca thyoides* thicket with scattered York gum; ME3, Shrublands - *Melaleuca uncinata* thicket with scattered York gum; **Saline units**:-SA1, Succulent steppe with open woodland & thicket - york gum over Melaleuca thyoides & samphire; SA2, Succulent steppe with open woodland - eucalypts over saltbush; SA3, Succulent steppe with sparse woodland & thicket - York gum & Kondinin blackbutt over tea-tree thicket & samphire; SA4, Succulent steppe with thicket - *Melaleuca thyoides* over samphire; SA5, Succulent steppe with thicket - tea-tree over samphire; SA6, Succulent steppe with woodland & thicket - york gum over *Melaleuca thyoides* & samphire; **Bare areas**:-B1, Bare areas - rock outcrops; B2, Bare areas - salt lakes

Table 21 Most common canopy taxa (in assemblage order) by frequency in quadrat groups, only taxa occurring in 10 or more of the 682 quadrats included. These canopy taxa were not represented in quadrat groups 11, 15 or 25. (Assem = Assemblage; Total = Total occurrences for each taxon; Quad. grps = Number of quadrats groups taxon occurs in.)

Assem	Taxon	Quadrat Groups																						Total	Quad. grps
		1	2	3	4	5	6	7	8	9	10	12	13	14	16	17	18	19	20	21	22	24	23		
1	*Eucalyptus capillosa* subsp. *capillosa*	3	9			4						4				1								21	5
1	*Eucalyptus loxophleba* subsp. *loxophleba*	3	32		1	3					4	9												52	6
2	*Eucalyptus loxophleba* subsp. *lissophloia*	4	1	1		2						5												13	5
3	*Eucalyptus celastroides* subsp. *virella*		4			5								1										10	3
3	*Eucalyptus longicornis*		3		10	9						1												23	4
3	*Eucalyptus salmonophloia*		28		5	25	7					1						1			1			68	7
3	*Eucalyptus salubris*		15		3	3	4															4		29	5
3	*Eucalyptus yilgarnensis*	3	4		5		2									2								16	5
4	*Eucalyptus hypochlamydea* subsp. *ecdysiastes*		1											4	1	4	2				1			13	6
4	*Eucalyptus incrassata*						1						1	1				1	1	4		4		13	7
4	*Eucalyptus phaenophylla* subsp. *phaenophylla*					1	2					1				2	6		1		1			14	7
5	*Eucalyptus astringens* subsp. *astringens*					6	1				1							10						18	4
6	*Eucalyptus calycogona*		1			1	9																	11	3
6	*Eucalyptus eremophila*				1	1	5								1	1		1			2	1		13	8
6	*Eucalyptus flocktoniae*				1	2	14							3			5			1	7	2		35	8
6	*Eucalyptus leptocalyx*					2										1					4		3	10	4
6	*Eucalyptus phenax*		1			5	7							3			2	1		2	1		1	23	9
6	*Eucalyptus pileata*				2	1	1										4				3			11	5
6	*Eucalyptus tenera*		1			1	4									1	1			1	2			11	7
8	*Eucalyptus calophylla*							21	8		3	3	1	2										38	6
8	*Eucalyptus marginata*							25	9															34	2
12	*Allocasuarina huegeliana*	3	1			2		1	1		7	31	4	12	1									63	10
12	*Eucalyptus occidentalis*				6			1		1	5	2												15	5
13	*Eucalyptus wandoo*		2			13		24	2	2	5	39	4		1									92	9
17	*Eucalyptus accedens*							5	2			1	2	3				1						14	6
23	*Eucalyptus pleurocarpa*																		12	4				16	2
24	*Callitris roei*												1			2	1	1	3	5	1			14	7
24	*Eucalyptus albida*		1										1	2	1					5				10	5

saline habitats are not strongly correlated with major climate parameters, Figure 13).

Phytogeographic patterning was also examined by comparing quadrat grouping (reflecting different compositional groups) in relation to Beard's structural mapping units (Table 20) and canopy species recorded at each quadrat (Table 21). If the structural units (from Beard's maps) or canopy species dominance (extracted from 682 quadrats) were strongly correlated with floristic groups then the two-way tables would show the structural units/canopy species being restricted to a limited number of floristic groups. This was generally not the case. The closest correlations are between Beard's *Acacia* forest and shrublands and quadrat groups 1 and 2. However, these floristic groups also occur in 27 other structural units (Table 20). Beard's mallee woodlands and shrublands units cover the broadest range of floristic groups. Similarly, the canopy species at any plot is not a good predictor of floristic grouping except at the very broadest scale (Table 21).

DISCUSSION

Flora

Precise figures on the richness of the SWBP are not yet available at the taxon (primarily species and subspecies) level. Hopper (1992) estimates a figure of 8000 taxa. The current survey of 682 terrestrial quadrats recorded 2609 taxa (32.6%) from a total area of just over 27 ha (7 ha of which was sampled intensively for all vascular plants and the remainder only for overstorey species). Eight new taxa were collected and perhaps 10% the flora of the study area (on current knowledge) still awaits formal description (Appendix 1). The poor state of knowledge of the flora of the southwestern Australia has been commented on previously (Brown, 1989; Gibson *et al.*, 1997; Gibson and Lyons, 1998a, b; Lyons *et al.*, 2000).

Family composition and the lifeform spectrum of the 2609 taxa recorded are in general agreement with previously published data with the ten largest families (Myrtaceae, Proteaceae, Papilionaceae, Asteraceae, Mimosaceae, Cyperaceae, Orchidaceae, Epacridaceae, Poaceae, and Stylidiaceae) representing 62.7% of the flora, and just four of the 21 lifeforms (shrubs, annual herbs, perennial herbs, geophytes) representing more than 80% of species (Pate *et al.*, 1984; Hopper *et al.*, 1996). Of these lifeforms, shrubs predominate (Table 4).

Species richness of 23 richest families were positively correlated with rainfall across the study area (cf. Brown's 1989 kwongan study), the exceptions being Asteraceae, Chenopodiaceae (both showed a negative correlation with rainfall) and Myrtaceae, Mimosaceae, Poaceae, Goodeniaceae, Rutaceae, and Lamiaceae that showed no correlation. These families would be expected to show correlations if the study area were expanded to include more of the Eremaean and high rainfall areas. Although there were highly significant relationships between species richness and rainfall for 19 families, the generally low r-values indicate that considering rainfall alone is not sufficient to explain species richness (Table 6).

Species richness at family level was very different between soil types for 22 of the 23 richest families (Mimosaceae again being the exception, Table 5). Quadrats on duplex soils showed lower average species richness than quadrats on granite, laterite and deep sand soils. However, species richness was not related to the major structural formations sampled (Table 9). These results support the observations of Yates and Hobbs (1997) that woodlands have similar richness to shrublands, but with a major shift from predominately shrubs in the shrublands to predominately annuals in the drier eucalypt woodlands. Our data do not support Beard and Pate's (1984) view that mallee formations are floristically intermediate between woodlands and shrublands but rather show a similar shift in understorey lifeform depending on soil type as seen the woodland formation (Figure 9).

Congruence between taxonomic levels

The ordination of the correlation matrix of the taxonomic association matrices shows large differences between the species level matrix and those derived from the genus, family and order matrices, which in turn show large differences to that derived from the class matrix (Figure 4). The pattern of an arching or fan effect in the ordination has been reported for similar analyses of marine benthic communities (Olsgard *et al.*, 1997; Olsgard *et al.*, 1998). Importantly, however, the pattern of arching or fan effects in the marine studies differs from the wheatbelt study in that there was a tighter clustering between species, genera and families and greater divergence at higher taxonomic levels. In the wheatbelt study congruence between the different matrices also does not parallel the percentage decrease in the number of taxonomic units between the adjacent levels. If the distance in the ordination between the full presence/absence matrix and the random matrix is taken as a coarse measure of order (noting that ordination distances are non-metric rank orders) then the distance from the full matrix to the genus matrix shows a 18% change and the distance to class matrix a 75% change. Differences between the genus, family and order matrices are less than 10% on this scale. Therefore, it can be concluded that considerable information would be lost if data matrices above the level of individual taxon were compiled for the wheatbelt study area.

Congruence between lifeforms

The patterns of congruence shown between broad lifeforms classes (Figure 5) suggests that no single lifeform class was a good surrogate for the full dataset. This implies that any survey undertaken that records only specific lifeform classes will not accurately reflect the pattern shown by the total flora. Overstorey species that are often used in structural vegetation mapping are clearly poor surrogates for the diversity patterns of the complete flora in the study area (Figure 5).

These findings show a remarkable similarity to cross-taxon congruence patterns reported by McKenzie et al. (2000) and McKenzie et al. (2004) where the combined biodiversity dataset was centrally positioned in relation to the different phylogenetic groups (plants, mammals, spiders, scorpions, frogs and reptiles). In those studies none of the individual phylogenetic groups proved a good surrogate for any other. The lack of congruence is not suprising, either for different phylogenetic groups reported by McKenzie et al. (2004) or the broad lifeform classes discussed here, given the apparent different physiology and life history traits of the subgroups.

Patterning in the distribution of uncommon species

Of the 2609 taxa recorded, almost 61% were recorded from < 5 quadrats, and just over half of these taxa were recorded from only a single quadrat. High percentages of uncommon taxa have been frequently reported from quadrat based flora surveys in Western Australia both at the regional (Keighery et al., 2000) and subregional scales (Gibson et al., 1994, Wardell-Johnson and Williams 1996). Analysis of the composition of these uncommon taxa both in terms of lifeform and taxonomic affinity showed no differences compared with the pattern of the total sampled flora. The frequency distribution of the uncommon taxa departed significantly from a random Poisson model and occurred at a much higher than expected frequency along the southern and western edges of the study area (Figures 7 and 8), suggesting a biogeographical sampling artifact.

Earlier work by Gibson et al. (1994) showed similar patterns on the southern Swan Coastal Plain where the uncommon taxa (occurring in only one quadrat) were concentrated along the inland edge of the study area. This was interpreted as resulting from under-sampling of a heavily cleared fertile soil unit. However, an equally parsimonious explanation would be a biogeographic sampling artifact since this edge abuts the floristically distinct Jarrah forests and woodlands of the Darling Plateau.

Quadrat analyses

Analysis of the dataset of the 682 quadrats x 1022 taxa recorded in five or more quadrats recovered much of the partition structure of the full dataset (Figure 8). The removal of 60% of uncommon taxa did result in reallocation of 20% of quadrats to different groups but the regional and edaphic patterning in the quadrat dendrogram was clearer (occurring at higher levels) than in the full dataset. As one of the primary purposes of the analyses was to examine regional patterning, the reduced dataset was considered the more appropriate for analysis.

The primary division between quadrats in the dendrogram largely corresponded to a split between the more fertile granite and duplex soils from the laterite and deep sand soils. The exceptions to this were (a) the inclusion of the mostly sandy, species-rich quadrats in groups 7 and 8 (from the higher rainfall southwest) with the quadrat groups of the duplex and granite soils and (b) the inclusion of the species-poor duplex and granite soil quadrats in groups 22 to 25 with the sand and laterite quadrat groups. The 3D ordination recovered the major edaphic patterning more accurately than did the dendrogram clustering with all the sand and laterite soil groups in the lower right quadrant (Figures 10 and 11). Interestingly, except for group 15, there was no obvious split between deep sand and laterite quadrats despite laterite soils being somewhat more fertile (Lamont and Markey, 1995). At lower divisions in the dendrogram geographic congruence between sites became obvious. These were also reflected in the ordination with strong correlations with climatic gradients and with longitude. These patterns are somewhat complicated by a number of strong intercorrelations between edaphic and climatic parameters (Appendix 5).

The geographical coherence of most groups can most easily be seen if quadrat groups are broken down according to the currently recognized biogeographic subregions (Table 13). While few quadrat groups are restricted to individual subregions there is a strong trend of occurrence in adjacent subregions (but not necessarily within individual biogeographic regions).

Environmental domains of the species assemblages

For 70% of assemblages it was possible to model assemblage richness patterns in relation to environmental domains. Robust models were generated for 16 of the 23 assemblages modeled. These models explained 49.1 to 84.2% of the scaled deviance and were consistent with the known distribution patterns and habitat preferences of the component species. Eighty-five percent of the 1022 taxa occurred in these 16 assemblages. All 16 assemblages showed a unimodal (14 cases) or bimodal (2 cases) relationship between species richness and composition (as recovered by a one

dimensional ordination) and all were significantly nested as measured by Atmar and Pattersons' (1993) temperature calculator. It should be noted, however, that recent work by Leibold and Mikkelson (2002) and Fischer and Lindenmayer (2002) suggests that Atmar and Patterson's approach can sometimes provide misleading evaluation of nestedness (generally overestimating the level of nestedness).

Of the remaining seven assemblages, four (assemblages 7, 9, 10,14) showed some level of coherence but had not been adequately sampled (their major area of distribution was beyond the study area boundary, or centred on the wetlands that are discussed in Lyons et al., 2004). They also showed inconsistent patterns in nestedness and richness in relation to composition, or only partial congruence with known distribution and habitat preferences (Table 18). Explanatory power of these models ranged from 47.8 to 74.0%.

The three remaining assemblages (assemblages 5, 15, 17) were not significantly nested nor did they show any relationship between species richness and composition. In two of these assemblages (5 and 15) species richness did not conform to a Poisson distribution (as assumed by GLM). Unsurprisingly the models of these assemblages had low explanatory power (17.3–25.8%) and were not consistent with the known distributions and habitat requirement of the component species. The third model made little ecological sense, but as the species-rich quadrats were localized, the model generated explained 47.8% of the scaled deviance. The species in these assemblages were also poorly sampled with their major area of distribution beyond the study area boundary or centred on the wetlands (Lyons et al., 2004).

The explanatory power of the 16 well-sampled assemblages was generally lower than the models developed for the full biodiversity analysis (which included plants, mammals, spiders, scorpions, frogs and reptiles) of 304 of the quadrats (McKenzie et al., 2004). Preliminary analysis including all species occurring in more than 2 quadrats (cf. ≥ 5 quadrats reported here) showed only a modest increase in explanatory power (generally < 10%). It is not clear if the generally lower explanatory of the plant species models reported here has resulted from factors such as broader sampling of the upland vegetation resulting in a less well stratified dataset than the biodiversity analysis; the general exclusion of the wet and/or saline ends of the environmental gradients; or the lack of the inclusion of fauna group responses.

The analyses also indicated that the explanatory power of a model on its own was not a good measure of the concordance with known distribution and habitat preference of individual assemblages. Even models that made very poor

ecological sense (i.e. species occurrence showed little congruence in terms of their overall habitat preference or distribution) could report high explanatory power if the species-rich quadrats had a localized distribution pattern where steep climatic gradients were evident. Surprisingly, the broad soil type parameter was often an important component of models either alone or in conjunction with other soil chemical parameters. This probably reflects the general similarity in soil chemistry of the sandy surficial layer of many samples. A discriminant function analysis of the soil chemical parameters was not able to recover the broad soil types based on soil profile characteristics which had been noted in the field.

Geographical patterns in plant biodiversity

Patterns in plant biodiversity elucidated in this study were examined in four comparisons between:

- the current biogeographic regionalization (IBRA) and the 25 group quadrat classification (Table 13),
- the current biogeographic regionalization (IBRA) and the distribution of maximum species richness of the 23 species assemblages (Figure 12),
- the current biogeographic regionalization (IBRA) and the 6 and 11 group classification of weighted assemblage occurrence (Table 19, Figure 13),
- current broad scale structural mapping and the 25 group quadrat classification (Table 20).

These comparisons showed some correspondence between floristic patterning and the Jarrah Forest bioregion but generally there was little support for the other currently recognized bioregions and subregions. The level of support for the Jarrah Forest bioregion needs to be treated with caution since only half of the bioregion was sampled and the bioregions to the west and south were not sampled at all. Similarly, structural mapping showed little correlation with floristic composition as has been reported previously (Havel, 1975a; Loneragan, 1978; Hnatiuk and Hopkins, 1981).

What is apparent in the analyses is the gradational nature of species turnover throughout the study area. Havel (1968, 1975a, b, 2000) has previously described the vegetation on the Swan Coastal Plain, the Jarrah Forest and the Warren bioregions as forming continua with gradual asynchronous species turnover, especially of understorey species, primarily in relation to climatic and edaphic factors. Similar patterns are clear across the six bioregions sampled in the present study.

CONCLUSIONS

In relation to the seven question this study set out to investigate it was found that:

- It is possible to produce robust models in terms of location, climate and soil parameters for 16 of the 23 species assemblages which encompassed 85% of the 1022 taxa. These models explained between 49 and 84% of the scaled deviance. Models of a further 4 assemblages (explaining between 48 and 74% of the scaled deviance) were largely consistent with known habitat preferences but had their major centre of distribution outside our study area or centred on wetlands which were not sampled. The remaining three assemblages did not show any relationship between species richness and compositional gradients.
- The primary environmental correlates with the quadrat classification were climatic variables (rainfall parameters) with soil variables (available K, exchangeable Mg, exchangeable Ca and pH) being important on orthogonal axes.
- The quadrat classification was poorly correlated with Beard's 1:250000 structural vegetation units, indicating a poor match between composition and dominant lifeform.
- The pattern in distribution of species assemblages and quadrat groups showed little correlation with the current biogeographical regionalization (IBRA) of the study area. The Jarrah Forest bioregion received some support but only half this bioregion was sampled and the regions to the west and south were not.
- The analyses of the dataset at different taxonomic resolutions recovered significantly different floristic patterning.
- The analyses of the dataset based on different lifeforms recovered significantly different floristic patterning.
- The high percentage of uncommon taxa (60% of 2609 taxa recorded occurred in less than 5 quadrats) were not randomly distributed but concentrated along the southern and western edges of the study area. It is most likely that this represent a biogeographical sampling artifact.

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