

The cushion plants of lowland southern Australia

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Abstract: A preliminary analysis has recorded the cushion lifeform in 60 taxa from lowland southern Australia (i.e. latitudes south of 26° S) encompassing six morphological forms from open, non-peat-accumulating species (58 taxa) to hard, dense cushions more typical of alpine and subalpine areas (2 taxa). Only two species appear to be obligate cushions. All but six cushion-forming species are endemic to southern Western Australia. Most species occur in the Transitional Rainfall Zone rather than the High Rainfall Zone or the more arid interior, with only one species being endemic to the arid zone.

In Western Australia cushion-forming species occur on exposed coasts, granites, edges of salt lakes and sandplains; almost half of the species also commonly occur across a number of other habitat types. The few plant communities dominated by cushion plants are generally restricted to small areas of a specific habitat type such as *Borya* herblands on shallow soils around outcropping granites. Lowland cushion species in Western Australia do not appear to be restricted to the most stressful habitats.

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Introduction

Cushion plants are a distinctive lifeform originally treated by some authors as being from alpine areas (e.g. Raunkiaer 1934), but also occurring in subalpine areas and on subantarctic islands (Gibson & Kirkpatrick 1985) and in various lowland areas with a range of climates other than subantarctic ones (Godley 1978). Despite work on lowland species in the Mediterranean and North Africa (e.g. Quezel 1967, Nimis 1981) little recent attention has been given to lowland cushion species. In Australia, as long ago as 1906, Diels drew attention to lowland Western Australian cushion plants in Boryaceae, Goodeniaceae, Fabaceae and Sterculiaceae (Diels 1906; translated 2007) but this has been overlooked by later workers. This paper brings together the little that is known about lowland cushion plants in the southern Australian vascular flora.

A precise definition of the term cushion plant is difficult (Raunkiaer 1934, Gibson & Hope 1986). Here, we will use the following: cushion plants are chamaephytes or hemicryptophytes that, growing singly, take on a hemispherical or subhemispherical shape due to the close branching of their shoots and their short internodes. This combines the definitions given by Gibson and Kirkpatrick (1985) and Gibson (1991). The hemispherical shape provisions allow mat plants to be excluded (see also Foweraker 1917). The leaves are small (Godley 1978), which allows the

shoots to be very closely compacted (Foweraker 1917). It is implied in the definition above that the margins of the shoot canopy normally extend downwards to reach ground level. As defined here, cushion plants form a continuum from hard, compact species that accumulate peat within their shoots to soft, loose, non-peat-accumulating species. Examples of intergradation between the various types defined below are common and some species only occasionally take on a cushion form (Rauh 1939).

In Australasian alpine and subantarctic areas, cushion plants are known in many different habitats, from ‘bogs to shattered rock and from snowpatch to herbfield’ (Gibson & Hope 1986). They are also common in similar habitats in the paramo, altiplano and alpine regions of the north, central and southern Andes (Bosman *et al.* 1993, Cavieres *et al.* 2002, Earle *et al.* 2003). This habitat range can be extended by examining the scattered Northern Hemisphere data from lowland areas, e.g. *Anabasis aretioides* Moq. et Coss. (Chenopodiaceae) occurs in the Sahara Desert (Hauri 1912) and *Centaurea horrida* Badaro (Asteraceae) occurs on Sardinian sea-cliffs exposed to strong, salt-laden winds (Mameli *et al.* 2008). The latter is one of a group of lowland Mediterranean cushion plants found in ‘thorny-cushions’ vegetation (Nimis 1981). This group includes species of *Anthyllis*, *Astragalus*, *Genista* (all Fabaceae), *Stachys* (Lamiaceae) and *Sarcopoterium* (Rosaceae) (Nimis 1981).

Methods

Using the definition given above, a list of cushion plants in southern Australia (i.e. latitudes south of 26° S) was developed using literature searches, by searching the collections database at the Western Australian Herbarium (PERTH) for specimens having the word ‘cushion’ in the plant description field and with input from the researchers listed in the acknowledgments. The resulting list should not be regarded as comprehensive and should be viewed as a list of species which can occur as cushions but do not always take on that form. Some species, such as *Schoenus calcatus*, we regard as obligate cushions but many others are not.

The most detailed classification of the types of cushion plants is that of Rauh (1939), published in German. We applied his basic typology here except that we excluded his ‘annual and biennial cushions’ and his ‘tree cushions’ categories. We also excluded mat plants that never form cushions or raised mounds. For some types, Rauh uses the German word ‘kugel’ which strictly translates as ‘spherical’. Here, we translate it as ‘hemispherical’ to better reflect cushion shape. Similarly, we translate ‘flach’ as ‘low’ rather than ‘flat’ given that Rauh uses ‘flach’ to include subhemispherical plants.

Distributional information for Western Australian species, based on the Interim Biological Regionalisation of Australia (IBRA) version 5.1 (Cummings & Hardy 2000), is available from the collections database at PERTH. Summary figures were compiled using all collections of each species. Typical habitat information for these species was compiled from the collections database and field observations by the authors. Species nomenclature follows current usage at PERTH unless species authors are given (Western Australian Herbarium 1998–). Taxa that have not yet been formally named are referred to by standardised phrase names.

Results

At least 60 southern Australian vascular plant species in 14 families fall within the definition of cushion plant given above (Table 1). The number of genera per family ranged from one to three. The genera with most cushion species are *Acacia* (9 species), *Andersonia* and *Stylidium* (8 taxa), *Borya* (6 species) and *Hibbertia* (5 taxa). All but six of these 60 species are endemic to southern Western Australia (Table 1).

Rauh types

Using the translations given above, the Rauh types represented on our list are ‘shrub cushions’, ‘turf cushions’, ‘radial-hollow-hemispherical cushions’, ‘radial-low cushions’ (both hollow and solid types) and ‘rosette cushions’.

Leucophyta brownii is the sole representative of Rauh’s ‘shrub cushion’ type (generally greater than 50 cm tall, taking

on an open, hemispherical shape). This species is typical of coastal habitats, where the hemispherical shape is common.

Rauh’s ‘turf cushions’ are a broad category primarily defined by the non-persistence of a tap root. They are represented in our list by the monocot taxa, with the exception of *Lomandra mucronata* (Table 1). All six *Borya* species and *Schoenus* sp. Cape Riche Cushion (G.J. Keighery 9922) occur as soft, hemispherical, non-peat-accumulating cushions with extensive adventitious roots from old leaf bases. *Schoenus calcatus*, in contrast, forms a solid, dense cushion that accumulates peat within its canopy and has similar morphology to the hard, bolster species of southern hemisphere alpine areas (Gibson & Kirkpatrick 1985).

Schoenus calcatus and five of the *Borya* species endure extended dry periods by altering the structure of their leaf cells, which change colour to orange or yellow (Table 1). With the onset of winter rains the leaves quickly revert to green and their functions are restored (Gaff 1981, George 2002a). These have previously been referred to as resurrection plants (Gaff 1981). George (2002a, 2002b) has recently documented that diallagy (colour change over dry periods) is much more widespread than previously appreciated in the Western Australian flora. In contrast, *Borya laciniata*, which only occasionally forms cushions, is a drought-avoider which sheds its leaves over the dry summer months (Churchill 1987).

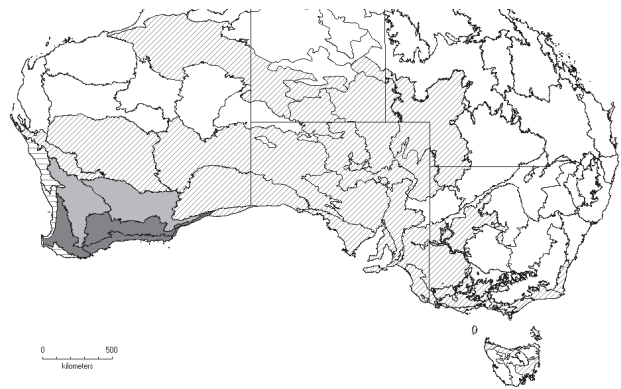


Fig. 1. Map of distribution of lowland cushion species across southern Australia by IBRA regions. Counts are derived from all collections of species that are known to form cushions, Western Australian records from the Western Australian Herbarium, other records from the Australia’s Virtual Herbarium. Diagonal cross hatching indicates 1–10 species per region; horizontal cross hatching indicates 11–20 species per region; light grey solid fill indicates 21–30 species per region; and dark grey solid fill indicates 21–38 species per region.

The ‘radial-hollow-hemispherical cushion’ type is represented by 14 species; 11 epacrids (*Andersonia*, 7 species; *Astroloma*, 4 species), *Ptilotus helichrysoides* (Amaranthaceae), *Argentipallium tephrodes* (Asteraceae) and *Lomandra mucronata* (Dasypogonaceae).

The most common cushion type is the ‘radial-hollow-low cushion’, represented by 30 species (Table 1), some of which can reach diameters of greater than a metre (e.g. *Acacia pulviniformis*).

Seven of the eight *Stylidium* taxa form small, ‘rosette cushions’, while *Stylidium pulviniforme* forms small ‘radial-solid-low cushions’.

Distribution

The distribution of lowland cushion species is not uniform across southern Australia; 58 of the 60 taxa are recorded from Western Australia, with only four of the Western Australian species extending into other States. Even within Western Australia, lowland cushions’ distributions are not uniform (Fig. 1) and they are more concentrated in the South West Floristic Region (an area of Mediterranean climate) than the

arid inland. Within the South West, cushion species are more common in the Transitional Rainfall Zone (300–600 mm rainfall) than either the High Rainfall Zone along the south and west coast or the more arid interior (zones as defined by Hopper & Gioia 2004).

The western and southern coastal areas have 50–60% of the numbers of species occurring in the Transitional Rainfall Zone, while in the more arid regions of Western Australia richness drops off very rapidly with only two species (*Hemichroa diandra* and *Ptilotus helichrysoides*), extending into the Great Victoria Desert.

Frankenia muscosa J.M.Black (Fig. 2) is the only strictly arid zone endemic in Table 1, occurring in sites with a mean annual rainfall of about 140 mm in the Northern Territory and South Australia.

Nine taxa (*Andersonia* sp. Mitchell River (B.G. Hammersley 925), *Hibbertia hibbertioides* var. *pedunculata*, *Schoenus* sp. Cape Riche Cushion (G.J. Keighery 9922), *Scholtzia* sp. Kalbarri (N. Hoyle 623), *Stylidium amabile*, *Stylidium coroniforme* subsp. *amblyphyllum*, *Stylidium coroniforme* subsp. *coroniforme*, *Stylidium ferricola*, *Stylidium* sp. Glabrous inflorescence (R. Davis 7917)) have quite restricted distributions, being only recorded from single IBRA regions in Western Australia. One species, *Borya mirabilis* Churchill, is restricted to a single location in the Grampians National Park in western Victoria (Coates 2000). The eight most common species (*Astroloma ciliatum*, *Astroloma pallidum*, *Borya constricta*, *Borya sphaerocephala*, *Frankenia pauciflora*, *Hibbertia acerosa*, *Lechenaultia tubiflora*, *Stylidium piliferum*) were recorded from between seven to 10 IBRA regions.



Fig. 2. Cushion plants of *Frankenia muscosa* 10cm high near Dalhousie Springs, South Australia. Photo by Reg Morrison; first published in van Oosterzee (1991).



Fig. 3. Cushion plants of *Borya constricta* 10cm high on shallow granitic soil, Peak Charles National Park, SW of Norseman, Western Australia. Photo by Bruce Fuhrer.

Table 1. Cushion type, habitat and distribution for lowland cushion plants in the southern Australian vascular flora.

Cushion types: RHH = 'radial-hollow-hemispherical'; RHL = 'radial-hollow-low'; RSL = 'radial-solid-low'; R = 'rosette'; SC = 'shrub'; T = 'turf'.

Habitat: the most typical habitats are listed. Where blank, the species occurs over a range of habitats.

Distribution: endemic to south-western Australia unless otherwise indicated in the Notes column by these codes: NSW = New South Wales; NT = Northern Territory; SA = South Australia; T = Tasmania; V = Victoria; WA = Western Australia. Some common names are given in inverted commas in the Notes column.

Family/Species	Type of cushion	Habitat	Notes	References
Monocots				
Boryaceae				
<i>Borya constricta</i>	T	Granite	A resurrection plant.	George (2002b); Fig. 3
<i>B. laciniata</i>	T	Granite	Only occasionally a cushion; drought-avoider with deciduous leaves.	George (2002b)
<i>B. longiscapa</i>	T	Granite	A resurrection plant	George (2002b)
<i>B. mirabilis</i>	T	Sandstone outcrop	V. A resurrection plant. 'Pincushion Lily' Threatened flora.	Coates (2000)
<i>B. nitida</i>	T	Granite	A resurrection plant. 'Pincushions'	Churchill (1987)
<i>B. sphaerocephala</i>	T	Granite	A resurrection plant.	George (2002b)
Cyperaceae				
<i>Schoenus calcaratus</i>	T	Sand	A probable resurrection plant. 'Newdegate Cushion'	Wilson (1997), George (2002b)
<i>S. sp. Cape Riche Cushion</i> (G.J. Keighery 9922)	T	Sand	'Cape Riche Cushion'	
Dasyopogonaceae				
<i>Lomandra mucronata</i>	RHH	Granite, Sand		
Dicots				
Amaranthaceae				
<i>Hemichroa diandra</i>	RHL	Coastal, Saline	NSW, SA, V, WA.	
<i>Ptilotus helichrysoides</i>	RHH			
Asteraceae				
<i>Argentipallium tephrodes</i>	RHH	Saline		
<i>Leucophyta brownii</i>	SC	Coastal	SA, V, T, WA.	
Chenopodiaceae				
<i>Roycea pycnophylloides</i>	RHL	Saline	Threatened flora	
Dilleniaceae				
<i>Hibbertia acerosa</i>	RHL	Granite		
<i>H. diamesogenos</i>	RHL	Granite		
<i>H. hibbertioides</i> var. <i>pedunculata</i>	RHL			
<i>H. priceana</i>	RHL		Threatened flora	
<i>H. turleyana</i>	RHL	Sand		
Ericaceae				
<i>Andersonia caerulea</i>	RHH	Sand	One form of variable species.	
<i>A. grandiflora</i>	RHH	Sand		
<i>A. geniculata</i>	RHH			
<i>A. setifolia</i>	RHH			
<i>A. sp. Mitchell River</i> (B.G. Hammersley 925)	RHH			
<i>A. sprengelioides</i>	RHH	Granite, Coastal		
<i>A. virolens</i>	RHH			

Family/Species	Type of cushion	Habitat	Notes	References
<i>Astroloma ciliatum</i>	RHH			
<i>A. compactum</i>	RHH			
<i>A. pallidum</i>	RHH			
<i>A. sp. Tutanning</i> (A.S. George 7779)	RHH			
Fabaceae				
<i>Eutaxia acanthoclada</i>	RHL			
<i>Kennedia microphylla</i>	RHL		Only occasionally cushion.	Diels (1906)
<i>Pultenaea purpurea</i>	RHL		One form of variable species.	Figs. 4 & 5
Frankeniaceae				
<i>Frankenia muscosa</i>	RHL	Saline	NT, SA. Species name means 'moss-like'.	Fig. 2
<i>F. pauciflora</i>	RHL	Coastal, Saline	SA, T, V, WA. Occasionally cushion, not restricted to coastal areas.	
<i>F. sessilis</i>	RHL	Saline	SA, V, WA.	
Goodeniaceae				
<i>Lechenaultia formosa</i>	RHL	Granite, Sand		
<i>L. pulvinaris</i>	RHL	Sand	The species name means 'cushion-like'.	
<i>L. tubiflora</i>	RHL	Granite, Sand		
<i>Scaevola crassifolia</i>	RHL	Coastal		
<i>S. humifusa</i>	RHL	Saline	Not restricted to saline areas.	
<i>S. pulvinaris</i>	RHL		The species name means 'cushion-like'.	
Mimosaceae				
<i>Acacia acanthaster</i>	RHL	Granite		
<i>A. brachyclada</i>	RHL			
<i>A. concolorans</i>	RHL			
<i>A. crassuloides</i>	RHL			
<i>A. lachnophylla</i>	RHL			
<i>A. poliochroa</i>	RHL			
<i>A. pulviniformis</i>	RHL		The species name means 'cushion-like'.	
<i>A. pusilla</i>	RHL			
<i>A. sorophylla</i>	RHL	Saline	Not restricted to saline areas.	
Myrtaceae				
<i>Eremaea fimbriata</i>	RHL			
<i>Scholtzia sp. Kalbarri</i> (N. Hoyle 623)	RHL	Coastal, Sand		
Stylidiaceae				
<i>Stylidium amabile</i>	R			Wege & Coates (2007)
<i>S. ciliatum</i>	R			
<i>S. coroniforme subsp. amblyphyllum</i>	R			Wege & Coates (2007)
<i>S. coroniforme subsp. coroniforme</i>	R		Threatened flora	Wege & Coates (2007)
<i>S. ferricola</i>	R			Wege <i>et al.</i> (2007)
<i>S. piliferum</i>	R			
<i>S. pulviniforme</i>	RSL	Sand	The species name means 'cushion-like'.	
<i>S. sp. Glabrous inflorescence</i> (R. Davis 7917)	R	Sand		

Habitat

The landscapes of the South West of Western Australia have developed on Archaean granites of the Darling Plateau that have undergone little mountain building since the Permian glaciations and as a result have undergone an extended period of weathering. This has resulted in Tertiary–Quaternary laterites and sandplains on the uplands and duplex soils in the broad valleys with sluggish, generally saline drainage lines, especially in the east (Gibson *et al.* 2004). Quaternary aeolian sands occur along parts of both the west and south coasts.

The typical distribution of lowland cushion species across this landscape can be considered in the following groups, although individual species generally occur across a number of habitat types.

Species occurring on exposed coasts

There are at least six species of cushion plants found in sites exposed to high levels of wind and salt spray in southern Australia (Table 1); a habitat which is shared with many of the ‘thorny cushion’ shrub species from the Mediterranean (Nimis 1981).

Of the six cushion species occurring along the coast only *Scaevola crassifolia* and *Leucophyta brownii* are restricted to that habitat, while *Hemichroa diandra* becomes restricted to this habitat in northern Western Australia. Both *Hemichroa diandra* and *Frankenia pauciflora* also occur on saline soils and around salt lakes in addition to occurring in coastal situations.

Species occurring on saline or subsaline soils

This group comprises the three *Frankenia* species, *Hemichroa diandra*, *Roycea pycnophylloides*, *Acacia sorophylla*, *Argentipallium tephrodes*, and *Scaevola humifusa*, although these last three species are not restricted to this habitat. (Table 1). *Roycea pycnophylloides* is only known from salt lakes in the central wheat belt and is listed as Threatened flora.

Species occurring on non-saline arid zone sites

A single species, *Ptilotus helichrysoideus*, extends into dry non-saline desert sites, in this case the Great Victoria Desert. Similarly, a range of cushion plant species can be found in non-saline parts of the Sahara Desert (Hauri 1912, Quezel 1967).

Species occurring on granites

Sixteen species occur on granitic soils but none are restricted to this habitat; they also occur on sandy or lateritic substrates. Some of the few plant communities in Western Australia dominated by cushion plants are the *Borya* herblands growing on the shallow soils on the edge of granite aprons. These communities, while restricted in size, are widespread around the granite outcrops of the South West (Fig. 3). As

with the majority of Western Australian *Borya* species, the rare Victorian species, *Borya mirabilis*, is a resurrection plant. Its single population occurs on a ferruginous sandstone outcrop which would suffer summer water stress similar to the granite habitats in the west.

Species occurring on sandplain or sand over limestone

A further nine species are recorded as occurring on sandplain or sand over limestone:– *Andersonia caerulea*, *Andersonia grandiflora*, *Hibbertia turleyana*, *Lechenaultia pulvinaris*, *Schoenus calcatus*, *Schoenus* sp. Cape Riche Cushion (G.J. Keighery 9922), *Scholtzia* sp. Kalbarri (N. Hoyle 623), *Stylidium pulviniforme*, *Stylidium* sp. Glabrous inflorescence (R. Davis 7917). A further three species, *Lechenaultia formosa*, *Lechenaultia tubiflora* and *Lomandra mucronata* are common on sand as well as granite substrates.

The remaining 28 species are not easily categorised, occurring over a range of habitat types (Table 1).

Discussion

Rauh’s (1939) comprehensive classification covers 12 basic cushion types including trees, shrubs, annual and perennial herbs, graminoids and mosses. These morphological types encompass soft, loose, non-peat-accumulating species to hard, compact species that accumulate peat within their canopies (‘bolster’ cushions of Gibson & Kirkpatrick 1985), with intergrades being common. Alpine bolster species would typically fall into his ‘radial-solid-hemispherical cushion’ (‘Radialvollkugelpolster’), ‘radial-solid-low cushion’ (‘Radialvollflachpolster’) and dense forms of his ‘turf cushion’ (‘Rasenpolster’).

We recorded only two hard, compact, peat-accumulating cushion species from lowland southern Australia, *Schoenus calcatus* (‘turf cushion’) and *Stylidium pulviniforme* (‘radial-solid-low cushion’), as well as 7 non-dense ‘turf cushions’, 13 ‘radial-hollow-hemispherical cushions’, 30 ‘radial-hollow-low cushions’, 7 ‘rosette cushions’ and one ‘shrub cushion’ type. We did not find any ‘radial-solid-hemispherical cushions’ which are typically alpine. The seven non-dense, ‘turf cushions’ were all monocots and did not accumulate peat, suggesting that these should probably be treated as a separate subtype. The most common features of the lowland cushions (with the exception of *Schoenus calcatus* and *Stylidium pulviniforme*) were that they did not accumulate peat within their canopies and that both cushion and non-cushion forms were common within the same species (Figs. 4 & 5).

While we record cushion plants in 14 different families from southern Australia (Table 1), it is likely that some families are genetically more likely to develop cushion morphology than others. For example, Ericaceae (previously Epacridaceae) has the largest number of species (11) and also figures prominently in lists of cushion species from elsewhere (Gibson & Hope

1986). Similarly, species of Cyperaceae and Stylidiaceae commonly form cushions in alpine and subalpine areas in the Australasian region (Gibson & Hope 1986). Frankeniaceae (three species in Table 1) includes the cushion plant *Anthobryum triandrum* (Remy) Surgis from NE Argentina, which occurs in saline sites at altitudes of 3 400–4 700 m (Ruthsatz 1978) and was formerly treated as a *Frankenia* (the generic name translates as ‘flowering moss’). Diels (1906) identified one species of Sterculiaceae, *Rulingia cuneata*, as forming cushions in Western Australia, no collection of this species could be located that exhibited that form.

Damage from salt spray causes many shrub species to share some characteristics with cushion plants, namely profuse shoot branching and a dense, compact canopy (Boyce 1954).



Fig. 4. Cushion plant of *Pultenaea purpurea* 10cm high on shallow sandy clay loam with metasedimentary surface fragments, Ravensthorpe Range, Western Australia. Photo by Adrienne Markey.



Fig. 5. Non cushion form of *Pultenaea purpurea* 30cm high growing under tall mallee shrubland on a sandy clay loam, Ravensthorpe Range, Western Australia. Photo by Adrienne Markey.

Most of these species exhibit asymmetric shoot growth forms which are not hemispherical or subhemispherical (Boyce 1954), excluding them from the cushion category; further work is needed on the extent to which salt spray can contribute to cushion morphology.

Cushion plants were found in 60 species across southern Australia but our finding that lowland species capable of forming cushions are heavily concentrated in Western Australia needs further validation, since only the collections at PERTH were used to identify cushion-forming species. Similar analyses of the collections at the other State herbaria are also needed.

Most cushion species within southern Western Australia are found in the South West Floristic Region, an area with a Mediterranean climate. Within the South West, cushion-forming species are concentrated in the Transitional Rainfall Zone, a very species rich area where explosive speciation in the woody perennial taxa has occurred in response to climatic perturbations in the late Tertiary and Quaternary (Hopper *et al.* 1996, Hopper & Gioia 2004).

Cushion plants in Western Australia rarely dominate the vegetation in which they occur, however, where this happens it is at a local scale in habitats of significant stress (e.g. *Borya* herblands on granite aprons, *Roycea* herblands on saline soils and *Scaevola* shrubland on exposed coasts). Cushion dominated vegetation in Western Australia supports Korner's (2003) view that cushions are typical of stressed habitats as has been reported in alpine areas. However the wider distribution patterns of Western Australian lowland cushion species are quite variable and are at odds with the view that cushion species are restricted to extreme sites. While some occur in restricted habitats or habitats where environmental stress would be considered high, other species occur across a wide variety of habitats as components of species-rich shrublands with at least half of the cushion-forming species occurring as minor components of species-rich shrublands on a variety of sandplain, laterite and clayey substrates.

Typically, cushion taxa in southern Western Australia occupy a variety of habitats coexisting in species rich shrublands with a number of other lifeforms, in contrast to both alpine (Korner 2003) and other lowland cushion species (Nimis 1981).

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