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Differing habitat defines two metapopulations of a threatened Hunter Valley eucalypt: *Eucalyptus parramattensis* subsp. *decadens*

Stephen A. J. Bell

Conservation Science Research Group, School of Environmental and Life Sciences, University of Newcastle, University Drive, Callaghan, NSW 2308, AUSTRALIA. stephen.bell@newcastle.edu.au

Abstract A review of existing records and analysis of occupied habitat was undertaken for the vulnerable tree *Eucalyptus parramattensis* subsp. *decadens* (Myrtaceae). This taxon is endemic to the lower Hunter Valley of New South Wales, where it occurs principally in two discrete metapopulations on the Tomago Sandbeds and in the Cessnock area. Fortunately, many areas supporting this taxon and its habitat occur on public lands, with part of both metapopulations contained within Werakata National Park and State Conservation Area or Tilligerry State Conservation Area. Despite this, existing and continuing threats to the taxon include development, high frequency fire, rubbish dumping and weed invasion.

Multivariate cluster analysis and non-metric dimensional scaling were performed on full floristic sample data to formally define occupied habitat. Five floristic groups were identified which differ across metapopulations and consequently increase the conservation significance of both. Differences in environmental variables (geology, soil, rainfall) were also identified and support floristic delineations. Previous estimates of between 15 000 and 25 000 individuals spread across the two metapopulations should now be refined and considered separately for conservation management purposes. Furthermore, applying phylogeographic principles suggests that both metapopulations should be managed as separate evolutionarily significant units to maintain the adaptive capacity of each genotype.

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Introduction

Many threatened plants occupy restricted geographical distributions due to habitat specificity, either at local or landscape scales (e.g. Keppel *et al*. 2017; Silcock & Fensham 2014, 2018). Although such taxa are often over-represented in listings of threatened species (Burgman 2002) compared to widespread species which have undergone population declines, the threats associated with human occupation and stochastic events nonetheless justify their inclusion. Requirements driving establishment and persistence in a location may be dictated by specific soil or water requirements, disturbance regimes, or interactions with co-occurring species of plants and animals related to pollination or dispersal (e.g. Prober & Austin 1990; Keppel *et al*. 2017; Coleby & Druitt 2021). In some cases, range-restricted floras can be explained by randomness and seed dispersal limitations rather than habitat availability (e.g. Robinson *et al*. 2019), but in general there is a higher probability of extinction for all taxa with small geographical ranges (Tucker *et al*. 2012). While widespread species commonly occur in a range of habitats, this rarely occurs in different populations of range-restricted taxa. Where taxa comprise several populations within a definable region, metapopulations (collections of interacting local populations where long-term persistence is dependent on colonisation and immigration outcompeting local extinction: Hanski *et al*. 1996) may be defined to better direct management and conservation initiatives. Some metapopulations possess a minimum viable population size whereby long-term persistence of a species cannot be assured without management intervention (Bulman *et al*. 2007). However, fragmentation related to agriculture and urban development will influence the long-term persistence of any metapopulation through interruptions to these ecological interactions and, as a consequence, conservation of a metapopulation will require management intervention to maintain colonisation processes (through dispersal or augmentation) and to reduce threats that may lead to extinction (Husband & Barrett 1996; Freckleton & Watkinson 2002).

Scheele *et al*. (2018) highlight that despite the long-recognised need to fully understand the ecology, habitat requirements and threatening processes affecting at-risk species, in reality this information is missing or undervalued for most taxa. They point out that understanding these basic attributes is required across the full distributional range of a target species so that management interaction can be planned in an informed manner. In this regard, range-restricted taxa present relatively easy targets where a greater understanding of species ecology and habitat requirements can be achieved, yet we still know relatively little about many of these. This is partly explained by a recognition that many listed range-restricted taxa have shown no evidence of decline (Silcock & Fensham 2018), and therefore do not rank highly in research priorities. The major threats operating on all Australian plant species centre on modifications to ecosystem structure and function, particularly through altered fire regimes and intensive agricultural activity (Kearney *et al*. 2019). In this context, it can be useful to apply phylogeographic principles (Avise 2000; Médail & Baumel 2018) to better manage at-risk and range-restricted taxa, allowing for future adaptations to changing environments and ensure that target taxa are managed appropriately. Evolutionarily Significant Units (ESUs), an important component of phylogeography, defines populations that have been historically geographically isolated and are therefore likely to possess distinct evolutionary heritage. ESUs are often supported by genetic investigations to identify their evolutionary heritage, but in other cases this may be assumed based on assessments of likely genetic exchange.

For the prominent Myrtaceous genus *Eucalyptus*, there is a diverse array of taxa occupying distributional ranges from <1 km^2 (e.g. *Eucalyptus imlayensis*) to entire continents (e.g. *Eucalyptus camaldulensis*). Some studies on range-restricted eucalypts have identified habitat peculiarity as key drivers in their distribution (Prober & Austin 1990; Shepherd & Keyzer 2014; Coleby & Druitt 2021), yet few have investigated habitat differences between metapopulations of the same taxon. Fensham *et al*. (2020) examined the range-restricted *Eucalyptus argophloia* and identified its presence within three vegetation communities of differing floristic and soil composition shared across six discrete locations; however, prior to fragmentation these all formed a single population. There are no studies in the literature where range-restricted eucalypts have been shown to occupy different habitat in different metapopulations.

This paper investigates aspects of the ecology and distribution of the range-restricted *Eucalyptus parramattensis* subsp. *decadens* across two metapopulations (c. 25 km apart), using co-occurring floristic data and key environmental variables to define occupied habitat. It compares the environmental niches of these two metapopulations to determine if, on the basis of disjuncture and assumed poor genetic exchange, conservation and management strategies should treat populations of this taxon as different phylogeographic units.

Study Area

Investigations were undertaken in the lower Hunter Valley of New South Wales, in the only areas known to support natural stands of *Eucalyptus parramattensis* subsp. *decadens* (Tomago and Cessnock). Both areas occur within the NSW North Coast region of Thackway and Cresswell (1995), and the North Coast botanical division of Anderson (1961). The vegetation of the Tomago (~10 000 ha) and Cessnock (~70 000 ha) study areas has been previously classified and mapped (Bell & Driscoll 2006; DECC 2008), and the extent of these investigations demarcate the study areas for the current work (Figure 1).

The Tomago Sandbeds ('Tomago') are comprised of Pleistocene sands forming the inner barrier of the Newcastle Bight Embayment (Thom *et al*. 1992) and are located approximately 15 km north-east of Newcastle. The sandbeds were gazetted as a Crown water reserve in 1939 to supply water to Newcastle in the 1930's, and extraction is facilitated through the use of 22 pumping stations controlled by the Hunter Water Corporation. Additionally, the Commonwealth Department of Defence established a RAAF fighter base and bombing range on the southern edge of Tomago near Williamtown in the early 1940's. The Sandbeds are well vegetated across the majority of its 100 km^2, apart from localised development associated with the RAAF Air Base and Newcastle Airport, and extensive areas of rehabilitated mining land where heavy minerals and silica sand have been extracted over many decades (URS Australia 2000). Much of Tomago now forms part of the Tilligerry State Conservation Area.

Cessnock is a major regional town approximately 40 km inland from Tomago. Sand sheets derived from old riverine alluvial deposits occur in broad areas between Cessnock and the neighbouring township of Kurri, colloquially known as the 'Kurri Sands' and giving name to the threatened Kurri Sands Swamp Woodland (NSW Scientific Committee 2011) that occurs in the area. The Cessnock district comprises a mixture of urban, agricultural, mining, viticultural and bushland areas, including large tracts of public bushland (e.g. Cessnock, Aberdare, Heaton, Pokolbin and Corrabare State Forests; Yengo, Watagans and Werakata National Parks; Werakata State Conservation Area; and Crown reserves).

Both Tomago and Cessnock lie in a warm temperate climatic zone, with warm wet summers and cool dry winters. Rainfall generally peaks in late summer and early autumn, although local variations due to topography are evident, with an annual average of 738 mm per year at Cessnock and 1127 mm per year at Tomago. Temperatures range from average lows of 16^{o}C at both Cessnock and Tomago in June and July, to highs of 33^{o}C (Tomago) and 36^{o}C (Cessnock) in January (Bureau of Meteorology 2022).

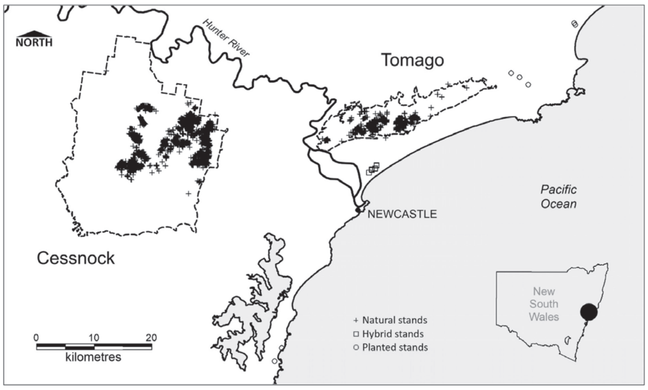

Figure 1. The study regions, showing extant records of *Eucalyptus parramattensis* subsp. *decadens*.

Methods

Study taxon

Eucalyptus parramattensis was first described in 1913 from type material collected at Fairfield in Sydney (Hall 1913). It forms part of subgenus *Symphyomyrtus* and section *Liberivalvae*, the 'Red gums' (Slee *et al*. 2020). Other members within this group include *Eucalyptus bancroftii, Eucalyptus prava, Eucalyptus seeana* and *Eucalyptus interstans* (Slee et. al. 2020), and of these only *Eucalyptus prava* also occurs within the Hunter catchment. Historically, there have been three subordinate ranks of *Eucalyptus parramattensis* recognised: subsp. *parramattensis*, subsp. *decadens* and var. *sphaerocalyx*. *Eucalyptus parramattensis* var. *sphaerocalyx* was described in 1934 and appears to be represented in collections solely by the type specimen: "*N.S.W. - Duck River, Parramatta (Dr. Woolls); Richmond, Bankstown and Cabramatta*." (cited in Hill & Johnson 1991). Although Blakely (1934) noted other localities, this was the only specimen fully referred to and was also the specimen labelled 'Type' by Blakely. However, Hill & Johnson (1991) did not recognise this variety when differentiating subsp. *decadens* from the type form but chose instead to include it within subsp. *parramattensis*. Slee *et al*. (2020) later raised var. *sphaerocalyx* to subspecies level, noting its presence from near Paramatta to the foothills of the Blue Mountains, but this was not adopted by NSW. It is probable that plants from the original collecting localities are now extinct due to urban development in Sydney.

Eucalyptus parramattensis subsp. *decadens* L.A.S. Johnson & Blaxell (Earp's Gum) is a small-growing eucalypt restricted to two distinct areas within the lower Hunter Valley, where it is locally dominant. It was considered allopatric with the type subspecies by Hill and Johnson (1991), and differs from subsp. *parramattensis* by its larger buds, fruits and leaves. The taxon is listed as vulnerable in the NSW *Biodiversity Conservation Act 2016* and the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999*. *Eucalyptus parramattensis* subsp. *decadens* is a long-lived tree which flowers and fruits sporadically under suitable conditions, and resprouts readily following fire or other disturbances (pers. obs.). Pollination is likely affected through the foraging activities of birds, bats and insects, and hence genetic material has the potential to spread great distances. In the Port Stephens area, *Eucalyptus parramattensis* subsp. *decadens* is a preferred Koala browse species (Knott *et al*. 1998; Lunney at al. 1998; Phillips *et al*. 2000) and is also foraged by the Grey-headed Flying Fox (Eby 1995).

Extant distribution

Two classification and mapping projects undertaken within the lower Hunter Valley across the Tomago Sandbeds (Bell & Driscoll 2006) and the Cessnock area (DECC 2008) provided the background to this study. During those projects, extensive field traverses were made in 4WD vehicle and on foot to record dominant plant species across each landscape as rapid data points, logging their locations into GPS units. These data were collected primarily to assist in the preparation of a classification and map of the natural vegetation in those areas (see Bell & Driscoll 2020 for further details). Newly collected field data for *Eucalyptus parramattensis* subsp. *decadens* were extracted from these projects and combined with publicly available locational records to create a single database to map the extant distribution of the taxon. Outlying records were inspected to determine currency and consider the possibility that their presence was a result of planting.

Floristic survey & data analysis

Existing plot-based floristic data for the lower Hunter region was examined and all sample plots supporting *Eucalyptus parramattensis* subsp. *decadens* extracted where this taxon dominated or co-dominated the canopy layer. These were largely drawn from Bell and Driscoll (2006) and DECC (2008), with minor additions from other projects. All floristic data were collected within standard sample plots of 0.04 ha (20 x 20m quadrats), located within homogeneous stands of vegetation. Modified (1-6 scale) Braun-Blanquet cover abundance scores (1 = few individuals, <5% cover; 2 = many individuals, <5% cover; 3 = 5-25% cover; 4 = 26-50% cover; 5 = 51-75% cover; 6 = 76-100% cover) were applied to all vascular plant species recorded within each quadrat. Plant nomenclature followed the National Herbarium of New South Wales (Plantnet: https://plantnet.rbgsyd.nsw.gov.au/floraonline.htm).

Multivariate cluster analysis and non-metric multidimensional scaling (nMDS) was performed on this dataset using *Primer* (Clarke & Gorley 2006), to delineate floristic groups where this taxon occurs. Analysis utilized the group averaging strategy, the Bray-Curtis association measure and a Beta value of –0.1. Both 2-dimensional and 3-dimensional nMDS routines were run, set at a minimum stress of 0.01 and running 25 iterations. Prior to data analysis, all plots were allocated to *a priori* floristic groups based on field observations and characteristic species composition, to be tested during analysis. The SIMPER routine in *Primer* was used to generate diagnostic species lists for each defined floristic group, identifying those species collectively contributing 90% to the distinctiveness of each defined community. Analysis of similarity within and between *a priori* floristic groups was undertaken using one-way pairwise analysis of similarity with the ANOSIM routine with 999 permutations, also in *Primer*. Final floristic groups defined were aligned to major regional classification units to assist future conservation planning for this taxon.

Environmental correlations

Intersection of *Eucalyptus parramattensis* subsp. *decadens* point data with a range of environmental variables was undertaken in GIS to examine habitat across floristic groups. Variables examined included geology, lithology, soil landscape, soil fertility, elevation and rainfall. Due to scale limitations inherent in digital environmental layers, analyses were stratified to the two known metapopulations to avoid potential errors associated with poor resolution. These analyses used geology and lithology resource layers from Rose *et al*. (1966), Rasmus *et al*. (1969), Colquhoun *et al*. (2020), soil and soil landscape layers from OEH (2019a-d), and rainfall data from the Bureau of Meteorology to determine the most frequent attributes. Chi-square goodness of fit testing was undertaken on each variable for each metapopulation.

Results

Extant distribution

In excess of 3750 records of *Eucalyptus parramattensis* subsp. *decadens* comprise the regional database for this taxon, distributed predominantly across two main meta populations (Figure 1). This total includes records of planted specimens at Catherine Hill Bay in southern Lake Macquarie, and at Salamander Bay to the east of the Tomago Sandbeds. Both of these occurrences are in rehabilitated lands associated with mining activities. Two records also exist north of the settlement of Hawks Nest in the Myall Lakes National Park area, however one of these occurs on a rehabilitated mining path, and the other is presumed to also have been planted. Neither of these more northern outliers were inspected during this study, and it is possible that a third small disjunct population occurs at that location. A small number of records also occur on the outer barrier of Stockton Bight which are currently considered hybrids, most likely with *Eucalyptus robusta*. Over 2900 records of this taxon were recorded during mapping projects at Tomago (791) and Cessnock (2115). The two areas are separated by the extensive Hunter River floodplain and its tributaries, which does not support habitat suitable for this taxon. Elevational ranges for occurrences of *Eucalyptus parramattensis* subsp. *decadens* ranged from <10 m asl at Tomago, to 20-80 m asl at Cessnock.

Floristic groups

Multivariate cluster analysis of 48 sample plots where *Eucalyptus parramattensis* subsp. *decadens* dominated the canopy layer resulted in two high level groupings (the metapopulations of Tomago and Cessnock), at an overall similarity of 20% (Figure 2). Five low level floristic groups were definable for the full dataset at 42% similarity: three at Tomago, and two at Cessnock. Finer resolution of the Cessnock clade potentially delineated a third floristic group, however differences observed are not consistent and overlap other data.

The 3-dimensional nMDS provided the more significant of the ordination plots produced, with a stress level of 0.09 for the definition of the two metapopulations. Finer resolution of the five defined communities is best illustrated in the 2-dimensional nMDS, at a stress level of 0.14 (Figure 3). The ANOSIM test confirmed initial groupings defined and showed significant differences in species composition among floristic groups (Global R = 0.89, P = 0.001). Pairwise tests found significant differences between all pairs of floristic groups, indicating that within group samples were more similar than between group samples (Table 1). Pairings of floristic groups 1 and 2 were the most similar (R = 0.573), while group 1 most differed from all other groups (R = 1 for groups 3 to 5).

Table 2 summarises the key features of each of the five defined floristic groups where *Eucalyptus parramattensis* subsp. *decadens* dominates the canopy, and representative images are shown in Figure 4. SIMPER analysis identified those species collectively contributing 90% to the composition of each community and can be used to profile those communities where *Eucalyptus parramattensis* subsp. *decadens* is most commonly found (see Appendix 1). Based on the mapping of Bell and Driscoll (2006) and DECC (2008), approximately 3300 ha of occupied habitat supports this taxon; 1789 ha at Cessnock and 1488 ha at Tomago.

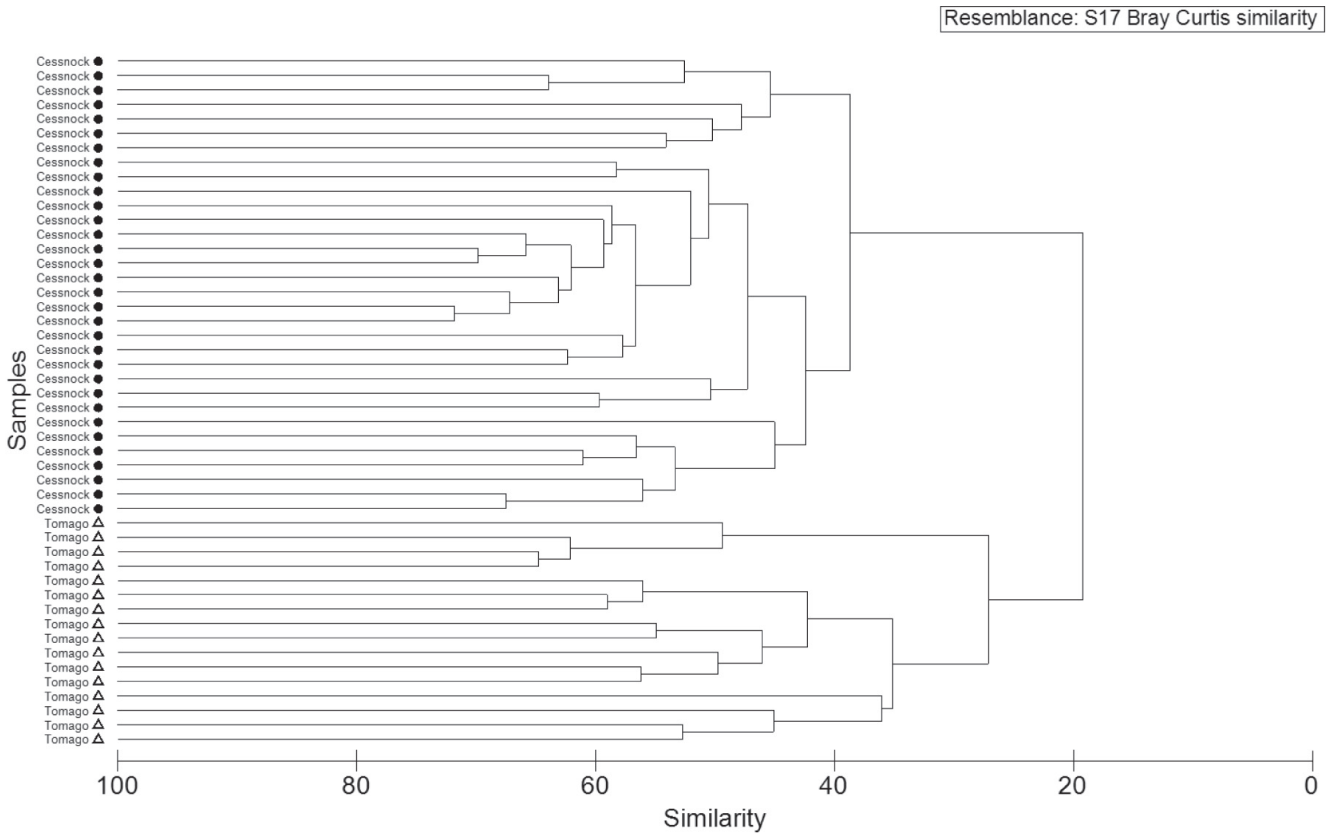

Figure 2. Dendrogram of sample sites, using the Bray-Curtis association measure, clearly showing a major dichotomy at ~20% similarity for Cessnock and Tomago locations.

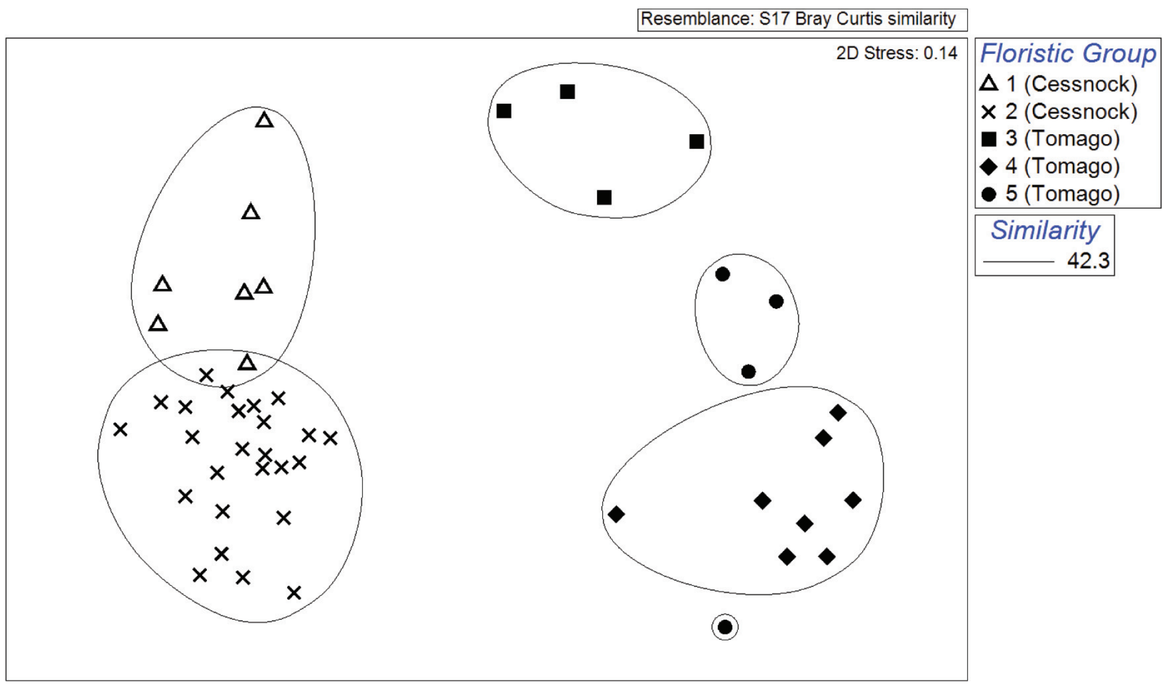

Figure 3. 2-dimensional nMDS plot of sample sites showing the three defined communities at Tomago, and two at Cessnock. Cut-points from the dendrogram in Figure 2 (at ~42%) are overlain, showing strong correlation.

Table 1. ANOSIM results (Global R & significance level, p) for pair-wise comparisons of *a prior* floristic groups.

	Group 1		Group 2		Group 3		Group 4		Group 5	
	R	p	R	p	R	p	R	p	R	p
Group 1										
Group 2	0.573	0.001								
Group 3	1	0.003	0.995	0.001						
Group 4	1	0.001	0.997	0.001	0.993	0.002				
Group 5	1	0.003	1	0.001	0.823	0.029	0.777	0.002		

Table 2. Summary of defined floristic groups.

Floristic group	Meta-population	Key canopy species	Structure	No. of samples	Mean spp./ sample	Species richness
Group 1	Cessnock	*E. parramattensis* subsp. *decadens, Angophora bakeri*	heath woodland	7	40.71	99
Group 2	Cessnock	*E. parramattensis* subsp. *decadens, Melaleuca nodosa*	scrub woodland	25	38.60	143
Group 3	Tomago	*E. parramattensis* subsp. *decadens, Banksia aemula*	scrub	4	39.75	73
Group 4	Tomago	*E. parramattensis* subsp. *decadens*	sedge woodland	8	24.25	78
Group 5	Tomago	*E. parramattensis* subsp. *decadens*	open forest	4	34.50	87

Floristic Group 1 (Appendix 1a, Figure 4a)

Floristic group 1 represents one of the more consistent communities defined and comprises part of the Kurri Sands Swamp Woodland EEC. Typified by the combination of *Eucalyptus parramattensis* subsp. *decadens* and *Angophora bakeri* in the canopy (cumulative 9% of total species contribution), over a diverse range of shrubs such as *Lambertia formosa, Bossiaea rhombifolia, Astrotricha obovata, Isopogon anemonifolius, Monotoca scoparia, Leucopogon virgatus,* and *Melaleuca nodosa* (cumulative 35%), and grasses and graminoids *Entolasia stricta, Aristida ramosa, Anisopogon avenaceus, Lomandra cylindrica* and *Xanthorrhoea glauca* subsp. *glauca* (cumulative 18%). Constancy ratios are highest for *Eucalyptus parramattensis* subsp. *decadens, Persoonia linearis* and *Astrotricha obovata*. Mapped extent: 1304 ha (DECC 2008).

Floristic Group 2 (Appendix 1b, Figure 4b)

Also falling broadly within the Kurri Sands Swamp Woodland EEC, floristic group 2 is dominated by *Eucalyptus parramattensis* subsp. *decadens* (cumulative 7% of total species contribution), but with dense shrub or tall shrub layers of *Melaleuca nodosa, Melaleuca thymifolia, Dillwynia retorta, Leptospermum parvifolium* and *Grevillea parviflora* subsp. *parviflora* (cumulative 24%), and the grasses/ graminoids *Aristida warburgii, Entolasia stricta, Anisopogon avenaceus, Lomandra cylindrica* and *Xanthorrhoea glauca* subsp. *glauca* (cumulative 23%). In some places, stunted, often mallee-like *Eucalyptus fibrosa* can also be present in the canopy layer. Other locations support a low open forest of *Eucalyptus parramattensis* subsp. *decadens* and *Eucalyptus beyeriana*, +/- *Eucalyptus punctata* and *Angophora bakeri*. Understorey vegetation here also includes *Melaleuca erubescens, Monotoca scoparia*, *Themeda triandra* and *Ptilothrix deusta*. Mapped extent: 485 ha (DECC 2008).

Figure 4. Habitat for *Eucalyptus parramattensis* subsp. *decadens* at Cessnock (a-c) and Tomago (d-f). a = Cessnock Scrubby Woodland; b = Cessnock Heathy Forest; c = Cessnock Low Open Forest; d = Tomago Wallum Scrub; e = Tomago Scrubby Open Forest; f = Tomago Sedge Woodland.

Floristic Group 3 (Appendix 1c, Figure 4c)

In poorly drained swales of the Pleistocene plain at Tomago, some sections of the more widespread *Banksia aemula* heathlands also support scattered individuals or dense stands of *Eucalyptus parramattensis* subsp. *decadens* in a very dense low scrub (cumulative 17% of total species contribution).

Melaleuca nodosa, Leptospermum polygalifolium subsp. *cistmontanum*, *Leptospermum trinervium, Monotoca scoparia* and *Isopogon anemonifolius* characterise the shrub layer (cumulative 23%), with dominant subshrubs *Trachymene incisa* subsp. *incisa, Euryomyrtus ramosissimus* subsp. *ramosissimus, Hibbertia fasciculata* and *Platysace ericoides* (cumulative 19%). Ground layer vegetation is less important in this group, but includes *Cyathochaeta diandra, Leptocarpus tenax, Haemodorum planifolium* and *Xanthorrhoea glauca* subsp. *glauca* (cumulative 8%). Mapped extent: 957 ha (Bell & Driscoll 2006).

Floristic Group 4 (Appendix 1d, Figure 4d)

A low open woodland of *Eucalyptus parramattensis* subsp. *decadens* (cumulative 18% of total species contribution), with few other canopy species. Characteristic shrubs include *Melaleuca thymifolia, Melaleuca sieberi* and *Banksia oblongifolia* (cumulative 18%), over a sedge-dominated understorey of *Leptocarpus tenax, Schoenus brevifolius, Ptilothrix deusta* and *Lepyrodia scariosa* (cumulative 34%), with grasses such as *Entolasia stricta* and *Hemarthria uncinata* var. *uncinata* (cumulative 11%). This vegetation type occupies claypans associated with the Pleistocene inner barrier of the Newcastle Bight Embayment. Mapped extent: 476 ha (Bell & Driscoll 2006).

Floristic Group 5 (Appendix 1e, Figure 4e)

An open forest of *Eucalyptus parramattensis* subsp. *decadens* (cumulative 16% of total species contribution), over a moderately dense understorey of *Leptospermum polygalifolium* subsp. *cistmontanum*, *Banksia oblongifolia, Acacia longifolia* subsp. *longifolia, Melaleuca thymifolia, Melaleuca nodosa* and *Platysace lanceolata* (cumulative 43%). Ground layer vegetation includes the sedges *Leptocarpus tenax, Cyathochaeta diandra* and *Ptilothrix deusta* (cumulative 11%), and the grasses *Entolasia stricta* and *Paspalidium distans* (cumulative 12%). This vegetation type occupies the poorly drained Pleistocene dunes of the inner barrier of the Newcastle Bight Embayment. Mapped extent: 55 ha (Bell & Driscoll 2006).

Table 3 equates the five floristic groups defined in this paper with major regional vegetation communities, NSW Plant Community Types, and the State classification of Keith (2004).

Environmental correlations

Chi-squared goodness of fit tests showed significant ($p<0.001$) differences in all environmental variables at both Cessnock and Tomago metapopulations (Table 4). Each metapopulation occurs in distinctly different environments displaying very few commonalities in geological, soil or rainfall properties, supporting the clear demarcation of vegetation groups defined in the floristic analysis. At Cessnock, *Eucalyptus parramattensis* subsp. *decadens* primarily occurs in moderately low fertility natric kurosol soils with restricted or very restricted water movement, derived from conglomerate and siltstone sediments of the Permian-aged Branxton formation, within the Wallalong soil landscape and in the 800-1000 mm/yr rainfall band. At Tomago, the taxon occurs in low fertility podosols of aeolian origin with free water movement through the profile, overlying sandstones of the Permian Tomago coal measures, within the Tea Gardens soil landscape and the 1000-1200 mm/yr rainfall band.

Table 3. Equivalent vegetation types in previous regional studies.

Current study	Previous Study	Equivalent Community
Floristic group 1	LHCCREMS [1]	Kurri Sands Swamp Woodland (EEC)
	Tomago Sandbeds [2]	-
	Cessnock-Kurri [3]	Kurri Sand Heath Woodland (EEC)
	NSW PCT [4]	1633: Parramatta Red Gum - Narrow-leaved Apple - Prickly-leaved Paperbark shrubby woodland in the Cessnock-Kurri Kurri area
	NSW vegetation [5]	Sydney Sand Flats Dry Sclerophyll Forests
Floristic group 2	LHCCREMS [1]	Kurri Sands Swamp Woodland (EEC)
	Tomago Sandbeds [2]	-
	Cessnock-Kurri [3]	Kurri Sands Redgum-Stringybark Forest/ Kurri Sands Shrub Forest
	NSW PCT [4]	not defined
	NSW vegetation [5]	Sydney Sand Flats Dry Sclerophyll Forests
Floristic group 3	LHCCREMS [1]	not defined
	Tomago Sandbeds [2]	Clay Wallum Scrub
	Cessnock-Kurri [3]	-
	NSW PCT [4]	not defined
	NSW vegetation [5]	Wallum Sand Heaths
Floristic group 4	LHCCREMS [1]	Tomago Sand Swamp Woodland
	Tomago Sandbeds [2]	Earp's Gum Sedge Woodland
	Cessnock-Kurri [3]	-
	NSW PCT [4]	1651: Parramatta red gum - Fern-leaved banksia - Melaleuca sieberi swamp woodland of the Tomaree Peninsula
	NSW vegetation [5]	Coastal Dune Dry Sclerophyll Forests
Floristic group 5	LHCCREMS [1]	not defined
	Tomago Sandbeds [2]	Earps' Gum–Peppermint Scrubby Forest
	Cessnock-Kurri [3]	-
	NSW PCT [4]	not defined
	NSW vegetation [5]	Coastal Dune Dry Sclerophyll Forests

[1] Lower Hunter & Central Coast Regional Environmental Management Strategy (NPWS 2000); [2] Bell & Driscoll (2006); [3] DECC (2008); [4] NSW Plant Community Types (https://www.environment.nsw.gov.au/NSWVCA20PRapp/default.aspx); [5] Keith (2004).

Table 4. Major environmental variables supporting the two metapopulations of *Eucalyptus parramattensis* subsp. *decadens* at Cessnock (n=66) and Tomago (n=809).

Variable	Location	Dominant attribute (%)	χ^2	df	Significance
Geology	Cessnock	Branxton formation (73)	151.6364	5	p<0.001
	Tomago	Quaternary sand (100)	-	-	-
Lithology	Cessnock	Conglomerate (71)	43.7273	2	p<0.001
	Tomago	Sandstone (93)	593.6329	1	p<0.001
Soil landscape	Cessnock	Wallalong (67)	65.0303	3	p<0.001
	Tomago	Tea Gardens variant a (70)	2827.9345	7	p<0.001
Soil fertility	Cessnock	Moderately low (96)	54.5455	1	p<0.001
	Tomago	Low (99)	1593.7994	2	p<0.001
Aust Soil Class	Cessnock	Kurosols, Natric (96)	54.5455	1	p<0.001
	Tomago	Podosols (99)	2347.7219	3	p<0.001
Hydrologic soil type	Cessnock	Group D (96)	54.5455	1	p<0.001
	Tomago	Group A (99)	1558.2933	2	p<0.001
Rainfall band	Cessnock	800 - 900 mm/yr (59)	27.9091	2	p<0.001
	Tomago	1100 - 1200 mm/yr (95)	1388.5269	2	p<0.001

Discussion

Eucalyptus parramattensis subsp. *decadens* is endemic to the Hunter Region, with two distinct and separate metapopulations on the Tomago Sandbeds and around Cessnock. Data collected as part of two major regional vegetation mapping projects have established a comprehensive picture of the natural distribution and occupied habitat of this taxon, and an estimated total population size of between 15 000 and 25 000 individuals has been previously made (Bell 2006). Despite considerable survey undertaken within the areas between each metapopulation, culminating in major mapping and classification projects (NPWS 2000; McCauley et. al 2006; DECC 2008), no further significant stands have been recorded and the two populations remain isolated. One small and fragmented group of plants has recently been discovered in former grazing land now largely cleared at Farley (D. Harman, pers. comm.), approximately 10 km north of Kurri, and a single individual in regrowth open forest has also been reported near North Rothbury, 15 km north of Cessnock (noted in Bell & Driscoll 2005). Historically, both locations may have adjoined the Cessnock metapopulation, given the large expanses of cleared grazing land now present between these areas.

At Tomago, *Eucalyptus parramattensis* subsp. *decadens* occurs exclusively on low elevation Pleistocene sand swales comprising the inner barrier of the Newcastle Bight embayment (Thom *et al*. 1992). Putative hybrids occur on the outer barrier of the Newcastle Bight embayment, on Holocene barrier depressions or strand plains, and require taxonomic clarification. The Cessnock metapopulation extends at slightly higher elevations from Wallis Creek in the east, to near Bellbird in the west, south to Mulbring, and north to Bishops Creek. The highly urbanised and cleared landscapes in the Cessnock area suggest that originally the species may have been largely contiguous across the whole district.

Prior to this study, information on the habitat of *Eucalyptus parramattensis* subsp. *decadens* was contained within various taxonomic texts. For example, Hill (2002) documents habitat as "*dry sclerophyll woodland on sandy soils in low, often wet sites*", and the original taxonomic manuscript describes it as "low-lying, often swampy areas on poor sandy soils, associated with *Eucalyptus signata, Eucalyptus globoidea* and *Angophora bakeri*" (Hill & Johnson 1991). The five floristic groups defined in this study provide a more detailed view of associated species and habitat, and mapping for each of these groups (Bell & Driscoll 2006; DECC 2008: available at https://www.seed.nsw.gov.au/) shows there to be approximately 3300 ha of occupied habitat across both metapopulations.

In addition to the five floristic groups defined as part of this study, *Eucalyptus parramattensis* subsp. *decadens* occasionally occurs as a minor component in some closely associated habitats. In the Cessnock area, DECC (2008) notes the presence of this taxon in four other communities; low forest dominated by *Eucalyptus beyeriana* and *Melaleuca nodosa*, scrubby forest of *Eucalyptus* sp. aff. *agglomerata*, low heath dominated by *Melaleuca nodosa* and *Leptospermum parvifolium*, and scrub dominated by *Melaleuca nodosa*, *Melaleuca decora* and stunted forms of *Eucalyptus fibrosa*. At Tomago, it may also occur on the fringes of *Melaleuca quinquenervia* swamp forests, widely scattered in some *Callistemon pachyphyllus – Hakea teretifolia* shrub swamps, and very occasionally in wet heath dominated by *Baeckea diosmifolia, Conospermum taxifolium, Leptospermum trinervium, Banksia oblongifolia, Leptospermum juniperinum* and *Hakea teretifolia* (Bell & Driscoll 2006). However, the five groups delineated in the current study define the main habitats for this taxon at both locations, where the bulk of the two populations occur.

Eucalyptus parramattensis subsp. *decadens* has been used extensively for rehabilitation following heavy mineral mining on the Tomago Sandbeds and has also been planted in small amounts elsewhere. Recognising its status as a threatened plant, the RZM Pty Ltd mining company frequently planted the species as part of the revegetation process, collecting seed from local provenance populations (URS Australia 2000). The taxon has also been planted near Salamander Bay following mining operations there by RZM Pty Ltd, but it is not known to occur naturally in this part of Port Stephens. Other plants occur in the Catherine Hill Bay area on Permian sedimentary substrates to the south of Newcastle, again associated with mining operations but along mine haulage roads. Further north, there are limited records on the northern side of Port Stephens near Hawks Nest, at least one of which occurs in heavy minerals mining revegetation areas, but it is unknown if any of these records represent a natural population.

Conservation and Management

Fortunately, a reasonable proportion of both metapopulations of *Eucalyptus parramattensis* subsp. *decadens* occur within existing conservation reserves. On the Tomago Sandbeds, almost all of the population lies in an area with restricted public access, managed jointly by Hunter Water and the NSW National Parks and Wildlife Service (Tilligerry State Conservation Area). In the Cessnock area, although some plants are present within Werakata National Park (Bell 2004) and Werakata State Conservation Area, the bulk of the population occurs within Crown or private lands with few restrictions on public access. Such ready accessibility may lead to increased rubbish dumping, weed invasion from garden refuse and arson.

For long-term management of this taxon, the distance separating both metapopulations (c. 25 km, with no known individuals or populations evident in the intervening fragmented or forested landscapes) suggests that gene flow is unlikely and has possibly not occurred for hundreds of years. Outcrossing between any eucalypt populations will be a factor of the mobility of pollinator vectors (Potts *et al*. 2003; Southerton *et al*. 2004), likely to be insects (bees, wasps, flies, ants, beetles) and vertebrates (birds, small mammals, bats). Unlike some other eucalypts (e.g. *Eucalyptus caesia, Eucalyptus incrassata*), *Eucalyptus parramattensis* subsp. *decadens* possesses small flowers adapted for insect pollination, although vertebrates also likely contribute as well. Pollen movement through insect foraging almost always results in local dispersal only (Potts *et al*. 2003), commonly at a scale of tens of metres. Where vertebrates comprise the main pollinators, evidence suggests outcrossing is limited to hundreds of metres only (e.g. Mimura *et al*. 2009; Breed *et al*. 2012; Bezemer *et al*. 2016). In Western Australia, Byrne *et al*. (2008) examined pollen dispersal in *Eucalyptus wandoo* (bird and insect pollinated) across fragmented agricultural lands and found pollination occurring at distances of up to 1 km, with closer distances reported in denser stands of this species. Such dispersal patterns align well with most foraging bee and insect behaviour (Southerton *et al*. 2004).

If similarly constrained pollen dispersal distances occur in *Eucalyptus parramattensis* subsp. *decadens*, one consequence of such restricted gene flow between the two identified metapopulations is that both should be managed as discrete, yet complimentary conservation units. Management of such geographically and genetically disjunct populations of the one taxon are included in the definition of Evolutionarily Significant Units (ESU) discussed by Moritz (1994), and much of this is now incorporated into the discipline of phylogeography (Avise 2000). The term ‘significant’ in this context refers to those populations that have been historically geographically isolated and likely to possess distinct evolutionary heritage. In most situations where ESUs have been proposed they are supported by genetic investigations to identify that evolutionary heritage, but in other cases this may be assumed. The two metapopulations of *Eucalyptus parramattensis* subsp. *decadens* defined in the current study, on the presumption that no or very limited genetic exchange is occurring between the two, can consequently be considered ESUs. This distinction is reinforced by the differing habitats in which the taxon occurs across these metapopulations, and in the absence of genetic profiling it is sensible that both be managed as equally significant. Médail & Baumel (2018) caution that considering all populations of a taxon as equal and exchangeable risks losing both irreplaceable evolutionary legacies and future adaptability to environmental changes. Application of phylogeographic concepts to other plant populations elsewhere are limited (Médail & Baumel 2018; and see Coates 2000; Gutiérrez-Ortega *et al*. 2018), but in fragmented landscapes and for taxa that naturally occupy disjunct distributions separated by distances greater than their pollinator and dispersal networks, such management may become more common.

Relative to some other threatened plant species, the list of threatening processes potentially impacting *Eucalyptus parramattensis* subsp. *decadens* are relatively minor and highly focused. Large areas of habitat occur on public lands, and ease of access by the public, particularly in the Cessnock metapopulation, subjects the taxon to ongoing threats. Principle among these are rubbish dumping, weed invasion, high frequency fire over an extended period, indiscriminate clearing or logging, habitat loss and fragmentation associated with development. On the Tomago Sandbeds, groundwater extraction during times of drought by Hunter Water may impact on the taxon and its habitat, although strict adherence to avoid such impacts are included in the legislated *Water Sharing Plan for the Tomago Tomaree Stockton Groundwater Sources 2003* (https://legislation.nsw.gov.au/view/whole/html/inforce/2011-08-12/sl-2003-0118) and monitoring of groundwater dependent vegetation has occurred there since 2013. Dryland salinity may also constitute a currently unrecognised long-term threat to the taxon and its habitat (Zeppel *et al*. 2003). Using 1 km^2 grid cells across NSW, these authors showed through GIS analysis that the Hunter Valley was the catchment most potentially threatened by dryland salinity, with *Eucalyptus parramattensis* subsp. *decadens* ranked fifth of 32 potentially *at risk* flora species.

Further research into the ecology of *Eucalyptus parramattensis* subsp. *decadens* might include: investigating the impacts of repeated fire in quick succession (particularly the primary juvenile period and time required to develop a fire-resistant lignotuber); understanding the long-term impacts of groundwater extraction from the Tomago Sandbeds on the taxon and its habitat; obtaining more accurate estimates of the total number of individuals within each metapopulation, including confirmation that new recruitment is occurring; and examining the genetic composition of both metapopulations to confirm the hypothesis that little genetic exchange has occurred historically. Further investigation into putative hybrid forms on the outer barrier of the Newcastle Bight embayment also require taxonomic resolution.

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Appendix 1 Floristic profiles for all defined groups, based on SIMPER analysis in Primer (Clarke & Gorley 2006). Contrib% shows the average contribution of each species to the total similarity within that group (to a cumulative 90%), while the similarity/standard deviation ratio indicates the consistency with which each species contributes to that group across all component plots.

Floristic Group 1

Group 1					**Average similarity: 48.16**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Eucalyptus parramattensis* subsp. *decadens*	2.14	2.73	8.92	5.67
	Angophora bakeri	2.29	1.83	1.19	3.79
Shrub	*Lambertia formosa*	3.29	3.94	3.38	8.19
	Bossiaea rhombifolia subsp. *rhombifolia*	2.57	2.49	3.07	5.16
	Astrotricha obovata	2.00	2.31	3.92	4.79
	Isopogon anemonifolius	2.14	2.24	1.95	4.65
	Monotoca scoparia	1.71	2.07	2.32	4.30
	Leucopogon virgatus	1.86	2.03	2.58	4.21
	Melaleuca nodosa	2.14	1.84	1.48	3.81
	Persoonia linearis	1.14	1.36	8.92	2.83
	Dillwynia retorta	1.57	1.34	1.34	2.79
	Leptospermum trinervium	2.00	1.32	0.91	2.73
	Banksia collina	1.43	1.26	0.92	2.61
	Leptospermum parvifolium	1.57	0.84	0.60	1.75
	Acacia ulicifolia	1.29	0.63	0.53	1.30
	Hakea laevipes subsp. *laevipes*	1.00	0.58	0.56	1.21
	Pimelea linifolia subsp. *linifolia*	0.86	0.35	0.40	0.72
Subshrub	*Dampiera stricta*	1.29	1.01	0.85	2.11
	Platysace ericoides	1.14	0.72	0.61	1.50
	Hibbertia pedunculata	0.86	0.46	0.59	0.95
	Melichrus procumbens	0.57	0.37	0.62	0.76
	Drosera peltata	0.86	0.36	0.40	0.75
	Pomax umbellata	0.86	0.35	0.40	0.72
	Hovea linearis	0.57	0.34	0.62	0.71
Sedge	*Lepidosperma laterale*	0.86	0.65	0.92	1.35
	Ptilothrix deusta	1.14	0.44	0.38	0.92
Grass	*Entolasia stricta*	1.86	2.31	3.92	4.79
	Aristida ramosa	1.71	1.55	1.38	3.21
	Anisopogon avenaceus	1.71	1.54	1.41	3.20
Graminoid	*Lomandra cylindrica*	1.71	1.89	1.52	3.92
	Xanthorrhoea glauca subsp. *glauca*	1.86	1.53	1.40	3.19
	Lomandra glauca	1.43	0.89	0.58	1.85

Floristic Group 2

Group 2					**Average similarity: 48.89**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Eucalyptus parramattensis* subsp. *decadens*	2.88	3.53	3.68	7.22
	Angophora bakeri	1.44	0.72	0.48	1.48
	Eucalyptus fibrosa	0.68	0.44	0.64	0.90
Shrub	*Melaleuca nodosa*	3.20	3.09	1.20	6.33
	Melaleuca thymifolia	2.24	2.59	2.30	5.31
	Dillwynia retorta	2.16	2.36	1.87	4.83
	Leptospermum parvifolium	2.16	2.03	1.12	4.14
	Grevillea parviflora subsp. *parviflora*	1.88	1.79	1.27	3.66
	Hakea sericea	1.52	1.31	1.01	2.68
	Callistemon linearis	1.32	1.16	0.79	2.37
	Isopogon anemonifolius	1.28	1.10	1.01	2.25
	Pimelea linifolia subsp. *linifolia*	1.08	1.08	1.36	2.21

Group 2					Average similarity: 48.89
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
	Leucopogon virgatus	1.04	0.88	0.93	1.79
	Acacia elongata	1.00	0.62	0.62	1.27
	Astrotricha obovata	0.84	0.59	0.69	1.20
	Lissanthe strigose subsp. *subulata*	0.88	0.50	0.50	1.03
	Banksia collina	0.84	0.36	0.43	0.75
	Exocarpos strictus	0.60	0.34	0.52	0.69
	Hakea laevipes subsp. *laevipes*	0.64	0.32	0.44	0.65
Subshrub	*Platysace ericoides*	1.08	0.81	0.74	1.66
	Hibbertia pedunculata	0.72	0.40	0.49	0.81
	Phyllanthus hirtellus	0.72	0.37	0.40	0.75
	Dampiera stricta	0.72	0.34	0.40	0.70
Sedge	*Lepidosperma laterale*	0.72	0.41	0.56	0.85
Grass	*Aristida warburgii*	2.24	2.47	2.02	5.05
	Entolasia stricta	1.92	2.25	2.00	4.60
	Anisopogon avenaceus	1.80	2.14	1.92	4.37
	Eragrostis brownii	1.40	1.30	1.04	2.67
	Aristida ramosa	1.48	1.03	0.75	2.11
Graminoid	*Lomandra cylindrica*	1.92	2.43	2.26	4.98
	Xanthorrhoea glauca subsp. *glauca*	1.68	1.93	1.83	3.94
	Lomandra glauca	1.64	1.32	0.79	2.69
	Dianella revoluta var. *revoluta*	0.84	0.63	0.77	1.29
Fern	*Cheilanthes sieberi* subsp. *sieberi*	0.76	0.43	0.55	0.89
Vine	*Cassytha glabella forma glabella*	1.24	1.22	1.27	2.50

Floristic Group 3

Group 3					Average similarity: 56.19
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Banksia aemula*	4.00	5.02	5.01	8.94
	Eucalyptus parramattensis subsp. *decadens*	4.00	4.96	8.91	8.83
Shrub	*Melaleuca nodosa*	3.50	3.82	3.03	6.79
	Leptospermum polygalifolium subsp. *cistmontanum*	2.50	2.85	18.18	5.08
	Leptospermum trinervium	2.50	2.22	0.91	3.95
	Monotoca scoparia	1.75	2.14	2.71	3.81
	Isopogon anemonifolius	2.00	2.11	3.10	3.75
	Bossiaea heterophylla	1.50	1.67	2.79	2.97
	Banksia oblongifolia	1.50	1.65	3.18	2.94
	Acacia ulicifolia	1.50	1.65	3.28	2.94
	Melaleuca sieberi	1.25	1.43	18.18	2.54
	Baeckea diosmifolius	1.25	0.97	0.83	1.73
	Pimelea linifolia subsp. *linifolia*	1.25	0.93	0.84	1.66
	Gompholobium glabratum	1.00	0.72	0.91	1.28
	Conospermum taxifolium	0.75	0.71	0.91	1.27
	Dillwynia glaberrima	1.00	0.71	0.91	1.27
	Aotus ericoides	1.00	0.68	0.91	1.21
Subshrub	*Trachymene incisa* subsp. *incisa*	2.00	2.85	18.18	5.08
	Euryomyrtus ramosissimus subsp. *ramosissimus*	2.00	2.85	18.18	5.08
	Hibbertia fasciculata	2.00	2.85	18.18	5.08
	Platysace ericoides	1.75	2.17	2.48	3.86
	Dampiera stricta	1.25	0.97	0.83	1.73
Sedge	*Cyathochaeta diandra*	2.00	1.59	0.88	2.83
	Leptocarpus tenax	1.75	1.44	0.91	2.56
Graminoid	*Haemodorum planifolium*	1.00	0.74	0.91	1.32
	Xanthorrhoea glauca subsp. *glauca*	1.00	0.74	0.91	1.32

Fern	*Selaginella uliginosa*	1.00	0.74	0.91	1.32

Floristic Group 4

Group 4					**Average similarity: 46.16**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Eucalyptus parramattensis* subsp. *decadens*	4.25	8.10	5.16	17.54
Shrub	*Melaleuca thymifolia*	3.13	5.10	4.39	11.04
	Melaleuca sieberi	1.75	1.68	0.90	3.64
	Banksia oblongifolia	1.13	1.33	0.91	2.89
	Acacia longifolia subsp. *longifolia*	0.88	1.18	1.05	2.55
	Hakea teretifolia subsp. *teretifolia*	0.63	0.49	0.51	1.06
	Leptospermum polygalifolium subsp. *cistmontanum*	0.75	0.47	0.51	1.01
Subshrub	*Hibbertia riparia*	0.88	0.77	0.71	1.67
	Dampiera stricta	0.88	0.59	0.49	1.28
Sedge	*Leptocarpus tenax*	4.38	8.33	4.70	18.05
	Schoenus brevifolius	3.63	5.99	3.48	12.98
	Ptilothrix deusta	1.38	0.70	0.34	1.52
	Lepyrodia scariosa	1.00	0.48	0.34	1.05
Grass	*Entolasia stricta*	2.63	3.93	2.75	8.51
	Hemarthria uncinata var. *uncinata*	1.00	0.95	0.68	2.07
	Paspalidium distans	0.75	0.52	0.49	1.12
Vine	*Cassytha glabella forma glabella*	1.00	0.99	0.68	2.15

Floristic Group 5

Group 5					**Average similarity: 41.84**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Eucalyptus parramattensis* subsp. *decadens*	4.75	6.65	5.31	15.89
Shrub	*Leptospermum polygalifolium* subsp. *cistmontanum*	4.25	6.34	10.92	15.16
	Banksia oblongifolia	3.00	3.95	4.72	9.43
	Acacia longifolia subsp. *longifolia*	1.75	2.41	2.45	5.75
	Melaleuca thymifolia	2.25	2.33	3.29	5.56
	Melaleuca nodosa	1.75	1.64	0.91	3.92
	Melaleuca sieberi	1.50	1.00	0.80	2.39
	Isopogon anemonifolius	0.75	0.82	0.91	1.96
	Persoonia lanceolata	1.00	0.82	0.91	1.96
Subshrub	*Platysace lanceolata*	1.75	1.35	0.72	3.24
Sedge	*Leptocarpus tenax*	2.50	3.40	7.86	8.13
	Cyathochaeta diandra	1.00	0.61	0.41	1.45
	Ptilothrix deusta	1.25	0.61	0.41	1.45
Grass	*Entolasia stricta*	2.25	3.17	10.92	7.58
	Paspalidium distans	1.50	1.67	0.91	4.00
	Microlaena stipoides var. *stipoides*	1.50	0.52	0.41	1.24
Fern	*Lindsaea linearis*	1.00	0.53	0.41	1.27