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A floristic survey of the Tingle Mosaic, south-western Australia: applications in land use planning and management

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Abstract

A floristic survey of the Tingle Mosaic, an area of 3 700 km^2 which includes the wettest, least seasonal and southern-most part of Western Australia recorded a total of 857 vascular plant taxa in 441 quadrats (20 m x 20 m). These included 825 indigenous and 32 introduced taxa. Important families included the Papilionaceae (74 species), Proteaceae (73), Myrtaceae (64) and Orchidaceae (63).

Cluster analysis and ordination techniques defined five floristic communities supergroups, 12 community groups and 44 community types. The Open-forest, Tall open-forest and Shrubland/ woodland Communities Supergroups included most of the quadrats (356 of 441), and also occupied the largest areas within the region. There was high alpha diversity for the Woodland and Open-forest communities supergroups, while there was low alpha and gamma diversity for the Tall open-forest Communities Supergroup. Considerable variation in vegetation structure, and high gamma diversity was found for the three non-forest communities supergroups. An expanded program of survey would be required to target the exceptional variety of sites in the Swamp and outcrop Communities Supergroup. The Tingle Mosaic had high levels of local endemism, many taxa (both wet and dry country taxa) which have range limits in the area, and several relictual high rainfall taxa whose distributions are centred in the area. A high proportion of the region lies within the conservation reserve network. Nevertheless the conservation significance and complexity of the fine-scale biotic pattern in the area urge increased attention in management and policy for the conservation of biodiversity. Methods to integrate site-based work, to define complexes of community types, and of the mapping of these floristic assemblages are presented. These applications would be invaluable in management for the conservation of biodiversity in the region.

Introduction

The south-west of Western Australia includes an extraordinary diversity of vascular plants in a generally subdued landscape (Hopper 1979; Hopper *et al* 1992). This diversity has been especially noted for the inland transitional rainfall zone (TRZ *sensu* Hopper 1992) which is dominated by speciose genera of woody perennials in families such as the Myrtaceae, Proteaceae, Fabaceae and Epacridaceae (Hopper 1979; 1992) but not the high rainfall zone (HRZ) closer to the coast. Nevertheless wetland monocotyledonous taxa, including genera of Cyperaceae, Xyridaceae, Juncaginaceae, Restionaceae and Orchidaceae, are species-rich in the region. For example at least 1947 taxa are known from the Warren Botanical Subdistrict alone, despite limited survey (Hopper *et al.* 1992).

The HRZ is also notable for its high diversity of eucalypts compared with similar areas elsewhere in the Darling Botanical District (Christensen 1980; Smith *et al.* 1991, Wardell-Johnson & Smith 1991; Wardell-Johnson & Coates 1996, Wardell-Johnson *et al* in press). At least four species of large forest eucalypts, *Eucalyptus brevistylis* (Rates tingle), *E. jacksonii* (red tingle), *E. guilfoylei* (yellow tingle), and *E. ficifolia* (red-flowering gum) are locally endemic to the south-west between Walpole and Denmark. Each occurs in several allopatric populations in an area of high landscape and vegetation structural diversity. Because it was the tingles that first drew attention to the conservation significance of this landscape mosaic (Fernie & Fernie 1989), the survey area is described as the Tingle Mosaic.

The Tingle Mosaic is also notable for its scenic diversity and has been the subject of intense public interest (Smith *et al.* 1991; Wardell-Johnson & Smith 1991; Wardell-Johnson & Horwitz 1996). It occurs in close proximity to the towns of Walpole, Denmark and Albany (Smith *et al.* 1991) but includes areas that are generally remote and have not been explored botanically. The vascular flora has been chosen for study because of its richness (Hopper *et al* 1992) and because of its propensity to describe landscape pattern (Havel 1981; Wardell-Johnson *et al* 1989). The identification and classification of plant community types is a useful first step in land-use planning (Havel 1981; Wardell-Johnson *et al.* 1989). This allows the identification of rare or vulnerable communities at a regional level and allows a management context to be provided. Historically, vegetation classification in Australia has been based on a structural or physiognomic basis (Diels 1906; Speck 1952; Webb *et*

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al. 1976; Beard 1981). More recent work has utilised floristic attributes (e.g Havel 1975a,b; Webb et al. 1984; Cresswell & Bridgewater 1985; Foran et al. 1986). However, the final choice of attributes used to classify vegetation remains a function of the aims of the research project at hand (Anderson 1981).

Here, we describe the variation in the floristic composition of the area within the range limits of four locally endemic forest eucalypts (Tingle Mosaic) and identify sites with similar species composition (community types; terminology after Whittaker 1973).

Methods

Study area

The study area in south-western Australia lies between latitudes 34° 45' and 35° 10' and longitudes 116° 30' and 117° 45'. This area of approximately 3 700 km^2 (Table 1, Fig 1) within the Warren and Menzies Botanical Subdistricts of Beard (1980) includes the wettest and least seasonal part of Western Australia, although isohyets decline rapidly eastwards and from the coast.

Peter Tille (Agriculture WA, pers. comm., 1995) defined 98 land systems within 16 zones for The Darling Botanical District of Beard (1980), based on geology and recurring landform patterns. This area includes almost all of the jarrah and karri forests and woodlands of south-western Australia. The Tingle Mosaic lies within three zones (the Warren-Denmark southland, the Stirling coastal, and the Stirling Sandplain) and nine Land systems. The area includes two geomorphic provinces within the South-west Land Division (the Avon and the Stirling).

Climate

The region has a mediterranean climate (Gentilli 1971) with dry, generally temperate summers and cool, wet winters. The high rainfall parts of the Tingle Mosaic receive more reliable summer rain than elsewhere in the south-west. There is a considerable range in temperature and rainfall with gradients from both south-to-north and west-to-east. Thus in the south-western parts, annual rainfall exceeds 1 400 mm (Fig 1), whereas in the north-east it is about 750 mm.

Geology, physiography and soils

The Tingle Mosaic includes the southern fringe of the Great Plateau of Western Australia (Jutson 1914). It is composed of Precambrian granite rocks, partially overlain by various consolidated and unconsolidated sediments. This land surface has been subjected to a long and complex history of weathering and denudation which is expressed as variations in topography, soils and hydrology.

These factors, together with the nature of the rock

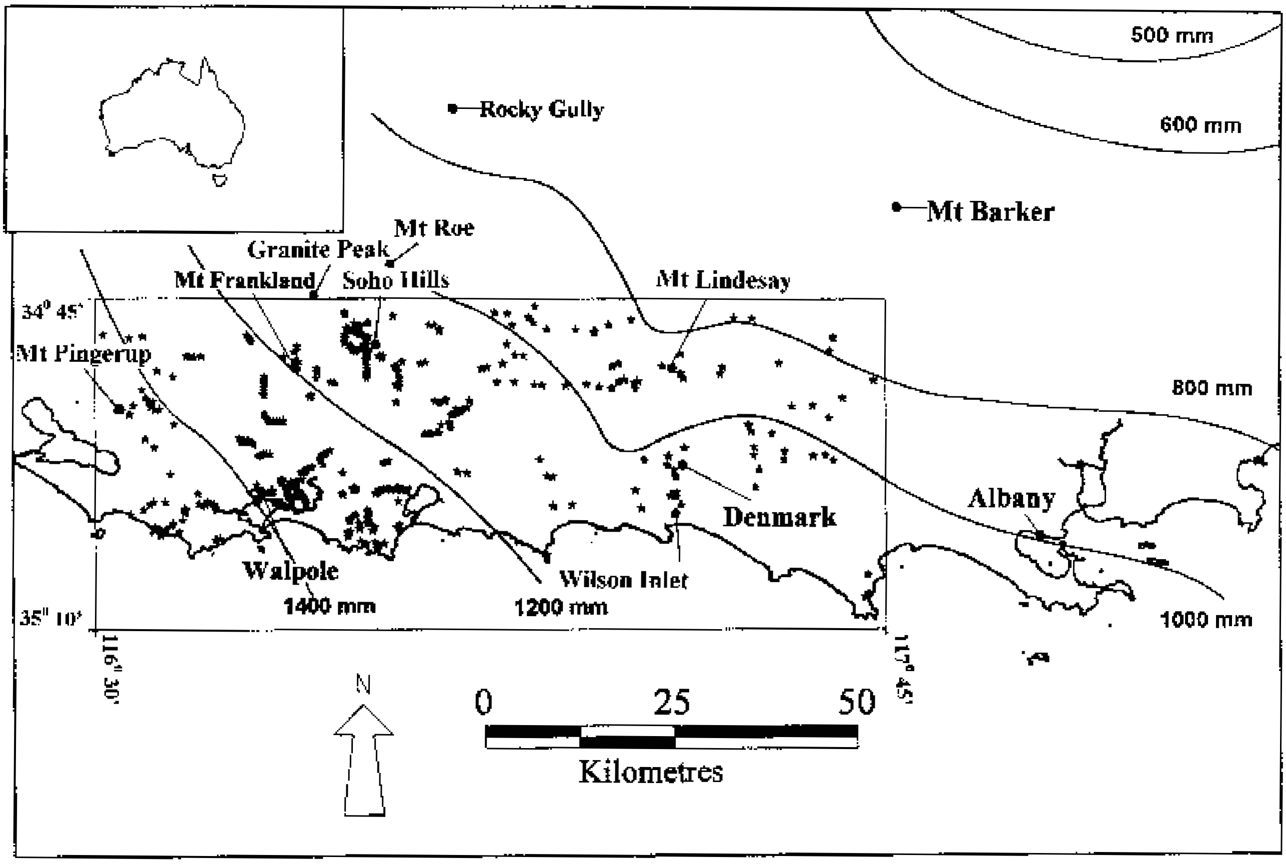

Figure 1. Study area showing the distribution of permanently located floristic quadrats, isohyets and major towns in south-western Australia.

Table 1

Tenure context of survey area. Reserves are National Parks, Nature Reserves and Conservation Parks. State Forest includes Executive Director lands, Timber Reserves and Other Reserves.

Location	Reserves km^2 (%)	State Forest km^2 (%)	Other km^2 (%)	Private Land km^2 (%)	Total Area km^2
Darling Botanical District	8 070 (11.3)	16 100 (22.6)	1 100 (1.5)	46 060 (64.6)	71 300
Warren Botanical District	2 870 (27.8)	3 290 (32)	430 (0.9)	3 709 (36)	10 300
Tingle Mosaic	909 (24.6)	686 (18.5)	387 (10.4)	1 717 (46.5)	3 700

types, formed the basis for the recognition of the landform/soils units defined and described by Churchward *et al.* (1988). These authors provided a detailed set of five 1:100 000 scale landform and soils maps covering an area between Windy Harbour eastward to Cheyne (Hassell) Beach, 80 km east of Albany, and extending inland to latitude 34º 31' S (as far north as Rocky Gully). Thirty-five units were mapped, based firstly on general geological features (*i.e.* units developed on granite or unconsolidated sediments, on siltstones and sandstones, on coastal aeolian and fluvial sediments and on drainage lines), and then on landform (plateau elements, hills and ridges, swampy terrain, dune systems, and major and minor valleys). They also provided further subdivision into individual units based on soils, local relief, slope and drainage patterns. The maps of Churchward *et al* (1988) provided a sound context for stratification in this survey (and also for broad-scale ecosystem management in the area).

Most of the Tingle Mosaic has soils which are developed on components of laterite profiles either exposed by erosion or as colluvial waste released by this process. Many of these soils have ferrugenous gravels in the surface horizons. In the unconsolidated sandy sediments, soil morphology is influenced mainly by drainage status, while in the coastal sand dunes, soil variation often relates to the age of parent material.

The headwaters of the Frankland River, a large river which rises well to the north of the Tingle Mosaic, are in broad valleys with salt lakes. Hence, there is a natural contribution of salts to the surface water. This is at a maximum following heavy winter rains. The headwaters of the Deep, Denmark, Kent and Hay Rivers also rise to the north of the Tingle Mosaic, and occur in areas with high soluble salts in the subsoil. Surface incidence of salinity is most evident in the north-east part of the Tingle Mosaic, and is expressed both as seepage on slopes and as saline valley floors. Salinity is not apparent on the plateau developed on marine sediments even though rainfall is low and the substrata known to be saline (Teakle 1953).

The general level of the Great Plateau gradually falls toward sea level in the area and forms part of the Ravensthorpe Ramp (Cope 1975). In the east, the landscape consists of a plateau developed on Pallinup Siltstone. The plateau surface represented by gently undulating plain slopes from about 180 m above sea level to about 40 m near the coast. In the remainder of the area, much of the terrain is developed on granitic rocks although there is a variable incidence of unconsolidated deposits as well as westward extensions of the Eocene sediments. This is at an elevation of from 260 to 180 m above sea level and is part of the Great Plateau underlain by deeply weathered granite. Some broad sandy, often swampy tracts are included.

To the west, extensive tracts such as the Pingerup Plains grade in elevation from 70 m inland, to less than 20 m where they abutt the narrow zone of coastal dunes. Granite is sometimes exposed as domes and pinnacles emergent above the sandy tracts (*e.g* Mt Pingerup). The terrain is dominated by a pattern of ridges of granitic rocks alternating with broad swampy corridors, having a west-north-west orientation. The crests of many of the ridges are in excess of 100 m above the corridors.

On the coastal fringe, both Precambrian and Tertiary rocks are overlain by Tamala Limestone of Pleistocene age (Logan 1968) and/or unconsolidated Holocene aeolian sands. The broad ridges of Tamala Limestone rise to about 100 m and often act as barriers behind which estuaries, such as Wilson Inlet, have developed. A system of Holocene parabolic dunes extend from the coast in a general east-north-east direction, overlying the broad ridges of limestone and of granite as well as alluvial and estuarine deposits. Much of the coastline is characterised by a succession of arcuate bays with granitic headlands linked by the barriers of Tamala Limestone in which steep cliffs have usually been cut. Most of these bays face south-west. The coastal plain in the immediate hinterland of the dunes is mantled by unconsolidated alluvium and/or aeolian sands.

Vegetation

Each of the 35 landform units defined by Churchward *et al* (1988) were described in terms of their physiography, geology, soil morphology and associated native vegetation. The latter was described structurally, and dominants were listed for each major stratum. This provided a means of determining quadrat locations to ensure a regional coverage of a complex area. The natural vegetation of the area has been mapped (scale 1:250 000) by Smith (1972) and Beard (1972-80).

Hopper *et al* (1992) provided a regional perspective for the flora of the Warren Botanical Subdistrict. They listed 1947 taxa including 1628 native and 319 naturalised introduced taxa for the area (roughly equivalent in size to the Perth Region; 8323 km^2 extending over 300 km from Yallingup on the Leeuwin-Naturaliste Ridge to Albany on the south coast).

Many site-based floristic studies have been carried out, in or nearby to the Tingle Mosaic. For example, Strelein (1988) presented an ordination using over 400 sample sites and 100 indicator species in the southern jarrah forest. He defined seventeen site types from this work using the methods of Havel (1968, 1975a,b) and discussed the regeneration, dieback susceptibility and productivity of each. Inions *et al* (1990) derived a floristic classification of regenerating karri forest in the Nornalup System of the Warren Subdistrict. They used 204 permanent inventory plots (Campbell *et al* 1985) and 105 species were sampled. Thirteen community types were defined by cluster analysis, ordination and discriminant analysis of the 312 m^2 quadrats. Wardell-Johnson *et al* (1989) developed a floristic classification of the Walpole-Nornalup National Park based on 219 quadrats and 233 species. Twelve community types were derived with clustering and ordination techniques. Several smaller site-based studies have also been carried out in the area (*e.g* Hopkins & Griffin 1984). These have been reviewed by Hopper *et al* (1992). Other opportunistic flora surveys have been carried out in the area over many years and a preliminary list of flora for the Warren Botanical Subdistrict is now available. Thus, over 2200 indigenous vascular plant taxa, many yet to be named, are known from this subdistrict alone (Hopper *et al* 1992; N Gibson, CALM *pers. comm*, 1995).

Sampling sites

This study was based on intensive sampling of the different vegetation types in representative areas. Areas were chosen on the basis of the landform / soils classification of Churchward *et al* (1988), although more intensive survey in the Walpole-Nornalup National Park was completed prior to the availability of this work (but see Wardell-Johnson *et al* 1989). Data from 144 sites of quadrat size 10 m radius (312 m^2) have been included from this work (see also Wardell-Johnson *et al*. 1989) Hence the survey effort is considerably greater for the WNNP than for the remainder of the Tingle Mosaic. The park does however include a major proportion of the populations of all three tingles as well as *E. ficifolia* (Smith *et al*. 1991, Wardell-Johnson & Smith 1991). Hence the concentration of quadrats in this area reflects the concentration of the rare eucalypts in the area.

The locations of sampling sites were selected to give as wide a range as possible of vegetation types from throughout the study area. All quadrats were located in undisturbed indigenous vegetation, with few weeds occurring in the area and no recent history of high intensity fire. Sampling preference was given to areas which were in existing conservation reserves rather than private property or road reserves.

Detailed studies have recognised that an appropriate sample area is about 400 m^2 in forested areas (Burbidge & Boscacci 1987; D Keith, Forests Commission of NSW, *pers. comm* 1994). This allows a representative floristic list for the site, and minimises the influences of individual large trees or logs within a quadrat. Quadrats larger than this risk encountering ecotones in the diverse vegetation of the HRZ of south-western Australia. All quadrats in this study were 20 m x 20 m, except those from the Walpole-Nornalup National Park survey mentioned above. All quadrats were established and permanently marked in the field by metal star pickets at centre points, and droppers at corners. The sites were checked at least twice, including at least once in spring. Species nomenclature follows Green (1985).

Analytical techniques

All sites (441) and all taxa (857) were analysed for plants presence / absence, which provides most of the information by ordination and classification of site-based data (Anderberg 1973). A matrix of pairwise associations between sites was calculated using the Czekanowski (1913) metric. UPGMA (Sneath & Sokal 1973) was used to derive clusters from the dataset; although this is sometimes prone to minor misclassification, it has the advantage of taking more than one species into account at any fusion. The clustering-intensity coefficient beta (β) was -0.10; under such conditions the clustering strategy is space-dilating and resists the formation of a single large group by forcing the formation of even-sized groups (Booth 1978).

The use of clustering techniques assumes that a population is discontinuous; the validity of this assumption depends on the species' response to environmental gradients and the nature of the gradients themselves (Austin & Cunningham 1981). In reality, vegetation is likely to vary from apparently continuous to apparently discontinuous with the nature of boundaries varying in width and level of diffusion throughout, and by how they are defined. The location of sample sites can also have an influence over the degree to which the vegetation of a region is considered continuous or discontinuous.

The acceptability of imposed groups was examined by ordinating the sites using semi-strong-hybrid multidimensional scaling (PATN; Belbin 1993), and examining the position of group members in component space. As analysis should not be performed across major data discontinuities (Green 1980), further cluster analysis was performed on each of the five major discontinuity's determined through initial analysis.

Results

Sites and species

A total of 857 vascular plant taxa were recorded in the 441 quadrats of the Tingle Mosaic. Important plant families included the Papilionaceae (74 species), Proteaceae (73), Myrtaceae (64) and Orchidaceae (63). Relative to the number of taxa represented in the Warren Botanical Subdistrict, the Orchidaceae (63), Cyperaceae (34), Restionaceae (34), Poaceae (24) and Asteraceae (19) were relatively poorly represented in quadrats (see Hopper *et al* 1992). The largest representation of genera included *Acacia* (23 species), *Stylidium* (36), *Leucopogon* (20) and *Eucalyptus* (22). *Caladenia* (12) and *Drosera* (12) were relatively poorly represented in quadrats in comparison with the Warren flora as a whole. A list of the taxa and their constancy (proportion of quadrats in which the species is present) in community groups is presented in Appendix 1. Several name changes occurred during the course of the study, and several taxa were found to have been misidentified once multivariate analysis was complete. These were few, thus providing little likelihood of influencing the overall classification. They are also shown in Appendix 1.

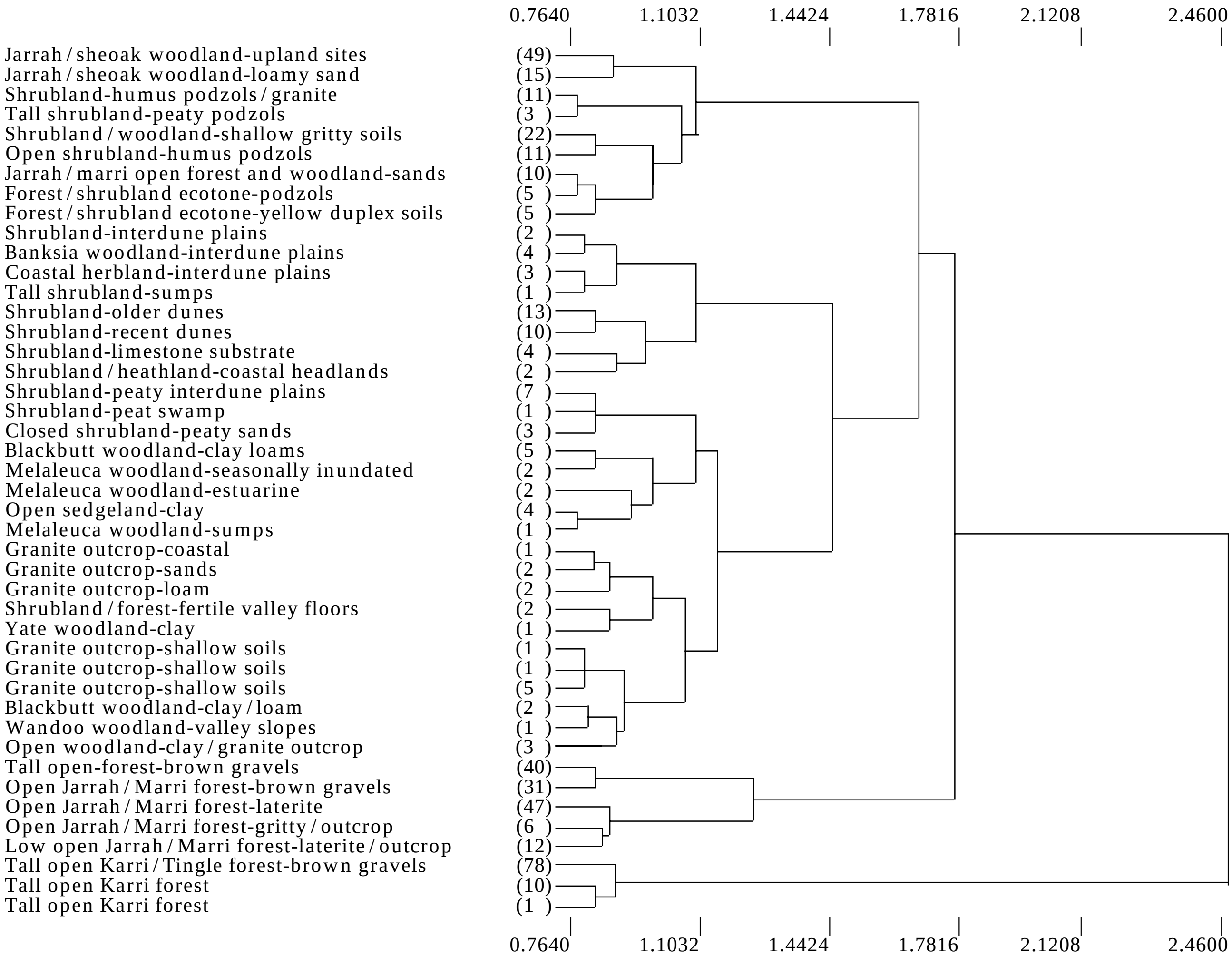

Figure 2. Dendrogram classification of 441 sites, based on 857 vascular plant taxa showing communities supergroups (A-E) and community types. The predominant vegetation and soil features of the 44 community types are shown with numbers of quadrats in brackets. Reprinted from Wardell-Johnson & Horwitz (1996) Forest Ecology and Management, 85(1-3) , Conserving biodiversity and the recognition of heterogeneity in ancient landscapes: a case study from south-western Australia, 219-238, 1996 with kind permission of Elsevier Science - NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

Cluster analysis and ordination defined five floristic communities supergroups, 12 community groups and 44 community types (Figs 2-3; Table 2). As the five communities supergroups represent a clear discontinuity in both cluster analysis and ordination, it is likely that this will mask differences amongst community types (Green 1980). Thus the five communities supergroups were each analysed separately for higher resolution within the supergroups and to define community sub-types.

A clear separation of sites at the 12 group level defined groups of similar sites according to broad topography, drainage and soils characteristics. These 12 groups are referred to as community groups and the constancy of taxa within these groups are presented as a summary of the floristics of the area (Appendix 1). All but the tall open-forest communities supergroup comprise more than one community group.

Shrubland/woodland Communities Supergroup. (A: 131 quadrats and 464 taxa) included four community groups (forest / sandplain ecotone sites, woodland communities in shallow soils, shrubland on sandplains, woodland on sandy crests and valley divides), nine types and ten sub-types (Fig 4, Table 3). These were generally sites in broad sandy terrain.

Dune Vegetation Communities Supergroup. (B: 39 quadrats and 268 taxa) included two community groups (Merrup Dunes, Interdune plain and swamp), eight types and ten sub-types in aeolian dunes (Fig 5, Table 4).

Swamp and outcrop Communities Supergroup . (C: 46 quadrats and 524 taxa) included three community groups (wandoo woodland and outcrop, saline swamps, and peat swamps) and 19 types (Fig 6, Table 5). These sites were in swampy terrain or areas of impeded drainage or outcrop. The limited sampling and heterogeneity of these community types prevented assessment below the 19 group level.

Open-forest Communities Supergroup . (D: 136 quadrats and 428 taxa) included two community groups (jarrah / marri / tingle open-forest, jarrah / marri open-forest), five types and 14 sub-types (Fig 7, Table 6).

Table 2

Summary statistics of communities supergroups and community groups of the Tingle Mosaic.

Community supergroup	Community types	Sub-community types	taxa	quadrats	Community group (community types)
A: Shrubland / woodland communities	9	10	464	131	A1; Forest / sandplain ecotone sites (3) A2: Woodland communities in shallow soils (2) A3: Shrubland on sandplains(2) A4: Woodland on sandy crests and valley divides (2) Walpole, Kentdale, King, Broke, King (swamps, plateau, valley divides)
B: Dune vegetation	8	10	268	39	B1: Merrup Dunes (4) B2: Interdune plain and swamp (4) Nullakai (dunes)
C: Swamp and outcrop	19	19	524	46	C1: Wandoo woodland and outcrop (11) C2: Saline swamps (5) C3: Peat swamps (3). All (swampy terrain, plateau and hills).
D: Open-forest	5	14	428	136	D1: Jarrah / marri / tingle tall open forest (2) D2: Jarrah / marri open forest (3) Walpole, Roe, Kentdale, King, Pardalup, King, Redmond (hills, ridges, plateau)
E: Tall open-forest	3	12	132	89	E1: Karri / tingle tall-open forest (3) Walpole (hills and ridges)

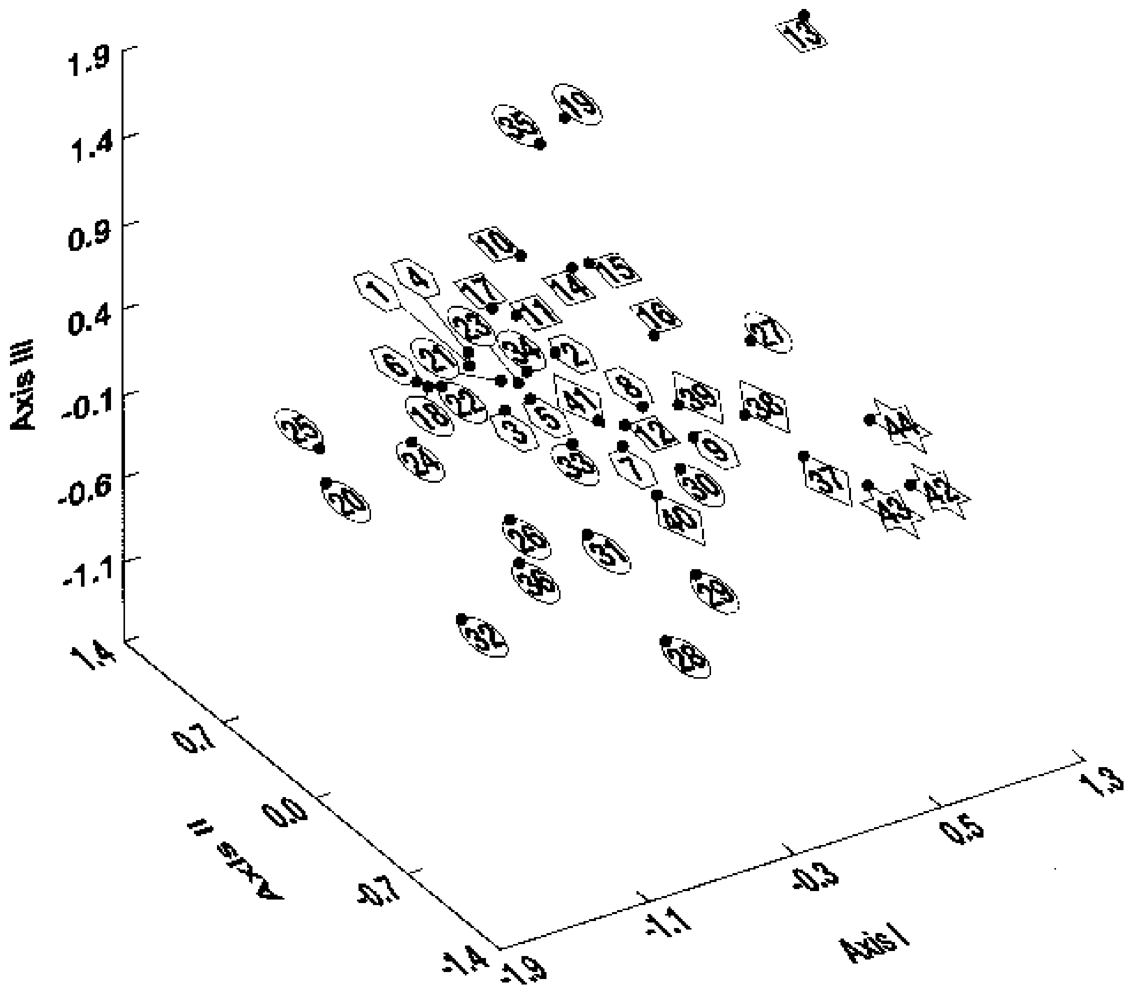

Figure 3. Centroids of the 44 community types clustered in three dimensions using semi-strong-hybrid multidimensional scaling.

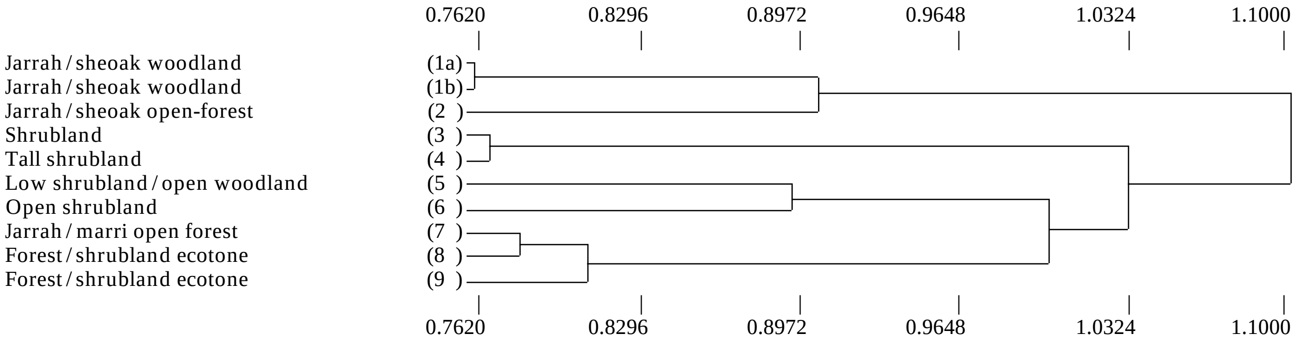

Figure 4. Dendrogram classification of the 131 sites (based on 424 vascular plant taxa) of the Shrubland / woodland Communities Supergroup (A); community type and sub-type are shown in brackets.

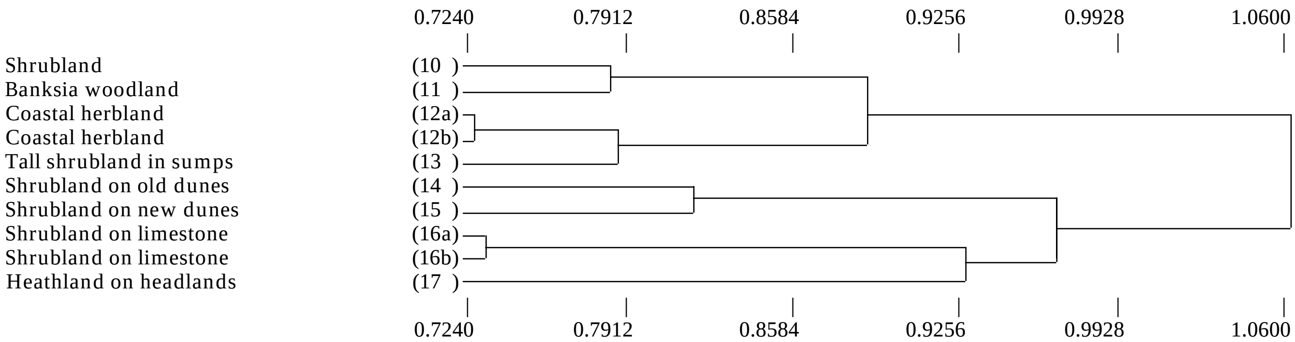

Figure 5. Dendrogram classification of the 39 sites (based on 241 vascular plant taxa) of the Dune vegetation Communities Supergroup (B); community type and sub-type are shown in brackets.

Table 3

Description of community types in Shrubland / woodland Communities Supergroup (Communities Supergroup A).

Community-type[a]	Description	Number of quadrats[a]	Species richness[a]	Landform / soils[b]
1(a,b)	Jarrah / sheoak	49 (39, 10)	43.0 (42.9, 43.6)	Freely drained sands in uplands and valley divides (CA, Bwp, Ds, Dc, Q).
2	Jarrah / sheoak open forest and woodland	15	36.3	Fertile sands with some loam (WA, CA, HA).
3	Shrubland to tall shrubland	11	23.4	Humus podzols in gently sloping sandy terrain (HA, A).
4	Tall shrubland	3	29.3	Peaty podzols in lower slopes of sandy terrain (HA, A).
5	Low shrubland to open woodland	22	47.2	Shallow gritty duplex soils / podzols (Lp, Kp, Mtp, Cop, BU).
6	Open shrubland	11	41.9	Humus podzols (F, CA).
7	Jarrah / marri open forest and woodland	10	40.7	Sands (HA, A).
8	Forest-shrubland ecotone	5	40.8	Leached sands and podzols (Gs, Ks).
9	Forest-shrubland ecotone	5	21.0	Sandy yellow duplex soils (A, HA)

[a] values for sub-communities is parentheses; [b] units of Churchward et al.(1988).

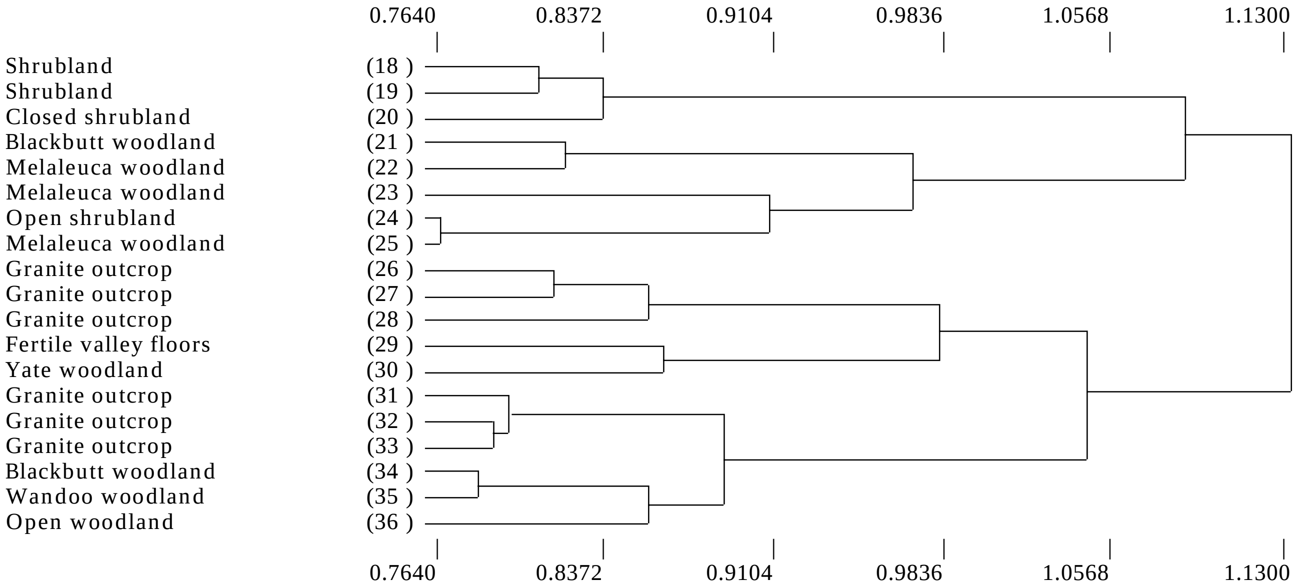

Figure 6. Dendrogram classification of the 46 sites (based on 524 vascular plant taxa) of the Swamp and outcrop Communities Supergroup (C); community type and sub-type are shown in brackets.

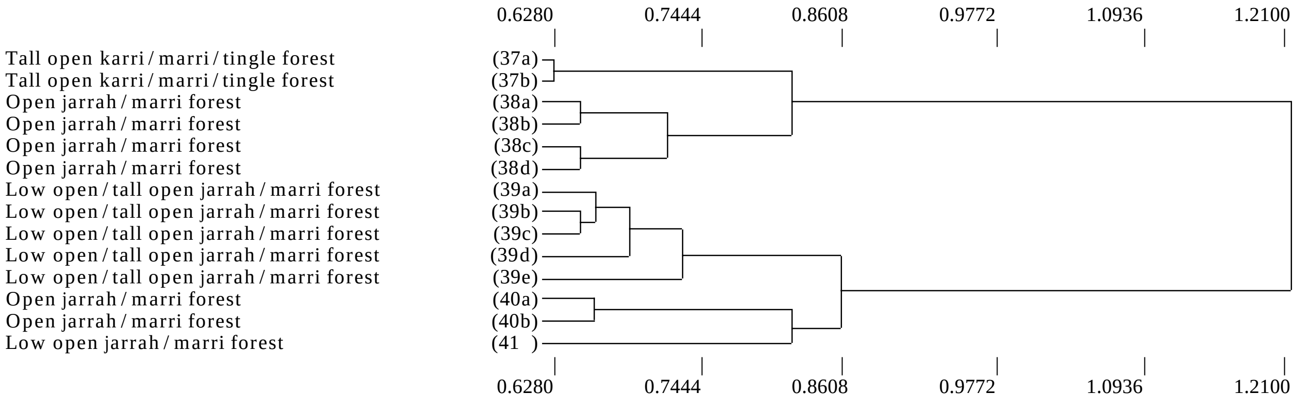

Figure 7. Dendrogram classification of the 136 sites (based on 428 vascular plant taxa) of the Open-forest Communities Supergroup (D); community type and sub-type are shown in brackets.

These were in hilly terrain, but with poor soils or moisture holding capacity

Tall open-forest Communities Supergroup. Separate community groups were not recognised in this community supergroup (E: 89 quadrats and 136 taxa). However, three types and 12 sub-types were defined in this supergroup (Fig 8, Table 7) which included sites occurring in loamy soils in freely drained upland areas with good moisture retention capabilities. Considerable variation in vegetation structure was noted in the three non-forest supergroups.

Community types and species richness

The Tingle Mosaic was rich in species, although quadrats in tall-open forest were species-poor (Table 7). Species richness between quadrats was not normally distributed (Fig 9). This distribution reflected the uneven sampling effort within the study area. There was a large number of quadrats in tall open-forest with low species richness, and in open-forest and woodland with high species richness. Community types are species-rich in all but relatively fertile freely-drained upland sites, and extreme areas such as outcrop or saline seepage. Species richness is very high in open-forest and woodland environments on shallow or sandy soils.

The high richness of the Tingle Mosaic manifested itself through a very high proportion of singletons within quadrats of the survey area, particularly in the Open-forest and Swamp and outcrop Communities Supergroups. Notably, over 25 % of species occurred in only a single quadrat (singletons - Table 8). A high pro-

Table 4

Description of community types in the Dune vegetation Communities Supergroup (Communities Supergroup B)

Community-type[a]	Description	Number of quadrats[a]	Species richness[a]	Landform / soils[b]
10	Shrubland.	2	34.0	Interdune plains in older D'Entrecasteaux dunes
11	Banksia woodland.	4	39.7	Seasonally inundated, interdune plains in D'Entrecasteaux dunes.
12 (a,b)	Seasonally inundated coastal herbland.	3(1, 2)	27.3 (27.0, 28.0)	Seasonally inundated, freely drained D'Entrecasteaux dunes.
13	Tall shrubland in sumps	1	20.0	Sumps in BWp.
14	Shrubland on older dunes.	13	40.1	Older D'Entrecasteaux dunes.
15	Shrubland on recent dunes	10	36.0	Recent D'Entrecasteaux dunes.
16 (a,b)	Closed shrubland on limestone substrate	4 (1, 3)	26.5 (28.0, 26.0)	Limestone substrate in D'Entrecasteaux dunes.
17	Open shrubland to low open heathland on coastal headlands	2	29.5	Coastal granite headlands in D'Entrecasteaux dunes.

[a] values for sub-communities in parentheses; [b] units of Churchward et al (1988).

Table 5

Description of community types in the Swamp and outcrop Communities Supergroup (Communities Supergroup C).

Community type	Description	Number of quadrats	Species richness	Landform / soilsa
18	Shrubland.	7	39.1	Broad peaty interdune plains.
19	Shrubland.	1	28.0	Permanently moist freely drained peaty swamps.
20	Closed shrubland.	3	23.0	Broad seasonally inundated peaty sands
21	Blackbutt woodland.	5	40.2	Seasonally inundated clay loams.
22	Melaleuca woodland	2	35.5	Seasonally inundated.
23	Melaleuca woodland	2	24.0	Seasonally inundated estuarine habitats.
24	Open sedgeland.	4	24.7	Seasonally inundated clay soils.
25	Melaleuca woodland	1	20.0	Seasonally inundated sumps.
26	Granite outcrop.	1	29.0	Coastal granite outcrop.
27	Granite outcrop.	2	29.5	Sand amongst granite outcrop.
28	Granite outcrop.	2	17.0	Loam amongst granite outcrop.
29	Tall Shrubland to Tall open-forest	2	17.0	Fertile minor valley floors.
30	Yate woodland.	1	55.0	Clay valley floors.
31	Granite outcrop.	1	66.0	Shallow soils on granite outcrop
32	Granite outcrop.	1	39.0	Shallow soils on granite outcrop
33	Granite outcrop.	5	60.2	Shallow soils on granite outcrop
34	Seasonally inundated blackbutt woodland.	2	55.0	Clay-loams on seasonally inundated valley floors
35	Wandoo woodland	1	26.0	Low valley slopes
36	Open woodland.	3	43.0	Clay in granitic outcrop

[a] units of Churchward et al (1988).

Table 6

Description of community types in the Tall open-forest Communities Supergroup (Communities Supergroup D).

Community-type	Description	Number of quadrats[a]	Species richness[a]	Landform / soils[b]
37(a, b)	Tall-open karri / marri / yellow tingle forest	40 (12, 31)	34.0 (33.4, 38.7)	Brown / yellow gravelly freely drained upland (Ky, My, COy, V1)
38(a, b, c, d, e)	open jarrah / marri forest	31(3, 8, 6, 14)	42.8(55.7, 41.1, 42.5, 40.0	Brown-gravelly freely drained upland (Kb, Mb, COb, V1)
39(a, b, c d, e)	Low-open to tall-open jarrah / marri forest	47(9, 17, 6, 9, 5)	53.5(65.2, 54.8, 50.3, 41.2, 45.8)	Gravelly upland sites - including block laterite (Ky, Kp, My, COy).
40(a, b)	Open jarrah / marri forest	6(5, 1)	47.5(46.0, 54.0)	Shallow gritty soils amongst rock outcrop (Ly, Ls, Lg, Ks).
41	Low-open jarrah / marri forest associated with granite outcrop.	12	55.4	Shallow gritty soils amongst rock outcrop with laterite (COp, COy Mtp, Mty, Ly, Lp).

[a] values for sub-communities in parentheses; [b] units of Churchward et al (1988).

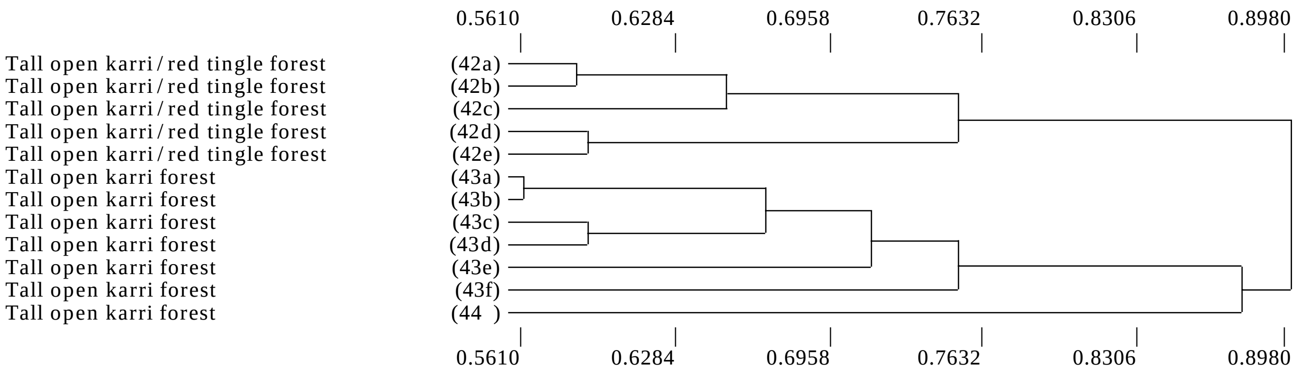

Figure 8. Dendrogram classification of the 89 sites (based on 132 vascular plant taxa) of the Tall open-forest Communities Supergroup (E); community type and sub-type are shown in brackets.

Table 7

Description of community types in the Tall open-forest Communities Supergroup (Communities Supergroup E).

Community-type[a]	Description	Number of quadrats[a]	Species richness[a]	Landform / soils[b]
42(a, b, c)	Tall-open karri / red tingle forest	78(12, 20, 10, 29, 7)	19.3(18.1, 21.8, 24.5, 17.0, 16.0)	Brown-gravelly freely drained upland (Kb, Mb, COb, Vl)
43(a, b, c, d, e, f)	Tall-open karri forest	10(1, 1, 5, 1, 3, 1)	19.1(16.0, 25.9, 17.2, 15.0, 33.0 16.0)	Brown-gravelly freely drained upland (Kb)
44	Tall-open karri forest	1	12.0	Brown=gravelly freely drained upland (Kb)

[a] values for sub-communities in parentheses; [b] units of Churchward et al.(1988).

Table 8

Comparisons between three floristic surveys of the high rainfall zone (HRZ) of south-western Australia.

Survey	Authors	Area km^2	Species (analysed)	Singletons (%)	Quadrats	Community types
Tingle Mosaic	Wardell-Johnson	3 700	(857)	214 (25)	441	44 (75 subtypes)
Swan Coastal Plain	Gibson *et al* (1994)	4 000	1485 (1097)	272 (25)	509	30 (43 subtypes)
South Coast	Gibson (pers. comm.)	2 000	910 (877)	214 (24)	301	40

portion of singletons has also been noted in other floristic studies carried out in the HRZ (Table 8).

Endemism in the Tingle Mosaic

A total of 20 taxa, endemic to the Tingle Mosaic were encountered in quadrats located in this study area (Table 9). At least another 13 taxa are known to be endemic to the study area, but were not located in quadrats (Table 9). This included four dominant forest eucalypts, a hybrid and a eucalypt taxon (*E. virginia* ms) previously collected in the area (1961) but not recognised as unique until the present study. Many of these locally endemic taxa are also rare (Table 9). A substantial number of collections made during this study require further clarification of taxonomic status. Thus additional taxa may subsequently be found to be restricted to the Tingle Mosaic. The considerable variation within what is currently accepted as a species suggests that several genera require major revision. These include *Hemigenia*, *Astartea*, *Baeckea*, *Agonis*, *Calandrinia*, *Aotus*, *Chorizema*, *Daviesia*, *Jacksonia*, *Latrobea*, *Leucopogon*, *Logania*, *Olearia* and *Hibbertia*.

The distribution of the endemic taxa is not even. For example 29 priority flora are known to occur within 10 km of Mt Lindesay (314 km^2) compared with 130 for the whole of the Southern Forest Region (14 400 km^2). This is a ratio of 10.2:1 on an area basis.

Many taxa found most commonly in drier or more seasonal environments than the Tingle Mosaic have limited ranges within the Tingle Mosaic (Table 10). These are usually confined to upland north-east facing slopes (*e.g Banksia gardneri* var. *brevidentata* in the Soho Hills) or deep sands (*e.g B. coccinea* in Redmond Forest Block) within the Tingle Mosaic. Many taxa that are confined to high rainfall, less seasonal areas and do not extend into the drier parts of the Tingle Mosaic, have range limits within the area (*e.g Anthocersis sylvicola*, *Lomandra ordii* and *Reedia spathacea*, the latter being confined to peat swamps west of the Bow River catchment). Other species occurring in peat swamp habitats, such as *Cosmelia rubra* and *Cephalotus follicularis* have distributions centred in the Tingle Mosaic.

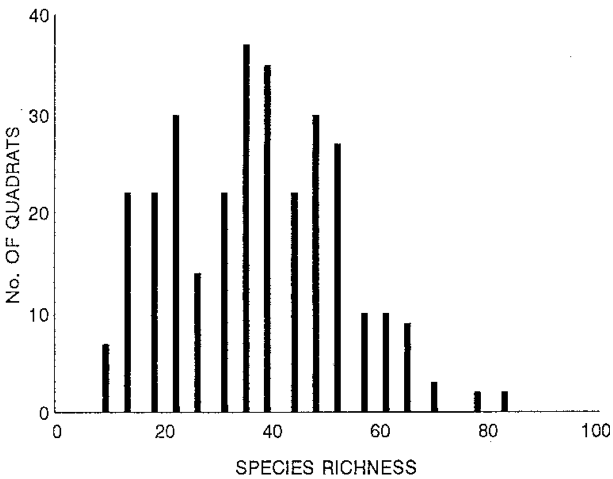

Figure 9. Numbers of quadrats plotted against species richness for 304 quadrats in the Tingle Mosaic.

Table 9

Taxa endemic to the study area.

	Taxon
#*	*Actinotus* sp Walpole (J R Wheeler 3786)
*	*Alexgeorgea ganopoda*
#*	*Andersonia* aff. *setifolia* (? *A. macronema*)
	Andersonia auriculata
*	*Andersonia* sp Collis (G Wardell-Johnson 5 A)
*	*Andersonia* sp Middle Rd (A R Annels 1059)
	Andersonia sp Mitchell River (B G Hammersley 925)
#*	*Andersonia* sp Mt. Lindesay (J A Cochrane 405)
*	*Anthocersis sylvicola* ms. (P G Wilson 6312)
*	*Boronia virgata*
*	*Borya longiscapa*
	Bossiaea webbii
#	*Caladenia evanescens*
#*	*Calothamnus* sp Mt.Lindesay (B G Hammersley 439)
#*	*Cryptandra congesta*
#*	*Eriochilus scaber* subsp *orbifolia* ms
	Eucalyptus brevistylis
	Eucalyptus ficifolia
	Eucalyptus ficifolia x *calophylla*
	Eucalyptus guilfoylei
	Eucalyptus jacksonii
	Eucalyptus virginia ms (A R Annels 3107)
*	*Gastrolobium brownii*
*	*Grevillea fuscolutea*
*	*Lambertia* aff. *uniflora* (A R Annels 1024)
#*	*Microtis globula*
*	*Rorippa dictyosperma* (G J Keighery 11945)
#*	*Sollya drommondii*
#*	*Spyridium riparium*
#*	*Tetratheca elliptica*
#*	*Thelymitra jacksonii* ms
	Trymalium venustum
#*	*Verticordia apecta*

* priority taxa; # taxa not recorded during this survey.

Table 10

Taxa with ranges ending in the Tingle Mosaic.

Western limit	
Acacia biflora	Grevillea umbellulata subsp acerosa
Acacia luteola	Hakea lasiantha
Acacia sulcata	Isopogon latifolius
Agonis marginata	Lambertia echinata subsp citrina
Banksia coccinea	# Latrobea sp South Coast (Ashby 1949)
Banksia gardneri var gardneri	# Lepidium pseudotasmanicum (SW limit)
Banksia gardneri var brevidentata	# Lepyrodia hermaphrodita
* Banksia goodii	# Lepyrodia monoica
* Banksia verticillata	# Lysinema lasianthum
Billardiera sp South Coast (A R Annels 227)	Melaleuca sp (A R Annels 863)
Brachysema sericeum	Melaleuca violacea
# Chorizema reticulatum	Monotoca tamariscina
# Conostylis misera	Nemcia crenulata
Dryandra serra	# Platytheca juniperina
Eucalyptus angulosa	Rinzia schollerifolia
# Eucalyptus buprestium	Schoenus trachycarpus
# Eucalyptus decurva	#* Sphenotoma drummondii
Eucalyptus dorotoxylon	# Sphenotoma parviflorum
Eucalyptus missilis	Synaphea polymorpha
Eucalyptus occidentalis	* Verticordia endlicheriana var angustifolia
Eucalyptus staeri	# Verticordia fimbrilepis subsp australis
Eucalyptus wandoo (SW limit)	# Xanthosia singuliflora
Eastern limit	
# Actinotus laxus ms	Lepyrodia extensa ms
Chaetanthus leptocarpoides	# Lomandra ordii
Chorizema retrorsum	* Melaleuca ringens
Eucalyptus calcicola	# Restio jacksonii
Gahnia sp Yelverton (G J Keighery 10820)	# Restio ustulatus
Hemigenia microphylla (SE outliers)	# Sporodanthus rivularis ms
#* Hypocalymma sp Scott River (A S George 1177)	Patersonia umbrosa var xanthina
* Reedia spathaceae	Stylidium laciniatum
# Hypolaena caespitosa ms	Stylidium pritzelianum
# Hypolaena viridis ms	Taraxis glaucescens ms
#* Kennedia glabrata	Taraxis grossa
# Lambertia orbifolia	
Southern limits and outliers	
# Chamelaucium forrestii subsp forrestii ms	#* Drakaea micrantha
# Darwinia thymoides	#* Epiblema grandiflorum var cyanea ms
#* Diuris drummondii	# Grevillea cirsiifolia

* priority taxa; # taxa not recorded during this survey.

Discussion

The Tingle Mosaic includes both great floristic richness and many rare and locally endemic plant species. Detailed taxonomic work on the collections made during this survey is likely to provide further insight into the historical biogeography, and evolutionary history of the area. Other floristic studies of the high rainfall zone (HRZ) in the Swan Coastal Plain and along the south-coast, which have included over 1200 quadrats and 2000 species, demonstrate the individualistic nature of the floristics of the HRZ and that over 25% of the quadrat-based flora records are of taxa recorded only in a single quadrat (Gibson *et al.* 1994; N Gibson, CALM, *pers. comm.* 1995). Although new taxa continue to be discovered in forest sites, these are the least variable of the community types at a landscape scale. Sites in tall-open forest tend to be poorest in species (excepting extreme sites), with least variation across the landscape. The overall floristic diversity of the HRZ is very high. The richness of the flora of the region is related to this rich landscape pattern, which in turn is associated with a diverse climatic and edaphic history.

Endemism in the Tingle Mosaic

The Tingle Mosaic is notable for high species richness of locally endemic species. Several other south-western areas are also notable for high richness of local endemic and rare species (*e.g.* Whicher Range, Darling Scarp). However, none are notable for the high numbers of locally endemic dominant species described by this study. For example, five species of dominant forest eucalypts are locally endemic to the Tingle Mosaic. These species were considered by Wardell-Johnson & Coates (1996) to be indicators of a non-mobile, small-scale relictual biota that is confined to the region.

Swamp and outcrop sites are likely to have been important refugia for both the mesic and dry country elements of the biota during the major climate fluctuations since the mid Tertiary (Hopper 1979; Hopkins *et al.* 1983). Isolation of populations in these sites has led to differentiation and speciation in some woody plant genera (*e.g. Agonis, Andersonia, Chamaelaucium* and *Leucopogon*). *Eucalyptus brevistylis*, a tall forest tree, is the largest species endemic to granite outcrop sites. This species is also locally endemic to the Tingle Mosaic and associated with the moisture gaining sites at the base of granite outcrops in areas of high relief.

The high levels of endemism associated with upland granite outcrop areas is no doubt associated with the geological and climatic history of the area. Thus sites relatively high in the landscape may have become islands during marine transgressions. Large islands such as Mt Lindesay may have retained a greater array of habitat-types than smaller islands such as Granite Peak, Mt Frankland and Mt Roe. These smaller peaks retain many rare and locally endemic taxa, but only a small proportion of the total within the region in comparison with Mt Lindesay.

Association of floristics with environmental attributes

The Tingle Mosaic features high landscape diversity encompassing hills and ridges, granite monadnocks, swamp, steep river valleys, dune systems and coastal cliffs. This area includes vegetation types ranging from tall open-forests to herblands and includes high levels of heterogeneity immediately adjacent to the forests and woodlands. Thus 36 of the 44 community types are outside the forests. Of these, six are community types occurring on outcrops and 22 occur in swamp habitat. Both these landscape features include high gamma plant diversity.

The degree to which community types are associated with the landform soils units of Churchward *et al.* (1988) is likely to vary between community types. Soil type appears to be stronger than landform in its associations with community types in hill and ridge areas of granitic base rock. However, at a fine-scale, considerable variation has been noted within the community sub-types of the tall open-forests of the area. For example, Inions *et al.* (1990) examined variation in floristics within regenerating karri forest over a major part of the range of karri. They defined 13 community types on the basis of floristic variation, each differing in productivity as measured by age-standardised top-height. This was despite the finding of Wardell-Johnson *et al.* (1989) that karri forest displayed the lowest alpha and gamma diversity of the 12 community types that they defined in the Walpole-Nornalup National Park. Twelve community sub-types are defined within the three community types of the Tall open-forest Communities Supergroup in this study.

The swamps of the area are important features of the landscape and exhibit great variation from peat swamps, estuaries, lakes and playas. This diversity of swampland has been recognised in landform-soils mapping of the south-west. Of the 37 landform-soils units mapped by Churchward *et al.* (1988) along the south coast, 2 are valley units (17 sub-units), and 16 are units in swampy terrain. Thus half of the units identified by Churchward *et al.* (1988) are based on riparian or swampy terrain, although these occupy a minor proportion of the total landscape of the study area. Although the topography is muted, the origin and expression of this variation is not, and sharp ecotones between communities supergroups are a feature of the Tingle Mosaic (Wardell-Johnson *et al.* 1989).

Floristic pattern in granite outcrop and swamp communities reflects high levels of complexity in landform soils mapping in these environments (Churchward *et al.* 1988). Swamp and outcrop communities have high gamma diversity. An expanded program of survey would be required to target the exceptional variety of environments in the Swamp and outcrop Communities Supergroup. The high water table in areas of swamp vegetation leads to a close link between water table and community structure in an area of great edaphic complexity. These community types are also likely to be most vulnerable to changes in land use.

There is considerably less floristic diversity occurring in tall open-forest than in other vegetational structural types. Two community supergroups (D and E), representing eight community types, occur in hills and plateau landform units and include forest. Open-forest, tall open-forest and woodland communities included most of the quadrats (356 of 441) and also occupied the largest area within the region. Thus hill and plateau units represent over 54% of the total survey area but include few of the community types. The open-forest areas include high levels of α diversity, and occur on shallow and infertile soils of this high rainfall zone.

Integration of floristic classifications and landform soil mapping

There are many site-based floristic studies for, or near, the Tingle Mosaic. Wardell-Johnson *et al* (1989) developed a floristic classification of the Walpole-Nornalup National Park based on 219 quadrats and 233 species. Inions *et al* (1990) defined 13 community types on the basis of floristic variation within regenerating karri forest over a major part of the range of karri. Strelein (1988) defined seventeen site types based on the floristic composition of over 400 sites in the southern part of the range of jarrah using the methods of Havel (1968, 1975 a,b). Both Inions *et al* (1990) and Wardell-Johnson *et al* (1989) provided a means of allocating independent sites to the classification using discriminant functions on species defined as indicators in the analysis (72 and 52 species respectively). Thus sites in one classification can be defined according to another. Classifications developed in both studies have used similar methods and both schemes can be mapped (Ward & Wardell-Johnson 1993). However, although Hopper *et al* (1992) concluded that an integration of site-based work (in the Warren Botanical Subdistrict) is desirable, considerable site revisiting would be required. The present study allows the integration of previous studies carried out over a small area, or within a subset of the variation in floristic composition (*i.e.* either in jarrah or karri forest) of the region. This work is required urgently and would allow an environmental context for the management of the region.

Floristic mapping

Previous maps of the floristics of the Tingle Mosaic area include a vegetation map (Smith *et al* 1991) which recognized the association of the twelve community types defined by Wardell-Johnson *et al* (1989) with the

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