Biogeography of Australian chenopods: landscape in the evolution of an arid flora

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Science

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May 2020

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ABSTRACT

Chenopod taxa are globally prominent in deserts and on coastlines which suggests an evolutionary link, known as a littoral connection, and that remains unexplained. Australia is a global centre of chenopod diversity, where serial invasions of eleven immigrant clades over the last 16 million years, produced *ca.* 300 species within the continent. Six of these clades adaptively radiated in the Late Miocene-Pliocene within the continental interior.

Assuming a littoral connection as a working premise, Australian landscape history can inform the course of chenopod evolution. Almost all species are endemic and each clade must exhibit the three elements of the connection. Coasts and deserts share related taxa, marshy, sandy or saline habitats and adaptive traits for habitat occupation.

Phytogeographic analysis defines three groups of Australian chenopods. A Subcontinental Arid-Mediterranean Group has 97% of all species with Centres of Diversity in the west (Yilgarn) and east (Eyre-Murray). Sharing 129 species, the centres are strongly linked through the Great Victoria Desert, suggesting a common migration route. The chenopod poor Northern Tropical and Eastern Highlands groups suggest the barriers to range expansions. Diversification largely occurred inland, with 246 species being remote from coastlines. Only the *Scleroblitum* Clade lacks coastal taxa, but it has an estuarine ancestor.

Under the habitat element of a littoral connection, migration landscapes should be marshy, sandy or saline. Chenopod taxa mainly inhabit Riverine Desert (141 species) and Desert Lake (113 species) within continental drainage systems. Most coastal species are of diverse coastal habitats, with a capacity for inland range expansion through marshy ecosystems. Riverine Desert developed as chenopod clades arrived, connecting coastlines to both Centres of Diversity. Youth and discontinuity of Desert Lake precludes initial continental migration but promoted Pleistocene speciation. Sand Desert has relatively few species; a Pleistocene age postdates inland range expansion and its formation contributed to species population disjunction in rich clades.

Molecular phylogeny of Australian *Atriplex* Clade 1 reveals west to east migrations in two lineages after immigrant landfall on the west coast. One lineage migrated through inland Australia, initially diversifying in Stony Desert. The other lineage is limited to the southern coast and Western Australian catchments. Poor phylogenetic resolution in *Atriplex* Clade 2 precluded further interpretation, but initial diversification post-dates that of *Atriplex* Clade 1. Coastal species possibly have basal phylogenetic positions in both clades.

These findings suggest evolutionary stages of Australian chenopods involve: coastal landfall, initial inland migration through declining palaeodrainage systems and diversification in drying landscapes, along two possible biogeographic patterns. Either an initial, widespread inland migration fragmented into the Yilgarn and Eyre-Murray Centres, or separate, incipient Centres subsequently enlarged and exchanged species. Species extinction may be associated with dune field formation and loss of ancestral coastal taxa. Riverine Desert provided the species pool for significant speciation in Desert Lake and Stony Desert land types.

Each immigrant clade observes the taxon, habitat and trait elements of a littoral connection, which remains the most likely evolutionary scenario for these iconic Australian arid taxa.

DECLARATION

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint award of this degree.

I give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

I acknowledge the support I have received for my research through the provision of an Australian Government Research Training Program Scholarship.

John Thomas McDonald Date: 5/12/2019

ACKNOWLEDGEMENTS

Numerous people and organisations assisted in the completion of this research and their cooperation and collaboration is enormously appreciated. Such assistance included analytical, technical, logistical and financial support as well as the equally necessary encouragement and criticism.

My initial thanks are to my supervisors Prof Andy Lowe for the encouragement to attempt a challenging project and Dr Ed Biffin for guiding me through molecular analysis given my lack of familiarity with genetics. Dr Nikki Thurgate provided a useful sounding board for ecological notions in the early stages of the project.

To the following I am indebted for scientific and technical expertise and advice:

Prof. Gudrun Kadereit, at Johannes Gutenberg University Mainz, who supervised DNA extraction and sequencing; along with staff and students attached to the Botanical Museum of the University of Mainz [Herbarium MJG].

From the State Herbarium of South Australia, Dr Peter Lang and Dr Robert Chinnock assisted with plant identification and collection. Curator Helen Vonow supervised access to plant samples for DNA sequencing. Additional species samples were also provided from the Western Australian Herbarium, Queensland Herbarium (Brisbane) and the National Herbarium of Victoria.

Dr. Greg Guerin assisted with analyses in R statistical computing environment.

For logistical support I greatly appreciate:

TERN group (Ben Sparrow, Emrys Leitch and Ian Fox) for enabling additional fieldwork and access to plant material.

State and Commonwealth authorities for collecting and import/export of field specimens, especially thankful to Frank Kutsche (DEWNR) and Kanksha Drews (PIRSA) both in South Australia. Similarly to Wildlife Trade and Biosecurity Branch (Australian Government Dept. of Environment & Energy); Victorian Dept. of Environment, Land, Water and Planning; New South Wales Office of Environment and Heritage and Western Australian Dept. for Parks & Wildlife.

My gratitude also extends to Lab Group members for advice, discussion and assistance in the laboratory and with fieldwork including Stefan Caddy-Retallic, Rainbo Belton, Dona Kireta, Nick Gellie, Duncan Jardine, Matt Christmas, Zdravko Baruch, Kor-jent van Dijk and Ellie Dormontt.

The Nature Conservation Society of South Australia provided funds for field collection.

All maps with bases derived through Atlas of Living Australia, courtesy of Google.

PREFACE

In 1989 I began a long period as a rangeland ecologist assessing land condition in outback South Australia, where chenopods are important to pastoralism. Methodologies rely on identifying species response to long-term grazing and utilising two aspects of chenopod association – species with a considerable degree of co-occurrence and suites of assembly tied to particular landscapes.

South Australian pastoralists, initially sceptical of assessment, could find these convincing. In the North-East Pastoral District, I was challenged by one landholder, to identify the pre-stocking vegetation of a paddock long degraded by grazing. This region features in Francis Ratcliffe's reports of *Soil drift in the arid pastoral areas of South Australia* (1936) popularised as *Flying fox and drifting sand* (1938). On a bare, alluvial plain of red loam with iron-stained pebbles and white quartz gravel, grew sparse, open patches of *Sclerolaena brachyptera*, *S. cuneata*, *S. lanicuspis* and *Atriplex lindleyi* amid exotic annuals. After venturing that a *Maireana astrotricha-Atriplex vesicaria* community was originally present, the owner disdainfully 'agreed to disagree' in the absence of proof. His outlook changed at the sighting of a decrepit and solitary *Maireana astrotricha* a little farther along the track.

Such assembly must relate to the nature of the landscapes. Many chenopods, even abundant ones like *Maireana sedifolia*, are unique to certain land types. A high degree of co-occurrence is apparent in up to nine genera being present at a single site; it can include up to seven *Sclerolaena* species. Tempering such patterns is that with a short walk uphill, chenopod diversity and richness reduces markedly.

Chenopods have other notable quirks that prompts much interest. Fresh saltbush foliage is the equal of lettuce in sandwiches; it probably fed diprotodons. Of six species of *Sclerolaena* at a site, only one or two species would infest my socks. Reduce the stocking pressure and chenopods can readily reappear; a single saltbush is the mother nucleus to colonial cohorts, coalescing in a broad, diffuse front that creeps across a landscape. Bluebushes are not as spontaneous. *Enchylaena* and *Rhagodia* always reappear first under trees. Many *Atriplex* spp. and *Sclerolaena* spp.are pioneer species of secondary successions.

With such a large arid zone, the origin of the arid flora features prominently in studies of Australian vegetation, especially in the later twentieth century. Recent discoveries enabling a renewal of interest include chenopod occupation marginally exceeding the period of aridity in Australia and occurring as a serial invasion. The very high species endemicity ties chenopod evolution to the history of Australian landscapes.

Initially I intended assuming that a littoral connection explains chenopod evolution. My initial aim was to identify how it operated within chenopods as a whole, given their common association. Findings would provide hypotheses for specific study of separate chenopod clades. As the study progressed it became apparent chenopods must be examined with respect to patterns defining a littoral connection as this also gives wider context for inferring biogeographic processes. In doing this I hope to have avoided circularity of argument that can arise in such case, but also provided a basis for examining other plant groups purportedly with a similar origin, so that littoral connections become better understood.

CHAPTER 1: INTRODUCTION TO A LITTORAL CONNECTION AND AUSTRALIAN CHENOPODS

The global diversification of chenopods over the later Cenozoic is attributed to a littoral connection (Shmida 1985), including the Australian complement (Burbidge 1960; Barlow 1981, 1994). The connection is a hypothesis of dispersal and diversification within and between coastal and desert floras (Shmida 1985). The genus *Atriplex* is ecologically prominent in coastal and desert ecosystems on different continents (Osmond *et al.* 1980). Phytogeographic similarity of coasts and deserts, observed on each continent except Antarctica, prompt notions of adaptation to one habitat facilitating ready colonisation of the other. In Australia, it has been proposed that the entire arid flora (Burbidge 1960), or at least a significant component of it (Beadle 1981a, 1981b), derives from coastal taxa, but the evolutionary course remains unknown.

Burbidge's original notions are now largely discounted, but the littoral connection is a persistent concept, deserving fresh examination. It provides chenopod evolution in Australia with a context of transition from coast to desert with 302 chenopod species evolving from at least eleven ancestors that arrived over the last 16 million years (Kadereit *et al.* 2005).

A littoral connection provides a beginning to biogeographic processes that end in the modern distribution of chenopods. A coastline is the initial condition from which processes of range expansion, adaptation, diversification and extinction, result in occupation of coast and desert landscapes by contemporary taxa. Diversification and range expansion are certainly the major evolutionary processes where serial immigrant invasions overcame a succession of barriers, including the distance between coast and desert and the variation in inland habitats.

The aims of this study are to biogeographically describe the evolution of Australian chenopods under the premise of a littoral connection and to examine the validity of such an assumption through molecular phylogeny. Such an account would be relevant to other taxa presumed to have similar connections.

BIOGEOGRAPHY OF AN AUSTRALIAN LITTORAL CONNECTION

Definition and application

A littoral connection is based on three, interrelated elements that coast and desert floras share (Burbidge 1960; Shmida 1985):

- Taxon: Closely related desert and coastal taxa across plant groups - the groups are polytopic
- Habitat: Environments that are saline and either sandy or marshy and prone to inundation
- Trait: Dominant life forms of herbs and suffrutescent shrubs, and physiognomy of leaf and stem succulence, related to salt-tolerance

The spatial patterns of shared floral elements would be symptomatic of movement between coastal and desert habitats and exploring such patterns is the core of biogeographic enquiry.

The plant families Aizoaceae and Chenopodiaceae feature commonly among Australian and global taxa presumed to have a littoral connection (Table 1.1). For Israel alone, Shmida (1985) lists 17 genera of both desert and coast, of which 10 are native to Australia, including five chenopod genera.

Littoral connections and arid floras: a literature review

Burbidge (1960) is commonly cited for the littoral origins of the Australian desert flora but the notions are older. In 1905, Ludwig Diels implied evolutionary links from coastal and arid habitats in Western Australia sharing plant taxa (Diels 1906; Doing 1981; Carolin 1982; Barlow 1994; Diels 2007). VL Komarov expressed similar ideas in 1908-09 (Shmida 1985), based on the global distribution of *Nitraria* sp. (Zohary 1973), a genus of Australian shores and desert. No terminology is consistently adopted for the ideas, but the term ‘littoral connection’ (Carolin 1982:122) is useful, emphasising phytogeographic pattern, without inferring a mechanism (Crisp *et al.* 1999).

	Source	**Burbidge (1960)**	**Beadle (1981a)**	**Heads (2014)**	**Barlow (1994)**	**Crisp et al (1999) #**	**Shmida (1985)**
	Scope	Australia	Australia	Australia	Australia	Australia	Global
Taxa: Family/Tribe							
	Aizoaceae	●	●	●	●	**()**	●
	Amaranthaceae					●	
	Asteraceae	**^**		●	●	●	
	Brassicaceae	**^**			●	●	
	Chenopodiaceae	●	●	●	●	●	●
	Convolvulaceae					**+**	
	Frankeniaceae		●			**+**	
	Goodeniaceae			●			
	Myoporeae			●			
	Plumbaginaceae						●
	Poaceae				●		
	Portulacaceae					**+**	●
	Zygophyllaceae		●				●
	Cactaceae						●
	Didiereaceae						●
	Tamaricaceae						●
Taxa: Genera					**$**		
	Artemisia						●
	Casuarina			●			
	Danthonia						**‡**
	Duma			●			
	Frankenia			●			
	Melaleuca			●			
	Pancratium						●
	Panicum						●
	Spinifex		●				
	Sporobolus		●				
	Stipagrostis						**‡**
	Zygochloa		●				

Table 1.1: Taxa for which littoral connection is posited in origins: *Italics* - not naturally occurring in Australia; # refers to endemic genera and species groups within listed families; **^** Burbidge lists as Cruciferae and Compositae respectively; **+** qualified as possibly; **‡** *Austrodanthonia* & *Aristida* are Australian equivalents; **()** Aizoaceae *s. lat*.; **$** un-named endemic genera.

Between Diels (1906) and Burbidge (1960) explanations for a littoral connection were not forthcoming, hampered by limited palaeogeographic understanding. Andrews (1916) explained the distribution, association and character of Australian genera in relation to past and present geology, but restricted arid taxa to that of the ‘hungry, siliceous sands’ and ‘rocky, arid ranges’. Without consideration of past environmental and ecological factors, Wood (1937) admitted limitations to his phytogeography of South Australia. Crocker and Wood (1947) proposed a “Great Arid Period” when severe desiccation derived the arid flora, but littoral considerations were omitted.

In a phytogeography of the Australian flora, Burbidge (1960) suggested a mechanism for the littoral connection in context of continental palaeogeography. More recently, Shmida (1985) set littoral connections within a phytogeographic analysis of the world’s desert flora, an ecological context of 14 rules for the distribution and evolutionary trends in desert flora and a conceptual evolutionary framework based on EO Wilson's Taxon Cycle.

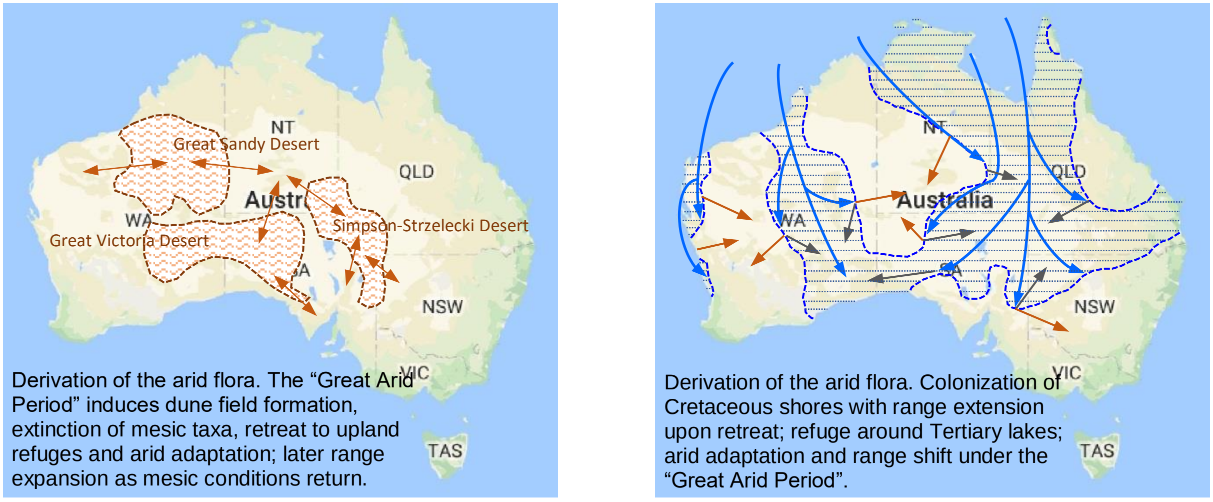
Burbidge (1960) broadly suggested (also see figure 1.1):

- Ancestors of the arid flora establish along Cretaceous sea shores in inland Australia
- Retreat of the seas facilitates adaptation to terrestrial conditions
- Taxa persist on coastlines and the shores of vast inland Tertiary lakes
- The lakes dry out under late Tertiary aridity, inducing range extension and adaptation

Four points are emphasised. First, Cretaceous arrival directly links Central Australian shorelines to Tethyan origins of prominent global desert flora. Later development of northern tropical regions effectively bars a direct migration. Aridity develops around ancestral species; later arrival requires range extension into the Australian interior. Second, the early to mid-Tertiary mega-lakes of Central Australia provided littoral habitats. Third, fossil assemblages in Lake Eyre clays, comparable to modern marshes of the Lower River Murray, identify a modern analogue of ancient environments. Finally, this origin complements the “Great Arid Period” (Crocker and Wood 1947), where newly forming dune fields destroyed older forests and plant taxa periodically retreated to and expanded from Pleistocene refuges. In modern terms, Burbidge's littoral connection is a sequence of Cretaceous invasion, Tertiary filtering and Quaternary sorting. With subsequent evidence for earlier aridity, the notion of the “Great Arid Period” waned, but Burbidge's ideas have endured.

A major problem with this scenario is that a Cretaceous origin is too early. Global angiosperm diversity was then insufficiently developed, and pollen types indicative of Australian arid flora evolved much later (Martin 1994). Dryland species are unlikely to survive in the Tertiary rainforest of Central Australia until the Miocene aridity (Beadle 1981a, 1981b). Burbidge (1960) admits this issue, expecting more endemic genera than is observed.

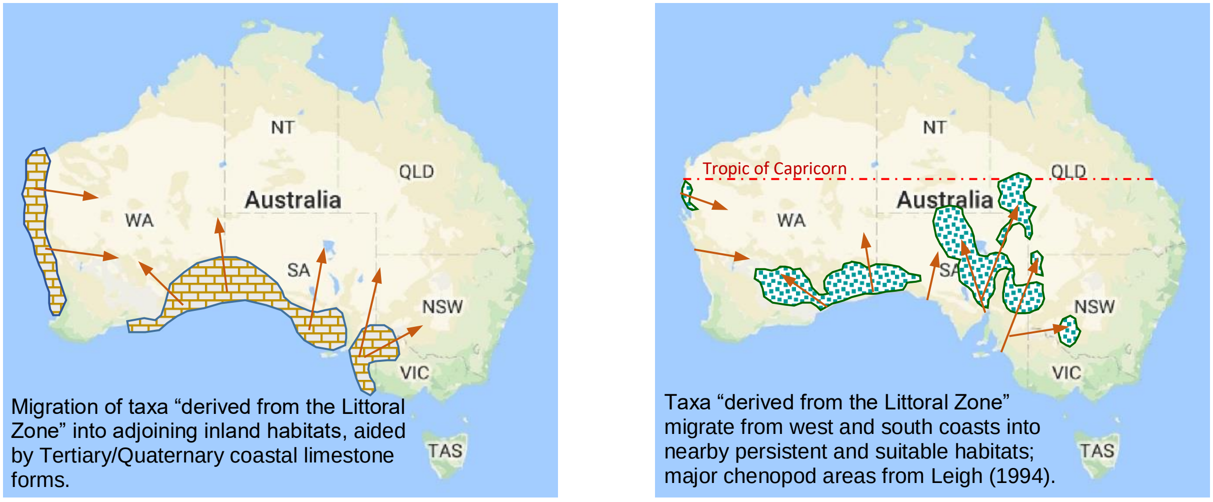
Crocker and Wood (1947) **Burbidge (1960); Heads (2014)**



Derivation of the arid flora. The “Great Arid Period” induces dune field formation, extinction of mesic taxa, retreat to upland refuges and arid adaptation; later range expansion as mesic conditions return.

Derivation of the arid flora. Colonization of Cretaceous shores with range extension upon retreat; refuge around Tertiary lakes; arid adaptation and range shift under the “Great Arid Period”.

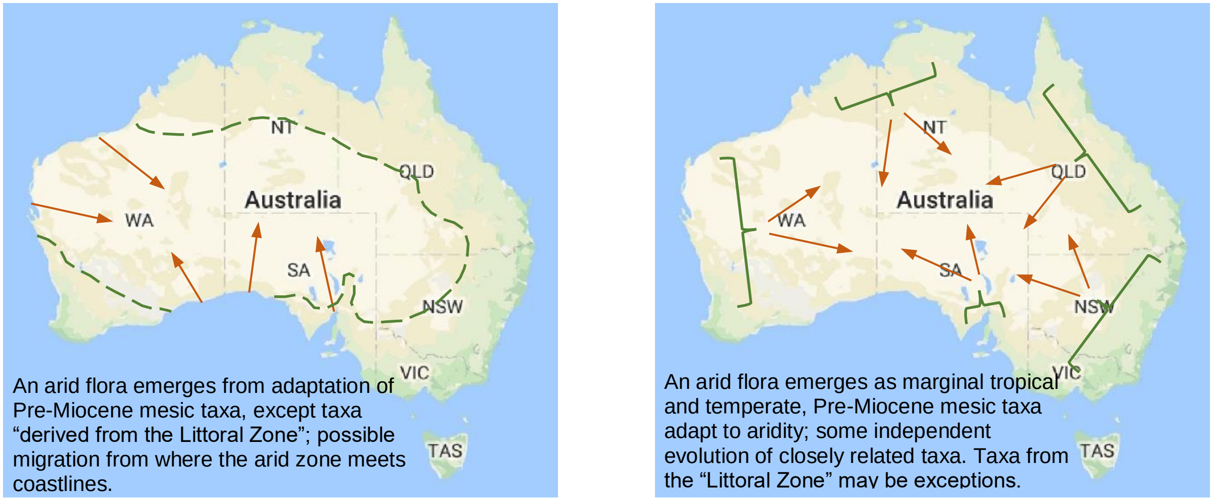
Specht (1972, 1981b) **Beadle (1981a, 1981b)**



Migration of taxa “derived from the Littoral Zone” into adjoining inland habitats, aided by Tertiary/Quaternary coastal limestone forms.

Taxa “derived from the Littoral Zone” migrate from west and south coasts into nearby persistent and suitable habitats; major chenopod areas from Leigh (1994).

Barlow (1981, 1994) **Crisp *et al.* (1999)**



An arid flora emerges from adaptation of Pre-Miocene mesic taxa, except taxa “derived from the Littoral Zone”; possible migration from where the arid zone meets coastlines.

An arid flora emerges as marginal tropical and temperate, Pre-Miocene mesic taxa adapt to aridity; some independent evolution of closely related taxa. Taxa from the “Littoral Zone” may be exceptions.

Figure 1.1: Notional development of Australian chenopods, as part of the entire arid flora or of taxa “derived from the Littoral Zone”. Barlow (1981, 1994) and Crisp *et al.* (1999) summarise more specific studies, emphasising taxa “derived from the Littoral Zone” may require different explanation to other arid taxa. Major areas of chenopods in green based on Leigh (1994); Cretaceous shorelines in blue based on Cretaceous 4 of BMR Palaeogeographic Group (1992).

Direct reference to the coastal origin of arid flora is also in Leigh and Noble (1969); Specht (1972); Beard (1976a); Williams (1979); Osmond *et al.* (1980); Barlow (1981); (Beadle 1981a); Beadle (1981b); Doing (1981); Specht (1981a, 1981b); Lange (1982); Parr-Smith (1982); Kuhn (1993); Barlow (1994); Martin (1994); Crisp *et al.* (1999); Crisp *et al.* (2004); Kadereit *et al.* (2005); Martin (2006); Byrne *et al.* (2008); Heads (2014). Most mention chenopods. For Shmida (1985), notable patterns with strong evolutionary implication are appealing, but conceptual. Carolin (1982:122) is optimistically blunt: "More work, particularly amongst the Caryophyllales, may vindicate this link, but I think that as yet it remains largely unestablished." Except for Parr-Smith (1982), no 'work' has eventuated, but Crisp *et al*. (1999) and Byrne *et al*. (2008) make suggestions.

Subsequent authors (see figure 1.1) revised the timeframe and noted habitat influences. The arid flora includes "Taxa derived from the littoral zone", with a Miocene origin (Beadle 1981b) confirmed by Kadereit *et al.* (2005). Furthermore, the southerly disposition of taxa, along with continuous presence of suitable habitat, suggests origins on southern or western coasts. Beard (1976) thought expansions of arid plant taxa more likely under Miocene rather than Pleistocene events. Diels' observations prompted suggestion of the calcicolous vegetation of ancient shorelines moving inland as deteriorating climate induced limey soils (Specht 1972, 1981b). Therefore, range extension inland, must explain the modern taxon range, not coastline regression. In contrast, Heads (2014) revives the Cretaceous Tethys connection, claiming molecular analyses underestimate true evolutionary age, also noting the weediness of littoral taxa enhances survival in the disturbance of shoreline regression.

For Barlow (1981, 1994) a littoral connection potentially resolves some evolutionary issues of the arid flora. The arid flora is generally non-distinct. It mostly comprises taxa from adjoining, mesic regions that successfully colonised the arid zone. However, endemic genera from five families, well represented in the world's desert taxa, are part of this young flora, especially Chenopodiaceae with *Maireana* and *Sclerolaena* having radiated widely in arid habitats along with the cosmopolitan *Atriplex*. Noting an earlier draft of Parr-Smith (1982), Barlow suggests range extensions most likely occurred where arid areas meet the coast (figure 1.1).

Parr-Smith (1982) proposes an evolutionary relationship between coastal and inland species of *Atriplex*. A littoral connection is not mentioned explicitly and Burbidge (1960) is cited for different purposes. All Australian *Atriplex* (except *A. australasica*) are assumed a single evolutionary line of several subgeneric groups. In a proposed phylogeny for a group of 10 dioecious shrub species, a west coast form of *Atriplex vesicaria* is identified as ancestral. Four lineages evolve from this coastal form, comprising the other shrub species and varieties of *Atriplex vesicaria*. Mapping species distribution and habitat to the phylogeny identifies two terrestrial lineages, one riparian/terrestrial lineage and two coastal lineages. Osmond *et al*. (1980) referring to an earlier draft of this work, treat this as a littoral connection in the sense of Burbidge (1960). However, molecular work of Kadereit *et al.* (2010) shows the subgeneric, shrubby group is polyphyletic.

Modern perspectives on the Australian arid biota, question concepts underpinning theories of origin of the arid flora and emphasise a physiological basis to adaptation (Barlow 1981, 1994; Crisp *et al*. 1999; Byrne *et al*. 2008). Invasions and migrations of elements in the Australian flora, which are central to the origin concepts of Crocker and Wood (1947), Burbidge (1960) and Beadle (1981b) while seen as questionable assumptions, would certainly apply to a littoral connection. For Crisp *et al*. (1999:326) the value of Burbidge (1960) is in emphasizing tolerance of coastal habitats pre-adapts plants to invade arid regions. Analyses of arid zone specialists like *Triodia* or Chenopodiaceae could confirm colonisation of the central desert from the continental periphery.

Byrne *et al*. (2008) broadly correlate evolutionary studies of plant, vertebrate and invertebrate taxa with landscape change, showing two main phases of speciation – radiation over the Late Miocene and Pliocene and maintenance through the Pleistocene. Two roles for a littoral connection are inferred. Occupation of ‘coastal and riparian sand dune habitats’ pre-adapts species to similar landforms of arid areas. The moderating climates of coastal fringes are refuges during intense arid periods, especially the west coast where the arid zone extensively meets ocean shore.

Martin (2006) attempted a palynological evaluation of the components of the arid flora (following Beadle 1981b), concluding pre-existing floras must be involved, except for the taxa derived from the littoral zone. A presence of *Eucalyptus* and *Acacia* pollen pre-dates their periods of dominance. Chenopod pollen dates to the Oligocene, but first appears abundantly in the Pliocene. Saline and alkaline littoral habitats certainly existed through the Tertiary, as halophytes other than chenopods e.g. *Wilsonia* (Convolvulaceae), were present.

Ward (2009) notes some key correlations of species distributions within global patterns reported by Shmida (1985). For example, psammophilous (sand tolerant) genera occur in both coast and desert and the distribution of halophytes and psammophilous taxa are similar. Such correlation in the Saharo-Mediterranean also includes a transitional group of halophilous-psammophilous taxa. Ward (2009) interestingly adds that eco-morphological adaptation to very saline environments, likely increases the probability of oceanic, long-distance dispersal from coastal areas.

Early twentieth century floristic studies of Eurasian Deserts may have inspired an Australian littoral connection hypothesis. Burbidge (1960:106) credits Prof. S. Smith White with suggesting that 'Eremaean' elements develop from coastal species, perhaps a tradition of thought since Diels and Komarov. Floristic studies of Middle Eastern and west Central Asian deserts prior to 1960, linked halophyte origins to progressive decline of the Tethys Sea during the Mesozoic or early Tertiary (Zohary 1973, Ch 10). Waisel (1972) posits all halophytes derive from seashore plants, exhibiting phytogeographic patterns of a Tethyan origin (citing Iljin 1946 and Chapman 1960). Migrations to inland areas follow coastline shift. Chapman (1974) reported a long-standing and widespread belief in the Tethyan origin of European halophytes, though doubted it applied to all halophyte taxa.

Evolutionary rationale to a littoral connection

Littoral connections would relate to plant habitation of terrestrial landscapes (Flowers *et al.* 2010). Sunlight, carbon dioxide and water are constantly required for photosynthesis; scarcity of any affects plant distribution and form (Taiz and Zeiger 2010). Sunlight and carbon dioxide are generally available, but water is not. Soil moisture after rain is the most reliable source for terrestrial plants (Evert and Eichhorn 2013) but geographically varies in availability. Plants must also tolerate the desiccation of atmospheric exposure (Delevoryas

1977; Grace 1997; Evert and Eichhorn 2013) favouring evolution of means to conserve water or to use any moisture that is available.

Salines in plant tissues enable water intake (Lambers *et al.* 2008; Taiz and Zeiger 2010; Evert and Eichhorn 2013). Selective uptake of soil cations concentrates cellular salines, osmotically inducing water entry. To create sufficient osmotic differential, cation intake increases to absorb water held tightly in dry soils or where soil water is saline. Sodium is the most commonly absorbed cation but has an attendant risk of toxicity (Flowers *et al.* 2010). Physiological adaptations for managing toxic levels of sodium and other cations, facilitate tolerance to aridity (Osmond *et al.* 1980; Colmer and Flowers 2008) and are linked to tolerance of inundation (Colmer and Flowers 2008).

A need for sunlight, carbon dioxide and water drives plant evolution (Tivy 1993; Evert and Eichhorn 2013). Competition for sunlight creates arborescent floras where water is abundant. Competition for scarce water induces low plant forms (e.g. shrubs, grasses) and exploitation of any available water.

Global development of salt-tolerant flora would predate modern arid floras. Angiosperms originating in the Mesozoic, initially diversifying through the Cretaceous and Early-Mid Tertiary under warm and wet climates, now dominate terrestrial floras (Soltis *et al.* 2008; Graham 2011) and are largely glycophytic (Waisel 1972; Flowers and Colmer 2015). The origins of modern aridity are Oligocene, as the initial, appreciably arid periods are in Early Miocene Asia (Guo *et al.* 2008). The oceans forming more than a billion years ago, have never completely enveloped the earth (Stacey and Hodgkinson 2013) and seawater salinity has been stable around 3.5% by volume for the last 100 million years (Wells 2011). Salt-tolerance in terrestrial flora is rare (Flowers *et al.* 2010; Bromham 2015) and did not likely appear distant from coastlines, until saline soils extensively developed under expanding aridity. Existing vegetation had to adapt or salt-tolerant species invaded.

Modern context for littoral connections

Since Burbidge (1960) and Beadle (1981a, 1981b), the evolution of Australian flora in relation to landscape change is now better understood (Barlow 1994; Hill 1994; Frakes 1999;

Martin 2006). Over the last two decades, molecular phylogeny and geochronology have shed light on the development of arid biota and landscapes by revealing the ages of clades and the diachronic formation of landscapes (Byrne *et al.* 2008; Fujioka and Chappell 2010).

A likely evolutionary course of Australian chenopods could be identified simply assuming a littoral connection operates. However its plausibility can also be evaluated, almost as a testable hypothesis, because a littoral connection, defined by landscape sharing patterns, also fits key biological concepts – niche conservatism and biological invasion.

Niche conservatism

A littoral connection is a specific instance of niche conservatism; the tendency of descendant species to retain the ecological character of a common ancestor (Wiens 2004; Wiens and Graham 2005; Wiens *et al.* 2010). Phylogenetic niche conservatism is the tendency for such conservatism to operate more strongly than expected across a species clade, but its measurement and nature (pattern or process) is uncertain (Wiens 2004; Losos 2008; Wiens *et al.* 2010; Crisp and Cook 2012). Studies in niche conservatism associate a clade with the niches of its component species, but those of phylogenetic niche conservatism also consider heritability of traits (Wiens *et al*. 2010; Crisp and Cook 2012).

Ideas of niche conservatism have antecedents (Wiens *et al*. 2010), being fundamental to palaeontology and palaeogeography (Wake *et al.* 2009). Reconstructing past environments assumes fossil organisms and their modern counterparts occupy similar environments.

Niche conservatism is commonly assumed for closely related species (Losos 2008) and has merit in broad studies (Wake *et al*. 2009). It operates strongly in the early stages of adaptive radiations of experimental bacterial populations (Flohr *et al.* 2013) and at biome scale (Crisp *et al.* 2009). Species in a range of taxa (not including chenopods) from overseas arid biomes, arriving in Australia since the Miocene, are predominantly found in the Australian arid biome.

Biological invasion

Arid flora with littoral connections can be effectively treated as a biological invasion through coastal regions. Biological invasion mainly focuses on human-mediated transport of species with significant economic or ecological impact (Groves and Burdon 1986; Drake *et al.* 1989;

Cronk and Fuller 1995; Davis 2009; Richardson *et al.* 2011; Richardson and Ricciardi 2013) but has clear parallels with natural invasions or migrations in ecological and evolutionary contexts (MacDonald 2003; Lomolino *et al.* 2010). Invasion science is rooted in biogeography (Wilson *et al.* 2009a; Richardson *et al.* 2011), given an Australian context in Prins and Gordon (2014) and with invasion broadly accepted as the arrival and spread of taxa that previously were absent.

The parallels are diverse, including the ecology of introduced plants successfully invading natural or semi-natural habitats (Cronk and Fuller 1995), generalizations in the geography, origin or taxonomic affiliation of invading plant species (Heywood 1989) and new selective pressures for invasive species (Suarez and Tsutsui 2008). Prentis *et al.* (2008) emphasise that genetic changes may enable rapid adaptation. Wilson *et al.* (2009b) consider invasions a specific form of range extension – human-assisted extra-range dispersal across biogeographic barriers.

Invasion is a sequence of stages e.g. dispersal, establishment, acclimatisation and range expansion (Groves and Burdon 1986; Heywood 1989; Hobbs 1989; Cronk and Fuller 1995; Shigesada and Kawasaki 1997; Richardson *et al.* 2000; Theoharides and Dukes 2007; Davis 2009; Richardson *et al.* 2011). Stages are not discrete, and comprise cyclic iterations of dispersal and establishment (Davis 2009), which could involve adaptation of invader species (Davis 2009) with diversification through genetic drift (Vellend *et al.* 2007). Such stages can be viewed as a succession of barriers to be overcome by a successful invader (Shigesada and Kawasaki 1997; Richardson *et al.* 2000). Variably successful migrations of taxa, involving dispersal, establishment, range extension and diversification, are significant in the origins of Australasian vegetation (Martin 1994).

Stages of invasion

Theoharides and Dukes (2007) describe plant invasions in stages of Transport, Colonisation, Establishment and Landscape Spread, identifying characteristics of successful invaders. With a final Diversification stage for biogeographic context, these stages are a useful framework for investigating a littoral connection.

Transport involves the intercontinental movement of species into new regions. Factors in successful transport and introduction relate to geographic origin, extent of native range and dispersal ability, which also influences later stages. Oceanic, long-distance dispersal most likely explains the arrival of indigenous chenopods (Kadereit *et al*. 2005).

Colonisation is the survival of arriving populations, mostly within local environmental conditions. Immediately following the transport stage, the first plants must germinate, grow, set flower and seed. Small populations are always at risk of random, severe disturbances. Plants with wide geographic ranges in their regions of origin are more likely to survive. Propagule pressure (the number of arrivals and number in each arrival) strongly influences colonisation success.

Bridgehead populations of chenopods will very likely survive on a coastline. Niche conservatism fundamentally applies to this stage with habitat of origin also being a coastline. Of some interest is whether coastal taxa and their nearest relatives, indicate the location of coastal landfalls.

Establishment is self-sustaining and expanding populations, taking longer than colonization and occurring at larger scale. Major factors are biotic interactions such as plant competition, trophic interactions that may be favourable (e.g. dispersal vector) or unfavourable (e.g. herbivory), or interactions that promote finding a niche in invaded ecosystems.

This stage comprises permanent coastal population with minor range extension along coastlines. Initial departure from coastlines into the immediate hinterland in coastal seral communities is likely. With niche conservatism, modern coastal taxa could ecologically resemble ancestral arrivals; a notion explored in habitat analyses of coastal species in Chapter 3. The youngest chenopod immigrants may possibly be at this stage.

Landscape spread is regional dispersal over notably longer time periods. It effectively comprises interacting populations at different stages of colonisation and establishment due to ongoing inter-regional transport. Landscape heterogeneity can vary rates of colonisation and establishment, through enhancing or retarding propagule production and dispersal.

Landscape structure and traits promoting dispersal are most important in this stage. Suitable habitats that connect regions would facilitate faster and more extensive spread. Adaptation could aid occupation and persistence in natural ecosystems, and may be achieved by isolation at the expanding edge of a population. Under a changing climate, invasive species with fast reproduction and high phenotypic plasticity are likely to respond with rapid genetic and phenotypic adaptation.

This phase would cover initial range extensions from coastlines. Under niche conservatism, the connecting habitats which facilitate rapid and extensive spread, would be those most like coastal habitats (see Chapter 3). Younger chenopod immigrants may currently be in this stage. Coastline advance and retreat could possibly assist intra-regional extension or induce contraction, and again, characteristics of coastal taxa may be informative.

Diversification comprises colonisation, establishment and landscape spread of related taxa under changing environmental conditions. Supra-regional range extension, with accompanying speciation in multiple lineages could include adaptive radiations. Successive range expansion of varied lineages, speciation process and possibly extinction and range contraction, add complexity.

Most chenopod clades would be in this stage. Distributions of taxa result from landscape spread and diversification and are examined in Chapter 2. Habitats of landscape spread and diversification are a subject of Chapter 3. Adaptive radiations in chenopod clades would broadly relate to continental scale of rainfall decline that creates the dry, saline habitats suited to chenopod taxa.

Invasion stages and Burbidge (1960)

Comparable stages of plant invasion are recognized by Burbidge (1960):

(1) Ancestors of the arid flora arrived on shores of inland seas in the Cretaceous; the last time marine conditions occurred in Central Australia. The Tethys Sea connected four Australian islands to an ancestral Mediterranean Region, where taxa of littoral connections are common. Oceanic dispersal is clearly inferred [*Transport*].

(2) Coastal habitats of principal occupation were the strand (the sandy beach above high water mark) and coastal salt-marsh [*Colonisation*].

(3) Littoral taxa were never shore-bound, but penetrated the interior along waterways emptying into marine environments [*Establishment*; initial *Landscape Spread*].

(4) With retreat of the seas, abandoned coastal species adjusted to drying conditions better than mesic species, aided by their ecological tolerances [*Landscape Spread*]; the shores of vast inland Tertiary lake systems still offered suitable habitat [*Establishment*].

(5) Episodic retreat and advance, within broad regressive trend at the end of the Cretaceous drove adaptation and outward expansion [*Landscape Spread, Diversification*]. Upon retreat, plants occupy newly exposed land, with subsequent advance juxtaposing newly divergent species or rendering some species extinct. Advance and retreat of later Cenozoic coasts and lake shores similarly affected more devolved species, but coastal shores never again breached the centre as in pre-Tertiary times.

(6) Littoral species occupy the beds of drying lakes, becoming psammophytes (sand species) as dune fields developed on the margins and expanded [*Landscape Spread, Diversification*].

AUSTRALIAN CHENOPODS: TAXONOMY AND BIOGEOGRAPHY

Chenopodiaceae are a particularly successful plant group of dry, saline or disturbed habitats of temperate and subtropical climates (Kuhn 1993; Kadereit *et al*. 2005). Global distribution is amphitropical (Hugget 2004), with several cosmopolitan genera e.g. *Atriplex*, *Chenopodium*, *Salsola* and *Suaeda* (figure 1.2). Plants are annual or perennial herbs and shrubs or rarely vines or small trees, with leaves or stems exhibiting degrees of succulence.

The global taxonomy of chenopods is currently under considerable revision. Close alliance to the Amaranthaceae (Kadereit *et al.* 2003) prompts recent treatments (Angiosperm Phylogeny Group I & II) to subsume Chenopodiaceae within the Amaranthaceae. Some current Australian treatments e.g. Wilson and Chinnock (2013), retain the familial distinction, also adopted for convenience in this study with the term ‘chenopod’ commonly substituted.

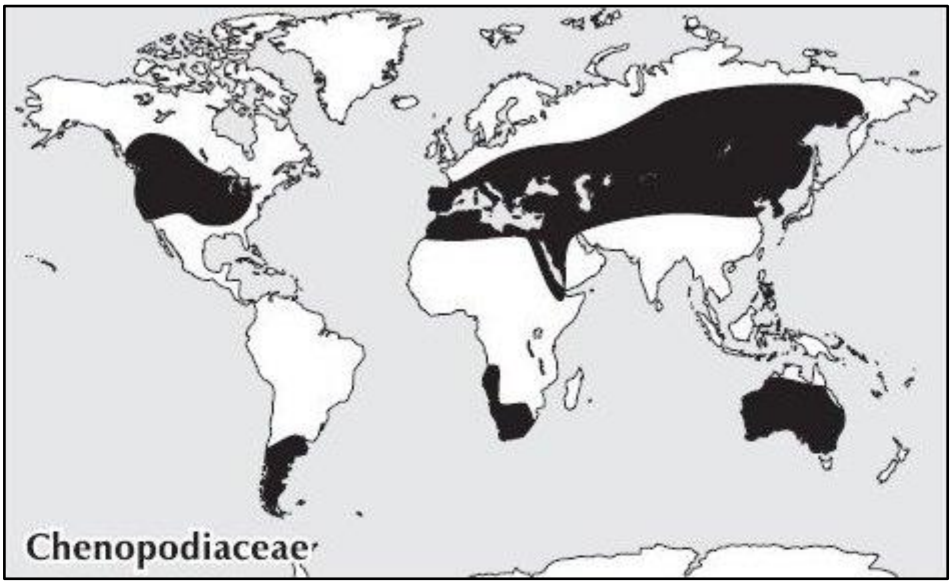


Figure 1.2: Amphitropical distribution of the Chenopodiaceae (from Huggett 2004), which likely emphasizes terrestrial chenopod taxa.

The family has approximately 100 genera and 1250 species, in 6 subfamilies and at least 10 tribes (Kadereit *et al*. 2005). The primary centre of diversity and origin, having all tribes and about 60% of the genera is the Mediterranean-Central Asian belt of the Old World. Australia is a secondary centre, in terms of species, followed by North America, South America and South Africa. Chenopods are of cosmopolitan ecological and economic importance (Kuhn 1993). Many species dominate plant communities of coast and desert. Native and commercial herds of large and small herbivores browse chenopods, additionally used in land rehabilitation as they readily colonize disturbed and saline lands. Some are domesticated for human consumption e.g. *Beta vulgaris* (silver beet, beetroot).

Australian chenopods are highly diverse, abundant and widespread in arid areas (Osmond *et al.* 1980; Graetz and Wilson 1984; Leigh 1994) and on coastlines (Osmond *et al.* 1980; Love 1981; Adam 1994; Saintilan 2009b, 2009a). The 302 indigenous species listed in the Australian Plant Census at the beginning of this study form the complement under study (listed in Appendix I). Species descriptions follow Wilson (1984, 1986); Jacobs (2000); Walsh (2002); Wilson and Chinnock (2013). Since 1984, nomenclature of *Chenopodium*, *Dysphania* and *Tecticornia* has been revised, and new species published for *Atriplex* and *Tecticornia*.

Molecular analyses of the last 20 years broadly reveal the global history of chenopods. Detail specific to each continent is scant but they are somewhat unique within the world's desert flora. Chenopodiaceae and Zygophyllaceae are the only two plant families, largely restricted to coast and desert habitats and found in all the world's desert regions (Shmida 1985). Though the world's major desert areas largely do not share taxa and their littoral connections very likely operated independently, the evolutionary course of Australian chenopods from coast to interior has global relevance.

Figure 1.3 plots diversity of eleven immigrant clades with estimated age of arrival. Clades arriving over the Mid-Late Miocene generally have more species than Pliocene and later arrivals. Only the Sclerolaenid (Miocene) and Chenopodieae I (Pliocene) clades generically diversified. Modern arrivals of deliberate or inadvertent introduction under European settlement are excluded from this study.

Subfamily Chenopodioideae

Atriplex clades

Australian *Atriplex* with 61 species in total, comprises three immigrant clades (Kadereit *et al*. 2010) in a secondary global centre of *Atriplex* (McArthur and Sanderson 1984). Clade names (Australian *Atriplex* Clades 1 and 2) follow Kadereit *et al*. (2010). An important study objective is to ascertain species membership of each clade. *Atriplex* are low to tall shrubs, perennial herbs, biennial or annual species. Some coastal species occur in New Zealand.

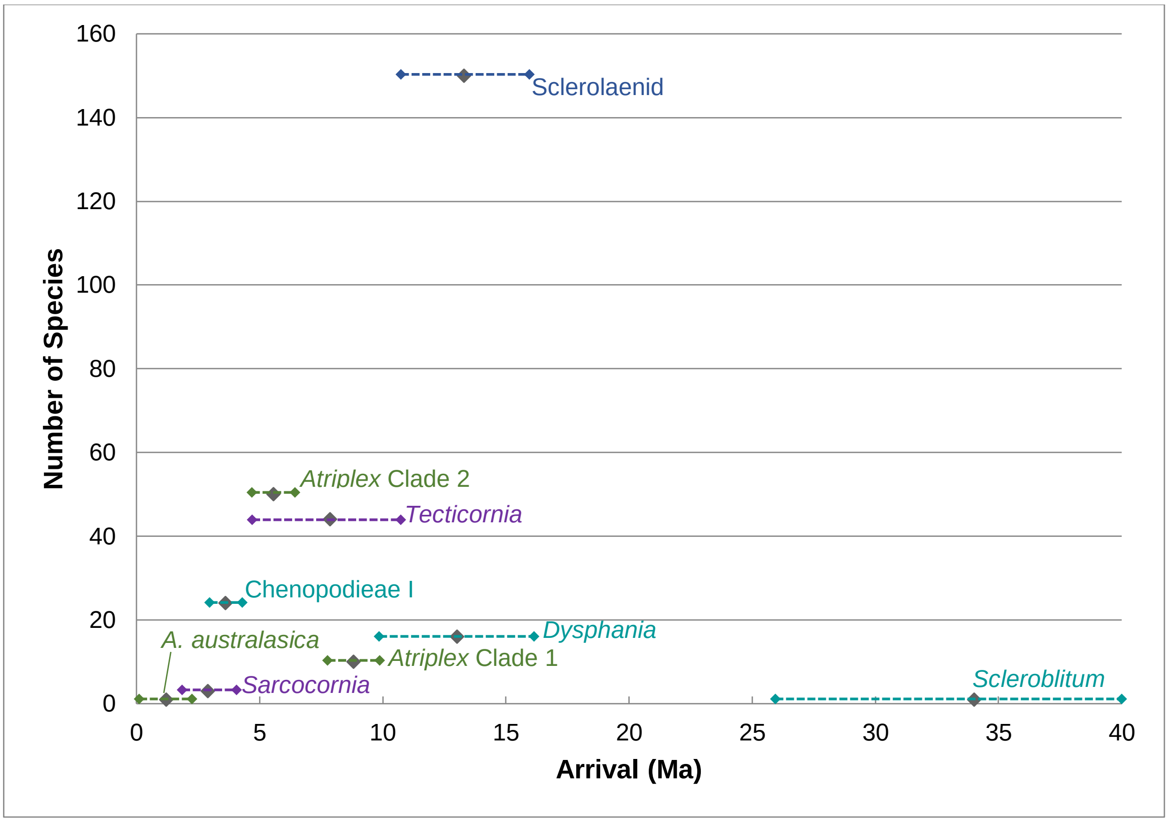


Figure 1.3: Estimated arrival time of nine chenopod clades with current clade richness in Australia. Time range indicated by bars; derived from Kadereit *et al*. (2005, 2010) and Kadereit and Freitag (2011). Arrival of *Salsola* and *Suaeda* clades is not known.

Cosmopolitan *Atriplex* has c. 300 species (Kadereit *et al*. 2010). All but one Australian species, are in a global lineage of C_4 species that emerged with increased aridity and seasonality of Miocene climates. *Atriplex* Clade 1 arrived 9.8-7.8 Ma and is related to Eurasian/American species. The richer *Atriplex* Clade 2, related to Central Asian stocks, arrived 6.3-4.8 Ma, radiating soon after. *Atriplex australasica* is a C_3 species of Eurasian origin, with estimated Pleistocene arrival needing confirmation (G. Kadereit, *pers*. *comm*.).

Chenopodieae I Clade

Australian Chenopodieae I includes 24 species from the cosmopolitan genus *Chenopodium* and from genera *Rhagodia* and *Einadia*, which are restricted to Australasia. Kadereit *et al*. (2005, 2010) estimate arrival of Australian Chenopodieae I at 4.7-2.9 Ma. Life-forms are tall shrubs, perennial and annual herbs and vine-like scramblers in *Einadia*.

The group likely comprises two immigrant clades. Mosyakin (2013) proposes adding *Chenopodium glaucum* and *C. erosum* to *Oxybasis*, a genus in East Asia, Australasia and North America; the cosmopolitan *C. glaucum* is regarded as a species aggregate. Only *C*.

glaucum ssp. *ambiguum* may be native to Australia (Wilson 1984). Pending confirmation, this group is treated singly.

The clade name is that for a group also with Russian, North Pacific and North American species (Kadereit *et al*. 2010). Fuentes-Bazan *et al.* (2012a) and Fuentes-Bazan *et al.* (2012b) put Australasian species in a large global clade, and regarded generic distinction of Australian taxa unwarranted. Both studies have too few Australian species, along with genera in conflicting positions, to be of interpretive value.

Dysphania Clade

Dysphania is a cosmopolitan genus with 16 species in Australia having common life forms of prostrate to erect annual herbs. Clade name follows the generic name (Kadereit *et al*. 2005). The cosmopolitan *Dysphania pumilio* has uncertain Australian status, being treated as native here; all other species are endemic. *Dysphania pusilla* of New Zealand is likely related.

Recent molecular work on *Dysphania* largely confirms the subgeneric structure of Australian taxa as developed in Mosyakin and Clemants (2002). The closest relatives are Asian stocks (G. Kadereit, *pers*. *comm*.). Arrival estimates of 16-10 Ma, are contemporary with the Sclerolaenid Clade (Kadereit *et al*. 2005; Kadereit and Freitag 2011). Similar to Australian Chenopodieae I, the few, published molecular studies focus on global taxonomy and involve small subsets, revealing little of Australian relationships.

Scleroblitum Clade

With arrival estimated between 42-26 Ma (Kadereit *et al*. 2005), the endemic *Scleroblitum* clade, comprising an annual herb, is Australia’s oldest. The age estimate should be improved (G. Kadereit, *pers. comm.*). Its closest relatives of the newly proposed genus *Blitum* are thought to be Eurasian species (Kadereit *et al*. 2005; Fuentes-Bazan *et al*. 2012b). Mosyakin (2013) includes North American taxa within *Blitum*. Current species range and estimated arrival time accord with the earliest physical evidence of chenopods in Australia, being pollen traces of Late Oligocene-Miocene age in estuarine deposits of the Murray Basin (Truswell *et al.* 1985; Kershaw *et al.* 1994).

Subfamily Salsoloideae

Salsola Clade

The herbaceous *Salsola* needs comprehensive taxonomic review. Collection before European settlement suggests Australian native status, but Pyankov *et al.* (2001) did not consider *S. australis* as endemic. At 17/5/2017, Australian Herbarium collections listed 1249 *S. australis* records, 191 *S. kali* records and 1274 *S. tragus* records. Date of determination influences species identity, but with floras listing only a single species at any time, this study treats all as *S. australis*. There are likely more species than currently recognized (Borger *et al.* 2008; Chinnock 2010). Confirming anecdotes of entry in Afghan camel harnesses would mean exotic and native elements have mixed. Akhani *et al.* (2007) include *S. kali* and *S. tragus* (synonym of *S. australis*) in the Kali clade of Central Asia and North Africa.

Subfamily Camphorosmoideae

Sclerolaenid Clade

With 12 genera and 150 species, this near endemic clade comprises half of Australian chenopod species and genera. *Enchylaena tomentosa* occurs in New Guinea and New Caledonia. Australian taxa dominate the subfamily which globally has *ca.* 19 genera and *ca*. 190 species (Kadereit and Freitag 2011). The clade name is adapted from Sclerolaeneae, a former name for Australian taxa. Kadereit and Freitag (2011) firmly establish monophyly of this clade with a close relationship to *Grubovia* in Central Asia, and estimated separation time between 16.4-10.3 Ma.

The molecular phylogeny of Cabrera *et al.* (2009, 2011) with almost half the clade’s species, used in a global phylogeny of Kadereit *and* Freitag (2011), suggest general speciation patterns. A broad polytomy is attributed to rapid radiation in the Late Miocene or Early Pliocene. The two main genera, which equally contain 40% of clade species, comprise the basal *Maireana* and the derived *Sclerolaena*. Remaining genera are loosely allied to these two genera which are polyphyletic.

To analyse patterns in this very large clade, it is grouped into taxa affiliated with *Maireana* or *Sclerolaena* as described in Appendix IV. *Maireana* comprises shrubs and perennial herbs while *Sclerolaena* comprises short-lived, weak shrubs or annual/biennial forms.

Subfamily Salicornioideae

Tecticornia and *Sarcocornia* clades

Tecticornia comprises 44 species, with about 12 collections in Western Australia awaiting determination. *Sarcocornia* has 3 species. Three species are newly described since 1984. Shepherd and Wilson (2007) list nomenclatural changes within *Tecticornia*. These genera are the only subfamily members in Australia, arriving as separate clades (Shepherd *et al.* 2004; Kadereit *et al.* 2006; Steffen *et al.* 2015). Clade names derive simply from the genus name. The succulent lifeforms are low growing shrubs or annual herbs.

Kadereit *et al*. (2006) placed *Tecticornia* within a larger *Halosarcia* clade, largely confined to Australia and the Indian Ocean periphery, with a small outlier on the Atlantic coast of Africa. The *Halosarcia* lineage formed at least by 14.6 Ma with Australian arrival at 10.9-4.8 Ma (Kadereit *et al*. 2005). Further taxonomic and molecular work within the larger clade is required to clarify relationships with Asian species and the arrival time in Australia, which most likely occurred through South East Asia (Kadereit *et al*. 2005). *Tecticornia* phylogeny has an unresolved polytomy (Shepherd *et al*. 2004), as does *Atriplex* Clade 2 and the Sclerolaenid Clade, attributed to rapid radiation over Late Miocene-Pliocene, synchronous with that of the Sclerolaenid Clade.

Australian *Sarcocornia* derive from South African stock, with a limited speciation in the Pleistocene (Steffen *et al*. 2015). With *Salicornia* from America and Africa, they are part of a sister clade to *Tecticornia* (Kadereit *et al*. 2006).

Subfamily Suaedoideae

Suaeda clade

Suaeda is a taxonomically difficult genus due in part to vegetative characters that vary greatly with salinity, competition and supply of water and nutrients (Schutze *et al.* 2003). Most *Suaeda* are annual species, but both Australian species can be weakly perennial. Wilson (1984) suggests some inland occurrences determined as the native *S. australis* could be the exotic *S. maritima*.

Australian species are from the global *Brezia* subclade, which has C_3 photosynthesis, and comprises mainly Eurasian lineages (Schutze *et al*. 2003). Australian *Suaeda* belong to a lineage with apparently primitive taxa, are in a basal position in the subclade and possibly isolated from sister species for some time. They may not be a sister pair, but separate incursions into Australia, though here are treated as a single immigrant group.

PURPOSE, SCOPE AND OUTLINE OF THESIS

Purpose and scope

The main aim of this study is to describe the geography of chenopod evolution by identifying the most likely course of a littoral connection in forging their modern Australian distribution. Salt-tolerance, as an exaptation for drought-tolerance among all chenopod taxa, puts focus on the whole chenopod complement.

Interpretation of origins using a littoral connection rests on plant taxa exhibiting patterns in the taxon, habitat and trait elements of the connection. Eleven immigrant clades of Australian chenopods conforming to these phytogeographic patterns increases likelihood of a littoral connection origin, but the evolutionary course may only become apparent in the nature of the patterns. Phylogenetic niche conservatism in each immigrant clade could reveal the evolutionary detail, but requires comprehensive phylogeny, functional understanding of adaptation specific to habitat and distributions of all chenopod species. Alternatively, the phylogeny of one rich clade may serve as an initial comparative reference for other clades.

Patterns of the three elements in Australian chenopods would greatly reflect Diversification and Landscape Spread, and some aspects of Colonisation and Establishment:

- For the taxon element: a phyletic group comprises basal coastal species and derived inland species. Basal coastal species may be ecologically similar to ancestral arrivals and colonizers. The derived inland taxa may be more similar to establishers and spreaders. All within the group would align along a route of Landscape Spread.

- For the habitat element: taxa from coastal habitats that are salty, sandy and inundated, progressively inhabit the inland by occupying coast-like habitats. This most ready access inland can occur incipiently in the Establishment stage, but mainly characterises Landscape Spread. Habitats dissimilar to coastal ones would be occupied in the Diversification stage.

- For the trait element: heritable traits relate to specific habitat characters of salinity and dryness, with distinct adaptation adding regional variation.

Patterns would be complex. Immigrant clades did not arrive simultaneously, nor likely landed on the same coast. Inland habitats are variably dissimilar to coasts, variably distant from shorelines and formed at different times. Younger clades would be in stages different to older ones, though current taxonomy indicates most clades are in the Diversification stage.

A complete investigation of the taxon, habitat and trait elements of a littoral connection would be in two parts. First, broadly correlate the regional diversification of taxa with migration and adaptation from coast to desert habitats under aridification – variation in habitat occupation and regional species concentrations reveals diversification patterns. Second, examine factors facilitating occupation of and adaptation to habitat – the interplay of intrinsic characters (e.g. heritable traits of eco-physiology, dispersal) with extrinsic conditions (e.g. increasing salinity, declining rainfall) influences divergence patterns in the sense of Wiens *et al.* (2010) and Crisp and Cook (2012).

The subject of this thesis is the first part of such an investigation – the influence of dynamic landscapes in a drying continent on the diversity of Australian Chenopodiaceae, covering three exploratory themes:

1. Phytogeography resulting from diversification and range extension based on modern richness and assembly of chenopod species through continental regions
2. Preference patterns in habitat occupation related to diversification and facilitation of species range extension
3. History of regional and habitat occupation in major lineages of *Atriplex*, based on a comprehensive phylogeny, that serves as an initial comparative reference

Additional principles, assumptions and observations are variably incorporated in each theme, to simplify biogeographic analysis and interpretation. Ecological opportunity is the main factor in adaptive radiation (Losos 2010; Yoder *et al.* 2010) and could involve degrees of niche shift (Wellborn and Langerhans 2015) because desert habitats can be dissimilar to coasts.

Coastal climates are generally more moderate than deserts (Ungar 1974). The floristics of coastal and desert dunes differ due to environmental variability (Danin 1996). Some desert habitats have no coastal analogue (e.g. arid ranges). For adaptation with niche shift, the probability of advantageous improvement is inversely proportional to magnitude of change. Great change is generally maladaptive (Parsons 1988); a hypothesis increasingly finding theoretical support (Ram and Hadany 2015). Consequently, the coast-inland migration of chenopods through inland habitats involves a successive overcoming of ecological and adaptation barriers.

Such considerations allow the following assumptions, given niche conservatism of the littoral connection and invasion of landscapes of the later Neogene:

- Marked adaptation has low frequency: range extension, begins at the coast (notably in Establishment stage) and is facilitated by dispersal through few, extensive, connected land types (Landscape Spread stage)
- Adaptation is minimal: extant adaptation allows movement into readily accessible land types, most similar to current habitat; the progressive trend is from halophyte to xerophyte (Landscape Spread and Diversification stages)
- Landscape chronology constrains diversification and range extension: occupation and adaptation conform to progressive emergence of arid land types and their formative processes (All stages except Transport)
- Overseas observation of exaptation facilitating habitat shift can apply in Australia
- Coastal species are more likely to be closest relatives of immigrant ancestor and indicative of the ancestral character (Colonization stage).

Such general findings may also apply to other taxa purportedly having a littoral connection. Findings may be a comparative benchmark in development of arid floras or a framework for evolutionary studies of particular plant groups. At the least, clarifying the detail of a long suspected, but poorly elaborated, evolutionary process will progress understanding of the development of our arid flora.

Thesis outline

Chenopod phytogeography – the modern distribution of Australian chenopods

Questions:

1. How are Australian chenopod clades distributed through regional Australia? Which rich regions reflect intense diversification or common migration (Centres of Diversity)? Can regional presence suggest ancient coastal landfalls?
2. What are the relationships between areas of richness? What chenopod taxa or clades are commonly shared, which suggest common migration routes? Which restricted (endemic) species suggests development of local lineages?
3. Do all Australian chenopod clades conform to the taxon element of the littoral connection? What is the nature of sister taxa patterns between coast and desert species? Do clades that don't conform, invalidate the notion?
4. Do congruent patterns in disjunct species suggest landscape influences?

Australian chenopods comprise *ca.* 300 species and descend from at least 11 ancestors, arriving mostly through the Late Miocene–Pliocene (Kadereit *et al*. 2005). Notable radiations occurred in three clades, in or before the Pliocene, and continued into the Pleistocene.

Australian chenopods are predominantly arid taxa (Graetz and Wilson 1984; Leigh 1994) and also coastal (Love 1981; Adam 1994), but variation within this distribution is poorly known. Measures of richness and assembly would identify aspects of Landscape Spread and Diversification stages. Regional species richness indicates where chenopods have diversified most and inhabited least. Assembly patterns would reveal common areas of occupation suggesting major migrations and routes of range extension. Congruent patterns of disjunction identify vicariance (disruptive events) in chenopod evolution.

Taxa of a littoral connection are a mix of closely related coastal and inland species. Such relationship should apply to each chenopod immigrant clade, which must have coastal taxa. A broad expectation is that older clades may have more species, with the inland relatives farther from the coast. Younger groups would have fewer species and inland relatives closer to the coast. Clades with cosmopolitan genera, should have ancestral coastal species of the same genus, and not a derived one. To overcome poor existing descriptions of chenopod distribution, Chapter 2 of this thesis develops a geography of Australian chenopod distribution, in exploring these ideas.

Chenopod habitats – occupation of Australian landscapes

Questions:

1. Through which landscapes are chenopods mainly distributed? Which landscapes do chenopods prefer and what variations occur among chenopod groups? How does landscape age, extent and connectivity influence species occupation and range extension?
2. Do all chenopod clades conform to the habitat element? What are the habitats of coastal species? Is there evidence of direct transition between the most similar (analogues) types e.g. coast dune species and desert dune species? How might habitat of extant coastal species indicate character of ancestral coastal species?

Mabbutt (1986, 1988) identifies eight major land types in Australian deserts, comprising characteristic assemblages of landforms, readily interpreted as species habitats from data in national, state and regional floras or compiled from ecological survey or herbarium collections. Three land types are xeric in nature (being arid, non-saline, non-alkaline) while five are variably halic and calcic (being arid, saline and alkaline) in nature.

Some coast and desert conditions are similar, with habitats that are effectively analogues, e.g. coast and desert dunes. Deserts are more varied having landscapes with no obvious coastal equivalents, e.g. gibber plain. Analogue types of coast and desert dunes, differ in floristic composition, life-form assemblages and ecosystem functions and processes (Danin 1996) and in salinity gradients, influencing eco-morphological variation in plant species (Waisel 1972). An evolutionary shift from coast to desert could involve appreciable adaptation, but where might it start?

Through different parts of Australia, different land types have connected coast and desert areas. Range extension is most likely facilitated through connecting land types of suitable chenopod habitat that existed around the arrival times of chenopod clades. Disconnected and youthful land types of largely unsuitable habitat are less likely to be occupied. Coastal habitats are diverse, but each has inland analogues (e.g. coast dune/desert dune; coast marsh/inland marsh) where direct transitions between them could enable coastal departures.

Comparing species occupancy across all land types, identifies habitats where diversification is abundant or limited. Land type age and extent helps identify the types potentially facilitating range extension. Occupancy of coastal habitats may reveal the species most resembling immigrant ancestors. Broad habitat analyses can characterise aspects of the stages of Colonization, Establishment and Landscape Spread in an invasion scenario.

Consistent with better understanding of regional chenopod distribution, Chapter 3 of this thesis develops a full description of chenopod habitats to explore these notions.

Phylogeny of Australian *Atriplex* – diversification and landscape formation

Questions:

1. Is progressive emergence of land types reflected in clade/subclade development? Do land types strictly control clade diversification or present varied opportunity for taxa? Are there lineages restricted to Centres or land types, of age coincident with land type age or are lag times notable?

2. What are the relationships of species shared by and unique to centres of diversity? Does this reflect migrations between centres or diversification confined to them?

3. Is phylogeny of chenopod groups consistent with a littoral connection? Where do coastal species sit? Are single or multiple migrations from coastlines evident within a single clade?

A complete phylogeny identifies the relatedness of extant species and the order of their emergence. Congruent patterns of species diversification, distribution and habitat across different groups identify common processes in evolutionary history (Morrone 2009; Wiley and Lieberman 2011). Chenopod clade arrival and diversification coincided with developing aridity but lineages can add complexity with multiplicity of range extensions (in time and space) and varied diversification.

Evolutionary relationships within and between Centres of Diversity is apparent in the phylogenetic position of species they share and species unique to each, identifying routes of movement. Shared species result from taxa early in diversification having widespread ranges or range extensions from one centre to another. Exact relationships reveal direction of movement and degree of exchange. Lineages restricted to a single centre identify diversification controlled by the centre's landscapes. Lineages containing restricted species from both centres, indicate vicariance or jump-dispersal, probably early in diversification.

Australian arid landscapes offered varied opportunity for occupation. Forming progressively from the Late Miocene (Fujioka and Chappell 2010), their size and location vary with time. Habitats are occupied as landscapes form (Byrne *et al.* 2008) or afterwards, with the lag time between habitat formation and species emergence being substantial for entirely novel habitats (Guerrero *et al.* 2013). Rapid occupation and extension of range could occur with pre-adaptation to aridity, perhaps repeatedly in older, rich clades as arid landscapes expand. The older *Maireana sedifolia* and much younger *Sclerolaena obliquicuspis* (Cabrera *et al*. 2009) co-occur on calcareous plains of varied age.

The phylogenetic position of coastal species is very informative. Coastal species in basal positions strongly supports a littoral connection hypothesis and identifies the modern taxa that are most like ancestors. Absence of coastal species refutes a littoral connection or indicates local extinction. Multiple coastal species result from the evolutionary taxon cycle (*sensu*. Shmida 1985) or diversification within coastal lineages. A combination of distribution, habitats and phylogenetic proximity to inland species identifies the region of origin and initial migration routes as well as the species that have a modern ecology indicative of colonizing and establishing ancestors.

As a complete phylogeny for each rich chenopod clade is beyond a single study, a molecular phylogeny of the two *Atriplex* clades in Chapter 4 explores patterns outlined above, with some comparison to the Sclerolaenid clade (Cabrera *et al.* 2011).

CHAPTER 2. CHENOPOD PHYTOGEOGRAPHY – THE DISTRIBUTION OF AUSTRALIAN CHENOPODS

INTRODUCTION

The modern distribution of chenopods stems from Neogene range extension, adaptation and diversification in eleven immigrant clades. Describing the distribution of taxa is an initial phase of biogeographic study from which likely evolutionary scenarios may be inferred (Stott 1981; Crisci *et al.* 2003). For example, concentrations of endemic species indicates local diversification, while regions that share suites of species could delineate common range extensions. Discontinuous distributions reflect extraordinary events. Species absence relates to unsuitable or remote habitat, or to extinction.

Distributions expand as barriers to range extension and adaptation are breached or diminish (MacDonald 2003; Cox and Moore 2010) and for chenopods, expansion comprises migration along coastlines and from coast to desert. Range extension inland can be akin to invasive species overcoming a succession of barriers (Wilson *et al*. 2009a).

The modern chenopod distribution is imprecisely known, often being described at continental scale and with emphasis on few, select species. Fortunately, modern digital platforms (e.g. Australasian Virtual Herbarium) readily depict species ranges for all Australian species, deriving distributions for given taxonomic rank and for immigrant clades.

Chenopods would readily occupy a vast, drying interior (Crowley 1994; Bui 2013). Salt-tolerance allows occupation of habitats most plants avoid (Flowers and Colmer 2015) and it is an exaptation for aridity (Osmond *et al*. 1980; Flowers *et al.* 2010). Continental decline in rainfall over the Neogene transformed mesic vegetation of the Late Oligocene into modern, xeric forms (Hill 1994; Barlow 1994; Martin 2006). Rainfall decline and increasing salinity sets adaptation challenges for existing taxa and creates opportunity for chenopod invasion.

In this chapter, a phytogeography of Australian chenopods reveals spatial patterns of range expansion and diversification in chenopod evolution. A much improved and needed description of the modern distribution of Australian chenopod taxa should also result. Supplementing this broad objective, is an examination of the taxon element of a littoral connection and disjunction of chenopod taxa.

BIOGEOGRAPHY AND DISTRIBUTION

Distribution concepts

Biological organisms are spatially arranged in a non-random and broadly predictable manner (Cox and Moore 2010; Lomolino *et al*. 2010). Taxon distribution is a basic analysis of spatial patterns, with studies of related taxa giving an evolutionary context (Tivy 1993; Lomolino *et al.* 2010). Concepts within taxon distribution are defined in Table 2.1 drawn from Pielou 1979, Stott (1981), Tivy (1993), Gaston (2003), Huggett (2004), Cox and Moore (2010), Lomolino *et al*. (2010) and Heads (2012, 2014); these can apply at any taxon classification.

Concept	**Definition**
Species range	Geometric aspects of a species area of occupation including location, size, shape and continuity of area of occupation
Range extension (or expansion)	Increase in species range by movement into unoccupied areas
Range contraction	Decrease in species range through local population extinction
Range shift	Change in location of species range due to combined extension and contraction
Allopatry	Two or more species with ranges that are entirely separate
Parapatry	Two or more species with ranges that overlap
Sympatry	Two or more species with ranges that coincide
Disjunction	Allopatric species with marked spatial separation
Population diffusion	Successive generations occupying different portions of the species range as offspring establish separately from parents

Table 2.1: Definitions in analysis of taxon distribution

The size and shape of species ranges is a balance of population diffusion maintaining occupation, and hostile regions which are dispersal barriers (Gaston 2003; Cox and Moore 2010; Lomolino *et al.* 2010). Aggregating the ranges of related species delineates taxon ranges of higher ranks (Stott 1981; Tivy 1993).

Ongoing extension, contraction and shift constitute a range dynamic. Species ranges extend as dispersal barriers weaken and diffusion enlarges contiguous populations. Alternatively, in long-distance (or jump) dispersal, a species breaches barriers that limit diffusion and establishes a separate stand in similar habitat. Further diffusion extends the species range. Long distance, oceanic dispersal best explains chenopod arrival, due to Australia’s Neogene isolation (Kadereit *et al.* 2005; Cabrera *et al.* 2011). Speciation and range dynamics create complex distributions of related species. Species ranges variably overlap, are entirely separate, or nest within ranges of widespread taxa.

Allopatry, parapatry and sympatry are also applied to speciation processes. Allopatry is the common form of speciation, resulting from geographic isolation of populations (Gaston 2003; Huggett 2004; Lomolino *et al.* 2010). Parapatry is a specific form of allopatry (Cox and Moore 2010) or a differential occupation of habitats common to a given area (MacDonald 2003), thus resembling sympatry. Parapatry and sympatry also arise from range extension of allopatric species (Heads 2012, 2014). Allopatry and sympatry are extremes separated by parapatry, and the genetics of trait change, rather than range pattern, best identifies speciation process (Phillimore 2013). Application in this study is only to range patterns.

In disjunctions, the separation area varies geologically, topographically, climatically, edaphically or biologically with the habitat of the taxa (Stott 1981). Disjunct taxa of low rank (e.g. subspecies) are assumed more recent separations than those of higher rank (e.g. genera). The cause of disjunct patterns is controversial – fragmentation of ancestral species ranges or long-distance dispersal (Lomolino *et al.* 2010; Cox and Moore 2010; Heads 2014).

Distribution and littoral connections

Two aspects of Australian chenopods provide the spatio-temporal context for analysing distribution. First, they comprise eleven immigrant clades from five subfamilies (Kadereit *et al.* 2005), likely with differing biogeographic history (e.g. landfall, ecological character). Species and clade distribution at broad scale is sympatric, with increasing parapatry and allopatry of species at finer scale. Sympatric patterns identified in phytogeography (Stott 1981; Crisci *et al*. 2003) would reflect migration from coast into desert through occupation of similar habitats. Second, salt-tolerance links species ranges to saline habitats, which are preserved in the geological record (see Chapter 3).

Analysis of chenopod distribution is two parts. Analyses of species richness and chenopod assembly at continental scale broadly reveals the course of chenopod evolution and clade histories. Two further aspects of distribution are also historically informative. Spatial patterns of the taxon element quantify outcomes of a littoral connection and crudely test it. Taxon disjunctions of continental scale indicate significant events affecting species range dynamics.

Distribution and invasion

Modern chenopod distribution relates chiefly to the invasive stages of landscape spread and diversification. However, aspects of colonization and establishment also feature in analyses because invasion stages are not discrete, nor strictly sequential. Niche conservatism also suggests the modern coastal taxa could ecologically resemble their colonizing ancestors.

The dynamics of initial stages to a littoral connection are identifiable. Colonization is the founding of a bridgehead on a coastline. Establishment immediately follows, as population diffusion enlarges the bridgehead within familiar shoreline habitat. Biotic factors e.g. competition, herbivory, parasites, are the major impediment to establishment (Theoharides *et al*. 2007) and can be assumed to be minimal for the first arrivals on a new coastline. A regional coastal presence would obscure a specific landfall site. The southern and western coasts have been suggested (Beadle 1981b; Specht 1981b); the south-west coast specifically for the Sclerolaenid clade (Cabrera *et al.* 2011). Coastlines shared by clades could reflect landfall location, particularly young clades of restricted range. Chenopods in coastal successions at varied distance from shore (Specht 1972; Waisel 1972; Love 1981; Specht 1981a; Adam 1994; Clarke 1994c) shows early capacity for inland movement.

Landscape spread, being inland and coastal range extension of regional scale, is an initial phase of diversification. Invader ecology is critical to this stage (Theoharides *et al.* 2007). Rates and location of spread through heterogeneous landscapes would vary. Exaptation for aridity assists movement as would the niche conservatism of a littoral connection that favours occupation of inland habitats similar to coasts. Attributes of coastal taxa would be important in earliest phases of spread. The inland extent and overlap of coastal taxa, including subspecies, could reflect the nature of range extensions e.g. sympatric, parapatric or allopatric patterns with the nearest inland relatives. Habitats influencing landscape spread are examined in Chapter 3. Nearest relatives are a topic of Chapter 4.

Landscape spread in continental Australia would facilitate reproductive isolation in two ways. First, extensive coastal migration creates opportunity for widely separate inland extensions. Second, with few topographic barriers to range extension initial migrant populations extend distantly, and later fragment if dispersal or diffusion is severely disrupted.

Chenopod diversification could relate to adaptation to varied landscapes and the reproductive isolation possible at continental scale. Regional species richness results from speciation and migration (Wiens 2011), so landscape spread and diversification can create regional centres of diversity, possibly with distinct lineages. Outcomes for immigrant clades depend on the time and location of their arrival and the dispersal rates and adaptive capacity of ancestral species. Congruent regional richness involving numerous endemic taxa and several clades is of special interest. Absence and paucity reflect dispersal or distance barriers, limited adaptive capacity (especially in younger clades) or possible extinction.

Current description of Australian chenopod distribution

Descriptions of chenopod distribution are exceptionally general, hampered by taxonomic issues and skewed by ecological and economic considerations but can be overcome with a phytogeographic approach. Specific issues are outlined in Appendix II.

Distribution would be complex due to substantial capacity for episodic, global travel, species range expansion and rapid diversification. Most subfamilies are intercontinental with seven Australian genera being cosmopolitan. Immigrant clades are from Eurasia, America and Africa (Kadereit *et al.* 2005, 2010; Cabrera *et al.* 2009, 2011; Kadereit and Freitag 2011; Steffen *et al.* 2015). Very rapid diversification rates of *Atriplex* in North America are attributed to Late Pleistocene adaptation and episodic hybridization accompanying species range shifts (Stutz 1978, 1984). Different chenopod taxa prefer different saline habitats (Kuhn 1993).

Migrations and invasions of chenopod taxa continue. Some Australian taxa are in neighbouring regions of South East Asia, New Guinea, Vanuatu and New Zealand (Wilson 1984, 1986). *Tecticornia* in South East Asia could relate to entry to Australia (Kadereit *et al.* 2005, 2006), but other occurrences are thought natural movement out of Australia. Australian chenopods are now naturalised in North America, Europe, Africa and Asia (Aellen 1939; Le

Houerou 1992) through wool exports and landscape rehabilitation. Conversely, weedy chenopod taxa have arrived from Europe, Asia and North America in modern times (Wilson 1984). However, the strong endemism of indigenous chenopod taxa (Wilson 1984) links their evolutionary history to continental Australia.

Chenopod phytogeography identifies variation in species richness and assembly over regions and clades. Such floristic analyses typically investigate the environmental factors in plant community assembly (Daubenmire 1978; Hegazy and Lovett-Doust 2016). Regional patterns of chenopod taxa would reflect evolution of assembly (Stott 1981; Crisci *et al.* 2003) especially on an island continent (Barlow 1994).

Richness and assembly of Australian chenopods

Speciation, dispersal and extinction determine species richness (Wiens 2011). Species rich regions result from local diversification, the survival of species already of widespread range and through being a common destination for species expanding their range. Species poor regions result from local or total extinction, unsuitable habitat that is beyond a taxon's adaptive capacity or suitable habitat that is inaccessible or remote. The latter would mainly apply to clades that are young or dispersal limited because several chenopod genera are continentally widespread.

Regional richness identifies significant processes for chenopods in total and for individual immigrant clades. For a single clade, diversification peaks in regions, rich with species of restricted range. Regions where several clades are rich with restricted species warrant particular investigation e.g. diversity under competitive exclusion. Older clades may be richest in the continental interior, but young clades may be richest nearer coastlines, an issue related to the taxon element (see below).

Species rich areas, that notably include endemic species, were previously and controversially considered centres of origin (Stott 1981; Morrone 2009; Lomolino *et al.* 2010). In a littoral connection, their interpretation as centres of differentiation following a mobile phase of the ancestors of clade lineages (Heads 2012, 2014) is more appropriate.

Regional assembly of chenopod taxa establishes regional associations that could suggest common migration. Taxa commonly shared by many regions are widespread species of marked range extension. Widespread taxa in older, rich clades possibly have lineages of serial migrations, which phylogenetic analyses can identify (see Chapter 4). A common co-occurrence of chenopod taxa reflects marked degrees of chenopod sympatry as species from richer clades have ranges of notable overlap. Systematic plant surveys of South Australia define floristic groups of chenopod formations with co-occurring taxa from at least three chenopod subfamilies, from most immigrant clade and from the same genus [e.g. Lake Eyre Basin (Hyde and Playfair 1997; Brandle 1998); Nullarbor Plain (Kenny and Thompson 2008); Murray Basin (Kinnear *et al.* 2000); Great Victoria Desert (Thompson and Foulkes 2008); Gawler Ranges (Hudspith *et al.* 2001)].

Regions that don’t share species arise in two circumstances. Prominence of unsuitable habitat makes at least one region species poor, in which instance a common boundary with a rich region is an effective barrier to expansion. Species rich regions can have few species in common, being occupied by different immigrant clades or distinct lineages within them.

Special distributions: Taxon element and disjunction

Taxon element

Distributions of coast and inland taxa describe the taxon element of a littoral connection. The element is a sister relationship of coast and inland taxa and may be simply the proportion of coastal and inland species. It can vary with factors such as clade age, richness or coastal landfall. Each immigrant clade should express the taxon element, as coastal species of one clade are not sister to inland species of another; each clade should have coastal species. Extinction can induce absence of coastal taxa in one clade, but absence in numerous clades refutes existence of the taxon element, undermining the concept of a littoral connection.

Species ranges of sister coastal and inland taxa express taxon element patterns. Floristic surveys indicate ranges of coastal taxa and inland sister taxa overlap. The coastal taxa *Atriplex paludosa* and *Maireana oppositifolia* are from different clades and together define several floristic groups on Eyre Peninsula, South Australia (Brandle 2010). Some are exclusively coastal, but others extend inland from the coast, including non-coastal taxa from the same clades. Both species are also in inland Western Australia. *Tecticornia* spp. exhibit similar patterns (Brandle 2010).

From such surveys and existing taxonomy, the taxon element of a clade comprises:

(1) Populations of a single species in coastal and inland habitats. This suggests broad environmental tolerance, possibly an ancestral characteristic. Wide ranges of environmental tolerance are important to successful colonisation in an invasion (Theoharides *et al.* 2007).

(2) Closely related species with common origin and sharing an Australian ancestor. Distinct suites of allopatric coastal and inland taxa would most strongly express the taxon element.

A rich immigrant clade could exhibit both patterns. In describing the taxon element, the exclusivity of coastal taxa to coastlines needs consideration.

Several evolutionary inferences emerge given such characteristics of coastal taxa and clade membership. As noted earlier, a littoral connection is doubtful for a clade of diverse inland species with no coastal taxa, though extinction may explain lack of coastal taxa in old clades. Lack of generic diversity in Salicornioideae is attributed to younger lineages replacing older ones (Kadereit *et al.* 2006). In older clades, inland taxa should outnumber and be more widespread than coastal taxa, given the extent of the arid zone. Coastal species richness could also be higher, and the sister taxa relationship includes related species. In younger clades, inland species should be fewer and of small ranges closer to coastlines. Very young immigrant clades would have few species with sister taxa patterns dominated by coast and inland populations of those species. Subspecies particular to coastal or inland habitats, may indicate adaptation with range expansion early in the landscape spread stage. A monotypic clade can only have sister pattern of coastal and inland populations.

Crude ratios of coastal to inland sister taxa for each clade can reflect clade history. Adaptive radiation or old age, creates Coast:Inland [**CI**] species ratio of 1:Many. Restricted diversification has ratios of low magnitude (**CI** is 1:1 or 1:Few) suggesting limited adaptive capacity, clade youth or extinctions. Substantial coastal diversification creates **CI** of Many:Many while newly arrived clades would have **CI** of 1:0. Repeated extension/speciation cycles (following Shmida 1985), more likely found in older clades, generates higher magnitude ratios (**CI** is Few:Many or Many:Many).

Disjunction

Disjunct taxa indicate extraordinary events in the evolution of immigrant clades, arising from vicariance or long distance dispersal (Stott 1981; Cox and Moore 2010; Lomolino *et al.* 2010). In vicariance, barriers form inside the range of widespread species, separating and isolating populations. In long distance dispersal, a maintained barrier is breached rarely. To identify the process from distributions, vicariance is generally invoked where multiple, unrelated taxa of similar ecology show congruent disjunction (Heads 2014). Disjunction occurs at any scale as the degree of gene flow is the critical factor (Stott 1981; Huggett 2004).

Disjunct distributions of Australian chenopod taxa would occur with the development of arid landscapes and along coastlines. Increasing aridity over the subcontinent, modified existing landscapes and created new ones, variably suited to chenopods (see Chapter 3). The Neogene history of Australia involves substantial shoreline shift in the north and south (BMR Palaeogeographic Group 1990, 1992; Quilty 1994; Belperio 1995; Voris 2000). Also, species buoyed across the ocean would easily disperse farther along the coast.

Taxa exhibiting disjunct patterns can indicate event timing. Disjunction of species populations is likely recent. Sister lineages, species and genera could represent increasing older separations. Additional phylogenetic studies are needed to determine disjunction of species and genera, but those of species populations are evident in species ranges. For this study, supra-regional patterns are of primary interest and especially congruent patterns across immigrant chenopod clades.

AIMS, OBJECTIVES AND METHODS

The major aim of this chapter is to describe regional patterns in the distribution of Australian chenopods, relating them to clade migration and diversification. Subsidiary aims are to describe the taxon element of a littoral connection and identify disjunct taxa.

Objectives are to:

- Describe chenopod distribution in terms of regional species richness and assembly:
    - Identify chenopod rich regions of intense speciation and for each immigrant clade
    - Describe the spatial assembly of chenopod species to suggest common areas of range extension
- Relate richness and assembly to understanding of chenopod origins
- Identify the taxon element of immigrant clades:
    - Describe the distribution of coast-inland taxa in each clade
    - Confirm each clade exhibits the taxon element of a littoral connection
- Identify congruent, disjunct populations of chenopod taxa at regional to subcontinental scale, across immigrant clades

Analyses chiefly rely on regional species presence/absence, aggregated to immigrant clades or to higher taxonomic rank.

Clade membership

Appendix I lists all chenopod species on the Australian Plant Census as of August 2014, taxonomy as per Wilson (1984) and clade membership as determined or presumed in this study.

Molecular analyses show clade membership broadly conforms to current taxonomy (Shepherd *et al.* 2004; Cabrera *et al.* 2009; Kadereit *et al.* 2010, 2011). *Atriplex* Clades 1 and 2 are exceptions, being resolved with molecular phylogeny (Chapter 4). Chenopodieae I possibly comprises two immigrant clades (Fuentes-Bazan *et al.* 2012a, 2012b), but is treated here as one. Unpublished molecular analysis broadly confirms the taxonomy of Australian *Dysphania* (Kadereit *pers. comm*.), comprising *Dysphania* (Wilson 1984) and *Chenopodium* subg. *Ambrosia* (Mosyakin and Clemants 2002, 2008; Shepherd and Wilson 2008, 2009).

The Sclerolaenid Clade is divided into two genus-based subgroups for distribution and habitat analyses. *Maireana* is basal and with *Sclerolaena* equally shares *ca.* 80% of 150 species in the clade. The derived *Sclerolaena* broadly marks evolution from perennial species with a winged perianth to semi-perennial/biennial species with a spiny perianth (Cabrera *et al.* 2009). The cause of such an adaptation is uncertain and differences in distribution may suggest the selection factors favouring spines and shorter life cycles. Species in these subgroups are identified in Appendix IV.

Distribution of taxa

Species range maps are digitally constructed on ALA platform (Atlas of Living Australia), deriving dot maps (following Stott 1981; Crisci *et al*. 2003; MacDonald 2003) from plotting location of collected herbarium specimens. Regional presence derives from an overlay of a suitable sampling layer. Taxon range maps are compared in the fashion of choropleth maps (MacDonald 2003), visually noting difference or similarity in presence/absence or plot point density through continental regions. Comparisons are broadly interpreted in context of range extent and occupation of landscape.

Lack of regional collection plots arises from regional absence of taxa (due to inability to survive abiotic or biotic conditions) or from limited collection efforts. Scarcity in the Great Victoria and Great Sandy Deserts in part reflects inaccessibility and remoteness. Rarity or true absence is reliably inferred with intense collection effort in areas of closer settlement.

Regional assembly and centres of diversity

Assembly and diversity are identified with floristic analyses, as in Stott (1981) and Crisci *et al*. (2003). A study area is partitioned into formal sampling units of appropriate size that are regular (e.g. grid system) or irregular (e.g. district).

Australian Physiographic Provinces (Pain *et al.* 2011) are used for diversity and assembly analyses, being of suitable scale and nature to investigate landscapes. They are Level 2 of a mapping hierarchy linking the continent to local soil types in the Australian Soil Resource Information System (ASRIS http://www.asris.csiro.au/) available as a sampling layer on ALA. Level 1 physiography comprises divisions of the Western Plateau (with 13 provinces), Interior Lowlands (3 provinces) and Eastern Highlands (7 provinces). Physiographic Provinces (APP) map and describe dominant landscape assemblages, are derived from Australian desert descriptions of Mabbutt (1969, 1977b, 1984, 1986, 1988), and utilised in an Australian physiography (Jennings and Mabbutt 1977, 1986) which underlies ASRIS (Pain *et al.* 2011).

Chenopod habitat analyses (Chapter 3) also use these desert landscapes, as they have ecological context. Cunningham (1981) and Mabbutt (1988) describe their vegetation. For a history of Australian vegetation, Taylor (1994) described landscape change with the physiography of Jennings and Mabbutt (1977, 1986). Whitford (2002) characterises the landscapes as desert ecosystems. Fox (1999) broadly relates physiographic divisions and provinces to major landform, soil and vegetation types, correlating provinces to natural regions described ecologically and identifying Murray Lowlands and Nullarbor Plain as typically chenopodiaceous.

Australian Physiographic Provinces are preferred to Biogeographic Regions (IBRA) for this sampling. Continental Australia has 23 physiographic provinces and 89 biogeographic regions. Neither APP nor IBRA offer uniform sampling size, but biogeographic regions have greater variation in shape and size, with smaller regions concentrated in eastern Australia, where chenopod occupancy is very low.

Variation in area prompted subdivision of the largest provinces. Sandland and Central Lowlands are divided into geographically recognizable areas of more equable size, using Level 3 boundaries of ASRIS (Physiographic Regions, also on ALA). Sandland North encompasses the Great Sandy and Gibson Deserts and Sandland South is the Great Victoria Desert. Central Lowlands is divided into West (Simpson-Strzelecki Desert, Sturt’s Stony Desert and Lake Eyre), Central (Channel Country and Mitchell Grass plains) and East (Brigalow Belt). Figure 2.1 shows the 26 sampling provinces.

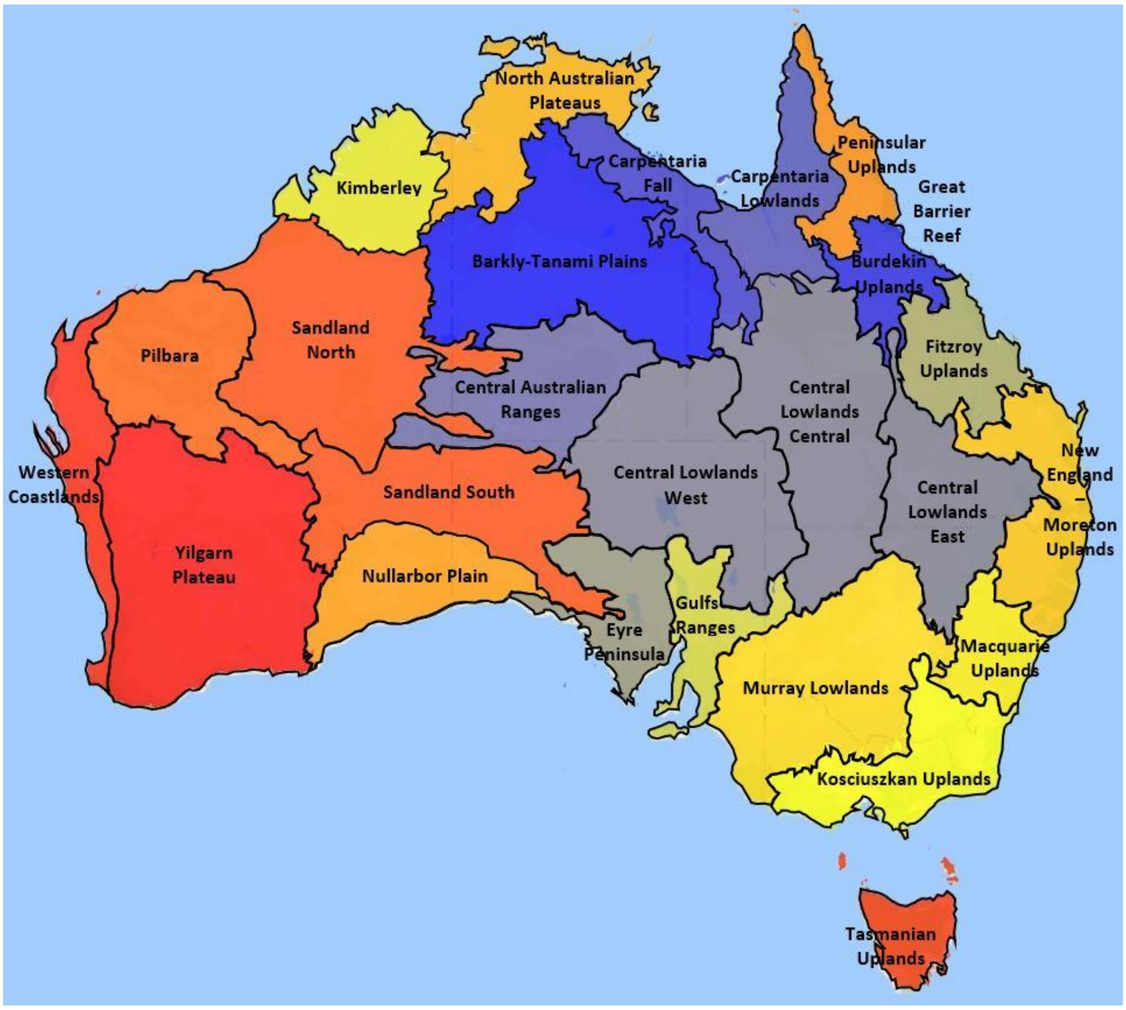


Figure 2.1: Modified Australian Physiographic Provinces (from Pain *et al.* 2011). Sandland is divided into Sandland North and South; Central Lowlands into West, Central and East.

Provincial species presence/absence is tallied from dot maps of AVH specimen collections superimposed on the APP layer of ALA, as follows:

- Presence is the occurrence of formally identified species collection with plot point of reasonably exact location. Absence is no occurrence within the province. Observation without collection is regarded as unreliable.

- Disregarding singular plots distant from a main species range where collection data clearly indicate incorrect plot position, grossly inexact or vague locality, a known introduction or cultivation, or strong likelihood of recent, mediated dispersal. Plot points are validated with an immediate check of collection information.

- To allow for gradational boundaries, a species is scored absent in provinces where the only plot points adjoin the boundary with a province in which the species is present. Boundary proximity was defined as less than the diameter of the default plot point size, on a dot map with the entire continent visible when viewed at maximum enlargement on a 24 inch monitor. The plots score as present, if the species is absent in the adjoining province.

Species ranges are rarely compact and continuous areal extents (Gaston 2003). Dot maps are plot points of varied density over both the species range and within provinces. They can include outlying populations, remote from a main range, being expansion or contraction under modern conditions. To investigate an influence of outlying populations on richness and assembly analyses, presence is recorded in Total (all populations included) and as Major (outlying populations ignored). Procedure for differentiating presence is in Appendix V.

Chenopod assembly is derived from Sorensen Index of dissimilarity for provincial composition calculated within the R statistical computing environment.

Coastal disposition

To investigate taxon element patterns, each species is assigned to a disposition class on a coast to inland continuum, based on species range. Classes reflect decreasing exposure to shoreline processes such as wind-borne salt-spray, tidal ebb and flow, wave splash or sea-storm surge:

- Coast obligate: species range is restricted to coastlines; shoreline processes strongly influence all populations
- Coast facultative: species range is largely along coastlines, influenced by shoreline processes; inland range of smaller extent is unaffected by coastal processes
- Inland facultative: terrestrial species of larger species range away from a coast; populations of smaller range are affected by shoreline processes
- Inland obligate: terrestrial species of inland range, generally remote from coasts; populations near a coast are little affected by shoreline process.

Each species is classified from combination of species ranges maps, floristic surveys of coastal areas, habitat notes in National, State and Regional Floras and compilation of collection records through AVH. Coast obligate and the two facultative classes are respectively similar to classification of saltmarsh species as ‘specialist’ or ‘generalist’ in (Saintilan 2009b).

Coast disposition classes resemble a simple diffusion/speciation model of range extension from the coast, but the classification is only for description of sister taxa patterns. Shifting coastlines (Quilty 1994) and the iterations of range extension and adaptation in taxon cycling (Shmida 1985) would suggest more complex processes, as outlined by Heads (2012, 2014).

Disjunction

Disjunction of species populations was noted from species range maps as regional presence/absence was recorded. Disjunction at continental scale was identified for coastal, temperate and arid areas.

RESULTS

Provincial species richness and centres of diversity

Provincial species presence and composition

Provincial presence/absence was readily tallied for the 302 species on the ALA platform. Plot points of collections remote from a main range could be quickly validated or disregarded. Problems encountered in such tallies and their remedies are briefly described in Appendix II.

Provincial species richness shown in figure 2.2, compares rankings derived from Total Presence and Major Presence. Data is tabled in Appendices VII and VIII. On a Total Presence basis, every province has chenopod taxa. Provincial richness ranking is generally conserved irrespective of how presence is noted, with one notable exception. The same eleven provinces are richest. Nine provinces rank identically. Difference in rank is only a displacement of 1 or 2 positions, even though difference in richness counts ranges from 22 species (Gulfs Ranges) to 48 species (Western Coastlands). The latter only realizes a rank change from 8th to 9th richest. The exception is Sandland North with rank changing from 12th (Total) to 17th (Major) because 51 species are treated as absent in Major Presence counts.

Provincial richness classes are broadly delineated with piecewise linear regression of provincial richness against richness rank (figure 2.3). Total Presence counts suggest four classes with Major Presence indicating two classes. The eleven richest provinces correlate strongly with rank order (R^2=0.9882 Total presence; R^2=0.9731 Major presence). Under Total Presence, these provinces individually comprise 60% to 33% of all chenopod species. The less rich provinces have less than 25% of chenopod species, also correlate strongly with richness rank (R^2=0.97) and include Nullarbor Plain. The poorest 7 provinces have less than 7% of all chenopod species (Total Presence).

Conservation of richness rankings indicates outlier populations have little influence on relative species richness. The eleven rich provinces notably rank as a distinct class. Provincial richness values subsequently reported are for Total Presence, based on the entire species range. However, the exceptional Sandland North province, requires some consideration as the 51 species treated as absent in Marked Presence counts, also produce a major anomaly in assembly analyses.

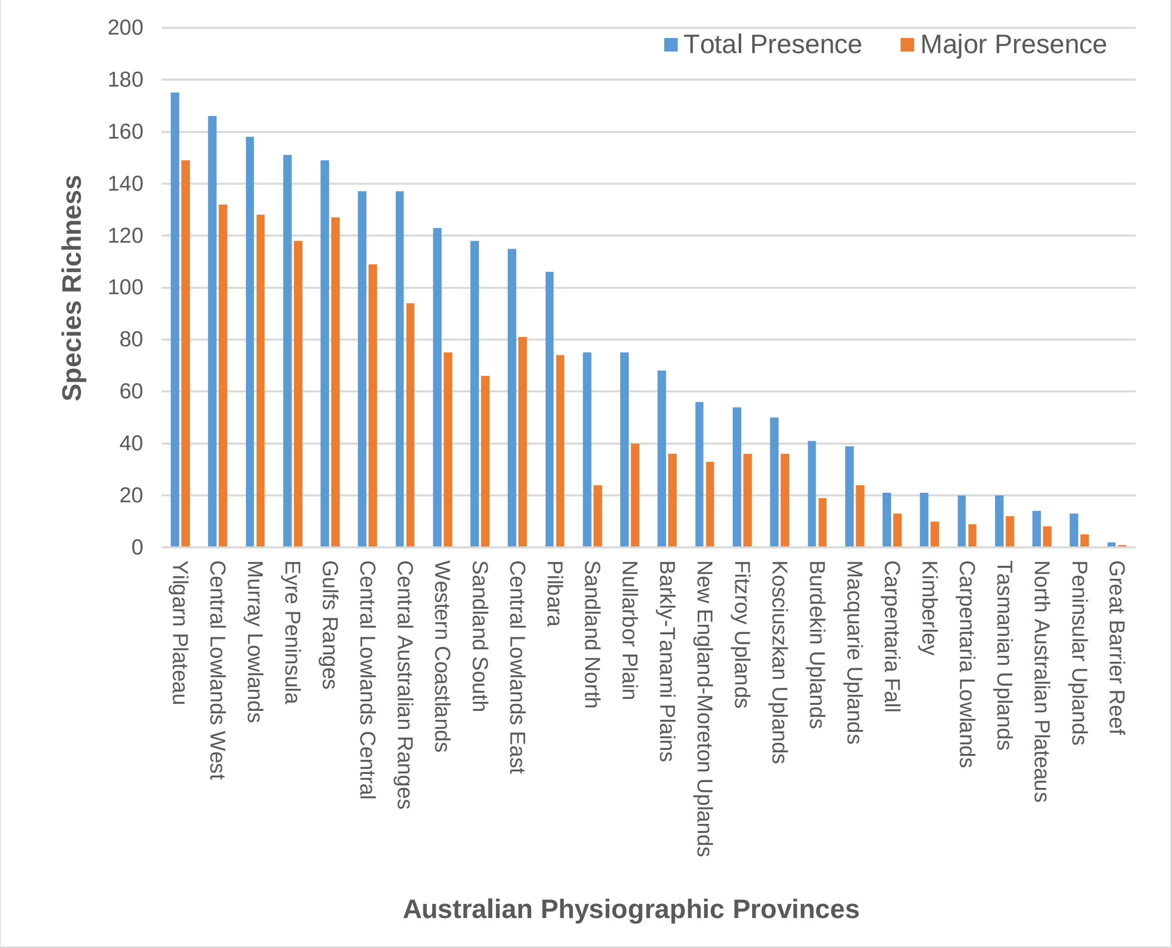


Figure 2.2: Comparative provincial chenopod species richness for Total and Major Presence, ranked by Total Presence richness counts. Sandland North province exhibits the largest difference.

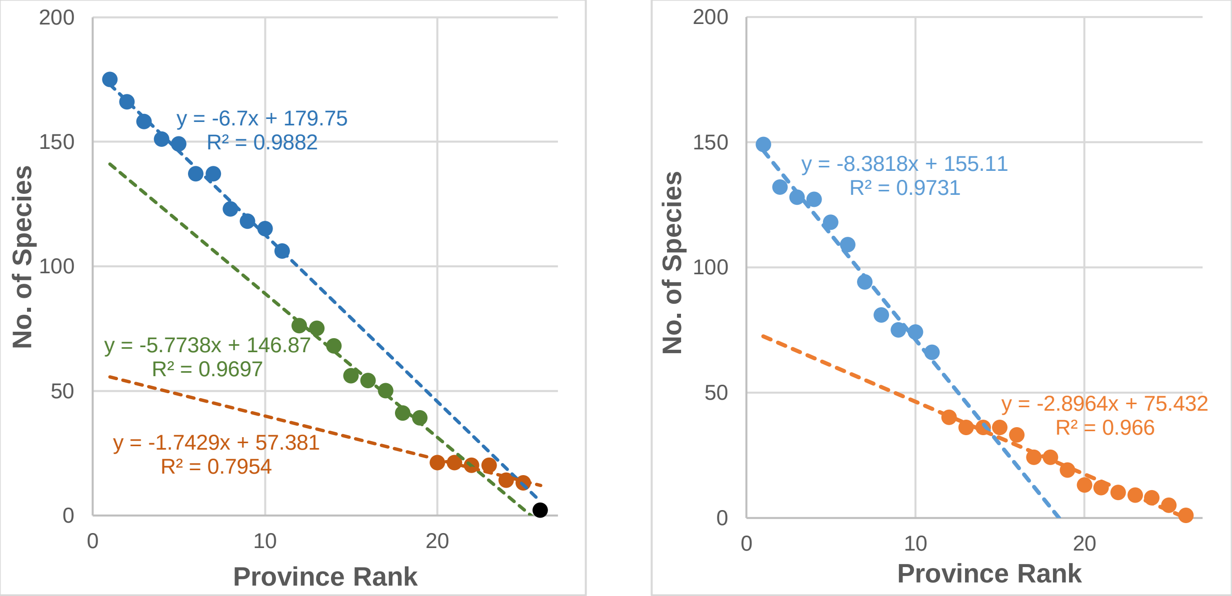


Figure 2.3: Piecewise regression analyses of provincial species richness with province rank. Total Presence counts (left) identify four richness classes and Major Presence counts (right) suggest two. The eleven richest provinces comprise the Yilgarn and Eyre-Murray Centres of Diversity and the province linking them.

Centres of diversity

The eleven richest provinces extend contiguously from the west coast to the margins of the Eastern Highlands, in two species rich centres of differing size. See figure 2.4 and Table 2.2. Both centres have coastlines, though of very different length.

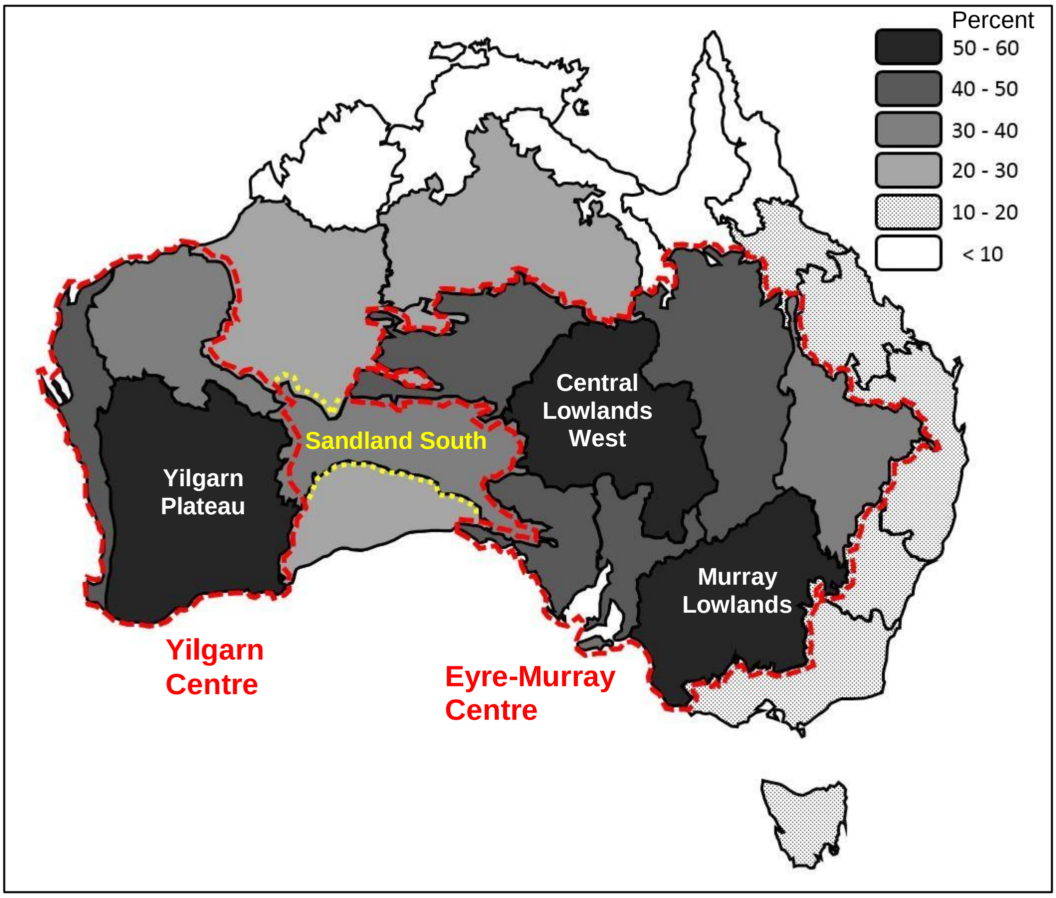


Figure 2.4: Chenopod centres and provincial species richness as percentage of all 302 species.

Taxa/Clade	**Shared Taxa**	**Yilgarn Restrict**	**Yilgarn Total**	**Eyre-Murray Restrict**	**Eyre-Murray Total**	**Outside Centres**	**Total Taxa**
Chenopod Species	129	70	199	96	226	7	302
Chenopod Genera	19	2	21	1	20	0	22
Atriplex	20	11	31	26	46	3	61
Clade 1	2	4	6	2	4	0	8
Clade 2	18	7	25	24	42	3	52
A. australasica	0	0	0	1	1	0	1
Chenopodieae I	15	3	18	5	20	1	24
Chenopodium	6	0	6	2	9	1	9
Einadia	1	0	1	3	4	0	4
Rhagodia	8	3	11	0	8	0	11
Dysphania	10	2	12	4	14	0	16
Scleroblitum	0	0	0	1	1	0	1
Salsola	1	0	1	0	1	0	1
Sclerolaenid	63	33	96	54	117	0	150
MaireanAff	32	20	52	23	55	0	75
SclerolaenAff	31	13	44	31	62	0	75
Tecticornia	17	20	37	5	22	2	44
Sarcocornia	2	1	3	0	2	0	3
Suaeda	1	0	2	0	2	1	2

Table 2.2: Shared and restricted species of Yilgarn and Eyre-Murray centres of chenopod diversity.

The three richest provinces of Yilgarn Plateau (175 species), Central Lowlands West (166 species) and Murray Lowlands (158 species) each have more than 50% of chenopod species. Yilgarn Plateau with Western Coastlands (123 species) and Pilbara (106 species) form the Yilgarn Centre of Diversity in the west. The Eyre-Murray Centre of Diversity comprises Central Lowlands West and Murray Lowlands along with five adjoining provinces (115 to 151 species). It is 10% richer in species than the Yilgarn Centre. Sandland South (118 species) links the two centres, more strongly than the Nullarbor Plain (75 species).

The centres share 129 species (43% of all species) and have species particular to each. Seventy species are restricted to the Yilgarn Centre (*ca*. 25% of all species), and that are endemic or their ranges extend into adjoining Sandland South, Nullarbor Plain or Sandland North. Almost a third of chenopod species (96) are restricted to the Eyre-Murray Centre. Some extend into adjoining Sandland South, Sandland North, Nullarbor Plain, Barkly-Tanami Plains or the Eastern Highlands provinces.Seven species are largely outside the centres, with four being coastal. *Atriplex billardierei* is in Bass Strait. *Atriplex humilis*, *Tecticornia australasica* and *Suaeda arbusculoides* are on tropical coasts. The three inland species are *A. cryptocarpa* (Nullarbor Plain), *Sclerolaena muelleri* (Sandland North, Barkly-Tanami Plains) and *T. bibenda* (Sandland North). Outlier populations of *A. cryptocarpa* and *Suaeda arbusculoides* occur respectively in adjoining Eyre Peninsula and Western Coastlands.

The centres share almost all 22 chenopod genera. Non-shared genera are *Roycea* and *Didymanthus* in the Yilgarn Centre and *Scleroblitum* in the Eyre-Murray Centre. Two genera of the Sclerolaenid clade are almost endemic. *Eremophea* is typically of the Yilgarn Centre with one species of minor occurrence in Central Australian Ranges. Conversely *Malacocera*, more typically of Eyre-Murray, has minor occurrence of one species in the Yilgarn Centre. In Chenopodieae I, *Rhagodia* diversity is strongly associated with the Yilgarn Centre and *Einadia* with the Eyre-Murray centre.

Provincial richness of immigrant clades

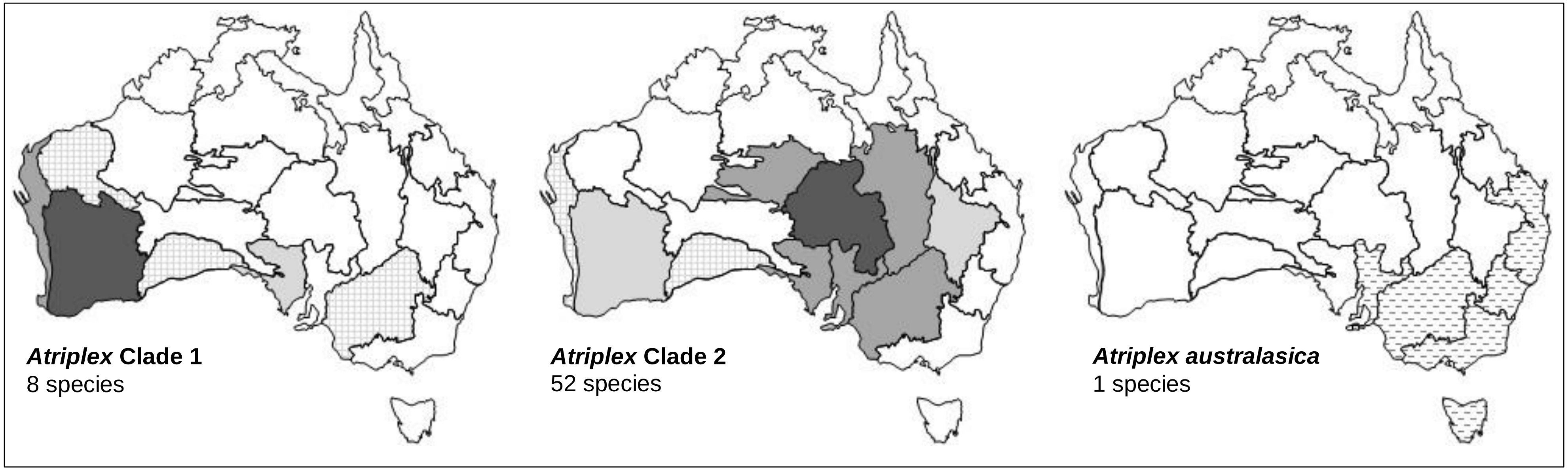
Figure 2.5 shows provincial variation in species richness for rich immigrant clades. *Sarcocornia* and *Suaeda* clades with few species, are not shown. Within Sandland South province, which links the two centres of diversity, the Sclerolaenid clade (both MaireanAff and SclerolaenAff subgroups), Dysphania and Chenopodieae I clades are notably richer than in the Nullarbor Plain.

Sclerolaenid clade richness matches that for all chenopod taxa. Central Lowlands West (*ca*. 60% of clade species) is richest, with Yilgarn Plateau, Central Australian Ranges, Murray Lowlands and Gulfs Ranges at 51%-53%. MaireanAff subgroup is richest in Yilgarn Plateau, which is poor in SclerolaenAff (22% of subgroup species). SclerolaenAff is richest in Central Lowlands West and adjoining provinces. Of the four provinces richest in MaireanAff species, three have coastlines. The three provinces richest in SclerolaenAff species do not.

Immigrant clades of the Chenopodioideae vary greatly in distribution. Chenopodieae I is mainly in a southern belt from west coast to east coast. The richest provinces have at least 60% of clade species and are coastal (Yilgarn Plateau, Gulfs Ranges and Murray Lowlands), excepting Sandland South with more species than the coastal Nullarbor Plain. Chenopodieae I is relatively poor in Central Lowlands West and Centre, which otherwise are rich in chenopod species.

Atriplex Clade 1 (eight species) is richest in coastal, western provinces. Yilgarn Plateau has six species and Western Coastlands has four. *Atriplex* Clade 2 (52 species) is richest in the Eyre-Murray Centre, particularly the inland provinces of Central Lowlands West (35 species) and Central Lowlands Centre (28). Yilgarn Plateau has 43% of Clade 2 species, including endemics. The monotypic *A. australasica* and *Scleroblitum* clades are of the southern Eyre-Murray Centre. Yilgarn Plateau is also rich with *Tecticornia* having 73% of 44 clade species.

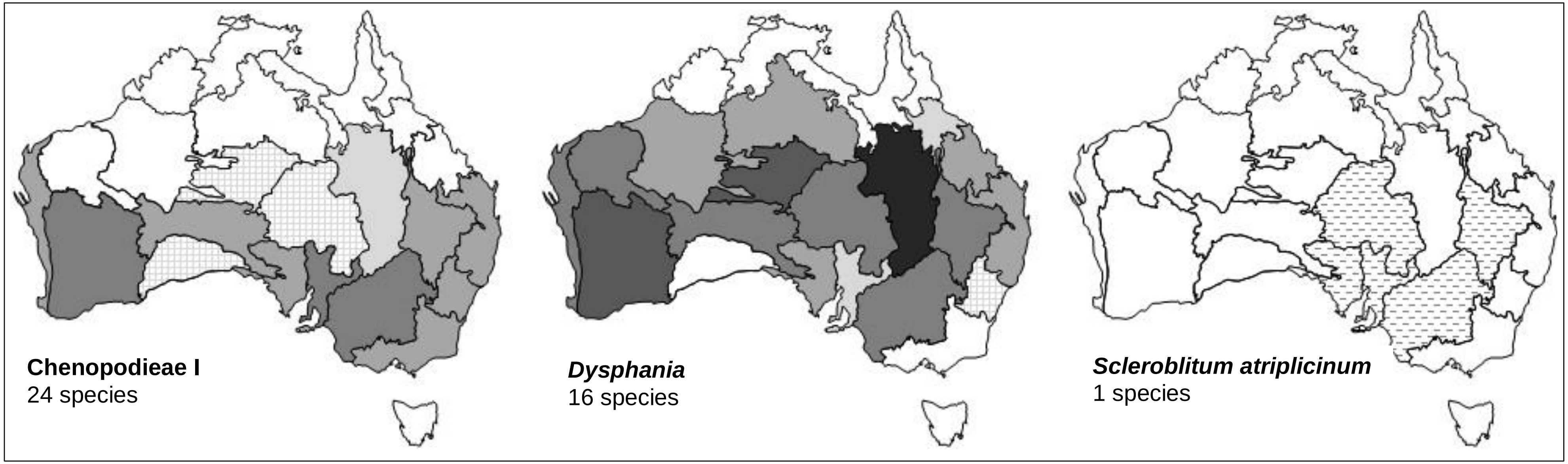
The *Dysphania* clade (16 species) has a range spanning the continent in a broad, central belt (Moreton-New England Upland to Western Coastlands). The northern arid provinces, otherwise scarce with chenopods, are included, but Nullarbor Plain is not. Eleven provinces exceed 56% of clade richness. Central Lowlands Centre with 13 of the 16 species, is the richest species proportion of any clade in a single province.



***Atriplex* Clade 1**
8 species

***Atriplex* Clade 2**
52 species

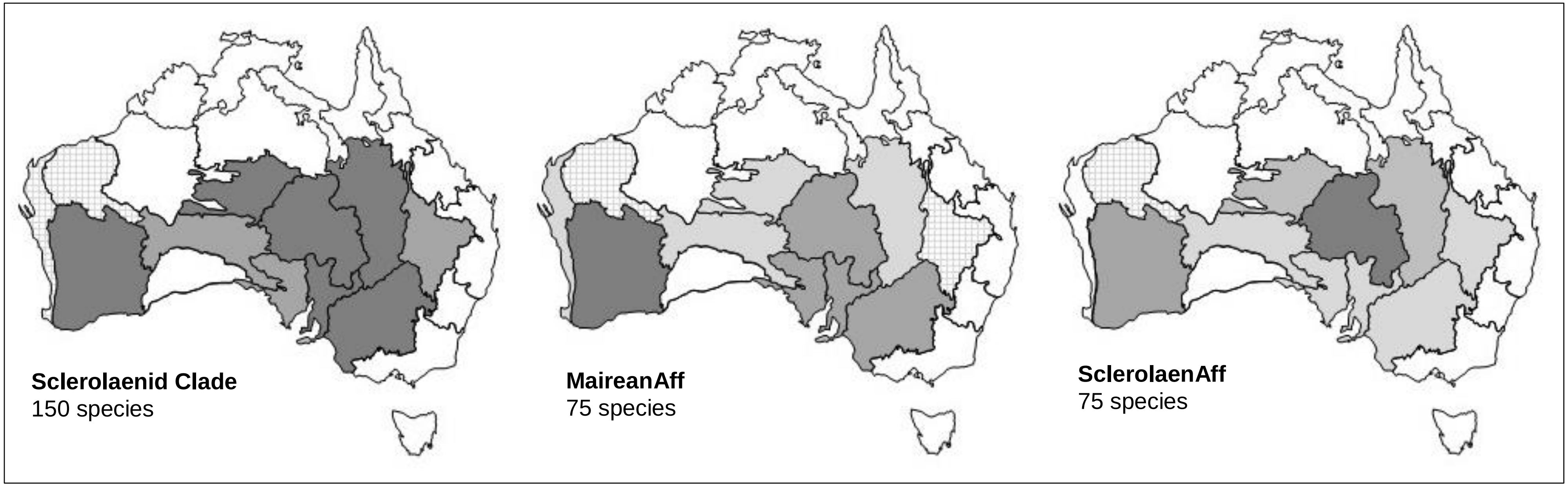
Atriplex australasica
1 species



Chenopodieae I
24 species

Dysphania
16 species

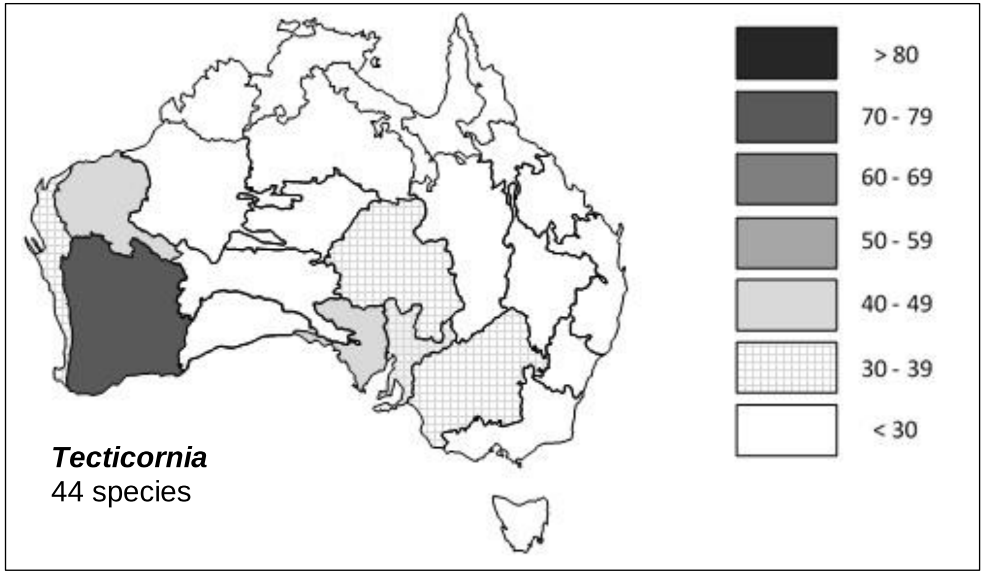
Scleroblitum atriplicinum
1 species



Sclerolaenid Clade
150 species

MaireanAff
75 species

SclerolaenAff
75 species



Tecticornia
44 species

Figure 2.5: Species richness of chenopod clades as percentage of clade richness. *A. australasica* and *S. atriplicinum* monotypic clades show presence only.

Widespread and limited provincial occurrence

The most widespread taxa and immigrant clades are identified in Table 2.3 listing species of the highest provincial frequency. Figure 2.6 shows clade cumulative species frequency through all provinces. The most widespread species in each clade have coastal populations; some are coastal species e.g. *Atriplex cinerea*.

Two species from different clades are exceptionally widespread. *Salsola australis* (*Salsola* clade) is in all 26 provinces. *Enchylaena tomentosa* (Sclerolaenid clade) is absent only from the most northern (North Australian Plateaus) and southern (Tasmanian Uplands). Both species are the only taxa in Great Barrier Reef, the poorest province. The least widespread clades are the oldest *Scleroblitum* (five provinces) and the youngest *Atriplex australasica* (six provinces). Of the rich clades *Atriplex* Clades 1 and 2 have the least widespread species. Each has a single species in 15 provinces at most, compared to the Sclerolaenid (24), Chenopodieae I (20), *Dysphania* (20) and *Tecticornia* (22) clades.

Similar to species-area curves, species richness of richer clades increases with the number of provinces, approaching limits set by the most provincially widespread species in each clade (figure 2.6). For the *Atriplex*, Sclerolaenid, *Dysphania* and Chenopodieae I clades, the approach is a near gradual increase. *Tecticornia* has a stepped approach, with 41 species in 11 provinces at most, and three species spread through 20-22 provinces.

Taxa/Clade	**Shared Taxa**	**Yilgarn Restrict**	**Yilgarn Total**	**Eyre-Murray Restrict**	**Eyre-Murray Total**	**Outside Centres**	**Total Taxa**
Chenopod Species	129	70	199	96	226	7	302
Chenopod Genera	19	2	21	1	20	0	22
Atriplex	20	11	31	26	46	3	61
Clade 1	2	4	6	2	4	0	8
Clade 2	18	7	25	24	42	3	52
A. australasica	0	0	0	1	1	0	1
Chenopodieae I	15	3	18	5	20	1	24
Chenopodium	6	0	6	2	9	1	9
Einadia	1	0	1	3	4	0	4
Rhagodia	8	3	11	0	8	0	11
Dysphania	10	2	12	4	14	0	16
Scleroblitum	0	0	0	1	1	0	1
Salsola	1	0	1	0	1	0	1
Sclerolaenid	63	33	96	54	117	0	150
MaireanAff	32	20	52	23	55	0	75
SclerolaenAff	31	13	44	31	62	0	75
Tecticornia	17	20	37	5	22	2	44
Sarcocornia	2	1	3	0	2	0	3
Suaeda	1	0	2	0	2	1	2

Table 2.3: Species in each immigrant clade with highest provincial frequency, given in brackets after species name. Coastal disposition: ^ Coast obligate; + Coast facultative; # Inland facultative.

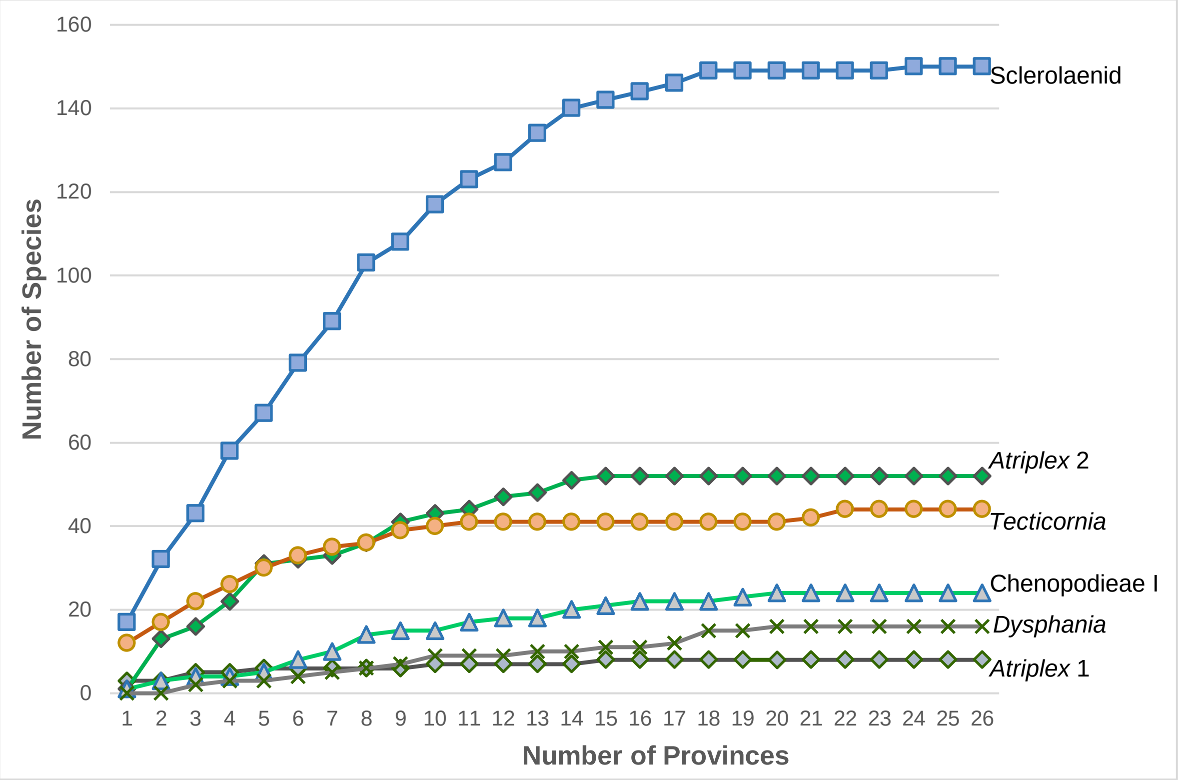


Figure 2.6: Cumulative frequency distribution of rich chenopod clades in Australian Physiographic Provinces.

The Sclerolaenid and *Tecticornia* clades exhibit the strongest endemism. The most species confined to a single province are 17 (Sclerolaenid) and 12 (*Tecticornia*). For two provinces or less it is 32 species (Sclerolaenid), 17 species (*Tecticornia*) and 16 species (*Atriplex* Clade 2). In contrast, *Dysphania* and Chenopodieae I have the fewest species in one province. The least widespread *Dysphania* species is in 3 provinces.

Distribution of chenopod taxa

The Australian distribution of chenopod subfamilies is described and mapped in Appendix XVI. Camphorosmoideae, Chenopodioideae and Salsoloideae occupy much of the continental interior extending into northern subtropical regions. Though also extensive in the arid interior, Salicornioideae is notably less widespread. The predominantly coastal Suaedoideae has inland populations in southwest and southeast Australia.

An odd, common scarcity of all subfamilies occurs in two southern subregions. Figures 2.7 and 2.8 show a common scarcity in the Upper South East of South Australia. The coastal Mediterranean climate is suited to chenopods (Kuhn 1993) which occur in adjoining districts and coast. The southern coastal plain of Western Australia exhibits a similar pattern (see Appendix XVI). Figures 2.7 and 2.8 also show variation in the distribution of clades.

Chenopodieae I and *Dysphania* clades tolerate temperate regions better than *Atriplex* or the Sclerolaenid clades.

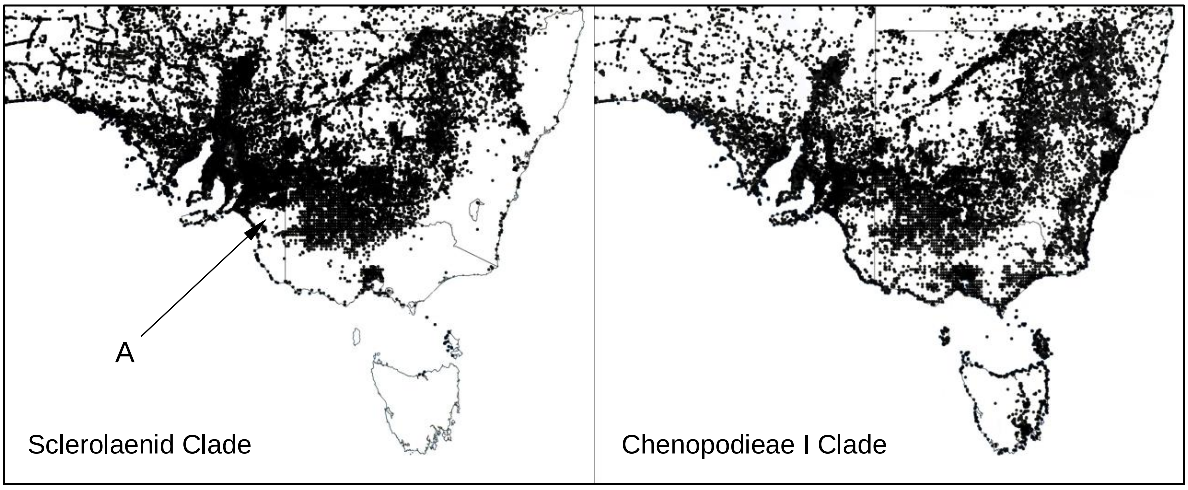


Figure 2.7: Scarcity of taxa in the Upper South-East of South Australia [A]. The Sclerolaenid Clade is also scarcer in uplands of the southern Eastern Highlands and Tasmania, in contrast to the Chenopodieae I clade.

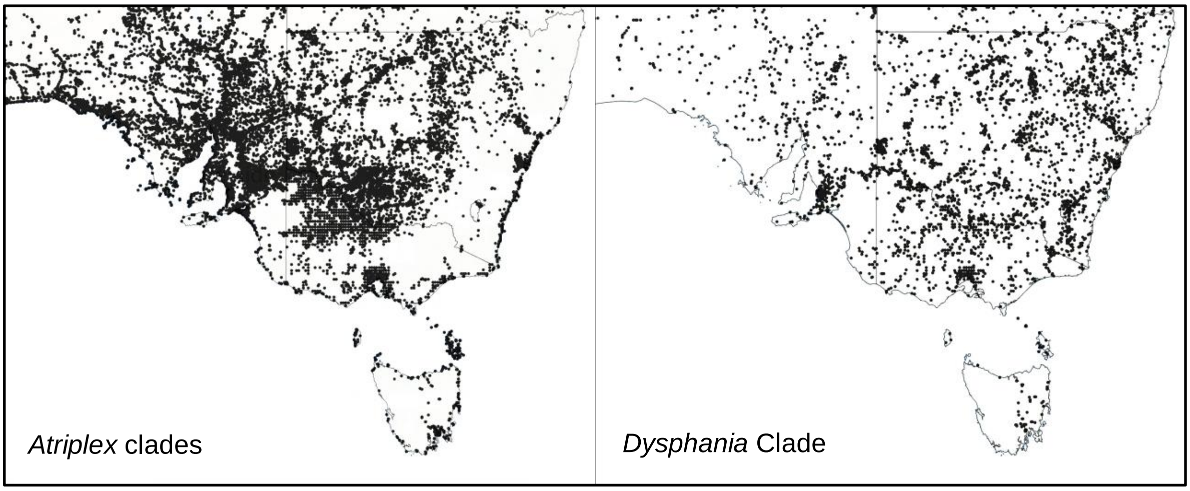
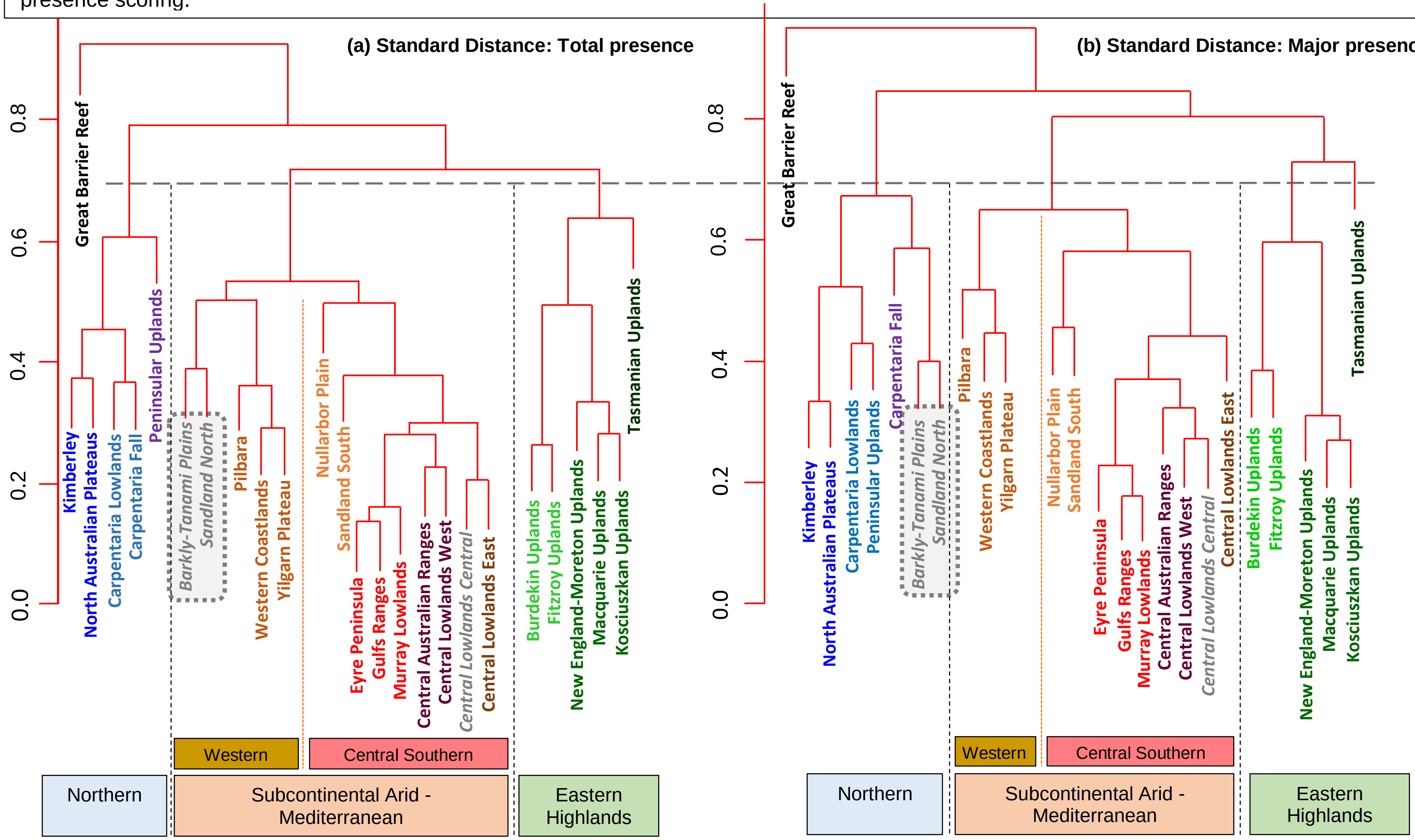


Figure 2.8: The absence of *Atriplex* (all clades) and *Dysphania* from the Upper South East of South Australia. *Atriplex* is also scarcer in the southern Eastern Highlands than *Dysphania* and Chenopodieae I clades.

Provincial assembly of chenopods

Figure 2.9 shows Sorensen dissimilarity of provincial species composition, schematically mapped to provincial richness in figure 2.10. Dissimilarity values are listed in Appendix IX. Topology of dissimilarity trees for Total Presence and Major Presence is broadly similar, but for the position of the northern arid provinces (Sandland North, Barkly-Tanami Plains) and Central Lowlands East province. Three continental groups are geographically recognizable.

Figure 2.9: Sorensen Dissimilarity of provincial chenopod composition. Main groups are defined arbitrarily at dissimilarity value of 0.68 for both Total and Major Presence. Trees are constructed using “hclust” function in R and show how the northern arid provinces change assembly groups with difference in presence scoring.



Northern Tropical Group

Species of the north coast mainly define this group of six provinces. Each province has less than 10% of all chenopod species; only two species are in Great Barrier Reef. Common coastal taxa are *Tecticornia australasica*, *T. halocnemoides*, *T. indica*, *T. pergranulata* and *Suaeda arbusculoides.* Shared inland taxa include continentally widespread species (e.g. *Einadia nutans*, *Dysphania rhadinostachya*, *Enchylaena tomentosa*, *Sclerolaena bicornis*, *S. lanicuspis* and *Salsola australis*) and northern arid species (e.g. *Chenopodium auricomum* and *S. cornishiana*).

Outlier presence significantly influences topology. The northern arid provinces (Sandland North, Barkly-Tanami Plains) are part of the Northern Tropical Group if outlier populations are ignored in provincial presence. Including outlier populations shifts the northern arid provinces to a different assembly group and more remotely places Peninsular Uplands in the Northern Tropical Group. A western and eastern division relates mainly to terrestrial taxa of minor presence. The eastern species are absent in the west and including the exceptionally restricted *A. humilis* along with *S. divaricata, S. muricata* and *S. tricuspis,* which are widespread in the Eyre-Murray Centre.

Comparability of dissimilarity values between provinces of the group, to provinces external it, indicate terrestrial species-sharing patterns with the east. Excluding the Great Barrier Reef, provincial dissimilarity values within the group are from 0.37143 to 0.64706 (Total Presence – Appendix IX). Comparable provincial dissimilarity occurs with Burdekin Uplands (all provinces: 0.4754-0.5926) and Fitzroy Uplands (all but Kimberley: 0.5676-0.6471). Three provinces show some affinity with Barkly-Tanami Plains. The affinity of Peninsular Uplands with Burdekin and Fitzroy Uplands is with three species not found in any other Northern Group province (*Einadia trigonos*, *Dysphania carinata* and *D. cristata*).

Eastern Highlands Group

The Eastern Highlands Group of six provinces has 10%-19% of all chenopod species. Provincial grouping largely arises from shared species of Chenopodieae I and *Dysphania* clades (refer figure 2.5) and coastal Suaedoideae and Salicornioideae. All four *Einadia* species are included, with 3 having species ranges predominantly restricted to the highlands.

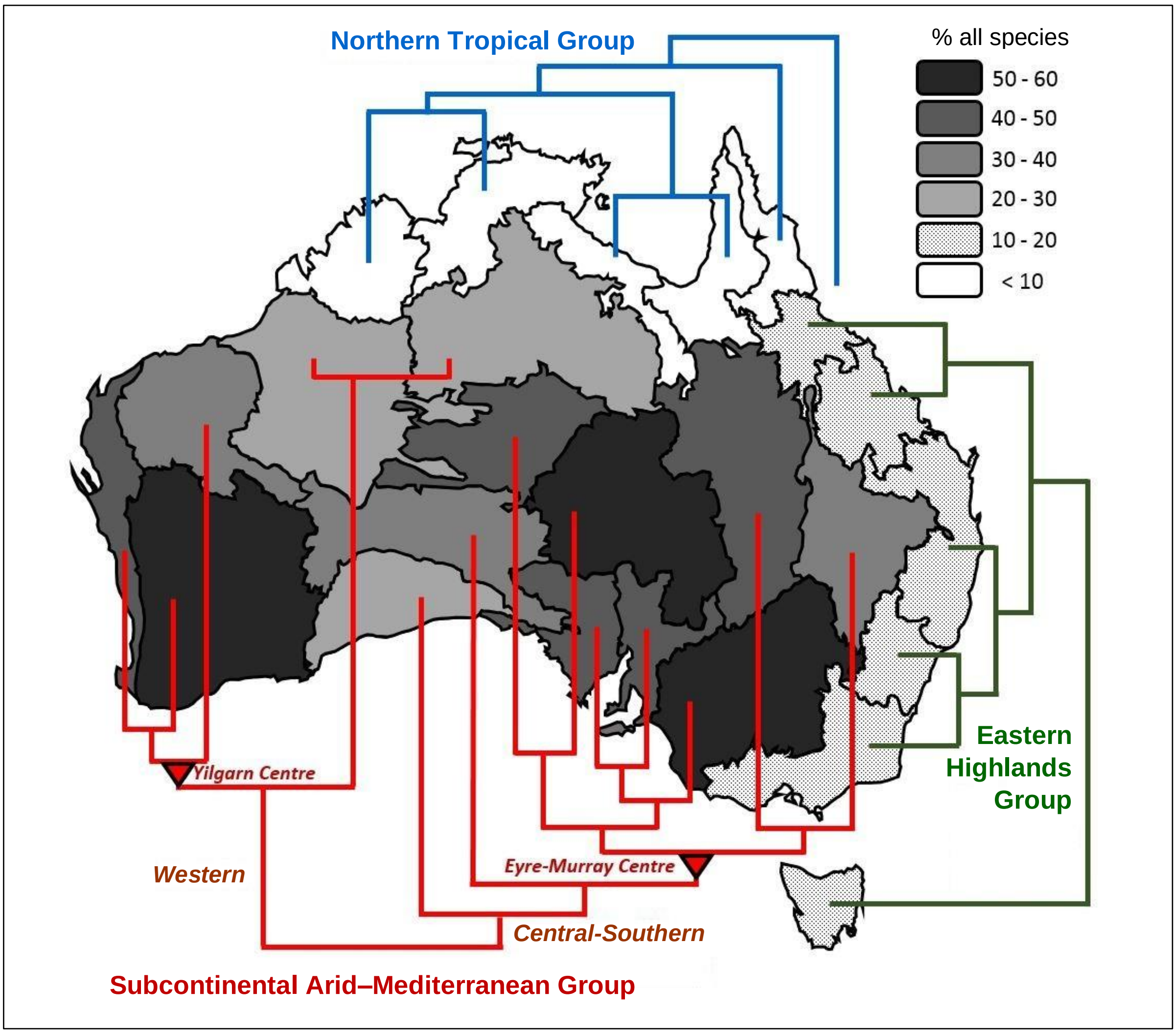


Figure 2.10: Schematic Sorensen Dissimilarity of provinces for Total Presence. Inverted triangles at nodes indicate Yilgarn and Eyre-Murray Centres of Diversity.

Three provincial subgroups are climatically recognizable: subtropical Burdekin and Fitzroy Uplands, mainland temperate New England-Moreton, Macquarie and Kosciuszkan Uplands and southern, temperate Tasmanian Uplands. The composition of coastal and inland species distinguishes subtropical and temperate subgroups. Four southern coastal *Atriplex* spp. (from 3 *Atriplex* clades) are absent in the subtropical north. The Sclerolaenid clade and *Salsola* are largely absent from southern regions. Inland species of *Atriplex* Clade 2 also differentiate north and south – a subtropical suite of *A. muelleri* and *A. lindleyi* contrasts with a temperate one of *A. suberecta*, *A. spinibractea* and *A. pseudocampanulata*.

The mainland subgroups significantly associate with provinces of the Subcontinental group to their west, particularly the immediate neighbours. Excluding Tasmanian Uplands, the group's provincial dissimilarity values are from 0.26316 to 0.62367 (Total Presence). Fitzroy Uplands has comparable dissimilarity to 6 provinces, having strong affinity with Central Lowlands East

(SD 0.4438), Central Lowlands Central (SD 0.5183) and Barkly-Tanami Plain (SD 0.5410). New England-Moreton and Kosciuskan Uplands have strong affinity with Central Lowlands East and Murray Lowlands (SD 0.4620-0.5758). Provincial similarities with the Northern Tropical Group are described above.

Subcontinental Arid–Mediterranean Group

The subcontinental group has 14 provinces, 97% of Australia's chenopod species and the two Centres of Diversity. Western and central-southern subgroups containing the centres share 129 species, and differentiate with 166 species restricted to either centre (Table 2.2). Two clusters in the western subgroup are the Yilgarn Centre (Pilbara, Western Coastlands, Yilgarn Plateau) and the northern arid provinces (Sandland North, Barkly-Tanami Plains). The central-southern subgroup has the seven provinces of the Eyre-Murray Centre with Sandland South and Nullarbor Plain. Eyre-Murray comprises a southern coastal cluster (Eyre Peninsula, Gulfs Ranges, Murray Lowlands) allied to a central-west inland cluster (Central Lowlands West, Central Australian Ranges) and slightly more distant central-east inland cluster (Central Lowlands Central & East). Nullarbor Plain is more distant than Sandland South to provinces of the Eyre-Murray Centre.

Assembly topology changes with exclusion of outlier populations, notably affecting three provinces. The western subgroup then comprises only the Yilgarn Centre; the northern arid provinces attach to the Northern Tropical Group. In the central-southern subgroup, Central Lowlands Central more closely aligns with provinces to the west, and Sandland South and Nullarbor Plain are closely paired.

The Subcontinental Group has closest relationship to the Eastern Highlands Group. As mentioned above, both northern and southern parts of the Eyre Murray Centre have an affinity with those Highland provinces immediately to the east. Central Lowlands East has an affinity with most mainland provinces of the Eastern Highlands.

Coastal disposition and taxon element patterns

Coast-Inland patterns of sister taxa within immigrant clades

Coastal disposition is readily classified from a combination of sources, with classes for all species listed in Appendix VI. Classification issues and their resolution are in Appendix II.

Frequency of disposition class along a coast-inland continuum is shown in Table 2.4. For chenopods in total, frequency generally increases with disposition inland. Six clades have a pattern of increase, and five clades are relatively static along the continuum. Of all Australian chenopod species, more than 80% are removed from coastal influence, only 8.3% are notably coastal and less than 2% are exclusively coastal.

Subfamily	**Immigrant Clade**	**No of Species**	**Coast Oblig**	**Coast Facult**	**Inland Facult**	**Inland Oblig**	**Estimated Arrival (Ma)**	**Group**
Chenopodioideae	*Scleroblitum*	1	0	0	0	1	42.2-26	Very Old
Camphorosmoideae	Sclerolaenid	150	0	3	8	139	16.4-10.3	Old
Chenopodioideae	*Dysphania*	16	0	0	3	13	16.1-9.9	Old
Salicornioideae	*Tecticornia*	44	1	5	5	33	10.9-4.8	Old
Chenopodioideae	*Atriplex* 1	8	1	1	1	5	9.8-7.8	Old
Chenopodioideae	*Atriplex* 2	52	3	1	7	41	6.3-4.8	Old
Chenopodioideae	Chenopodieae I	24	0	4	8	12	4.2-2.9	Old
Salicornioideae	*Sarcocornia*	3	0	2	0	1	4.0-1.8	Old
Suaedoideae	*Suaeda*	2	1	1	0	0	Not known	Young
Chenopodioideae	*A. australasica*	1	0	1	0	0	2.4-0.1	Young
Salsoloideae	*Salsola*	1	0	0	1	0	Not known	Young
	TOTAL		6	18	33	246		

Table 2.4: Frequency of chenopod species in coast disposition classes.

Immigrant clades loosely fall into three groups, based on age, species range and ratio of Coast species (obligate + facultative):Inland species (obligate + facultative) [**CI**]:

(1) **Very Old Group**: the monotypic, Oligocene *Scleroblitum* clade lacking coastal taxa has no sister taxa pattern; **CI** is 0:1. The clade range is six provinces of drier, south-eastern Australia.

(2) **Old Group**: The rich clades of Miocene-Pliocene age have the most coastal species. **CI** ratios are variably Few:Many, being 2:6 [*Atriplex* Clade 1], 6:38 [*Tecticornia*] and 3:147 [Sclerolaenid Clade]. Sister taxa patterns include different coastal and inland species and inland populations of coastal taxa. Species range size varies from very small to subcontinental, occurring on and remote from coastlines. The largest proportion of coastal taxa is in Chenopodieae I (16.7% of clade species) and with 50% of clade species somewhere on a coast. *Dysphania* has no species primarily regarded as coastal. *Sarcocornia* is anomalous, with age comparable to the Chenopodieae I clade and few species, but includes the Inland obligate *S. globosa* of south-west Western Australia.

(3) **Young Group**: These are clades of few species, including Pleistocene *A. australasica* along with the presumed young *Suaeda* and *Salsola* clades. Sister taxa patterns notably are

coastal and inland populations of the same species; Coast facultative types are prominent and coastal species dominate (**CI** ratios respectively 1:0, 2:0 and 0:1). For *A. australasica* and *Suaeda*, inland ranges are nearer the southern coastline, and of extent smaller than clades of the Old and Very Old groups.

Coast facultative types are more prominent than Coast obligates, outnumbering them by more than 3:1. Coast facultative types are in eight of eleven clades. Coast obligates are in four clades and unique to none. Coastal ranges of Coast facultative species are larger than Coast obligate species. The oldest clades (*Scleroblitum*, Sclerolaenid, *Dysphania*) have no Coast obligates. The oldest clades with Coast obligates are *Tecticornia* (*T. australasica*), which also has five Coast facultative species, and *Atriplex* Clade 1 (*A. isatidea*). The Coast obligate *Suaeda arbusculoides* is from a clade that is dominantly coastal in distribution.

Scleroblitum, *Dysphania* and *Salsola* apparently lack coastal species. *Scleroblitum* is described earlier. Apparent paucity in *Salsola* is an artefact of classification where inland range overwhelms coastal range. Three *Dysphania* species similarly have small coastal range within a large species ranges, and on different coasts. *Dysphania pumilio* is on the eastern, southern and western coasts, *D. plantaginella* on the west coast and *D. littoralis* on the north-east coast. *Dysphania* and *Scleroblitum* are also similar in life form and of low diversity given clade age.

With six immigrant clades, Chenopodioideae is richest in coastal species (11 species/10.8%). The greatest proportion of coastal taxa is in Salicornioideae (8 species/17%). Camphorosmoideae has three coastal species (2%). Chenopodioideae has four of the six Coast obligate species; all are *Atriplex* – *A. isatidea* (Clade 1) and *A. billardierei*, *A. hypoleuca* and *A. humilis* (Clade 2).

The endemic genus *Rhagodia* dominates the coastal taxa of the Chenopodieae I clade. Of cosmopolitan *Chenopodium*, only the annual *C. glaucum* is considered coastal. Inland facultative species comprise taxa from all three genera of the clade, including three *Rhagodia* spp., of which *R. preissii* ssp. *obovata* curiously is a Coast facultative type.

Distribution of coastal types

The linear species ranges of Coast obligate types are mostly of provincial to subcontinental extent, collectively widespread and occur where chenopods are scarce in the immediate hinterland. The north coast *Tecticornia australasica* and *Suaeda arbusculoides* lie between the Pilbara and Gold Coast. *Atriplex billardierei* is in Bass Strait with *A. hypoleuca* in south-west Western Australia. Exceptions are the northern range of *A. isatidea* with a chenopod shrubland hinterland and the very small range of *A. humilis* in the Gulf of Carpentaria.

Coast facultative species have large species ranges, mostly on the west and south coasts. Of all 18 species, twelve have coastal ranges of subcontinental size or larger and six are of provincial scale. Fourteen species are on the west coast between Carnarvon and Cape Leeuwin, with five in a similar span of latitude on the east coast. *Tecticornia indica* and *T. halocnemoides* are widespread inland and the only taxa found on all coasts. *Neobassia astrocarpa* and *T. auriculata* are on the northwest coast, occurring with few other chenopod species. In species poor clades of *Atriplex* Clade 1, *A. australasica*, *Sarcocornia* and *Suaeda*, Coast facultative and Coast obligate types are among the most widespread taxa.

Some Coast facultative species have Coast obligate subspecies that are variably sympatric with Coast obligate species. The range of *Rhagodia baccata* ssp. *dioica* lies within the northern extent of *Atriplex isatidea*. Both are coastal dune species. In *Atriplex* Clade 2 that of *A. billardierei* is within the range of *A. paludosa* ssp. *paludosa*, but are from different habitats.

Most Coast facultative species have inland populations contiguous with their coastal range. A few are notably disjunct. Of contiguous distributions, populations most distant from a shoreline variably extend from 10 km (e.g. *Rhagodia baccata*), to 150 km (e.g. *R. candolleana*), to beyond 300 km (e.g. *A. cinerea*, *T. indica*). The disjunct *Tecticornia auriculata* in the Fortescue Marshes is 200 km from coastal and near-coast populations of north-west Australia. Three disjunct populations of *T. flabelliformis* are in coastal South Australia, inland Western Australia and north-western Victoria.

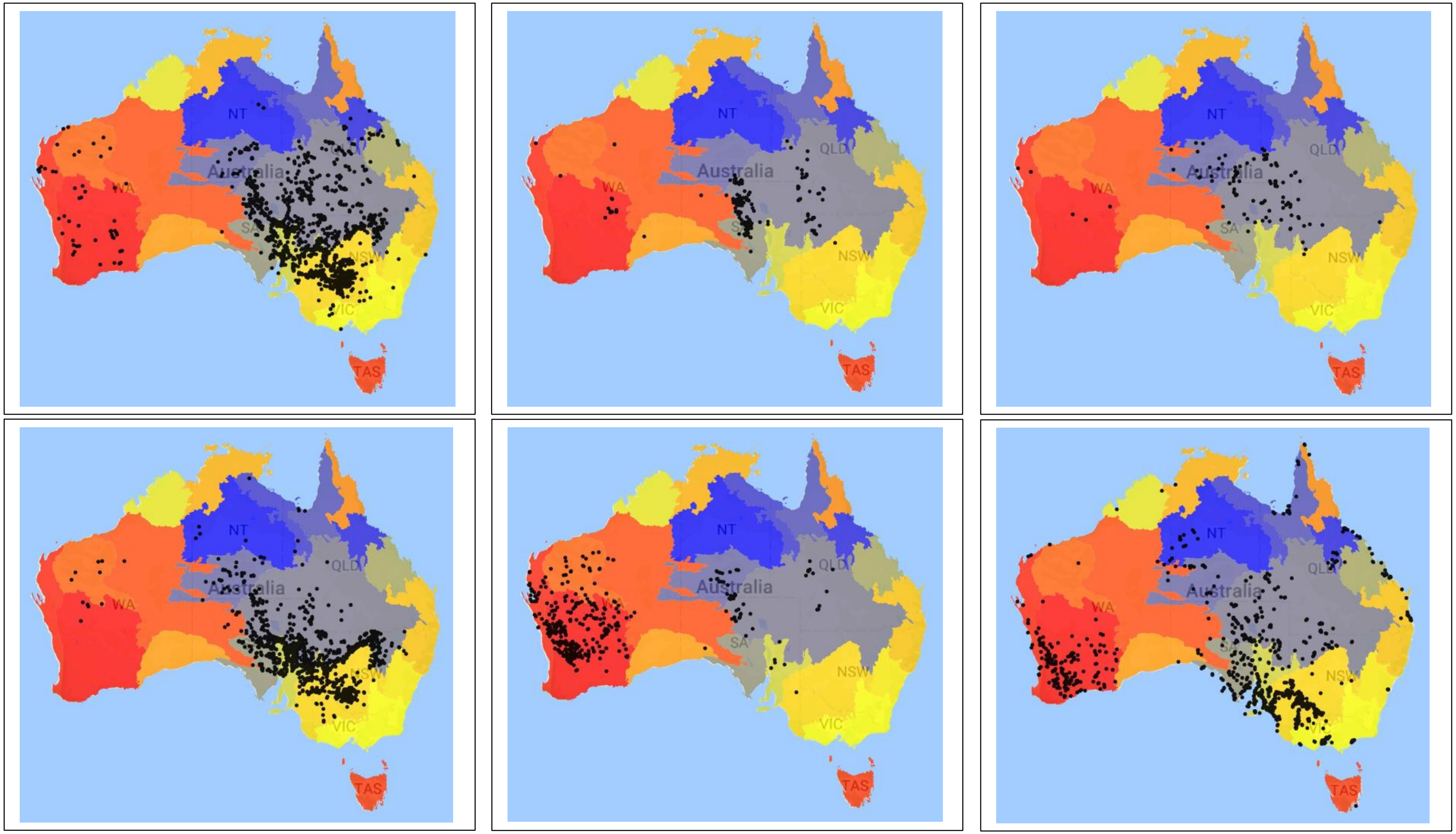


Figure 2.11: Disjunct populations in interior arid regions of *Atriplex lindleyi* (top left), *Atriplex quinii* (top centre), *Dysphania platycarpa* (top right), *Sclerolaena divaricata* (bottom left), *Maireana carnosa* (bottom centre) and *Tecticornia pergranulata* (bottom right) within Australian Physiographic Provinces.

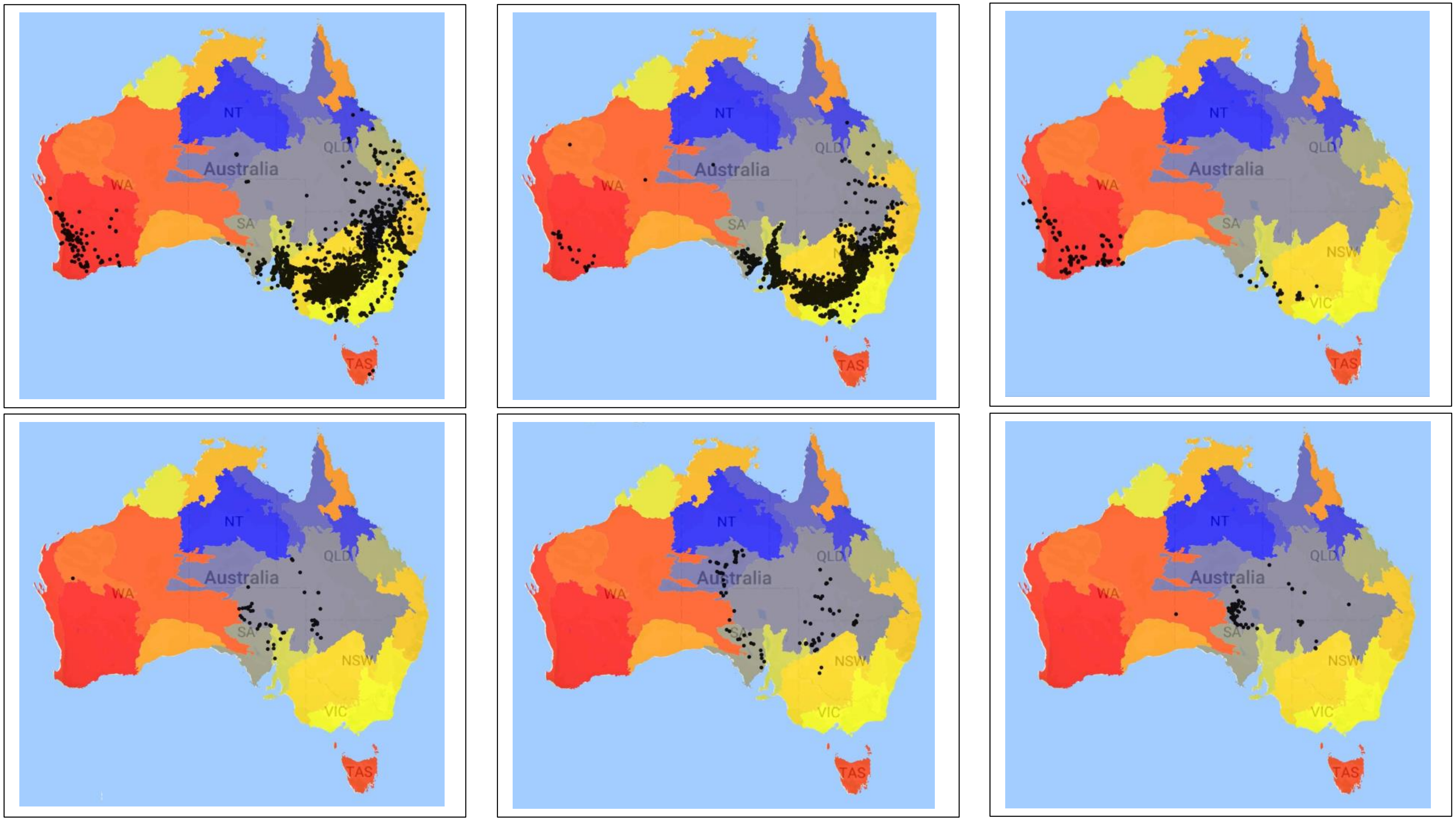
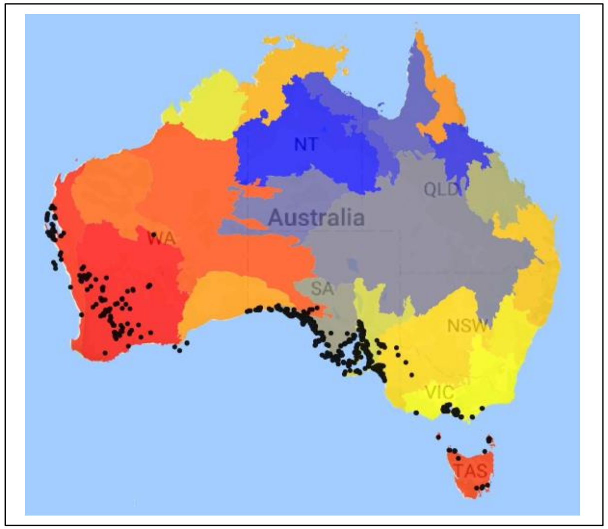
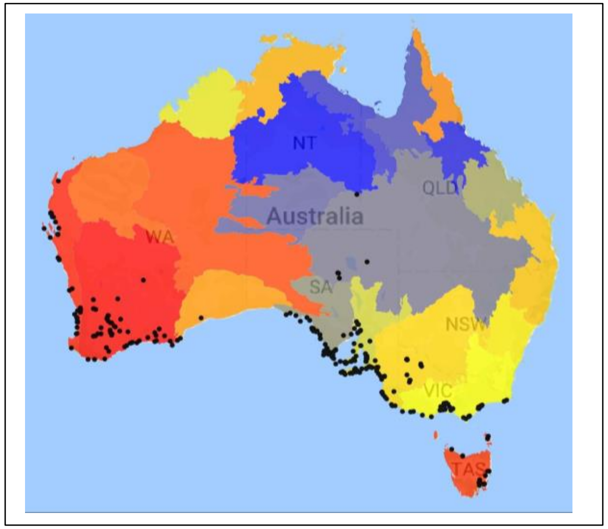
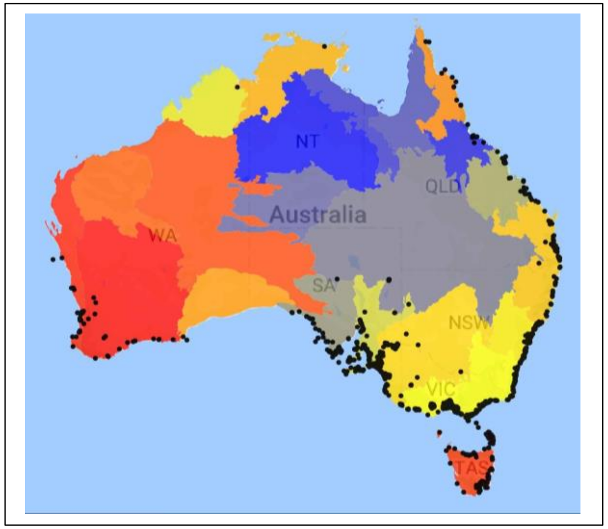


Figure 2.12: Disjunct species populations in southern temperate regions at top: *Atriplex semibaccata* (left), *Maireana enchylaenoides* (centre) and *Tecticornia syncarpa* (right). In Eyre-Murray centre at bottom *Atriplex macropterocarpa* (left), *Maireana schistocarpa* (centre) and *Sclerolaena blackiana* (right).







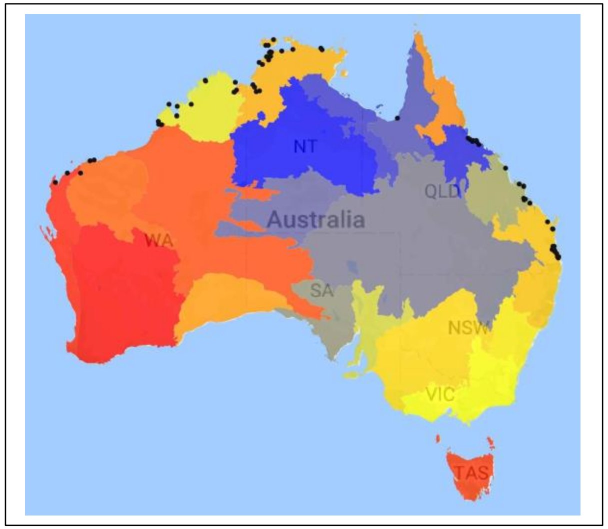
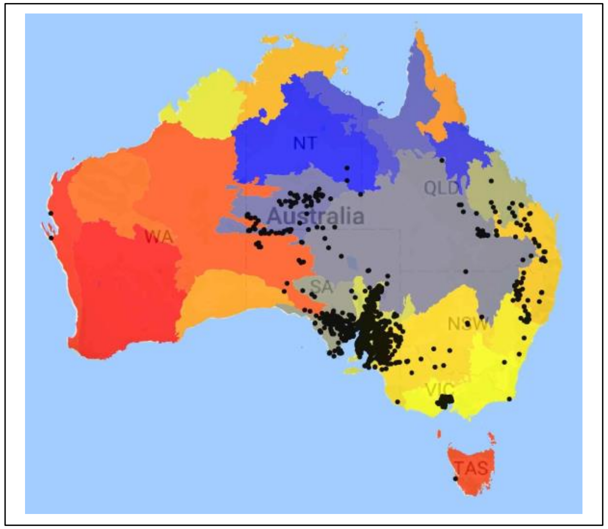


Figure 2.13: Disjunct species populations on the southern coast, at top: *Atriplex paludosa* (left), *Sarcocornia blackiana* (centre) and *Suaeda australis* (right). *Suaeda arbusculoides* shows disjunct populations on the northern coast (bottom left). *Rhagodia parabolica* (bottom right) is peripheral to the Lake Eyre Basin.



The coast and inland ranges of Inland facultative species vary in size. Coastal ranges commonly adjoin arid and semi-arid areas of Shark Bay, the Great Australian Bight and Gulfs of South Australia. They include the most widespread and common species e.g. *Enchylaena tomentosa*, *Atriplex vesicaria*, *Einadia nutans, Salsola australis* and *Sclerolaena diacantha*.

Disjunct Species

Many species from eight immigrant clades exhibit similar patterns of disjunct populations. Disjunct genera are unlikely. Currently they could only be in Chenopodieae I or Sclerolaenid clades, but their genera have widespread, parapatric ranges. Table 2.5 lists taxa from three latitude-climate zones with strongly disjunct western and eastern populations. Some species occur across two zones.

Figures 2.11-2.13 show the species ranges. For each species, the ranges of western populations markedly overlap, as do those of eastern populations. Range gaps coincide with all or part of Sandland South, Sandland North and Nullarbor Plain provinces that also separates the Yilgarn and Eyre-Murray Centres. The Great Australian Bight divides temperate mesic and coastline taxa.

	Atriplex	**MaireanAff**	**SclerolaenAff**	**Tecticornia**	**Other**
Arid					
	A. lindleyi 2 *A. nummularia* 1 *A. quadrivalvata* 2 *A. quinii* 2 *A. stipitata* 2	*M. aphylla* *M. appressa* *M. carnosa* *M. lanosa* *M. pyramidata* *M. suaedifolia* *Eremophea spinosa*	*S. articulata* *S. costata* *S. cuneata* *S. deserticola* *S. divaricata* *S. glabra* *S. minuta* *Osteocarpum acropterum*	*T. flabelliformis* *T. lylei* *T. moniliformis* *T. pergranulata* *T. tenuis* *T. triandra* *T. verrucosa*	*Chenopodium desertorum* *Dysphania cristata* *D. platycarpa* *D. sphaerosperma*
Temperate					
	A. semibaccata 2 *A. suberecta* 2	*M. brevifolia* *M. enchylaenoides*		*T. syncarpa*	*Dysphania pumilio*
Coast					
	A. paludosa 2	*M. oppositifolia*		*T. arbuscula* *T. lepidosperma*	*Chenopodium glaucum* *Sarcocornia blackiana* *S. quinqueflora* *Suaeda australis*

Table 2.5: Disjunct species populations of subcontinental distribution across climatic zones in Yilgarn and Eyre-Murray centres of chenopod diversity. Numbers after *Atriplex* species refer to clade of origin.

Disjunct species populations within the Eyre-Murray Centre are of taxa from different clades (Figure 2.13, Table 2.6). Western populations lie in the western Lake Eyre Basin (Central Australian Ranges, Central Lowland West and Eyre Peninsula). Eastern ones are in the central Lake Eyre and Murray Basins (Central Lowland Centre, Murray Lowland). Eyre-

Murray populations of the continentally disjunct *Maireana carnosa* and *Atriplex quinii* are also divided, separating their entire species ranges each into three main populations. Eyre-Murray separations also include *Rhagodia parabolica* in uplands bordering the Interior Lowlands and the unusual ring distribution of *Maireana campanulata*.

Atriplex	**Maireana**	**Sclerolaena**	**Other**
A. macroptercarpa *A. nessorhina* *A. quinii* + *A. sturtii*	*M. carnosa* + *M. schistocarpa* *M. spongiocarpa*	*S. birchii* *S. blackiana* *S. parallelicuspis*	*Dissocarpus latifolius*

Table 2.6: Terrestrial species of disjunct populations in Eyre-Murray centre of chenopod diversity (+ also subcontinental disjunct). All *Atriplex* species are from Clade 2.

Subspecies of continentally disjunct *Atriplex* species are peculiar to a centre of diversity, including the coastal *Atriplex paludosa*. The near-allopatric *A*. *paludosa* ssp. *moquiniana* and *A*. *paludosa* ssp. *baudinii* are unique to the Yilgarn Centre. *Atriplex paludosa* ssp. *paludosa* is restricted to the Eyre-Murray Centre. Of inland species, the centres share three of four subspecies of *Atriplex lindleyi* and one of *A*. *quadrivalvata*. *Atriplex lindleyi* ssp. *inflata* and *A*. *quadrivalvata* ssp. *quadrivalvata* are widespread. The Eyre-Murray taxa *Atriplex lindleyi* ssp. *lindleyi* and *A*. *lindleyi* ssp. *conduplicata* are scarce in the Yilgarn Centre, while *A. lindleyi* ssp. *quadripartita* and *A*. *quadrivalvata* ssp. *sessiliflora* are only in the Eyre-Murray Centre.

More species with disjunct populations occur at provincial and smaller scale. The western plains of the Murray Lowlands province separates South Australian and Victorian stands of *Maireana decalvans*, *M. rohrlachii* and *M. excavata* in a near congruent pattern. Disjunct populations occur within provinces e.g. *Maireana cheelii* in Murray Lowlands and several *Tecticornia* spp. in Yilgarn Plateau. Coastal *Suaeda arbusculoides* extends from the Pilbara to Queensland but is absent from Torres Strait.

DISCUSSION

General distribution of Australian chenopods

Most Australian chenopod taxa are inland species. Some are coastal or from the drier, mesic regions. No clade is uniquely arid. A broad sympatry of clade distribution in species rich provinces is due to extensive suitable inland habitat, especially landscapes with saline elements, indicating ecological factors in range extension and diversification (see Chapter 3 p129ff). These analyses provide definitive findings at continental scale, but they give strong indication of evolutionary influences at smaller scale and within each clade.

Chenopod species are distributed far more widely than chenopod shrubland. The range of all chenopods is much larger than indicated by Burbidge (1960), Leigh (1972, 1981, 1994), Beadle (1981b) and Graetz and Wilson (1984) due to the ubiquity of coastal taxa, species ranges of subcontinental scale and presence in subtropical regions.

Chenopod scarcity is easier to note, and identifies climatic and edaphic barriers to occupation. Low diversity along the northern and eastern coasts contrasts with a notable presence in coastal salt marsh systems. At finer scale, common scarcity in the western Murray Lowlands and southern Western Coastlands, on sandy plains of Mediterranean and coastal climate, contrasts with chenopods on nearby heavier soils, saline waterways and coastlines. Glycophytic species outcompete halophytes (Waisel 1972; Flowers *et al*. 2010; Taiz and Zeigler 2010) on these sandy soils.

Provincial richness and assembly

Centres of diversity

A subcontinental expanse of 14 desert provinces holds 97% of chenopod species and includes the Yilgarn and Eyre-Murray Centres of Diversity, linked through the Great Victoria Desert. The centres have mutual and separate elements in their development. Outside this expanse, chenopods are prominently coastal.

Mutual development is evident in the taxa shared through range expansions of widespread species. The centres share 43% of all chenopod taxa, from nine immigrant clades which are mostly inland species with a few southern coast species. The main linking axis is Sandland South Province, which has no modern coast, not Nullarbor Plain. The shared taxa mostly have continuous species ranges, but species from six clades have disjunct species populations with gaps in and adjacent to Sandland South. Numerous shared genera suggests adaptation has an associated capacity for expanding range.

Separate elements are the species restricted to each centre, which identify supra-provincial areas of greater diversification within clades. The Yilgarn Centre has 23.2% of all chenopod species including greater proportion of restricted species from *Atriplex* Clade 1 and *Tecticornia* clades. The Eyre-Murray Centre with 31.8% species restricted to it, is richer in restricted species from *Atriplex* Clade 2, and from the SclerolaenAff subgroup.

The geography of restricted taxa further distinguishes the centres. Being half the size of the Eyre-Murray Centre, speciation is more concentrated in the Yilgarn Centre, possibly due to several factors. The Yilgarn Centre has a greater length of coastline, with four restricted coastal species that are from different clades, arriving in the Pliocene or earlier (*Tecticornia auriculata*, *Rhagodia latifolia*, *Atriplex isatidea* and *A. hypoleuca*). Except for the Pleistocene *A. australasica*, all Eyre-Murray coastal species are shared. Aridity developed earlier in the Yilgarn Centre (Hill 1994; Martin 2006) giving chenopods a longer occupancy period. The two immigrant clades restricted to the Eyre-Murray Centre, are the oldest (*Scleroblitum*) and youngest (*A. australasica*) with implications for landfall (see below).

Numerous migrations have occurred and at different times. Each rich clade must expand initially, and lineages with widespread shared species also indicate distinct expansions. Generic distribution shows several migrations between the centres in the Sclerolaenid clade. *Maireana*, *Sclerolaena*, *Eremophea*, *Dissocarpus, Malacocera* and *Osteocarpum* are in both Centres, though not uniformly. Asymmetry of *Eremophea* and *Malacocera* presence suggests either a recent migration of one species or radiation after migration. Three subcontinental migrations occurred in Chenopodieae I if generic status is verified.

Landscapes in the centres of diversity

Landscapes of the Yilgarn and Eyre-Murray Centres are similar (Taylor 1994; Pain *et al.* 2011) but not in the same proportion. Both are extensive, subdued landscapes with climatic gradients of Coast-Mediterranean-Arid. The Eyre-Murray Centre is depositional with dune fields, gibber plains, alluvial plains, floodplains and terminal salt-lakes in Cenozoic sedimentary Basins; there are some shield plains and folded uplands. The Yilgarn Centre has an erosional landscape of a sand-covered igneous and metamorphic platform, with arid ranges, chains of salt lakes on linear alluvial plains and some gibber plains. Saline and calcareous soils are common to both centres, but broad plains of heavy soils are much more extensive in the Eyre-Murray than in the Yilgarn (McKenzie *et al.* 2004).

The length of coast-arid climatic gradients differ in each Centre. The arid zone reaches the Yilgarn Centre's north coast. In the Eyre-Murray Centre, Mediterranean climates separate coastal and arid areas. As already noted, coastlines of the Yilgarn Centre are much longer than in the Eyre-Murray.

Chenopod species richness of the Yilgarn Centre is consistent with southwest Australia being a global centre of plant species biodiversity (Gole 2006; Lambers 2014) though reasons are unclear. Characteristic sandy soils of subdued upland and sandplain in the Yilgarn Plateau (Tille 2006) support much of this plant biodiversity. Central Lowlands West and Murray Lowlands also have sandplains and dune fields. A common presence of sandy habitats accords with Burbidge's notion of inland occupation facilitated by habitat sharing. Chenopod diversity here may mainly relate to cycles of drainage cessation and resumption as suggested by Shepherd *et al.* (2004).

Assembly groups, expansions and barriers

Chenopod evolution is mainly tied to the Subcontinental Group, but the Northern Tropical and Eastern Highlands groups are not of evolutionary insignificance. Species poor regions peripheral to a principal range also indicate past barriers. Pre-Miocene vegetation grew in cool to warm, mesic climates and in which many taxa still survive (Hill 1994; Crisp *et al.* 1999; Martin 2006). Under increasingly dry conditions chenopods invaded the realm of the pre-Miocene floras as barriers moved north and east.

Common boundaries of the groups comprise range limits of numerous taxa, identifying significant barriers. Abrupt boundaries where species range limits coincide are strong barriers. The most strongly evident is at the southern Eastern Highlands boundary with the south-eastern Subcontinental Group. Where species limits do not strongly coincide, boundaries are diffuse, as with the Subcontinental group with the Northern Tropical group and northern Eastern Highlands group.

How barriers function is difficult to specify (Gaston 2003). Understanding limits to species expansion, at the least, includes abiotic and biotic factors to further spread and variation in population dynamics near range edges, but they likely operated similarly in the past as they do now. Current boundaries suggest cool, mesic uplands are a more formidable barrier than subtropical regions. Chenopod taxa of the northern and eastern groups also show how coastlines allow skirting of regions that otherwise are strong barriers of unsuitable habitat.

Assembly patterns of the Subcontinental, Eastern and Northern groups broadly accord with saltmarsh biogeography of Bridgewater and Cresswell (2003) and Saintilan (2009b, 2009a). See Appendix XI. Variation arises with the saltmarsh studies including taxa that are not chenopods and excluding chenopods not found in saltmarsh. Broad accord and adoption of chenopod taxa for floristic nomenclature emphasises importance of chenopod taxa in saltmarsh assembly and a continuity of saltmarsh systems from coast to inland. The studies also differentiate coastal and inland taxa in chenopod rich regions.

For Bridgewater and Cresswell (2003) the origins of saltmarsh distribution lie in species shared among saltmarsh groups. Inland halophytic vegetation has strongest links with southern and western coasts, implying the beginnings of inland colonisation. Furthermore, a prominence of ‘generalist’ types (Coast facultative) suggests ongoing colonisation, with climate change at coastal fringes inducing inland species to move to the coast.

Saintilan (2009a, 2009b) presents a cluster analysis of biogeographic regions from a larger pool of marsh taxa. The main northern and southern clusters parallel the Northern Tropical and Subcontinental groups, though differing in extent. Northern limits of the chenopod Centres are about 20 ^{o} S latitude. The northern saltmarsh cluster extends south to 23 ^{o} S latitude (Saintilan 2009a), being the southern limits of north coast taxa that are not chenopods (e.g. *Portulaca bicolor*, *Fimbristylis ferruginea*). The east-west span of the main southern cluster accords with the combined Yilgarn and Eyre-Murray Centres, with sub-clusters reflecting separation of the centres.

Subcontinental Arid-Mediterranean Group

Major chenopod range expansions and diversification give rise to this group. Inland taxa dominate assembly patterns, defining the Yilgarn and Eyre-Murray centres. The coastal taxa are the most diverse in Australia. Relationships of shared and restricted species in each clade are key to a detailed history of chenopods.

Saltmarsh phytogeography (Bridgewater and Cresswell 2003) has parallel relationships of coast and inland taxa and assembly of coastal taxa. The strictly coastal *Tecticornia arbuscula-Juncus kraussii* Group spans the southern coast from west to east, including Tasmania and reflects the shared coastal taxa of the two Centres. Two subgroups *Tecticornia halocnemoides-Limonium bivernosum* and *Tecticornia halocnemoides-Rhagodia baccata*, respectively characterize coastal regions of the Eyre-Murray and Yilgarn Centres. Inland areas of the Subcontinental assembly group belong to two other saltmarsh groups, largely reflecting the non-shared taxa, as well as coast to inland transitions. The *Tecticornia doleiformis-T*. *leptoclada* Group occupies most of the Yilgarn Centre. The *Tecticornia tenuis* group has a substantial range, from eastern margins of the Yilgarn Centre to the central Eyre-Murray Centre, including Sandland South. Both have northern and southern subgroups.

A saltmarsh group in each centre that links coast and inland taxa, suggests migration from coastal regions (Bridgewater and Cresswell 2003). The *Tecticornia doleiformis-T*. *leptoclada* group on the northern and western coastlines of the Yilgarn Centre, extends into the Yilgarn Plateau. In the Eyre-Murray Centre the *Tecticornia pergranulata* Group extends from coastal Murray Lowlands into the Central Lowlands provinces.

Assembly patterns suggest easterly expansion at the margins of the Subcontinental group. The Barkly-Tanami Plains and Sandland North have an affinity to the Yilgarn Centre, which adjoins Sandland North. Yilgarn Plateau, Sandland North and Barkly-Tanami Plains are edaphically similar, having dissected silcrete tablelands and sandplains over granitic substrates. The younger aridity of the Eyre-Murray Centre would limit expansion opportunity from there into the adjoining Barkly-Tanami Plains.

The diffuse boundary with the Northern Tropical Group lies across an arid-tropical climatic gradient. The major variation in assembly, as revealed in outlier analyses, identifies the boundary as a provincial belt of scattered populations of numerous species where the northernmost populations are at different latitudes. The climatic gradient extends across a subdued landscape, from a hot region of very low, unpredictable rainfall to a warm, seasonally wet and dry region with moderate rainfall in the warmest months (Hutchinson *et al.* 2005). Salt-tolerance exaptation for aridity, would contribute to surviving a warm, dry period that lasts the greater part of a year.

The boundary with Eastern Highlands is also indicative of past barriers. Taxon ranges of the Sclerolaenid, *Salsola* and *Atriplex* 1 and 2 clades end abruptly in a sharp transition to the southern uplands. In the north, the Sclerolaenid and *Atriplex* 2 clades extend across the subtropical ranges from the Eyre-Murray Centre to the coast, with species that are of subcontinental range (e.g. *Atriplex lindleyi, Dissocarpus biflorus*) or from adjoining lowlands (e.g. *Sclerolaena ramulosa*). The southern highland climate is of winter moisture and cool temperatures but the subtropical north has warm, moist seasons alternating with mild, dry ones (Hutchinson *et al.* 2005). This diffuse northern boundary is a similar climatic transition to that with the Northern Tropical Group. Radiations of the Sclerolaenid and *Atriplex* 2 clades are Late Miocene-Pliocene events (Cabrera *et al.* 2009; Kadereit *et al.* 2010) when central Australian climates were warm with a marked dry season (Martin 2006). Climatic niche conservatism possibly controls chenopod expansion.

Deep sandy soils of higher rainfall areas are edaphic barriers. Abrupt boundaries in the Sclerolaenid, *Salsola* and *Atriplex* 2 clades coincide on eastern margins of the Western Coastlands Province.

Some extinction has occurred. Species disjunctions point to local population extinctions. Species extinction is less certain, but possible within *Scleroblitum*. A Pliocene Wet reversal disrupted the long-term drying trend, with rainforest returning to eastern Central Lowlands and Murray Lowlands provinces (Martin 2006; Fujioka and Chappell 2010). Competitive mesic species would temporarily displace chenopod taxa on an advancing periphery, but expanding younger chenopod clades may also be as competitive. Extinction may also result from dune field formation (see Chapter 3).

Eastern Highlands Group

A coastline and an inland border with the subcontinental group, both of which span subtropical to temperate latitudes, control the assembly of this group. Characteristic coastal taxa are saltmarsh clades while inland taxa are mostly from the Chenopodioideae subfamily. Southern and northern subgroups are distinguished by coastal and inland taxa of more limited range, and with affinities to adjoining provinces of the Eyre-Murray Centre that suggests expansions.

The distinction of northern and southern subgroups closely parallels saltmarsh patterns of Bridgewater and Cresswell (2003). The northern subgroup is the eastern range of the tropical *Suaeda arbusculoides-Tecticornia indica* julacea saltmarsh group. The southern subgroup relates particularly to a *Stipa stipoides-Agrostis billardierei* saltmarsh subgroup ranging from eastern Tasmania to northern New South Wales, being the eastern range of the extensive *Tecticornia arbuscula-Juncus kraussii* saltmarsh group. It includes *Atriplex* spp. and *Rhagodia sp*. of the southern coast that further extend along Eastern Highlands coastlines.

Historic and current range extensions of coastal taxa are suggested. Clade ranges of *Tecticornia* and *Sarcocornia* on the seaboard represent past expansions. Late Miocene arrival on the northern coast (Kadereit *et al.* 2005) and Pliocene chenopod pollen in the marine Capricorn Basin (Hekel 1972; Martin 2006) infers southerly extensions of the *Tecticornia* Clade - possibly earlier, if Late Miocene chenopod pollen is confirmed [compare Hekel (1972), Martin and McMinn (1993) and Martin (2006)]. For *Sarcocornia*, a Late Pliocene arrival from South Africa (Steffen *et al.* 2015), probably through West Wind Drift (Munoz *et al.* 2004; Sanmartin *et al.* 2007), and absence on the northern coast implies a northerly direction of movement.

Species currently extending range northward from coastal ranges on the southern coast would be *Atriplex cinerea* (*Atriplex* Clade 1), *A. australasica* and *Rhagodia candolleana* (Chenopodieae I). Though the East Australia Current flows south close to the coast, complex eddies of the Tasman Sea (Ridgway and Godfrey 1997) and surface currents driven by South East trade winds (Gentilli 1977, 1986) aid northerly migration. Avian consumption of *Rhagodia candolleana* berries reduce dependence on coastal currents for dispersal, and promotes a faster rate of range extension. *Rhagodia candolleana* from a much younger clade, extends north to Brisbane while *A. cinerea* approaches Newcastle. Dispersal of the species is evident in their presence (or close relatives) in coastal New Zealand. *Atriplex cinerea* occurs in New Zealand (de Lange *et al.* 1998; Heyligers 2001) as does *Atriplex australasica* (see AK100625, AK247261 Auckland War Memorial Museum Herbarium) and *Chenopodium triandrum* (syn. *Einadia triandra*, *Rhagodia triandra*)1.

Some taxa from clades of the Chenopodioideae subfamily are peculiar to the Highlands Group. The ranges of *Dysphania* and Chenopodieae I clades straddle the boundary with the Subcontinental Group in contrast to other clades. Inland species are *Dysphania carinata, Chenopodium erosum* and three *Einadia* species, with species ranges largely within and aligned to the north-south orientation of the highlands. *Einadia*'s semi-succulent perianth is likely spread by woodland bush birds, similar to *Rhagodia* (Wood 1937; Lang *et al.* 2003; Brown 2014). *Dysphani*a can be spread by fur bearing animals (Grozeva and Cvetanova 2013). Species ranges extend marginally west onto the drier plains, suggesting the boundary with the Subcontinental group is one of species exchange as well as a landscape filter, with ranges of *Atriplex* Clade 2 and the Sclerolaenid Clade extending over the subtropical provinces. *Atriplex billardierei* from Bass Strait is also in New Zealand (de Lange *et al.* 2000).

Northern Tropical Group

The amphitropic distribution of chenopods (MacDonald 2003; Huggett 2004) ties the northern group to tropical barriers, most likely competition with tropical species (MacDonald 2003). Coasts are the only available habitat for salt-tolerant taxa, commonly co-occurring in high

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1 [http://www.nzflora.info/factsheet/taxon/Chenopodium-triandrum.html: accessed 10/4/2019]

stress habitats of estuaries and tidal rivers. Tropical saltmarsh is spatially discontinuous (Saenger *et al.* 1977; Adam 1994) with high evaporation rates creating prolonged hypersalinity and dry, salt crust that prevents vegetation growth (Ridd *et al.* 1988), including mangroves (Adam 1994). Salicornioideae and Suaedoideae are on tropical coastlines (Schutze *et al.* 2003; Kadereit *et al.* 2006) but coastal *Atriplex* are largely temperate (Osmond *et al.* 1980). *Salsola* largely occurs on dry sand sheets on tropical coasts.

The Northern Tropical Group is part of the Australian Monsoonal Tropics biome (Bowman *et al.* 2010), coincident with the *Suaeda arbusculoides-Tecticornia indica* julacea saltmarsh floristic group (Bridgewater and Cresswell 2003). Western and eastern elements astride the Gulf of Carpentaria are attributed to a continuing vicariance (mostly of pre-Miocene times), migrations from south-east Asia and range shifts due to Pleistocene sea level change. Chenopod patterns would relate to later events, especially coastal expansions in *Tecticornia*, *Sarcocornia* and *Suaeda*.

Recent shoreline change likely induced range shift and extension. Pleistocene shoreline oscillations exposed and submerged regional land surfaces, including the Gulf of Carpentaria (BMR Palaeogeographic Group 1992; Voris 2000). Range continuity of *Tecticornia* in the Gulf, shows rapid occupation following the last advance. Marine mammals show distinct genetic signatures from such cycling (Blair *et al.* 2014), which may similarly occur in disjunct populations of *Suaeda arbusculoides*. *Suaeda* and *Sarcocornia* may be expanding into the gulf, with recent initial collections of *Suaeda* [NSW 496174, 9/6/2002, Jacobs] and *Sarcocornia* [NSW 370834, 26/5/1992, Clarkson] which is absent from the north coast.

Tecticornia possibly migrated from south-east Asia (Kadereit *et al.* 2005). If so, the northern coastline is the region of landfall, longest occupancy and a bridgehead for early coastal range extension to west and east. *Tecticornia halocnemoides* and *T. indica* are widespread along Australian coasts and in central Australia, but are not inland taxa of the northern coastal provinces. Burbidge (1960) and Beadle (1981b) considered these areas a barrier to inland migration, which accords with their restriction to the coastline. Inland migrations of *Tecticornia* occurred farther south.

Rich clades from Chenopodioideae and Camphorosmoideae may be extending their range northward into the Northern Tropical provinces. The desert to monsoon coast transition is a broad rainfall gradient with a long warm, dry season that chenopods in lower rainfall areas could tolerate. The broad coincidence of northern clade margins would relate to tropical barriers associated with the amphitropic distribution, while the varied limits of species in the northern arid provinces indicate barriers acting as dispersal filters at finer scale. The northward movement may have ancient roots. Eocene vegetation mosaics of Central Australia are most similar to the modern, northern monsoon regions (Alley 1998; Alley *et al.* 1999) and the arid zone may have expanded northward after forming in the south of the continent (Bowler 1982).

Nullarbor Plain and Northern Arid anomalies

Sandland South Province is floristically richer than Nullarbor Plain, and more strongly links the two Centres. Leigh (1972, 1981, 1994) and Fox (1999) identify the Nullarbor Plain as a distinctively chenopodiaceous region, but twelve other provinces, including Sandland South, have at least 30% more chenopod species. Chenopod formations dominate the alkaline and saline habitats (Kenny and Thompson 2008), with a suite of lime-tolerant taxa from five clades, including the provincial endemic *Atriplex cryptocarpa*. This issue is further discussed in Chapter 3 (p 153). Curiously Sandland South was a coastal province at the time of arrival of the older clades (Hou *et al.* 2008).

The northern arid provinces have with outlier populations of many species that have main ranges to the south. Variable distribution through the provinces, indicates a diffuse periphery of current range expansion or contraction between the Subcontinental and Northern groups. Both provinces share more taxa with the Yilgarn Centre, than with the Eyre-Murray Centre, suggesting earlier range expansions from the Yilgarn Centre that could arise from earlier aridity in the west offering more opportunity for migration. Curiously, the taxa includes the Coast facultative *Neobassia astrocarpa*, part of a near-basal subclade of the Sclerolaenid clade, with origins in the Yilgarn Centre (Cabrera *et al.* 2009).

Coastal disposition: taxon element of littoral connection and evolutionary significance

Australian chenopods exhibit the taxon element of a littoral connection. Nine of eleven clades have at least one distinctive coastal species. *Dysphania* lacks distinctive coastal taxa and the very old *Scleroblitum* clade exhibits a taxon element insofar as its ancestor was estuarine.

The taxon element is not a discrete separation of coast and inland taxa. Some coastal species are exclusively shoreline, but most have inland populations parapatric with inland species; inland ranges can be large The presence of Coast facultative types in most clades, their prominence in younger clades and proximity of their coast and inland ranges strongly indicates adaptation is not necessary for coastal departure.

Variation in sister taxa ratios, coastal disposition and clade range broadly fit invasive processes of arrival, range extension, diversification and extinction. Younger clades have fewer species, are predominantly coastal and have smaller inland ranges proximate to coastlines. Time since their arrival is insufficient for substantial inland range extension or speciation. For the older clades, ample time has brought subcontinental occupation and diversification exceeding 40 species. Strongly asymmetric ratios of rich clades reveal adaptive radiations are inland phenomena, accentuating the limited coastal diversity.

The very old, monotypic *Scleroblitum* clade lacks coastal taxa, suggesting population extinction. Each of the three oldest clades (*Scleroblitum*, *Dysphania* and Sclerolaenid) expresses the taxon element less strongly, having very low **CI** ratio or no coastal taxa. Coastal taxa of old clades may be displaced by that of younger clades or possibly by coastal species derived through taxon cycling.

Some taxon element and coast disposition issues remain. The presumed youth of *Suaeda* needs confirmation and the taxonomy and arrival time of *Salsola* must be resolved. Estimate of 6-10 *Salsola* species (Borger 2008; Chinnock 2010) with affirmation of youth and native status would indicate very rapid rates of range extension and diversification.

Disposition and location of coastal taxa reveal features of colonization and establishment:

(1) Western and southern coastlines are regions of initial landfall and coastal departure. The origin of the Sclerolaenid clade is in the south-west (Cabrera *et al.* 2011). Other old clades

have similar continental distribution and co-occurring coastal taxa. Inland species ranges of the younger *Sarcocornia*, *Suaeda* and *Atriplex australasica* clades adjoin the southern coastline. Small ranges of the *Scleroblitum* and very young *Atriplex australasica* clades in southeast Australia suggest specific landfall and coastal departure locations (see Clade distribution below). Coastal taxa migrating from western landfalls could also depart the southern coast where *Scleroblitum* and *A. australasica* did.

(2) The prominence of Coast facultative taxa, readily enabling coastal migration and departure, means establishment quickly follows colonisation. Coastal range extension would be the first general stage of landscape spread for chenopods. This character of modern coastal species is likely ancestral.

(3) Chenopod clades have few coastal species. This may result from ready coastal dispersal, few habitat types and intra-familial competition. Low species diversity coupled with large species ranges is globally common with coastal *Atriplex* (Osmond *et al.* 1980). Kadereit *et al.* (2006) attribute lack of generic diversity in Salicornioideae to global uniformity of coast habitats. Chapman (1976) identifies only three coastal habitats important to terrestrial species and the mean number of coastal taxa is 3.3 species per clade. Coastal species of younger clades would compete with established taxa.

Cosmopolitan taxa and oceanic and coastal migration

Coastal species are cosmopolitan genera in *Atriplex*, *Sarcocornia*, *Suaeda* and *Dysphania* clades. The Sclerolaenid clade comprises Australian genera. *Tecticornia* is prominently an Australian taxon, generically centred on the Indian Ocean (Kadereit *et al*. 2006).

Oceanic movement of cosmopolitan chenopod taxa and continental coastal migration can result from West Wind Drift (Munoz *et al*. 2004; Sanmartin *et al*. 2007). Chenopod seed and containers are notably buoyant (van der Pijl 1982; Kuhn 1993). *Sarcocornia* arrived from South Africa (Steffen *et al.* 2015). *Atriplex* Clade 1 is related to American *Atriplex* (Kadereit *et al.* 2010) and South American taxa could reach Australia through West Wind Drift. After floating south in the Agulhas Current east of Africa, the cosmopolitan Eurasian taxa (*Atriplex* Clade 2) may be carried by West Wind Drift. Within Australia, West Wind Drift would extend species ranges eastward along the southern coastline, accounting for coastal *Atriplex cinerea* (*Atriplex* Clade 1) and *A. billardierei* (*Atriplex* Clade 2) occurring in New Zealand (de Lange *et al*. 1998, 2000; Heyligers 2001). West Wind Drift increases chances that western coastlines are the initial landfalls.

The Chenopodieae I clade oddly has the endemic *Rhagodia* typically coastal, rather than the cosmopolitan *Chenopodium*. Clade taxonomy has a history of frequent revision (Wilson 1984). Fuentes-Bazan *et al*. (2012a, 2012b) considers the generic distinctions unwarranted, treating all species as *Chenopodium*. *Rhagodia* and *Einadia* have a fruiting berry (Kuhn 1993) unlike *Chenopodium* from overseas, but so do Australian *Chenopodium curvispicatum* and *C. gaudichaudianum* (Wilson 1984) which are not coastal species. If *Rhagodia* is derived, it would exemplify the Evolutionary Taxon Cycle (Shmida 1985), with an ancestral coastal *Chenopodium* being replaced in very short time.

Taxon cycling and coastal taxa

Shmida (1985) proposed an Evolutionary Taxon Cycle within a littoral connection, promoting diversification. Phylogenetic studies could confirm the number of cycles completed and the clades in which it features. Cyclic diversification is repeatedly episodic departures from and returns to the coast as new taxa evolve (Shmida 1985). It has created new coastal taxa in the Sclerolaenid Clade and is suspected in *Atriplex* Clade 2 and Chenopodieae I.

Taxon cycling in the Sclerolaenid clade, possibly involves extinction and replacement of ancestral coastal species. Coastal taxa are in distinct genera (Cabrera *et al.* 2009), and a coastal ancestor is difficult to identify among the modern taxa. *Maireana* is recognized as the basal genus with *Maireana oppositifolia* in a basal grade of lineages. *Neobassia astrocarpa* is near basal, from the *Eremophea* subclade that is mostly inland. *Threlkeldia diffusa* is derived having a coastal range from Broome to Bass Strait, overlapping *N. astrocarpa* on the northwest coast and enveloping *M. oppositifolia* on the southern coast. The clade's coastal ancestor may have been replaced in later coastal migrations.

The unusual location of the coastal *A. humilis* most likely arises from taxon cycling in *Atriplex* Clade 2. It is the only Coast obligate of restricted range and is endemic to the Gulf of

Carpentaria, which formed in the latest Pleistocene (Voris 2000; Holt 2005). The region was arid terrestrial during the last glacial maximum (Barlow 1981) and as the gulf formed, its margins would have approached the northern limits of *Atriplex* Clade 2 range. With *Atriplex* preferring temperate coasts (Osmond *et al.* 1980) and a very recent emergence, coastal range extension has been limited.

Taxon element and suitability of disposition class

Coastal disposition classes coarsely distinguish coastal and inland taxa. Exacting ecological classification could better differentiate Coast and Inland facultative types, especially in *Dysphania* and *Salsola* clades, which weakly express a taxon element. Suggested means are in Appendix II.

Chenopod taxa are a substantial component of saltmarsh communities that have coastal specialist and generalist species (Bridgewater and Cresswell 2003; Saintilan 2009b). Chenopod patterns strongly resemble saltmarsh assembly, so with more exacting ecological classification and resolved clade phylogeny evolution of chenopod taxa would suggest the evolution of halophytic communities. However, this coarse classification illustrates that barriers to initial inland movement or along coastlines are readily overcome.

Uncertain relationships of Inland facultative species to coastlines, makes disposition classes an unsuitable model for inland expansion. Species once distant from shorelines could become coastal through shoreline transgression (likely for *Atriplex humilis*) or range extension toward the coast.

A model coastal species

The species range of the Coast facultative *Atriplex paludosa* (*Atriplex* Clade 2) extends from Shark Bay to Tasmania. Its four subspecies vary in coastal disposition that may reflect distinct coastal and inland migrations. They form a near allopatric complex of two western and two eastern types separated by the Nullarbor Plain (see figure 4.6e). The Coast facultative *A. paludosa* ssp. *moquiniana* around Shark Bay has inland populations close to the coast. It grades abruptly into the Inland facultative *A. paludosa* ssp. *baudinii* that occurs up to 400 km inland in south-west Western Australia and has few coastal populations scattered from Abrolhos Islands to Esperance. South Australia is the main range of Coast facultative *Atriplex paludosa* ssp. *cordata*, which occurs up to 50 km inland on Eyre Peninsula. The western range of the subspecies is the southern margin of the range of *A. paludosa* ssp. *baudinii*. *Atriplex paludosa* ssp. *cordata* grades into the Coast obligate *A. paludosa* ssp. *paludosa* in the Gulfs-Ranges province, disjunct from Bass Strait populations.

Disjunct Species

Areas that separate the disjunct populations of widespread, shared chenopod taxa coincide with separation of the Yilgarn and Eyre-Murray Centres. The gap extends north from Nullarbor Plain to Sandland North across coasts, climate zones and desert regions. Congruent patterns across immigrant clades, suggest vicariance events, related to climate and landscape change of varied age. Current landscapes of the gap are limestone plain (Nullarbor Plain) and desert dune field (Sandland South and North). Disjunct sister species pairs of the two centres are as yet unknown.

Subcontinental disjunctions in species of arid habitat occurred late in chenopod evolution. All 31 species are from older clades; three clades have at least four disjunct species. Disjunction post-dated marked range expansion and diversification. The youngest clade is Chenopodieae I (*Chenopodium desertorum*), arriving in the mid-Pliocene at the earliest. Four species are from *Atriplex* Clade 2 occurring after initial diversification of the Late Pliocene (Kadereit *et al*. 2010). Fifteen species are from four genera of the Sclerolaenid Clade; eight from the derived SclerolaenAff subgroup (Cabrera *et al.* 2009, 2011). All disjunct *Sclerolaena* have 4-5 perianth spines, which overall are as numerous as those with 2-3 spines.

Provincial species disjunctions of the Eyre-Murray Centre are also dune field separations. Interestingly the subcontinental disjunct species *Maireana carnosa* and *Atriplex quinii* are included, with three main population ranges, separated by the Great Victoria Desert and by the Simpson-Strzelecki Desert in the Eyre-Murray Centre. Eastern and western populations of the Eyre-Murray restricted species *Atriplex fissivalvis*, *A. macropterocarpa*, *A. nessorhina* and *Maireana spongiocarpa* are similarly divided by the Simpson-Strzelecki dune field.

Vicariance associated with dune fields seems contrary to a littoral connection, but identifies event timing. Local extinction from desert dunes counters the habitat element, as they should promote occupation. However, desert dunes form as land surfaces are exposed to wind-drag in dry conditions (Twidale and Wopfner 1990; Laity 2008; Nichols 2009), which principally occurs when vegetation cover is removed. Conditions immediately preceding dune formation possibly initiate disjunction. The Great Victoria and Simpson Deserts dune fields developed most extensively in the Late Pleistocene under very arid conditions (Sheard *et al.* 2006; Fujioka *et al.* 2009; Hesse 2010) being the culmination of a vicariant drying trend (Crisp *et al.* 2004; Crisp and Cook 2007). The intensity and extensiveness of Pleistocene aridity is consistent with the scale of disjunction, with a dry, but less arid Pliocene promoting expansion, not extinction. This issue is further examined in Chapter 3.

The climatic nature of vicariance is seen in other species ranges of the Eyre-Murray Centre. The centre’s inland is the driest Australian region especially for eco-geomorphic processes (Dunkerley 2010). On the periphery of the Lake Eyre Basin, the species ranges of *Maireana campanulata*, *M*. *schistocarpa* and *Rhagodia parabolica*, almost form ring distributions enclosing both the driest areas and disjunct species of the Centre’s restricted taxa.

Origins of coastal and temperate disjunct population are manifold. The Bunda Cliffs are an exceptionally inhospitable continuous habitat for 200 km, where colonisation and establishment is near impossible even for freely dispersing coastal taxa. Either their Late Miocene formation fragmented existing populations, or the taxa later bypassed them. Disjunction in the temperate species is probably climatic. In the separate SouthWest and SouthEast sclerophyll biomes (Crisp and Cook 2007), the disjunct species *Atriplex semibaccata*, *A. suberecta*, *Maireana enchylaenoides* and *M. brevifolia*, from the older clades arriving in the Early Pliocene or earlier, are groundcover species of woodland and mallee communities. Separation of the biomes is attributed to events leading up to and the emergence of the arid zone.

Other disjunct species populations show congruent patterns at provincial scale. Of some interest are disjunctions in *Maireana excavata*, *M. rohrlachii* and *M. decurrens* across South Australia and Victoria, with formative events being of Quaternary age. Populations are divided by the Mallee Dunefield, the vast Lake Bungunnia and calcareous pedogenesis in the western Murray Lowlands. Quaternary shoreline shifts divide South Australian populations of

M. excavata and *M. rohrlachii* as Spencer Gulf and Gulf of St Vincent, repeatedly formed and disappeared, while those in Torres Strait (Voris 2000) can explain disjunct populations of *Suaeda arbusculoides* on the northern coast.

Similar floristic and biogeographic patterns

Assembly, richness and subcontinental disjunctions of chenopods complement other floristic and biogeographic studies. Crisp *et al.* (1999) describe western and eastern centres for Myrtaceae, Fabaceae, Proteaceae and Ericaceae (as Epacridaceae), with disjunct genera concentrated in provinces of the Yilgarn Centre and Eastern Highlands. Gill (1981, 1994) reports similar patterns for open forest Eucalypt species. The mallee species lineages now linking eastern and western Eucalypts arose through an easterly migration (Parsons 1994).

Crisp and Cook (2007) describe disjunct sister species pairs from several plant genera of the SouthWest and SouthEast sclerophyll biomes. Chenopod centres adjoin the sclerophyll biomes on their drier margins. A mid-Miocene aridity and shoreline movements separated the sclerophyll biotas, kept apart by the edaphic barrier of the Nullarbor Plain. The youngest separations coincide with the earliest chenopod presence, probably initial range extension of older chenopod clades. Disjunction of mesic chenopod species in sclerophyll plant communities, may be the final stage of separation of the sclerophyll biomes.

Saltmarsh phytogeography and coastal chenopod diversity follow a climatic zonation of Australian coastlines. Davies (1977, 1986) identifies the richer western and southern coasts as arid. Clarke (1994c) classifies coastal dune floristics of these coasts into tropical arid and temperate arid segments. Arid coast is defined by low average river discharge to the sea where tidal flats are more prevalent than estuaries. Bridgewater and Cresswell (2003) tie Australian saltmarsh distribution to the amount of cool or warm season rainfall on wet or dry coastlines. Bioregional clusters also relate to humid or dry, tropical or temperate coasts with extensions inland (Saintilan 2009a, 2009b) that emphasise a continuity of marshy habitats. For Beadle (1981b), the proximity of the richest provinces to coasts of high clade diversity with habitats persistently suited to chenopods, most simply explains landfall, shoreline range expansion and ready inland migration. Such climatic zonation is modern; and may not have been the conditions of initial chenopod movement.

Clade distribution and evolutionary histories

Provincial richness and coastal disposition of immigrant clades offer insights and contrasts in their course of evolution.

The very old Oligocene clade – *Scleroblitum*

Scleroblitum arrived near the start of the Oligocene drying trend, prior to the onset of aridity. Very old clade age is certain but the molecular estimate (42-26 Ma) needs refining (Kadereit *pers. comm.*). Major questions are clade persistence of at least 26 Ma, loss of coastal populations and the time of inland range expansion.

The oldest chenopod pollen known in Australia is in Oligocene estuarine sediments of the Murray Basin (Truswell *et al.* 1985; Kershaw *et al.* 1994) and very likely is *Scleroblitum*. All other immigrant clades are younger. The sediments containing the pollen lie within its current distribution. Alternatively, the pollen is from an extinct clade and *Scleroblitum* was elsewhere in Australia, possibly estuaries and coastal lagoons of the Eucla Basin (Benbow *et al.* 1995b; Hou *et al.* 2008). Later migration eastward could occur with West Wind Drift which has operated since the Oligocene (Sanmartin *et al.* 2007). However, chenopod pollen of Oligocene age has not been identified in the Eucla Basin.

The Murray Lowlands conceivably hosts landfalls and coastal departures. The region is the landfall of the very young *Atriplex australasica* clade, and location of its only inland populations. *Scleroblitum* is largely confined to the Murray Basin. The pollen-bearing, estuarine clays occur north of the Murray River in South Australia and east of Mildura in Victoria (Macphail *et al.* 1993), distant from the current coast. Abandonment by retreating shoreline, leaving beach ridges in its wake, may have created inland populations, which moved farther inland as inland areas became drier.

Expansion inland would have been difficult for much of clade history though possible in seasonal climates. Mesic vegetation persisted extensively in the Murray Basin until the Pleistocene (Martin 2006). Pliocene pollen assemblages with chenopod traces in central-eastern New South Wales, point to dry, closed forest with marked seasonal drought (Martin 1979). The alluvial sediments lie within the modern range of *Scleroblitum*. Found mostly in damp habitats, it is a low-growing, herbaceous, cryptic annual of decumbent to prostrate form (Wilson 1984). A Wet Reversal interrupted the Neogene long term drying trend in the Early Pliocene (Martin 2006; Fujioka and Chappell 2010; Sniderman *et al.* 2016) with mesic taxa returning to inland landscapes, replacing less competitive halophytes.

Persistence of a monotypic clade for at least 26 Ma raises issues. Eastern coastal chenopods persist in coastal habitats, with hinterland ones being unfavourable. For a net result of one species, any radiation requires an extinction of similar size. The Wet Reversal could initiate this, but with resumption of the drying trend and inland expansion *Scleroblitum* would face competition from the younger chenopod clades.

Scleroblitum is singularly noted for a modern lack of the taxon element, possibly arising under a combination of events. Shoreline retreat could occur too rapidly for *Scleroblitum* dispersal. Populations currently nearest to coastlines are in the northern South Australian gulfs, where episodic advance and retreat were frequent in the Pleistocene. The most similar, modern habitat nearest the Oligocene landfall is the Lower Murray Lakes where *Scleroblitum* is currently absent. Formation and demise of the vast Lake Bungunnia in the last 3 million years would separate inland and coastal populations with plants having to survive in unfamiliar beach-dune habitats, competing with diverse chenopod species.

Scleroblitum and *Atriplex australasica* clades are a curious contrast, being monotypic, the oldest and youngest clades, and of near allopatric distribution restricted to the southern Eyre-Murray Centre. Lifeform is similar to some species from *Dysphania* and Chenopodieae I.

The Miocene-Pliocene clades

Chenopod clades of this age are widely spread, and variably diversified, through coast and inland regions of the continent. Major geographic factors in landscape spread and diversification are inland regional histories and population isolation at subcontinental scale.

All clades have coastal species that span the continent, but coastal diversity is relatively low. The continental ranges of coastal taxa indicates major coastal migrations are few. Extensive coastal migration increases the possibility of departure as broad diffusion fronts, given the inland ranges of Coast facultative species that are the most common form of coastal taxa. Each separate departure is an incipient lineage.

Seasonality in mesic conditions could influence inland range expansion. The Sclerolaenid, *Dysphania* and *Atriplex* 2 clades extend into warm, seasonally wet and dry climates. Such climate prevailed over much of the continent at the time these clades arrived (Martin 2006). *Sclerolaena* may have diverged from *Maireana* as the dry season became more intense or of longer duration. Furthermore, the modern climate zones with extreme aridity are of Pleistocene age (Martin 2006; Fujioka and Chappell 2010). Initial chenopod diversification may be a response to seasonality and the onset of aridity, rather than its attainment.

Sclerolaenid Clade

The Sclerolaenid Clade is the richest in species and genera and is very widespread, surpassed only by *Salsola*, a close relative. Scarcity in Kosciuszkan and Tasmanian Uplands show cool, mesic conditions are a major barrier to dispersal. The sharing of most genera between the centres indicate migrations of emerging lineages, likely also repeated within *Maireana* and *Sclerolaena*.

The derived *Sclerolaena* seem better suited to subtropical conditions. SclerolaenAff is proportionately richer in the north and east, having species particular to northern arid regions (e.g. *Sclerolaena crenata*, *S. muelleri*) and the subtropical north-east (e.g. *S. ramulosa*). Subtropical regions have most soil moisture in the warm season. MaireanAff is predominantly in the south and west, within Mediterranean conditions of hot summers and cool season moisture. *Maireana* in subtropical regions includes some of the most widespread chenopod taxa, so the particular lineage from which *Sclerolaena* derives is of interest.

Duration or intensity of dry periods may drive selection for a spiny perianth. More *Sclerolaena* occur in the Eyre-Murray Centre, which is Australia’s driest region. Spiny forms developed independently within the clade e.g. *Eremophea*, *Dissocarpus* spp. (Cabrera *et al.* 2009). These are in the MaireanAff subgroup with species ranges in the driest regions. If drier conditions drive such adaptation, spatio-temporal patterns of emergence of spines might reflect the provincial nature of post-Miocene climate change.

The early stages of Taxon Cycling are evident in this clade, possibly involving extinction and replacement of ancestral coastal species. *Threlkeldia diffusa* shows a substantial coastal migration, in later clade history.

The Sclerolaenid and *Dysphania* clades are Late Miocene arrivals from Asia (Kadereit and Freitag 2011; Kadereit *pers. comm.*) having subcontinental distribution with few coastal taxa. The Sclerolaenid clade has 12 genera and is ten times richer in species. Each *Dysphania* is markedly widespread.

Tecticornia and Sarcocornia clades

Tecticornia and *Sarcocornia* clades are from the same subfamily, having very similar lifeform and ecological niche. The major biogeographic difference is the age and location of arrival. *Tecticornia* likely arrived through South East Asia (Kadereit *et al*. 2005), while *Sarcocornia* came from South Africa (Steffen *et al.* 2015) likely through West Wind Drift. The absence of *Tecticornia* from middle and upper catchments of rivers draining to the north coast, indicates migration inland occurred elsewhere to the south.

Tecticornia arrival is near contemporary with *Atriplex* Clade 1. Both are most diverse in the Yilgarn Centre, but *Tecticornia* has 5.5 times as many species. *Sarcocornia* and Chenopodieae I are contemporary. With one sixth the richness, it has smaller inland range and greater coastal range.

Tecticornia is the most coastally widespread chenopod clade, being on all coasts. Its substantial inland range is notably less than other rich clades, being largely absent from the Ord and Victoria River catchments and in the northern and eastern Lake Eyre Basin. Presence in drainage of the lower Lake Eyre Basin, suggests combination of the volume and downstream reach of annual monsoon driven flows may be a major limit in species range because these determine the basin’s saline character. *Sarcocornia* is coastally widespread, and though absent on much the tropical north coast, the clade exemplifies extensive coastal migration preceding inland occupation.

Clade age would account for contrasting distribution of the two clades. The older *Tecticornia* has numerous, widespread inland and coastal species. The younger *Sarcocornia* has few species and small inland ranges proximate to southern coasts. Episodic isolation of regional populations under dry conditions drove diversification in *Tecticornia* (Shepherd *et al.* 2004) especially in the Yilgarn Centre, where the clade is richest. Using arrival estimates, *Tecticornia* diversified at 4-9.2 species/Ma and *Sarcocornia* at 0.75-1.7 species/Ma. *Tecticornia* arrived at the onset of aridity. *Sarcocornia* arrived with aridity well established over the continent, likely retarding range extension of taxa largely reliant on hydrochory for dispersal (Kuhn 1993).

Sarcocornia collections suggest a recent, rapid range expansion. Initial collections of 1848-1849 are from coastal southern Australia. All collections prior to 1880 were coastal, as were all but four up to 1919. *Sarcocornia* was first collected in the Avon Wheat Belt of Western Australia in 1890-1891 then not until 1951-1952. Initial collection in the Lake Eyre Basin was in 1897 with a second in 1975. Such an expansion could not involve water-borne dispersal, because inland collection sites are in unconnected watercourses.

Atriplex Clades 1 and 2

Atriplex Clade 1 arrived 1.5-5 Ma earlier than Clade 2. Forms are very similar, with molecular analyses determining clade membership. Taxa from both clades are in coastal New Zealand (de Lange *et al.* 1998, 2000; Heyligers 2001).

Atriplex Clade 2 is more widespread inland, extending farther into subtropical dry regions. Both clades span the continent from west coast to east coast, with the southern coastal ranges of *Atriplex cinerea* (Clade 1) and *A. paludosa* (Clade 2). Inland taxa from Clade 2 also extend from the northern Eyre-Murray Centre through the subtropical highlands to the coast and to the Gulf of Carpentaria. The location of *A. humilis* (assumed in Clade 2) on the Gulf coast relates to taxon cycling (see earlier).

Ecological prominence of Clade 1 species contrasts with clade species poverty. *Atriplex isatidea* and *A. cinerea* dominate coastal dunes in the west and south (Specht 1972; Beadle 1981b). *Atriplex nummularia* dominates shrubland plains and understorey of riverine woodland in the Lake Eyre and Murray Basins (Beadle 1981b; Eldridge 1988). *Atriplex rhagodioides* and *A. amnicola* are similarly prominent, respectively along the lower River

Murray (Stewart and Brandle 2010) and the Gascoyne and Murchison Rivers (Curry *et al.* 1994). *Atriplex incrassata* dominates the dry, stony plains of central Australia, which have few resident shrubs (Brandle 1998). *Atriplex cephalantha* and *A. yeelirrie* are of restricted range, but locally abundant (Clarke *et al.* 2012). Clade species rehabilitate landscapes that are degraded by drought, grazing, flooding, erosion and salinity (Leigh 1972, 1994).

Atriplex Clade 2 has six times the species of Clade 1 with greater variation of life-form. All Clade 1 species are shrubs. Of Clade 2 shrub species, only *A. vesicaria* is north of the Tropic of Capricorn. Annual/biennial forms from Clade 2 extend farther north than *A. vesicaria*, and include species with main range in northern arid regions e.g. *A. cornigera*, *A. humifusa*.

Clade 2 distribution resembles the SclerolaenAff subgroup of the Sclerolaenid Clade. Both are richest in the very dry central-eastern interior, but have species restricted to the Yilgarn Centre. Clade and subgroup range extend east and north from the Eyre-Murray Centre into subtropical uplands and lowlands. Both have species of annual/biennial form with their main range in northern arid regions. The prominent coastal taxa, *Atriplex paludosa* and *Threlkeldia diffusa*, have a common eastern range limit of eastern Bass Strait. The coastal range of *Threlkeldia diffusa* would be a late coastal migration, which *A. paludosa* may also have only recently attained. It is absent from the eastern seaboard where *A. cinerea* (Clade 1) and *A. australasica* (the youngest clade) are found.

Dysphania and Chenopodieae I clades

Similarity in lifeform and reproductive elements led to long standing taxonomic confusion of these clades. Recent molecular analyses have verified (Kadereit *pers. comm*.) revisions of Mosyakin and Clemants (2002). Clade differences are strong expression of the taxon element in Chenopodieae I and a weak expression in *Dysphania*. All *Dysphania* are annual or biennial lifeforms. Chenopodieae I includes shrubs, especially in its coastal taxa. *Dysphania* arrival is contemporary with the Sclerolaenid Clade, being more than 10 Ma, but with only a tenth of the species. Chenopodieae I is contemporary with *Sarcocornia*, arriving no more than 4 Ma, but has six times the species richness.

Both clades occur in inland Eastern Highlands more than other clades, distributed in an east-west belt across the southern and central arid zone from coast to coast. *Dysphania* is richer in the subtropical ranges than the cooler southern uplands, similar to *Atriplex* Clade 2 and the Sclerolaenid clade. In this same region is *Dysphania littoralis*, perhaps the species with the strongest ecological claim to being coastal. From Chenopodieae I, the genus *Einadia* is near-centred in the Highlands, and *Chenopodium* spp. occur throughout.

Dysphania and *Scleroblitum* can be similar in lifeform. Both clades are relatively poor in species, given their age, weakly express the taxon element and each species is widespread. Similar to *Scleroblitum*, *Dysphania* could be intolerant of return to mesic conditions, such as in the Wet Reversal of the Early Pliocene (Martin 2006). However, tolerance of temporarily disturbed, open areas (Grozeva and Cvetanova 2013) enables persistence in drier regions, unlike for the older *Scleroblitum*. *Dysphania* exhibits the least endemicity of any rich chenopod clade.

The distribution of Chenopodieae I has notable elements. Clade range expanded to near continental scale in less than 4 Ma. The clade is species poor in the Central Lowlands, where other rich clades are diverse. Chenopods generally prefer open, sun-lit areas (Kuhn 1993), but the clade's ecological niche includes being an understorey plant tolerant of shade. In contrast, *Dysphania* richness is greatest in the northern Eyre-Murray Centre, where Chenopodieae I richness is poor.

Dispersal capacity contributes to rapid expansion and explains mesic associations. The semi-succulent fruit of *Einadia* and *Rhagodia* is dispersed by birds (Wood 1937; Lang *et al*. 2003; Brown 2014). *Enchylaena* has a similar berry, and is the most widespread species in the older Sclerolaenid clade. Consumption by woodland birds may favour *Einadia* in the Eastern Highlands. The coastal range of *Rhagodia* is comparable to coastal taxa of other clades, especially older *Atriplex* clades. Its greater extent along the Eastern Highlands coast, infers faster rate of range extension.

Chenopodieae I has few species that are extensively dominant. Some widespread inland taxa dominate or co-dominate understoreys in *Eucalyptus*, *Acacia* or *Callitris* woodland, including *Rhagodia parabolica* (Brandle 2001; Brandle *et al.* 2010), *R. drummondii* (Pringle 1998) and *R. eremaea* (Payne *et al.* 1988; Curry *et al.* 1994; Lang *et al.* 2003). In the dry Central Lowlands, they occur beneath trees and tall shrubs e.g. *Rhagodia spinescens*, or are sparse groundcover species e.g. *Chenopodium desertorum*. Only in drainage systems are they abundant e.g. *Chenopodium auricomum*, *C. nitrariaceum* (Boyland 1974; Mollenmans *et al.* 1984; Brandle 2001; Lang *et al.* 2003). Such occupation points to "Boyko's Rule" (Shmida 1985) – taxa of mesic environments occupy mesic habitats of adjoining drier environments.

Taxonomic revision of Chenopodieae I is essential to resolving clade membership and generic status. The cosmopolitan annual *C. glaucum* is the only coastal type other than *Rhagodia* spp., has non-indigenous varieties (Wilson 1984) and possibly belongs to a global *Oxybasis* clade (Fuentes-Bazan *et al*. 2012b).

Young coastal clades

Atriplex australasica and Suaeda

Distribution of youthful clades represents the early phases of invasion. Recent arrival limits diversification and the extent of inland ranges. Youth should be confirmed for all clades.

Characteristics of young clades are species poverty, prominence of coastal taxa and lack of inland species. Inland taxa are coastal species of limited range close to coastlines. The largely coastal *Suaeda* clade has species richness and range extent of inland populations between that of *A. australasica* and *Sarcocornia*. Inland ranges of *A. australasica* and *Suaeda* coincide in the western Murray Basin where the coastal littoral existed in the Pleistocene (Bowler *et al.* 2006). Estimated arrival of *A. australasica* of 2.4–0.1 Ma (Kadereit *et al.* 2010) relates to divergence from the Eurasian *A. glabriuscula*; Central Asian species are poorly sampled in molecular analyses. From exact dates for *Suaeda* and *Atriplex* arrival, rates of continental coastal range extension and of inland range extension in South Australia could be estimated.

This youngest clade identifies regional coastal landfall and departure in the Gulfs Ranges and Murray Lowlands provinces. Combination of date, range location and coast disposition would exclude arrival elsewhere with a subsequent range shift. Landfall to the west would be in very suitable habitats where extinction would be unlikely. Westerly coastal movements are unlikely with West Wind Drift, discounting landfall east of its current range.

Clade age provides movement rates subsequent to landfall. Populations farthest from the current coast indicate *A. australasica* departed the coast in the western Murray Lowlands. Current coastal range extension north along the eastern seaboard follows easterly movement through Bass Strait. *Atriplex australasica* could model the colonization and establishment stages of chenopod invasion. Current range and estimated arrival give expansion rates of 0.87–17.5 km each 1000 years.

Atriplex australasica is also in New Zealand similar to coastal *Atriplex* of Clades 1 and 2 though of uncertain status (see AK100625, AK247261 Auckland War Memorial Museum Herbarium).

Suaeda is on all Australian coasts, similar to *Tecticornia*. Though not contiguous on the north coast, coastal range exceeds that of *Sarcocornia*. An inland range in Mediterranean regions of southern Australia similar to *Sarcocornia*, and having comparable richness, suggests a similar age for *Suaeda*.

Taxonomic issues and arrival date for *Suaeda* need resolution. Australian *Suaeda* may not be a single clade and was possibly isolated from the global *Brezia* clade for a long time (Schutze *et al*. 2003). Exotic species are not clearly distinct from natives (Wilson 1984).

Salsola

Salsola is the most widespread of Australian chenopods. It is on all coasts, but as widely scattered populations on the northern and eastern coasts. Taxonomic status and arrival time of *Salsola* needs resolution. If proven native, young and diverse, an extraordinary range extension and diversification of continental scale has occurred.

Interpreting origins from richness, assembly and coastal presence

In the Centres of Diversity, the shared taxa reflect migrations and non-shared taxa reflect diversification that would in part be formative processes. Both are likely episodic within rich clades, given varied arrival time and lineages that emerge in a subcontinental expanse of increasing area and newly forming habitats.

Two major routes of range expansion between the centres are evident. An inland route with dominant axis through Sandland South Province (the Great Victoria Desert) is the main floristic link for the two centres. A coastal route is the southern coast that now has the shared coastal taxa. For the earliest clade arrivals, the south coast was the southern border of Sandland South province.

An easterly direction of range extensions is more likely. West Wind Drift is a recurring, easterly coastal movement. Aridity expanded from western to eastern Australia (Hill 1994; Martin 2006). An easterly speciation trend is noted in the Sclerolaenid clade (Cabrera *et al.* 2011). Being a general trend it could disguise a less common, westerly movement. More importantly, a propensity for easterly migration, means western landfalls would best explain the shared taxa.

A third migration is from coast to inland, which could occur in either centre. That in the Eyre-Murray centre would be from the southern coast, arising through an eastern landfall or following subcontinental coastal migration from a western landfall. Inland migrations in the Yilgarn Centre could begin at western landfalls on the western or southern coast or after coastal migrations of provincial scale.

Species restricted to a centre most likely arise in two ways. Adaptive radiation follows range expansion from a centre’s coastline or follows migration of an inland ancestral species from one centre to another. In the latter case, the more species that migrate, would reduce the size of the radiation. Partial extinction of widespread species leaving them resident in a single centre is unlikely, under conditions that increasingly favour chenopod survival.

Phylogenetic relationships of shared and restricted taxa should reflect formative processes. Major lineages of shared taxa and restricted taxa from either centre indicate migrations between centres, while domination by species restricted to a single centre represents adaptive radiation in coast to inland migration. Comprehensive phylogeny is necessary to identify distinct migratory episodes. Regional congruency of clade patterns identifies taxa and environments for detailed study. The phylogeny of *Atriplex* is examined in Chapter 4.

CONCLUSION

At least eleven coastal ancestors derive a modern flora of 302 species, distributed mostly in arid areas, through serial invasions involving range extension of continental scale and varied diversification. Fourteen provinces have 97% of all chenopod species. Ten provinces form the large and distinct Yilgarn and Eyre-Murray Centres of Diversity linked strongly through the Great Victoria Desert. All but two clades occur in both centres. Minor extinction is associated with disjunct species populations and possibly of ancient coastal species.

Two broad evolutionary scenarios are not mutually exclusive and likely varied within each immigrant clade. The Centres developed with initial range extensions of subcontinental scale followed by fragmentation of widespread populations. Alternatively, separate initial radiations in western and central-eastern regions, later merged with range expansions.

The chenopod assembly groups reflect barriers to range expansion. Northward movement from a retreating tropical zone has a notably diffuse boundary. Tolerance of seasonal warm subtropical climates enables easterly movement from the Eyre-Murray Centre, with similarly diffuse boundary. A sharp boundary at the cool, mesic Eastern Highlands shows a strong barrier to most clades.

Distribution of immigrant clades is broadly consistent with age. Older clades have more species and larger inland ranges. Young clades have few species and are predominantly coastal. Notable clade characteristics in evolutionary context are listed in Table 2.7.

The taxon element pattern of a littoral connection is observed in 10 chenopod clades and recognizable in all. Coast facultative types dominate coastal taxa, enabling arrivals to readily colonize, quickly establish and spread extensively along coastlines, which continues in modern times on the northern coast and eastern seaboard. However, coastal diversity of clades is generally low.

Clade	**Age (Ma)**	**Genera/ Species**	**Distribution**	**Taxon Element**	**Major Coastal Presence**	**Biogeographic importance, indicator or comparative interest**
Scleroblitum	42.2-26	1/1	South East Australia	None	None	Landfall in Murray Lowlands Oldest clade; parapatric with youngest clade Extinction (or abandonment) of coastal population
Sclerolaenid	16.4-10.3	12/150	Continental	Moderate	West, South, East	Richest in genera and species Migration of genera between centres and along coastlines Taxon cycling and possible coastal extinction Contemporary with *Dysphania* Clade
Dysphania	16.1-9.9	1/16	Continental	Weak	West, South, East	Species with sizeable ranges Notable mesic presence Contemporary with Sclerolaenid Clade
Atriplex Clade 1	9.8-7.8	1/8	Continental South	Strong	West, South, East	Richest in Yilgarn Centre Ecological prominence with low diversity Contemporary with *Tecticornia* Clade Similar niche to Sarcocornia Clade
Tecticornia	10.9-4.8	1/44	Continental	Strong	All	Near continuous coastal range Richest in Yilgarn Centre Contemporary with *Atriplex* Clade 1
Atriplex Clade 2	6.3-4.8	1/52	Continental	Strong	West, South	Richest in Eyre-Murray Centre
Sarcocornia	4-1.8	1/3	Continental Coastal	Strong	West, South, East	Potential coastal range expansion rate Extending range onto northern coast Contemporary with Chenopodieae I Clade
Chenopodieae I	4.2-2.9	3/24	Continental	Strong	West, South, East	Notable mesic presence Potential terrestrial range expansion rate Contemporary with *Sarcocornia* Clade
Atriplex australasica	2.4-0.1	1/1	South East Australia	Strong	South, East	Landfall in Murray Lowlands Youngest clade; parapatric with oldest clade Potential coastal and terrestrial range expansion rate
Suaeda	Unknown	1/2	Continental Coastal	Strong	All	Potential coastal range expansion rate Scant in arid regions
Salsola	Unknown	1/1	Continental	Moderate	All	Most widespread clade Very rapid expansion rate if proven young

Table 2.7: Notable distribution characteristics of Australian chenopod clades in evolutionary context

CHAPTER 3. CHENOPOD HABITAT – OCCUPATION OF AUSTRALIAN LANDSCAPES

INTRODUCTION

A littoral connection is a form of biotic exchange between coasts and deserts (Shmida 1985). Exchange occurs along corridors, through regional filters or over sweepstakes routes (Lomolino *et al.* 2010). Filters operate at landscape level selectively allowing passage of some forms while retarding that of others. Major factors are the suitability and distribution of habitat and the dispersive and adaptive capacity of taxa.

Migration and diversification of chenopods coincided with the developing arid landscape and coast to desert transitions occur where barriers are weakest. With the niche conservatism of a littoral connection, inland habitats most similar to the habitats of coastal chenopods would be preferably colonised, assisting range extension. Dissimilar habitats may be barriers to species occupation and range extension, requiring adaptation for occupation. Barlow (1981, 1994) implies direct edaphic transitions (e.g. where coast dunes meet desert dunes) while Burbidge (1960) suggested transitions between any saline habitats.

The connectivity and continuity of suitable habitat would control range extension in heterogeneous landscapes. These are important factors in the landscape spread stage of plant invasions (Theoharides and Dukes 2007) and in biogeographic context of migrations (Lomolino *et al.* 2010). In particular, they diminish the barrier of vast distance between coast and central desert. Where connectivity and continuity is lacking, migration from shorelines could require adaptation to each habitat dissimilar to coastlines.

Australian desert habitats were not equally available in time or space (Mabbutt 1988; Hill 1994; Fujioka and Chappell 2010). Some pre-existing landforms were notably modified e.g. arid uplands, but others are novel, having no prior equivalent e.g. gibber plains. Significantly for chenopods, the greater retention of surface salt as rainfall declines, creates suitable habitat out of less suitable habitat, enhancing connectivity and continuity of desert habitats. In this chapter, the role of the physical landscape in the broad geography of chenopod evolution is broadly examined, especially the filtering of chenopod migrations by and speciation within inland habitats, in a context of Neogene landscape history.

BIOGEOGRAPHY AND HABITAT IN LITTORAL CONNECTIONS

Habitat, diversification and adaptation as used in this study are defined in Table 3.1

Item	Definition	Source
Habitat	The abiotic and biotic environmental conditions under which a species persists, often expressed as ranges within limiting variables e.g. temperature	Crawley 1997; Lomolino *et al.* 2010
Diversification	Numerous species descending from an ancestor	Lomolino *et al.* 2010
Adaptive radiation	Diversification of form and lifestyle over different niches in a relatively short time, occurring at any scale	Lomolino *et al.* 2010
Adaptation	The possession, or attainment, of functioning traits that allow an organism to better persist in its habitat	Smith 1993; Cox and Moore 2010; Lomolino *et al.* 2010; Evert and Eichhorn 2013
Exaptation	A functional change to a trait enabling the occupation new habitats	Thain and Hickman 2004
Filter	Dispersal route in a biotic migration that selectively allows some forms to pass while retarding others	Cox and Moore 2010; Lomolino *et al.* 2010

Table 3.1 Definitions for biogeography and habitat

Niche conservatism strongly influences diversification, with descendant species in habitats resembling that of an ancestor (Wiens and Graham 2005; Wiens *et al.* 2010; Crisp and Cook 2012) and is prominent in the early generations of an adaptive radiation (Flohr *et al.* 2013). Adaptive radiations are noted in Australian chenopod clades (Shepherd *et al.* 2004; Cabrera *et al.* 2009; Kadereit *et al.* 2010). Adaptation arises from mutation in gene components or structures (Pierce 2014). In the micro-mutationalism hypothesis, small mutations more likely realise an adaptive benefit, but large mutation is disadvantageous (Parsons 1988; Ram and Hadany 2015).

Clade history is an interplay of niche conservatism and niche divergence (Wiens and Donoghue 2004; Holt 2009; Donoghue and Edwards 2014). Descendants are constrained to ancestral niches but micro-mutationalism enables shifts to new ones. Salt-tolerance is an exaptation for drought tolerance, enabling occupation of arid areas (Osmond *et al.* 1980; Flowers *et al.* 2010), with migration filtered through the distribution of habitats variably suited to occupation.

Habitat and trait elements in littoral connections

Habitat element

The habitat element in a littoral connection is the sandy, marshy and saline habitats that coast and desert taxa share. Specific conditions plants must tolerate are dry and mobile sands (Clarke 1994c; Danin 1996), marsh inundation and anoxia (Colmer and Flowers 2008) and salt toxicity (Lambers *et al.* 2008; Taiz and Zeiger 2010). Desert habitats that are not salty, sandy or marshy (e.g. arid ranges) would be barriers, as these support glycophytes which are more competitive (Waisel 1972; Flowers *et al.* 2010).

Landscape filters operate in time and space. A gradual onset of aridity weakens barriers to chenopod range extension as rainfall becomes insufficient to leach soil salt. Diversification may begin as micro-mutationalism facilitates expansion into habitats slightly different to those already occupied. Conversely, strong barriers of unsuitable habitat prevent easy chenopod entry and could require a notable adaptation for occupation.

Trait element

The trait element is the common adaptations of sister taxa for occupying the shared habitats of coast and desert. A trait may be an exaptation; in this context, an attribute enabling desert occupation, but with a different function at the coast.

Salt tolerance is a major adaptation. Chenopods are mainly coast and desert species, associated with high incidence of alkali salts (Kuhn 1993). Salt tolerance gives halophytes an advantage over glycophytes, which otherwise out-compete halophytes in non-saline conditions (Waisel 1972; Flowers *et al.* 2010; Flowers and Colmer 2015). About 0.14% of all plant species are halophytes (Flowers and Colmer 2015) but chenopod formations cover about 6-7% of Australia (Graetz and Wilson 1984; Leigh 1994). Salt tolerance make plants tolerant of aridity (Osmond *et al.* 1980; Flowers *et al.* 2010) as the added intake of soil cations without toxic effect, increases soil moisture capture. Also, salt glands which regulate salt content, have the form of hairs or scales that reflect radiation and conserve moisture in very dry and hot regions (Kuhn 1993).

A coast-desert comparison of occupied habitat ideally includes the traits facilitating occupation. Such comparison is beyond the scope of this study due to the nature of salt-tolerance and poor knowledge of niches specific to chenopod taxa, even among particular groups e.g. saltmarsh flora (Saintilan 2009b). Salt tolerance is a complex trait of physiological processes and part of a syndrome for handling inundation (Flowers *et al.* 2010; Flowers and Colmer 2015). Also, the adaptations in speciation may not relate directly to coast and desert conditions e.g. dispersal traits.

Habitat variation and occupation traits

Difference in coast and desert habitat

Chenopod differentiation within major factors of plant distribution variation is broadly understood. Salicornioideae and Suaedoideae are commonly of flooded, saline habitats (Schutze *et al.* 2003; Kadereit *et al.* 2006) while Chenopodioideae, Camphorosmoideae and Salsoloideae are commonly of drier, less saline habitats (Pyankov *et al.* 2001; Kadereit *et al.* 2010; Kadereit and Freitag 2011). Australian chenopod ancestors arrived with capacity to occupy a wide range of habitats.

Temperature, moisture and solar radiation along with edaphic influences are major abiotic factors in plant distribution at local to global scale (Woodward 1987; Crawley 1997; Lambers *et al.* 2008; Evert and Eichhorn 2013). Coasts and deserts differ markedly in specific variables of temperature and moisture, particularly in diurnal and seasonal extremes (Strahler 1971). The resultant physiological impact of heat and water stress ultimately affect growth, longevity and reproduction (Crawley 1997). Selection pressure in deserts consequently promotes low-growing, open vegetation in contrast to arborescent forms of mesic conditions (Laity 2008).

Western North American plant communities indicate the climatic variations of coast and desert that chenopods tolerate (Chabot and Mooney 1985). Suites of chenopod taxa, particularly of *Atriplex*, are prominent in adjoining cold desert, warm desert and coastal regions. Coastal proximity moderates radiation, temperature and humidity (Barbour *et al.* 1985). Seasonal and diurnal temperature variations in deserts are extreme. In warm deserts, temperatures for much of the day in growth periods may exceed 30^{o} C, with summer maxima above 38^{o} C (Ehleringer 1985). In cold deserts, the mean daily minimum is below freezing for 5 months of the year; the few shrub species being only from Asteraceae or Chenopodiaceae

(Caldwell 1985). High radiation and low humidity induces extreme soil surface temperature (Ehleringer 1985), placing sustained moisture stress on desert plants (Caldwell 1974), but coastal humidity with fog and cloud greatly ameliorate coastal radiation (Barbour *et al.* 1985). In this region, *Atriplex confertifolia* is photosynthetically active from 5° C to 50° C, one of the widest ranges known (McArthur and Sanderson 1984). Chenopods occur at altitudes from *ca*. 1500 m to *ca*. 3500 m in the deserts of North America (Welsh 1984; Caldwell 1985), Central Asia (Grubov 2000) and South America (Reiche 1911), while also being at sea level on these continents. Such variations exceed Australian conditions.

Salinity controls plant distribution (Tivy 1993; Crawley 1997; Bui 2013) and may be the major edaphic factor in natural habitats (Osmond *et al.* 1980). Surface and soil moisture availability, as affected by soil texture, along with alkalinity and salinity, largely control the distribution of chenopod formations in western New South Wales (Eldridge 1988).

Coast and desert habitats vary in surface hydrology, saline chemistry and nutrient cycling. In coastal marsh, salt-water inundation and immersion is regular and frequent and subsoils always saturated, compared with erratic, desert flooding (Waisel 1972; Ungar 1974). On the coast, relatively greater nutrient cycling produces vegetated stable dunes, in contrast to bare, mobile desert dunes (Danin 1996). The organic nutrient poverty of coastal foredunes (Specht 1972; Beadle 1981b; Clarke 1994c) is similar to that of desert dunes, especially in a characteristic lack of nitrogen (Caldwell 1974).

Salt chemistry of Australian coast and desert habitats is marginally different. Saline moisture regimes of coast and desert in North America and around the Mediterranean, differ in salt type, source and influx (Waisel 1972; Caldwell 1974; Ungar 1974; Danin 1996). The origin of salt in Australian landscapes is largely cyclic, concentrated through evaporation of surface run-off or emerging, shallow groundwater flow (Chivas *et al.* 1991; George *et al.* 2008).

The adaptive requirements of invading taxa are reduced if they possess a broad tolerance to a range of abiotic conditions. Chenopods are tolerant of marked ranges in temperature, humidity, elevation and soil type, including coast and desert differences. Tolerance of broad ecological ranges is an attribute of invasive plants colonising new habitats (Theoharides and Dukes 2007; Cox and Moore 2010).

Salt-tolerance and other shared traits

Morphologies of salt-tolerance are common characters of coast and desert species. Succulent leaves or stems hold extra water to manage salt toxicity (Kuhn 1993; Hegazy and Lovett-Doust 2016). Stem succulence is characteristic of Salicornioideae. Leaf succulence is most prominent in Suaedoideae, Chenopodioideae and Camphorosmoideae.

Chenopods in low salinity habitats exhibit xeromorphic characters (Kuhn 1993). Ancestral Australian chenopods likely arrived with traits functionally suited to desert conditions. Moisture conservation mechanisms such as microphylly, sunken stomata and thick, epidermal coatings are common (Kuhn 1993). Chenopods are generally light demanding plants, requiring conditions of high exposure (Kuhn 1993). A predominance in hot and dry habitats is attributed to C_4 photosynthesis, widespread within *Atriplex* (Kadereit *et al.* 2010; Kadereit *et al.* 2012) and Salsoloideae (Kuhn 1993; Pyankov *et al.* 2001) but rare within *Tecticornia* (Shepherd and Van Leeuwen 2007). Australian *Atriplex* Clades 1 and 2 are part of a global C_4 clade, but the distantly related *A. australasica* is C_3.

Species of sandy substrates have particular xeromorphic traits. Sands drain freely and store no moisture in the common root zone during dry conditions (McKenzie *et al.* 2004). Chenopods grow ephemeral roots in response to rain for exploiting temporary stores and may have deep roots to access permanent reserves (McArthur and Sanderson 1984).

Tolerance of salt and immersion likely co-evolved under stress of saltwater inundation (Colmer and Flowers 2008; Flowers *et al.* 2010) and saline inundation is central to sharing coastal and inland habitats (Osmond *et al.* 1980). Salt tolerance is a complex of physiological processes that operate variably across plant taxa (Flowers and Colmer 2008; Flowers *et al.* 2010). Halophytes originating in coastal marsh survive flooding and hypoxia, compartment toxic ions, select essential potassium over the chemically similar and little-needed sodium and exclude toxic salts from shoots (Flowers *et al.* 2010). Most adaptation in plants of warm deserts is in the physiological interaction of photosynthesis and water use (Anderson 1982;

Ehleringer 1985). An additional problem is the energy cost of physiology, given small leaf size, low plant stature and presence in nutrient-poor ecosystems.

For these reasons, analysing distribution patterns of trait sharing across sister taxa of coast and desert habitats is an impractical exercise. Traits may not be simple and discrete, readily noted as present or absent and not easily observed morphologically e.g. root structure, physiological. With exaptation, a trait in coastal taxa functions differently in related desert taxa. However, desert conditions impose stresses similar to those of coastal existence.

The radiation of modern *Atriplex* exploits a “gamut of strategies associated with growth form, perenniality, reproductive behaviour and physiological processes”, for coping with climatic, edaphic and biotic disturbance and that may apply generally to chenopods (Osmond *et al.* 1980:131). *Atriplex* commonly shows weedy and ruderal character in the secondary succession of disturbed environments, especially anthropogenic ones, not unlike drift-line processes of beaches and estuaries. A weedy character is useful in surviving episodic, shoreline change (Heads 2014).

Habitats of seashores, marshes and desert conditions favour ruderal species (Grime 1979, 2001; Ward 2009). Tolerance of inundation and immersion explains much of the global range of *Atriplex* (Osmond *et al.* 1980), selecting for adjustment of plant life cycle to disturbance periodicity (Tivy 1993) e.g. rapid growth and early maturation before the next disruption. Plants marginal to open water of rivers and lakes, in zones reflecting water level, adopt similar strategies (Grime 1979, 2001). Desert species unable to reliably access sufficient water, and sensitive to temperature and humidity extremes, favour growth and reproduction strategies of brief life cycles and seed longevity (Caldwell 1974). This rapid response needs nutrients. Both coastal and inland chenopods cope with nitrogen scarcity (Caldwell 1974), probably through a complex association with soil-bacteria (Macdonald *et al.* 2015).

Major adaptations of desert plants are the enhanced capture, storage, minimal loss and efficient use of water. Such means are classed as drought tolerance, resistance or endurance or drought evasion, avoidance or escape (McCleary 1968; Crawley 1997; Ward

2009). An ephemeral or ruderal life strategy is a form of drought escape and the shedding of leaves is a form of drought tolerance.

In summary, habitat and trait sharing patterns of a littoral connection relate to coastal and inland habitats that are sandy or saline marsh. Adaptation is not needed for habitat sharing but could be expected for occupying dissimilar ones. Chenopods tolerate greater ranges of environmental variables than occurs in Australia. Salt-tolerance largely links coast and desert, but is relatively uncommon among plant taxa, operating within a complex of stress tolerance that includes flooding, is an exaptation for drought-tolerance, and is largely managed physiologically. The major attributes for desert habitat occupation, arrived with coastal ancestors.

LANDSCAPE CHANGE AND BIOGEOGRAPHIC PROCESS IN AUSTRALIA

Chenopods migrated into a drying interior prior to extensive formation of arid landscapes. Older chenopod clades arrived at the onset of Australian aridity, when mesic, arborescent floras covered much of inland Australia (Hill 1994; Martin 2006). Pliocene floras with *Acacia*, composites, grasses and chenopods, considered diagnostic of arid vegetation (Martin 2006), coincide with the arrival of younger clades. Landforms symptomatic of modern aridity are of Pleistocene age.

Neogene landscapes

Continental landscape change

The Neogene evolution of terrestrial Australia is described in Hill (1994), Drexel and Preiss (1995), Frakes (1999) and Fujioka and Chappell (2010). Martin (2006) and McLaren *et al.* (2014) describe changes in climate and vegetation. From a drying trend starting in the Eocene, the modern, arid climate began to emerge in the later Miocene and fully developed in the Pleistocene. Stratigraphy of the Eucla, Lake Eyre and Murray sedimentary basins, which cover much of the Yilgarn and Eyre-Murray Centres, reveal broad changes that increasingly favoured chenopod occupation.

Late Tertiary sedimentary sequences of the Eucla Basin reveal gradual drying trend across south and west Australia (Quilty 1994; Benbow *et al.* 1995a; Benbow *et al.* 1995b; Hou *et al.* 2008) where arid woodlands, arid grasslands and chenopod low shrubland replaced early Neogene rainforest (Benbow *et al*. 1995a, Martin 2006). The basin is part of a vast catchment with negligible modern flow, but once drained the Yilgarn Craton in Western Australia, Musgrave Block in Central Australia and Gawler Craton in South Australia. Drainage discharge declined over the Mid-Eocene to Miocene, changing marine sediments from alluvial sand and silt to limestone. Very high rainfall is required for the high river discharge needed to carry voluminous alluvium over a vast, flat landscape. Marine limestone forms in the absence of fluvial sediment and rivers emptied into lagoons behind coastal barrier dunes. In the west, rivers met the coast up to the Early-Middle Miocene and in the east an oceanic exit may have existed in the later Miocene on western Eyre Peninsula.

Basins on Australia's west coast present similar histories (Hocking *et al.* 1987; Hocking and Preston 1998).

Continuing rainfall decline and further discharge reduction is evident in Late Miocene and younger sediments of catchment drainage (Clarke 1994b, 1994a; Benbow *et al.* 1995a; Benbow *et al.* 1995b; Alley *et al.* 1999; Hou *et al.* 2003; Hou *et al.* 2008). Dolomitic and gypsic evaporites dominate sequences on eastern and western margins of the Eucla Basin, with gypsic-saline deposits more abundant in younger sediments. Dolomite forms in ponded lakes of limited annual flow under a marked dry season. Gypsic sediments are residues of lakes drying completely, indicating long periods of no flow at all.

Under the drying trend, vegetation type changed from mesic to sclerophyllous to xeric, but not uniformly (Kershaw *et al.* 1994; Benbow *et al.* 1995a; Martin 2006). Over the Eocene and into the Oligocene, rainforest taxa in the northern Eucla Basin, changed to mainly sclerophyllous *Casuarina* with some eucalypts. Rainforest taxa dominated eastern South Australia. This west-east contrast lasted into the Early Miocene. By the later Miocene, *Acacia* had emerged in the west and sclerophyllous taxa had largely replaced rainforest taxa in the east. Prominence of *Casuarina* with increasing eucalypts and *Acacia*, indicates sufficient rainfall to support arborescent formations, and a significant dry season with an associated fire regime (Martin 2006). Over the Late Miocene to Early Pliocene, chenopod shrubland in the eastern Eucla Basin contrasted with dry open woodland to the east (Benbow *et al.* 1995a). In the southwest Lake Eyre Basin the woodland also had chenopod scrubland, but in Eyre Peninsula and Gulfs Ranges provinces it had rainforest patches.

When arid landscapes became dominant is uncertain. Arid climates are inferred if pollen from grasses, composites and chenopods dominates sediment cores, relative to that of arborescent or sclerophyllous taxa (Truswell and Harris 1982; Kershaw *et al.* 1994). Such a pattern is absent in the Miocene, episodically interrupts dominance of sclerophyllous *Casuarina* and *Eucalyptus* in the Pliocene and is common in the Pleistocene (Kershaw *et al.* 1994). Sampling issues of discontinuous sequences and imprecise dates confound analyses.

The warm Australian Tertiary climate was humid with relatively dry and regionally variable seasons (Kershaw *et al.* 1994; Quilty 1994; Benbow *et al.* 1995a; Martin 2006). Dolomite deposition in vast lakes shows substantial rainfall with a marked dry season in Central Australia until the Late Miocene. An aseasonal aridity developed by the Pliocene. Charcoal fossils of the Oligocene to Early/Mid-Miocene in central and south-eastern Australia reflect burning in dry seasons and the emerging prominence of eucalypts. It is more abundant throughout eastern Australia in the Late Miocene.

Change processes and selection pressure

Increasing aridity alters land surface hydrology, affecting land forms, soils and vegetation. Resistant forms (e.g. hills, ranges) are retained in erosional landscapes, but in depositional ones (e.g. alluvial plains) new land types with no mesic equivalent can emerge.

Change in soil-water balance changes land surfaces (McKenzie *et al.* 2004; Bui 2013). Precipitation is intercepted above ground, evaporates, runs across the land surface or infiltrates the soil. Infiltration may be stored, taken-up by plants, evaporated from shallow depth or drain to groundwater. As rainfall declines, the partition amounts change variably, depending on soil type, land surface and mesoclimate. Deep sand changes least in proportions of the partition. In non-sandy soils, that part lost to deep drainage becomes negligible and that lost to evaporation and plant interception greatly increases. Evaporation from soil induces salinity or alkalinity (Smith 1968; Laity 2008). Across all soil types, desert soils are generally drier at the surface, and organic matter content is much reduced, especially of nitrogen (Fuller 1974; McKenzie *et al.* 2004; Laity 2008). Salt washed downslope accumulates in low-lying parts (Walter and Stadelmann 1974; Laity 2008), with variation markedly influencing local ecology (Whitford 2002).

Rainfall decline transforms landscapes through effects on vegetation, which protects land surfaces from meteorologic impacts e.g. heavy rainfall and run-off, strong winds (Marshall 1972; Fuller 1974; Laity 2008). Low rainfall induces open and low vegetation with bare surfaces between shrubs in the driest times. Dune fields form when land surfaces are exposed to the wind (Twidale and Wopfner 1991; Laity 2008, Nichols 2009), due to reduced vegetation. Similarly, desert pavements form where wind and water remove soil from unprotected surfaces (Mabbutt 1977a; Ward 2009), forming gibber plains with large surface run-off in Australia (McKenzie *et al.* 2004).

Dune fields and stony pavements are of greatest extent in deserts, actively forming in the driest desert conditions (Fujioka *et al.* 2005; Fujioka *et al.* 2009; Fujioka and Chappell 2010), but are not unique to them as they are also coastal and glacial forms (Mabbutt 1977a; Thornbury 1985). Stony pavements occur in subtropical granite country of moderate rainfall, prompting suggestion of edaphic aridity as a factor in angiosperm evolution (Stebbins 1952; Axelrod 1972). The only unique arid land form is disorganised drainage (Mabbutt 1977a; Thornbury 1985), which is widespread in Australia (Mabbutt 1969). Limited rainfall, lack of gradient and sediment blockage create discontinuous catchment tributaries where channel segments have terminal salt flats. Salt-pans and salt-lakes are also in temperate coastal regions. Co-occurrence of dune fields, stony pavements and disorganised and saline drainage does represent aridity (Fujioka and Chappell 2010), but more importantly they are novel landforms with vacant habitats.

Drying landscapes create evolutionary opportunities for resident and invading plant taxa. Xerophytes develop enhanced moisture capture, storage and efficient water use for drought tolerance or evasion strategies. Xerohalophytes use soil salt for drought-tolerance (Zohary 1962; Waisel 1972; Batanouny 1994) and share some xerophyte features (McArthur and Sanderson 1984). To survive emerging aridity and salinity, resident taxa fit to a halophyte-xerophyte spectrum. As salt-tolerance evolved independently and rarely in plant taxa, and in association with coastal flooding (Flowers *et al.* 2010), resident taxa more likely become xerophytes. Emerging saline habitats are migration opportunities for salt-tolerant plants, but do they become xerophytes?

Provincial Land Types – content, age and dynamics, coastal similarity

Mabbutt (1969, 1977b, 1984, 1986, 1988) maps and describes eight Australian desert landscapes: their tectonic setting and landforms, geomorphic processes (soil development and hydrology) and vegetation. The landscapes are the physiographic basis of ASRIS (Pain *et al.* 2011) and the provinces for sampling chenopod distribution (Chapter 2). Table 3.2 lists them in context of landscape change. Novel land types have no mesic counterparts in inland areas. Modified land types are inland landscapes retaining elements of mesic forms but with critical climatic transitions in their evolution.

The landscapes have been used to describe Australian vegetation (Cunningham 1981; Fox 1999) and to explain desert ecology (Whitford 2002) and arid geomorphic processes (Yang and Goudie 2007). The interaction of climate with regional, base geology (structure and lithology) and geomorphology (landforms and processes) determines soil characteristics and shapes ecosystem processes. With the principal character of deserts being water scarcity, the influence of landforms on hydrology (e.g. infiltration, run-off, erosion, moisture storage, salt accumulation) determines the nature and distribution of vegetation (Whitford 2002).

	Novel	**Area %**	**Modified**	**Area %**
Saline/Alkaline	Desert Lake Stony Desert	1 15	Karst Plain Desert Clay Plain Riverine Desert	3 4 9
Xeric	Sand Desert	38	Desert Upland Shield Plain	16 14

Table 3.2: Classification of desert land types based on relationship to pre-Arid forms and substrate chemistry. Area is percent area of Arid Zone as listed in Mabbutt (1988).

Table 3.3 describes landforms and processes, salinity and vegetation of Mabbutt landscapes and identifies analogous coast habitats based on Chapman (1976). These coast habitats and desert landscapes share form and process despite different geomorphic scale. Table 3.4 indicates particular aspects of habitat ecology or origin that could influence plant occupation. Coast and Mesic Plain & Range types are added for a complete range of potential habitats.

Four coastal habitats are significant for terrestrial plant species (Chapman 1976): salty and brackish marsh, sand dunes and slacks, shingle beaches and coastal cliffs. Shingle beaches are restricted in occurrence and have little vegetation, due to pebble movement and absence of soil. The main coastal plant habitats of marsh, dune and cliff, are also the major coastal forms in Australia (Specht 1972, 1981a; Beadle 1981b; Love 1981; Davies 1977, 1986; Adam 1994; Clark 1994c).

Land Type	**Landforms/Processes**	**Soil/Salinity/Vegetation**	**Coast Analogy**
Novel			
Desert Lake	Disconnected, saline complexes in pans, flats with marginal lunettes; or vast lakes of regional lowlands; irregular inundation with saturated subsoils; highly saline lowlands of temperate plains.	Common salts of sodium chloride, calcium sulphate and calcium carbonate. Vegetation zones of different chenopod taxa across sharp salinity gradients from bare salt crust to slight salinity on margins.	Saline marsh similar to coastal marsh, with inundation of muddy substrates. Lunettes marginal to inland marshes can be deep sand.
Sand Desert	Aeolian dune fields and sandplains; discontinuous or in long, linear dunes; occupy basin lowlands or mantle Shield Plain and pediments of Desert Upland. Stable slopes under vegetation cover, with mobile sand on dune crests.	Deep, red sands of neutral reaction trend; saline where thin sand sheets cover older landscapes. Hummock grassland, *Acacia spp.* tall shrubland or *Eucalyptus spp.* open woodland/mallee is major vegetation.	Coast and desert dunes have deep sands prone to surface disruption, mass movement and dry subsurface soil (Danin 1996). Coastal vegetation when present is generally stable.
Stony Desert	Dissected tablelands and plains of pebbly pavements (gibbers); with or without gilgai. Complex drainage networks due to lack of infiltration that causes high surface run-off (McKenzie *et al.* 2004).	Clayey soils, moderately to strongly saline; much varied lime and gypsum; calcium and magnesium salts near surface. Low grassy/chenopod formations (Brandle 1998) due to extreme exposure and very dry conditions.	Stony Desert (and Desert Clay Plain) have no obvious geomorphic analogues to coastal habitats; salt presence and exposure are common conditions.
Modified			
Riverine Desert	Desert drainage systems mainly in Lake Eyre and Murray Basins. Occasional channel flows with infrequent inundation of extensive floodplains. Sheet flooding on alluvial plains when rain abundant. Annual monsoonal or alpine flow of varied volume, in the northern and eastern arid zone.	Regularly inundated features less saline than more distant plains of mild to moderate salinity. Clay flats hold water. Vegetation open and arborescent along channels and floodplains; grassy and chenopod formations in broad flats; extensive chenopod low shrubland on dry alluvial plains.	Flow regimes resemble upper estuarine systems and tidal flats. Channel/flood flows and tides scour land surfaces and deposit sediment; alternate inundation with fresh or saline water; salinity of floodplain standing fresh water increases under evaporation.
Desert Clay Plain	Broad, alluvial plains of heavy soil in north-east Australia. Eco-physiologically similar to Stony Riverine Desert.	Strongly alkaline or mildly saline dark clays. Open *Astrebla* spp. grasslands; chenopod species in groundcovers.	Salt presence and exposure are common conditions; no recognizable geomorphic element.
Desert Upland	Rocky ranges, hillslopes and tablelands of sedimentary rock (sandstone and quartzite); stone mantled foot-slopes. Includes major uplands such as MacDonnell, Flinders and Barrier Ranges and Kimberley Plateau.	Thin, stony soils; non-saline and non-alkaline except on limestone substrates. Saline or alkaline sections downslope. Sclerophyllous woodland, *Acacia* shrubland and hummock grassland (*Triodia*, *Plectrachne*).	Coastal cliff and Desert Upland commonly share high exposure, steep slope and thin soil with much outcrop, but critically differ in the presence of salt-spray.
Shield Plain	Subdued, rocky landscapes of igneous and metamorphic rocks in Western, Central and South Australia, that has sandplain mantles.	Exceptionally varied soils being neutral, saline or calcareous, deep or shallow with surface sand or clay. Vegetation similarly varied with sclerophyllous woodland, shrubland and grassland.	Coastal cliff and Shield Plain commonly share high exposure and thin soil with much outcrop; critically differ in the presence of salt-spray.
Karst Plain	Bunda Plateau on the Nullarbor Plain is a flat plain of low elevation on crystalline limestone; undulating plains of pedogenic sheet calcrete across southern Australia.	Shallow, alkaline loams over thin calcrete; saline near the coast. Prominently chenopod (*Atriplex* and *Maireana*); "limestone taxa" dominates shrub layers and groundcovers.	Karst Plain resembles rocky cliff coastal habitats of a calcareous nature and coral cay islands in tropical waters.
Mesic Plain and Range	Temperate to subtropical ranges and plains of eastern, southern and western continental margins; includes igneous peneplain, alluvial plain and fixed dunes.	Soils commonly acid-neutral trend, but alkaline in drier regions. Sclerophyllous vegetation dominant; chenopod taxa in very seasonal climates or on heavy soils in drier areas.	Largely dissimilar to coastal habitats; higher rainfalls readily leach salt.
Coast	Beach-dune complexes; coastal lagoons and estuaries; rocky shores or cliffs; shingle beaches in Bass Strait and Tasmania.	Marine chemistry determines saline characteristics; dominated by sodium chloride. Coastal shrubland, heath and saltmarsh.	

Table 3.3: Land types based on Mabbutt (1988) and their similarity to coastal habitats. Soil description largely derived from Stace *et al.* (1968), McKenzie *et al.* (2004).

	Land Type	Ecological process/associations	Origin
Novel	Desert Lake	Some saltmarsh communities of coast and inland are floristically very similar (Bridgewater & Cresswell 2003; Saintilan 2009a,b).	Desert Lake emerged from Riverine Desert landscapes, forming disconnected flats in the vast, flat Australian continent.
	Sand Desert	Substantial water storage capacity of sand dunes assists survival of tree and tall shrub forms in dry areas (Walter & Stadelman 1974) especially in South Australia (Sparrow 1989).	Formation of dune fields is associated with substantial denudation of landscapes (Twidale & Wopfner 1990; Laity 2008).
	Stony Desert	The driest desert land type: lack of infiltration results in very high surface run-off; intense attraction of water molecules to clay particles in dry soil (Walter & Stadelman 1974; Laity 2008).	Maximum Australian development occurred in areas of least rainfall during global dry phase (Fujioka & Chappell 2009).
Modified	Riverine Desert	Floristically similar coast and inland saltmarsh communities are in Riverine Desert (Bridgewater & Cresswell 2003; Saintilan 2009a,b).	Emerged in the west in mid-Miocene when palaeovalleys ceased to flow (van der Graaff *et al.* 1977).
	Desert Clay Plain	For chenopods, this habitat is similar to Riverine Desert clay floodplains and Stony Desert, where gibber cover is scarce.	Tertiary lacustrine and alluvial clay deposits, exposed in the later Neogene (Christian *et al.* 1954; Turner 1993; Edgoose 2003)
	Desert Upland	Major uplands grade across climatic boundaries into subtropical and temperate ranges.	Uplands are younger than their constituent rock types. Major uplands in place through the Neogene (except maybe the Flinders Ranges).
	Shield Plain	Shield Plain climatically grades into Mesic Plain & Range, in coastal Mediterranean regions of Western and South Australia.	Cratonic platform that retains past elements of peneplanation and deep-weathering
	Karst Plain	The development of alkaline soils is critical process. Karst Plain also climatically grades into Mesic Plain & Range. The Gambier Karst of south-east South Australia only has coastal chenopod taxa.	The Nullarbor Plain has always been arid. The atypically flat surface of the Bunda Plateau is interpreted as evidence of little rainfall since the Late Miocene uplift (Benbow *et al.* 1995a).
	Mesic Plain & Range	The land type grades climatically into Desert Upland, Shield Plain and Riverine Desert.	Present since the earlier Miocene.
	Coast	Two primary coastal segments are defined on average river discharge rates (Davies 1988). A humid northern and eastern coast has more estuarine habitat than an arid western and southern coast.	The arid and humid coastal contrast likely developed over the Neogene

Table 3.4: Ecological and formative particulars of land types.

Specht (1981b) suggests shared calcareous substrates feature in littoral connections. Taxa of coastal calcareous outcrops of Western Australia have desert relatives (Diels 1905, 2007). Marine waters are saturated in calcium (Krumgalz 1982; Stacey and Hodgkinson 2013) and lime commonly occurs in desert soils (Brady and Weil 2008). Limestone has been extensive along western and southern coasts since the Miocene (Benbow *et al.* 1995b; Hocking and Preston 1998). Calcareous soils occupy drier southern Australia and adjoining agricultural regions (Stace *et al.* 1968; McKenzie *et al.* 2004).

Lime tolerance is advantageous for halophytes. As calcium intake off-sets sodium toxicity (LaHaye and Epstein 1969), lime-tolerance would assist occupation of saline habitats. For plants, excess calcium can inhibit the uptake of phosphorous, induce deficiency in mineral trace elements and render soils alkaline (Brady and Weil 2008), so halophytes tolerant of lime also gain competitive advantage.

In summary, the Tertiary sedimentary basins reveal rainfall decline with diminished catchment flows and associated vegetation change. Chenopods occur inland in the Late Miocene. Xeric vegetation emerges earlier in the west, is briefly episodic in the Pliocene and establishes in the Pleistocene. The mesic to xeric vegetation transition involved marked seasonality. Plant desiccation in warm and dry seasons exerts the initial selection pressure for xerophytism. Existing landscapes were modified climatically (Shield Plain, Karst Plain, Desert Upland, Riverine Desert and Desert Clay Plain). New landscapes were created (Stony Desert, Desert Lake and Sand Desert). Dry, saline or alkaline land surfaces favour xerophytes and halophytes.

Invasion, range extension and adaptation in littoral connections

Previous models of occupation and adaptation

Burbidge (1960), Barlow (1981, 1994) and Parr-Smith (1982) proposed littoral connections for Australian desert chenopods that variably incorporated habitat, range extension and adaptation.

Burbidge (1960) detailed an evolutionary model for the entire arid flora. Habitat affects range expansion and diversification, through shoreline shift, emergence of arid landforms and combined salt/flood-tolerance. Ignoring the impossible timeframe, the process involves:

- initial migrations through estuarine connections to inland lakes
- species range changes with lateral shift of coast and lake shorelines
- adaptation to arid habitats as the lakes dry up and dune fields form
- allopatric speciation with initial separation of coast and lake populations and subsequent isolation of populations within drainage systems

That dune field taxa emerge much later, fits the Late Cretaceous origin Burbidge favoured and complements the demise of mesic vegetation in the “Great Arid Period” (Crocker and Wood 1947).

Salinity and soil impose similar physiological conditions in deserts and at coasts, initiating species range extensions with direct edaphic transitions (Barlow 1981, 1994). Movement inland begins on arid coasts, with direct shifts to adjoining habitats requiring no adaptation. Transitions from coast dune to desert dune and coastal marsh to desert marsh would be a parallel diffusion through those habitats. Barlow (1981, 1994) also noted within the arid flora, general diversification trends of hybridisation and polyploidy and a shift toward self-compatibility, under fluctuating environmental conditions that include marked aridity.

Parr-Smith (1982) proposed an early evolution of *Atriplex*, based on morphological characters of shrub species, chromosome numbers and species ranges. A ‘primitive’ west coast form is identified as ancestral to two coastal migrations and three inland migrations. Habitats and ranges of listed species suggest the landscapes of transition. The general evolutionary trend is toward drought-enduring perennials and drought-avoiding annuals. *Atriplex* is now known to be two distinct clades.

Biogeographic plant invasion

Habitat influences all stages of biogeographic plant invasion and in complex manner for chenopod taxa. A major role in Landscape Spread and Diversification includes further transport, colonisation and establishment (Theoharides and Dukes 2007; Lomolino *et al.* 2010; Hampe 2011). Chenopod clades do not have equal opportunity to occupy land types that form in different places, at different times and in different ways. However, considering the nature of invasion, the development and distribution of land types and the evolution and distribution of chenopod clades, patterns in land type occupation can be expected.

The niche conservatism inherent in a littoral connection constrains the transformation of ancestral coastal bridgeheads into modern distributions. Transformation involves the least adaptation with migration mainly through familiar landscapes and adaptation to dissimilar land types is infrequent. Such a parsimonious outlook underlies biogeographic studies (Lomolino *et al.* 2010; Wiley and Lieberman 2011). The exactitude of parsimony is controversial, but it usefully infers and predicts from gathered data (Brower 2017).

Transport stage

Transport of seed or spore is very common in plants, and habitats where seed disperses without mortality are freely occupied (Lomolino *et al.* 2010). Chenopods arrived through long-distance, oceanic dispersal (Kadereit *et al.* 2005; Cabrera *et al.* 2009). Seeds are notably buoyant and germinate after saltwater storage (Ridley 1930; van der Pijl 1982; Kuhn 1993; Heyligers 2001) and can further disperse along shorelines after landfall. Chenopods are not solely reliant on water borne dispersal, being present in seral communities at varied distance from shorelines.

Colonisation and Establishment stages

The role of habitat differs in Colonisation and Establishment stages (Theoharides and Dukes 2007). Colonization success depends most on suitable abiotic conditions, while biotic conditions are critical to Establishment (e.g. plant competition, herbivory, pathogens and parasites). Invasive plants more readily make bridgeheads in habitats similar to a native range, because the required conditions of temperature, light, moisture and for breaking seed dormancy and initiating growth are most likely met (Lomolino *et al.* 2010). Coastal species from elsewhere are eminently suitable colonizers.

The native range of invaders has other influences (Theoharides and Dukes 2007; Lomolino *et al.* 2010). Wide, geographic native range permits survival in diverse habitats. Successful invaders tolerate temporal heterogeneity in resource availability stemming from disturbance that inflicts lethal stress on plant populations. Taxa adapted to such regimes colonize better than those that struggle, or that respond over longer periods, because fluctuating environments can select for dispersal ability. In seral coastal communities, the spatial and temporal nature of resource availability, is most acute near shorelines (Adam 1994; Clarke 1994c). Severe coastal disturbance concentrates resources in strandline debris or removes them in storm surges. Highly fluctuating and unpredictable resource availability, selected for the tumbleweed *Salsola iberica*, an effective dispersal and persistence of isolated plants, through hermaphroditism and reversion to self-compatibility (Lomolino *et al.* 2010).

The inland ranges of Coast facultative chenopod taxa suggest ecological tolerances wider than in Coast obligate taxa, which could have habitat limitations. Wider tolerances of Coast facultative taxa could be seen in occupation of diverse coastal habitats, which along with their prominence could signify an ancestral condition.

Landscape Spread stage

The nature and structure of landscape affects range extension. Most critical is how dispersal, landscape heterogeneity (including disturbance), patch dynamics and connectivity influence local extinction and migration, because these determine how species populations constitute regional presence (Theoharides and Dukes 2007). Organisms with large and continuous populations through non-uniform habitats tend to be successful at expansion (Lomolino *et al.* 2010). Habitat similarity allows ongoing colonization. Expansion also depends on spatial patterns of landscape heterogeneity, including the size and orientation of suitable habitat, the extent of unsuitable habitat between suitable patches and their variation in size or arrangement under disturbance regimes. A parsimonious view is that range extension proceeds through the least number of land types.

Range extension precedes diversification. A landscape younger than the earliest speciation cannot facilitate migration from the coast. Shepherd *et al.* (2004), Cabrera *et al.* (2009), Kadereit *et al.* (2010) and Kadereit and Freitag (2011) estimate radiation times of rich clades that would discount younger landscapes as facilitators.

Availability and connectivity of suitable habitat ultimately determine the capacity of plant species for rapid, large-scale range expansions at landscape to regional level (Hampe 2011). For Australian chenopods, a subcontinental landscape mosaic of continuity and connectivity comprises habitats variably suited to occupation and variably similar to coasts. Continuity is an unbroken length of suitable habitat, linking coast and interior. Connectivity is the contiguity of variably suitable habitats, including where dispersal overcomes intervening unsuitable habitats. Burbidge (1960), Barlow (1981, 1994) and Specht (1981b) emphasise continuity and connectivity of shared habitats, particularly of coast with Sand Desert, Desert Lake, Riverine Desert and Karst Plain.

An immediate impact of continuity is range extension along coastal habitats that begins Landscape Spread. Inland migration need not start at initial landfall but from any part of a regional coastline. Continuity and connectivity increase under a drying trend. At any one time, suitable habitats need not reach the deep interior, but extend as aridity expands or intensifies. Unsuitable habitats turn variably suitable as saline and alkaline soils develop under declining rainfall.

Habitats facilitating expansion would connect past coastlines to regions currently rich in chenopods. The only land types sharing habitats with coastlines and extending continuously from coasts into the Centres of Diversity are Riverine Desert and Sand Desert. Desert Lake is near continuous through the Yilgarn Centre, and almost connects to coastlines. In the Eyre-Murray Centre, it is discontinuous and disconnected from coasts.

Diversification stage

Within a geographic area, different habitats accumulate species of a given clade at varied rate, due to differing periods of occupation and rates of speciation (Stephens and Wiens 2003; Wiens 2011, 2012). A clade may invade one habitat before it occupies another. Habitat heterogeneity could exert diverse selection pressures under changing abiotic conditions. The degree of chenopod diversification can only relate to habitats present at the time of invasion and those of its subsequent transformation. Very young land types generally have less time available for diversification.

Wiens (2011, 2012) emphasises net diversification rate. Immigration readily raises the number of taxa in a habitat, while extinction reduces it. Extinction seems unlikely, given chenopod tolerance of coast and desert and increasing continental aridity, but it is suspected in the *Scleroblitum* clade.

Landscape pattern promotes diversification or local extinction through isolation at population edges (Theoharides and Dukes 2007). Persistent, vigorous isolates may become reproductively isolate and initiate allopatric speciation. Other isolates risk loss of variation, and their local extinction slows range extension. Hybridization from the mixing of once geographically isolated populations under renewed expansion could explain a rapid speciation of North American *Atriplex* (Stutz 1978, 1984; McArthur and Sanderson 1984).

For chenopod diversification in relation to inland habitat occupation and migration:

(1) Most species would be in land types with the longest period of occupation. Extensive land types that induce population isolation, or with diverse micro-niches variably selecting for adaptation could diversify at high speciation rate. The coast is extensive and the longest occupied, but the few species make extent, nature and age of inland habitats of primary interest. Shared inland habitats would be the first occupied in migrations and, if extensive, could be species rich, including endemics.

(2) The oldest habitats with the least chenopod species are barriers to occupation, particularly those with no species restricted to them. These would be dissimilar land types of Mesic Plain and Range, Shield Plain and Desert Upland, where habitat unsuitability prevents chenopod establishment. In Australia, areas of Shield Plain and Desert Upland are also distantly separated habitats that may not be reached simultaneously by chenopod clades.

(3) A significant proportion of species occupying a land type dissimilar to coast habitats would indicate notable adaptation. From a parsimonious view, eventual occupation of the most dissimilar habitat would be progressive adaptation to the least number of intermediary land types.

(4) The youngest habitats should have few chenopod species. Conversely, young land types with a high proportion of chenopod taxa, identify habitats of high diversification rate, especially if there are species restricted to that habitat.

(5) The prominence of Coast facultative species indicates adaptation is not necessary for coastal departure and occupation of similar inland habitats. Ready occupation of land types similar to and connected with coastal habitats i.e. Sand Desert, Desert Lake, Riverine Desert and perhaps Karst Plain, most likely enable departure.

In summary, a major influence of landscape is in Landscape Spread and Diversification. Transformation of coastal to desert flora involves inland migrations facilitated by continuity and connectivity of shared habitats that allows ongoing diffusion and exaptation for drought-tolerance. Adaptation may only be necessary for dissimilar habitats. Comparative species occupation of habitat in relation to age and distribution of inland land types, identifies the roles of habitat as accommodating expansion and diversification or as a barrier to them. Habitats facilitating expansions would be Sand Desert, Desert Lake, Riverine Desert and perhaps Karst Plain.

Disjunction

Habitats separating disjunct species populations are barriers of unsuitable habitat, irrespective of vicariance or long-distance dispersal (Cox and Moore 2010; Lomolino *et al*. 2010). Dune fields are strongly implicated vicariously in disjunct chenopod taxa of the arid inland (Chapter 2). Barlow (1981, 1994) suggests a dual role of dune fields – developing their own adapted plant associations and increasing disjunction between other taxa, but the exemplifying taxa are not chenopods.

Disruption caused by dune fields seems counter to being a shared habitat facilitating occupation in a littoral connection. The degree of chenopod occupancy and the habitats of disjunct taxa are of interest in identifying the nature of disjunction. The habitats of arid taxa with markedly disjunct populations should be those with preference for other than Sand Desert. Dune fields appear to be a disruptive event in the evolution of Australian chenopods as well as other plant taxa.

AIMS, OBJECTIVES AND METHODS

The major aim of this chapter is to identify the role of landscape in chenopod range expansion and diversification by analysing habitat occupation, distribution, formation.

Specific objectives are to:

- Establish the regional sequence of chenopod presence from existing molecular studies and landscape histories
- Identify the preferred land types of chenopod species, including species restricted to a single land type; Riverine Desert, Desert Lake and Sand Desert, being those inland land types most similar to coastal habitats, should be the preferred landscapes.
- Identify significant adaptation through notable occupation of inland habitats that are dissimilar to coastal ones
- Determine ecological ranges of tolerance for coastal species by comparing habitats of Coast obligate and Coast facultative species
- Identify transitions between shared habitats through comparison of habitats of coastal and inland populations of Coast facultative species
- Describe the nature of the landscapes separating disjunct populations of species with continental distribution (especially in arid areas) to identify occupation barriers.

Broad framework of expansion and diversification

A broad landscape framework for chenopod immigration is compiled from landscape and chenopod biogeography studies. Fujioka and Chappell (2010) summarise landscape history from specific studies. Regional chenopod presence is drawn from Kershaw *et al.* (1994) that develop vegetation histories for nine Australian regions. Stoian (2004) and Sniderman et al. (2016) describe the eastern Eucla Basin. Chenopod arrival and diversification is drawn from Shepherd *et al.* (2004), Kadereit *et al.* (2005, 2010), Cabrera *et al.* (2009, 2011), Kadereit and Freitag (2011) and Steffen (2015). Specific observations from sources are in Appendix X.

Habitat classification

Species habitats

All taxa are classified into Mabbutt land types, or as Coast or Mesic Plain & Range, using:

- National, state and regional floras, including online versions. National and state floras with the same source are assumed tailored to each state
- Published and online reports of systematic surveys e.g. Biological Survey of South Australia, Western Australia Technical Bulletins of Inventory and Condition, Queensland Regional Ecosystem Description Database
- Modern and historical regional ecological surveys and mapping e.g. (Blake 1937; Jessup 1948, 1951; Purdie 1984)
- Species information and fact sheets for land management, horticulture or conservation
- Herbarium specimen collection details as available through ALA/AVH, contained in Occurrence, Locality and Habitat fields and Additional Properties Data Sets
- Author's observations and experience

National, state and regional floras are primary sources, where listed habitats are matched to those listed in Table 3.3. Alternatives were checked where specific information is lacking or not easily classed to land type or a habitat. Ultimate resort was to build an occupancy profile from specimen collection data in AVH.

Coast and Mesic Plain & Range supplement the Mabbutt land types. Coast covers any habitat influenced by marine shoreline processes. Mesic Plain and Range covers tropical and temperate regions, largely applying to drier areas. Species poverty of tropical areas rendered unnecessary distinguishing tropical from temperate regions.

Frequency of occupation of coastal habitats is similarly compiled. Coastal species limited to a single coastal habitat are treated as a narrow range of tolerance; those with two or more have a broad range. Coastal taxa are classed in four habitats: three from Chapman (1976) being Beach-Dune, Estuary-Tidal flat and Cliff/Rocky, with Karst used for calcareous stony substrates. Frequency of occupation derives from sampling of AVH collection records. Results for South Australia taxa were compared with coastal floristics of Oppermann (1999), Heard (2003), Kenny and Thompson (2008), Neagle (2008) and Brandle (2010) to check consistency of observations.

Habitat class terminology and consistency

Classification criteria resolved issues of the Mabbutt landscapes intermixing and extending into non-arid regions. Desert Lake also includes saline lake complexes of temperate and subtropical areas because the vegetation is halophytic. Sand Desert only applies to arid and semi-arid regions. Sandplain and dune field with mesic vegetation of higher rainfall areas is classed as Mesic Plain and Range. Similarly, Shield Plain and Desert Upland where extending into temperate zones, become Mesic Plain and Range. Riverine Desert includes broad, alluvial valleys of uplands, similar to extensive alluvial plains which define the type. Karst Plain includes extensive, thick, pedogenic calcrete of southern Australia, where chenopods are dominant or in understoreys and groundcovers.

Land type terminology is based on desert landscapes of Mabbutt (1988). The names varied over the years in which the physiography was developed. “Land Type” is the term adopted here, with landscape retaining a general meaning and application. For clarity and consistency, the Land Types are initially capitalized and in singular form.

Disjunct species populations

Geomorphic mapping and description identifies landscapes that separate disjunct populations, along with age and process of formation. Focus is on disjunct species of arid areas, that are more numerous and have populations most broadly separated. Taxa from coastal, temperate and arid areas show disjunctions at continental and provincial scale, so the disjunction events are likely complex and possibly independent.

RESULTS

Chenopod presence and landscape history

Landscape and chenopod clade history is illustrated in figure 3.1. Lack of sediment core or analyses and uncertain stratigraphy, confounds identifying presence through time and it is not possible to distinguish chenopod clades using pollen. Initial diversification in *Dysphania* and Chenopodieae I clades is a crude estimate from a very limited clade sample (Kadereit *et al.* 2010) and could be earlier. Event dates are as reported or drawn from chronograms in source documents.

The environments of sediment cores are those of pollen capture (Truswell and Harris 1982), not necessarily of specific chenopod habitat. Vegetation histories of northwest and northeast Australia derive from offshore marine sequences.

Broad patterns of chenopod presence and landscape are:

(1) Earliest diversification of the oldest rich clades (Sclerolaenid, *Dysphania*) occurs later than their arrival in mid-later Miocene. These clades arrived prior to desert landscapes forming. For all other rich clades, diversification closely follows or coincides with arrival and with initial formation of desert landscapes, particularly Desert Upland, Shield Plain, Karst Plain and Riverine Desert.

(2) Chenopods are in western and central Australia before being generally found in the east. Middle Miocene traces in the western Murray Basin, contrasts with absence elsewhere in eastern Australia. The mid-late Miocene pollen presence of northeast Australia is uncertain (Martin and McMinn 1993; Martin 2006). Sclerolaenid, *Dysphania* and *Scleroblitum* seem the only possible sources of Mid-Miocene pollen. Only *Scleroblitum* fits Oligocene traces of the western Murray Basin.

(3) Sand Desert formed after seven clades initially diversified; Stony Desert after five. The rich Sclerolaenid Clade diversified before Desert Lake, Stony Desert and Sand Desert formed.

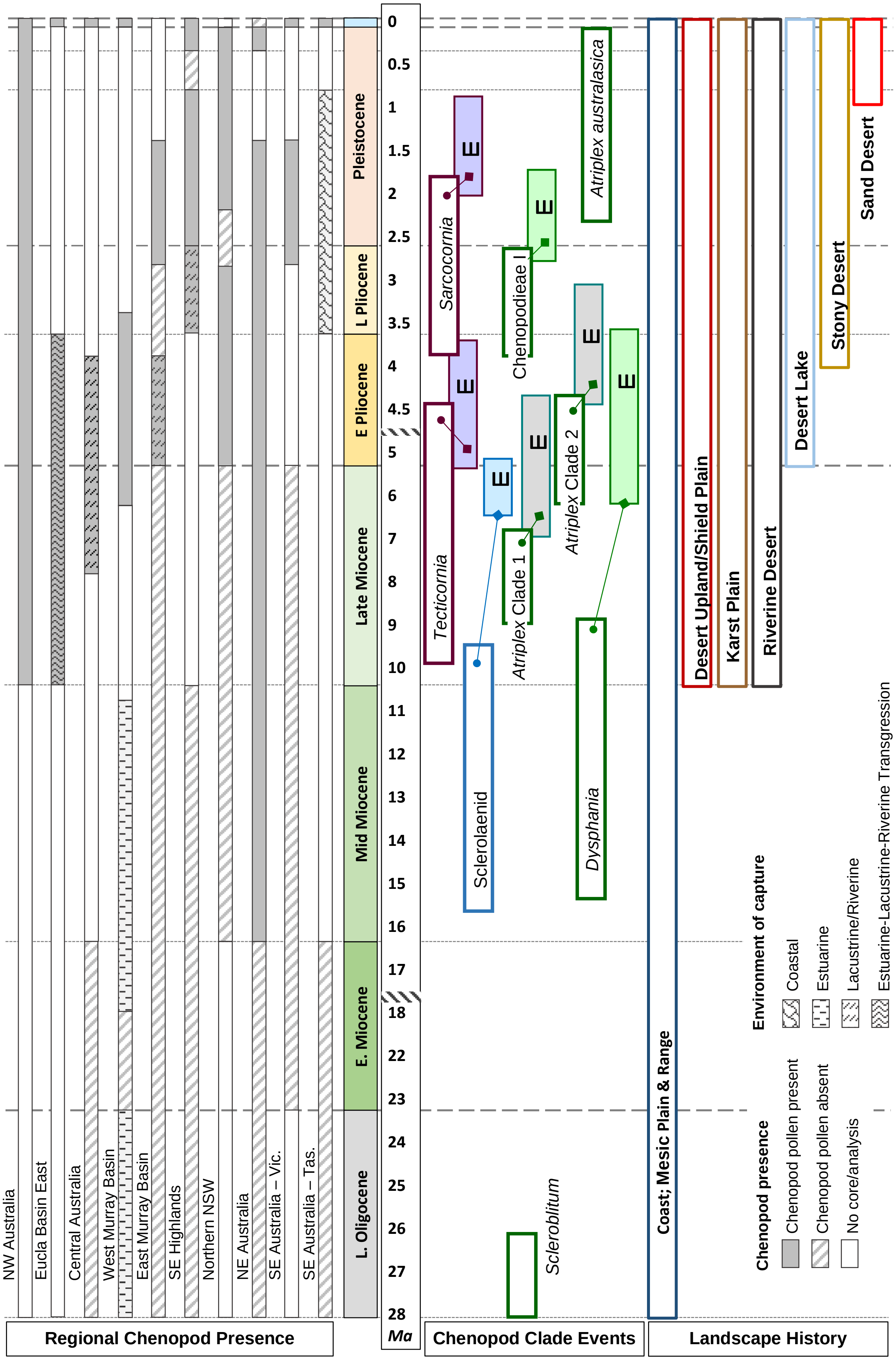


Figure 3.1: Chenopod regional presence, clade arrival and early diversification [Ш] and landscape history since the Early Miocene. Note: Dating means differ: pollen presence has the Geological Time Scale as main reference, but clade and landscape relate to age in million years (Ma). Scale breaks at 5-6 Ma and 18-22 Ma. In Landscape History, land types in the west develop earlier than similar ones in the east.

(4) Pollen assemblages indicate regional vegetation. Sediment cores reveal the environment of pollen capture, some of which match modern chenopod habitat:

- Northeast and Northwest Australia: Miocene pollen is in offshore marine sequences (Hekel 1972; Martin and McMinn 1993, 1994). That from northwest Australia is the taxa of coasts and regional waterways draining the interior of northern Western Australia. Northeast Australia sources are coastal, and regional waterways draining coastal catchments of the Eastern Highlands.
- Eastern Eucla Basin: Late Miocene to Early Pliocene presence in upper sections of Garford Formation is associated with estuarine, riverine and lacustrine environments in marine transgressive/regressive cycles, that are likely extensive in the Eucla Basin (Stoian 2004; Sniderman *et al.* 2016).
- Lake Frome: Late Miocene and Pliocene presence coinciding with the ‘drying of the lakes’ phase (Krieg *et al.* 1990) is associated with regressive beach ridges (some with lunettes) and exposed calcareous, lacustrine sediments. Lake shore forms include deltas, floodplains and channels of stream inflow. Lakes are fresh or brackish, but saline in places.
- Western Murray Basin: Oligocene traces in Geera Clay of Late Oligocene to Early-Mid Miocene age, are deposited in tide affected, shallow marine, deltaic channels (Truswell and Harris 1982; Macphail and Truswell 1989).
- Eastern Murray Basin, Northern NSW: Pliocene presence in clay of perennial, riverine, still-water habitat – swamp, lake or billabong, possibly abandoned river courses (Martin 1980); climate at least markedly seasonal, but closed forest was likely present (Martin 1979, 1980).
- South East Highlands: Dry river valleys at the end of the Pliocene. Forest and woodland present (McEwen-Mason 1989; Kershaw *et al.* 1994).

- Tasmania: Sediments of coastal sites; not abundant until the Holocene, but traces as early as Late Pliocene (Hill and Macphail 1985; Kershaw *et al.* 1994) and Macphail *et al.* (1995) reporting traces associated with flooding in near coastal habitats.

Shoreline transgressions that may have aided inland presence are evident in the Tertiary basins. Neogene coastlines largely approximated their current position with some exceptions (Langford 1990; BMR Palaeogeographic Group 1992). In the Oligocene to Middle Miocene, shorelines were along the western Pilbara Province and adjoining the Yilgarn Plateau Province on its north-western (Carnarvon Basin) and south-eastern (Eucla Basin) margins. Coastlines advanced and retreated in western Gawler Craton palaeovalleys (Eucla Basin) in the Late Miocene (Stoian 2004; Hou *et al.* 2008). The western Murray Basin was a shallow marine bay throughout the Miocene and Pliocene (Brown and Stephenson 1991; Bowler *et al.* 2006).

Continental habitats of chenopod species

Most species were easily classified into Land Type from primary sources and are listed in Appendix XIII. Many species are in various land types, consistent with widespread taxa. Habitats of coastal taxa were as readily typed. Absence of information or inconclusive descriptions are the chief issues, particularly for less common taxa and in collection records. Other issues and their resolution are also in the Appendix. Collection records for determining frequency of habitat occupation (occupancy profile) are summarised in Appendix XII.

Habitat occupancy of all species

For the rich immigrant clades, the frequency of species in ten land types is shown in figure 3.2. Many species are in more than one land type. Observed patterns of land type occupation are:

(1) Riverine Desert and Desert Lake have 2-2.5 times as many species as the third most occupied land type of Stony Desert (56 species). Coast occupancy (43 species) exceeds all remaining land types including Sand Desert. Chenopod occupancy of Mesic Plain & Range, Desert Upland, Shield Plain, Karst Plain and Sand Desert ranges from 34 to 38 species.

(2) Desert Clay Plain has the least number of species and clades. It is the least recognizable land type in habitat descriptions, resembling clay floodplain of Riverine Desert and gibber-less plains of Stony Desert. Many Stony Desert species likely occur in Desert Clay Plain.

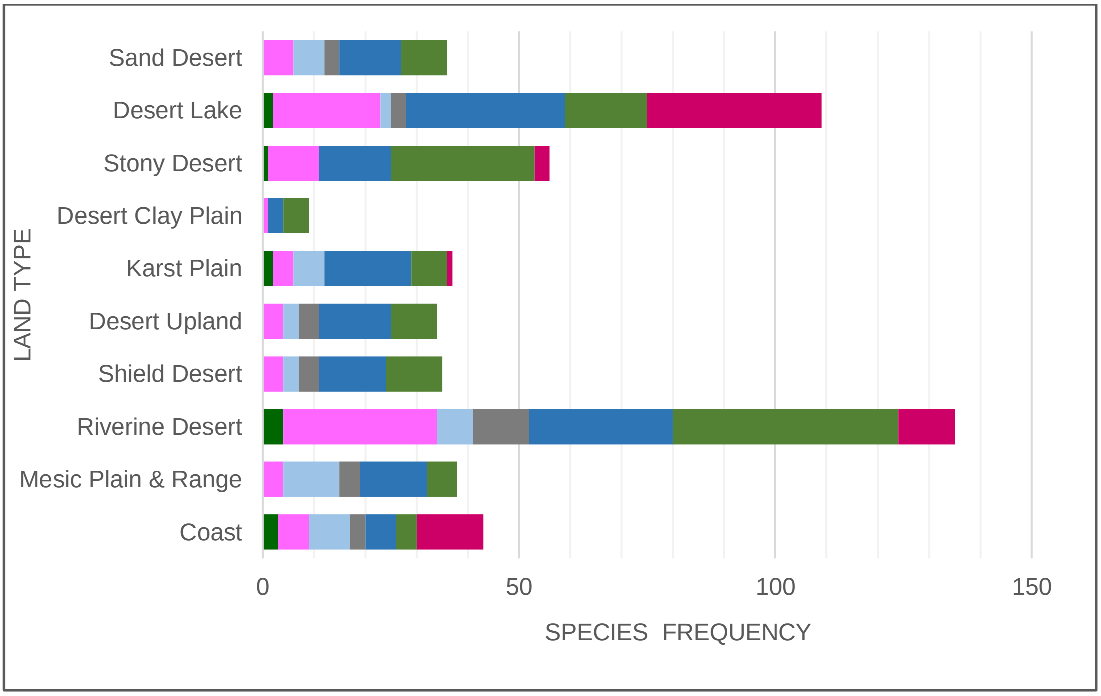


Figure 3.2: Occupation of land types by richer chenopod clades (> 7 species).

■ *Atriplex* Clade 1 ■ *Atriplex* Clade 2 ■ Chenopodieae I
■ *Dysphania* ■ MaireanAff ■ SclerolaenAff ■ *Tecticornia*

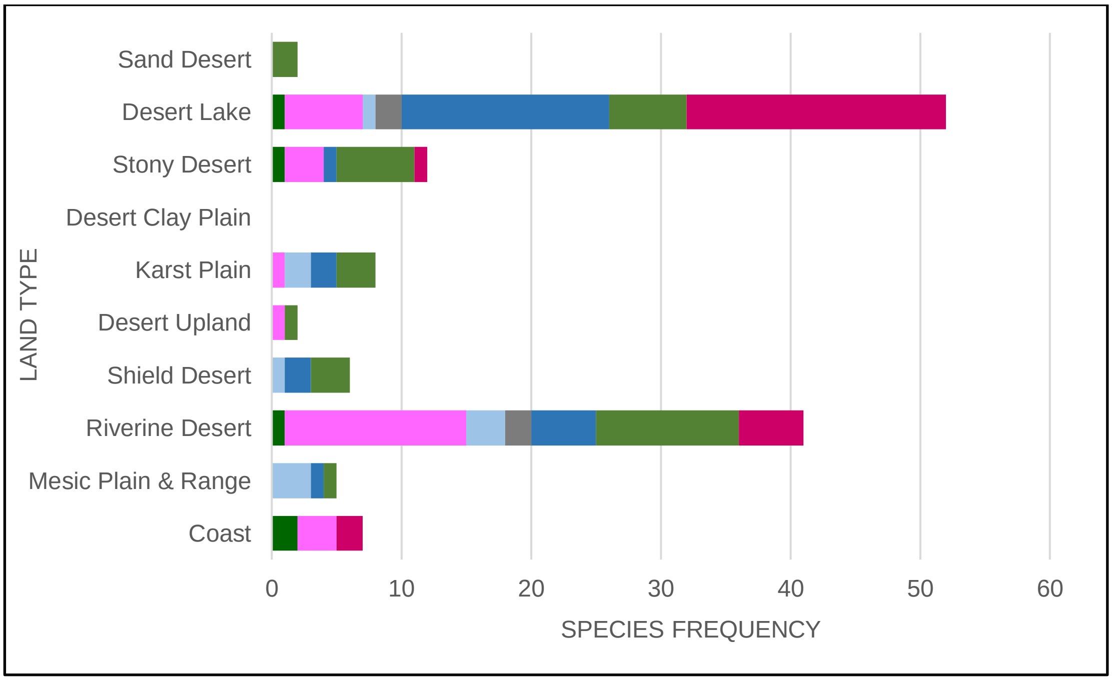


Figure 3.3: Species of richer chenopod clades (> 7 species) that occupy a single habitat type.

(3) In rank order, the species most occupying Riverine Desert are from SclerolaenAff, *Atriplex* Clade 2 and MaireanAff. Desert Lake mostly comprises species from *Tecticornia*, MaireanAff and *Atriplex* Clade 2, with notably less species from SclerolaenAff.

(4) All but two species in Stony Desert are from SclerolaenAff, MaireanAff and *Atriplex* Clade 2. SclerolaenAff species exceed that of MaireanAff and *Atriplex* Clade 2 combined. The single species from *Atriplex* Clade 1, is a low shrubland dominant, endemic to the southern Stony Desert.

(5) Most occupants of Mesic Plain & Range are from MaireanAff and Chenopodieae I.

(6) Sand Desert has species from six clades, but less species than Coast. More than half are from MaireanAff and SclerolaenAff. AVH records suggest more species are on sand plain than on dunes.

Immigrant clades also reveal some patterns:

(1) Every major clade has species in Riverine Desert and Desert Lake. Except for Chenopodieae I, the highest species occupancy of each rich clade is also in these land types. Only *Atriplex* Clade 2 and the Sclerolaenid clade have species in all ten land types.

(2) The dominance of the Sclerolaenid clade and *Atriplex* Clade 2 has a general pattern of greatest occupancy by either MaireanAff or SclerolaenAff, exceeding *Atriplex* Clade 2. However, *Atriplex* Clade 2 species exceeds SclerolaenAff in Desert Lake and MaireanAff in Riverine Desert. Sclerolaenid Clade species are least in Coast land type.

(3) Chenopodieae I occurs most in Mesic Plain & Range (11 species), Coast (8 species) and Riverine Desert (7 species). It is scarce in Desert Lake and absent from Stony Desert and Desert Clay Plain.

(4) *Dysphania* is richest in Riverine Desert (11 species) and of near equal occupancy (3-4 species) in six land types. Absence from Karst Plain, Stony Desert and Desert Clay Plain seemed inconsistent with species range maps showing presence in those regions. The few *Dysphania* in Stony Desert are on alluvial plain, sandplain and rocky ridges (Brandle 1998). The few *Dysphania melanocarpa* on Nullarbor Plain karst are in depressions or around rock-

holes (e.g. PERTH 2539195, PG Wilson, 23/7/1963; CANB 252139.1, ERL Johnson, Aug 1939; PERTH 2539012, MG Brooker, 4/6/1971).

(5) The species poor *Atriplex* Clade 1 is richest in Coast and Riverine Desert and absent from Shield Plain, Desert Upland and Desert Clay Plain.

(6) *Tecticornia* is abundant in Desert Lake, Coast and Riverine Desert but absent from Mesic Plain & Range, Shield Plain, Desert Clay Plain and Sand Desert. Single species occur in Stony Desert, Desert Upland and Karst Plain. That in Karst Plain is in locally saline depressions of the southern Nullarbor Plain, while that in Stony Desert is in heavy soils of stony tableland (*pers. obs.*).

Chenopod habitat specialists

Within the rich clades, 136 species are restricted to a single land type (figure 3.3):

(1) Desert Lake (54) and Riverine Desert (43) have the most species; almost 1/3 of all Australian species, and from each rich clade. Habitat specialists of *Dysphania* are only in these land types.

(2) Six species are restricted to Coast, which equals or exceeds restricted species of six land types.

(3) Sand Desert and Desert Clay Plain have the least restricted species and all are *Sclerolaena*. *Sclerolaena forrestiana* is on sandplains of Western Australia and *S. johnsonii* on sandplains and dune fields in Central Australia. Sand Desert occupants are mostly habitat generalists, including very widespread and common species (*Rhagodia spinescens*, *Chenopodium desertorum*, *Einadia nutans*, *Atriplex vesicaria*, *Sclerolaena diacantha*, *Enchylaena tomentosa* and *Maireana georgei*).

(4) Restricted species in Desert Lake largely are from *Tecticornia* (21 species) and the Sclerolaenid Clade (23 species) with 16 species from the MaireanAff subgroup. *Tecticornia* is richest in the Yilgarn Centre. Restricted species of MaireanAff are predominantly Western Australian and include *Maireana atkinsiana*, *M. diffusa*, *M. polypterygia* and allied genera *Roycea* and *Didymanthus*.

(5) Species from *Atriplex* Clade 2 and the Sclerolaenid Clade provide more than 2/3 of species restricted to Riverine Desert. SclerolaenAff and MaireanAff are in near equal proportion. Most *Atriplex* species are of alluvial plains, floodplains and watercourses of the Lake Eyre and Murray Basins, such as *A. crassipes*, *A. leptocarpa*, *A. muelleri* and *A. pseudocampanulata*.

(6) Stony Desert is third richest in species of a single land type (12 species), with most from the SclerolaenAff subgroup (6) and *Atriplex* Clade 2 (3) and taxon ranges in the Eyre Murray Centre. Species include *Sclerolaena articulata*, *S. bicuspis*, *S. blackiana*, *S. blakei*, *S. longicuspis* and S. *parallelicuspis*. No species from *Dysphania* or Chenopodieae I is restricted to this land type. *Atriplex incrassata*, the sole species from *Atriplex* Clade 1, dominates plant communities of this habitat (Brandle 1998). *Tecticornia papillata* is unusual given halophytic nature of *Tecticornia* habitat, noted in quartzite rubble (Shepherd 2008).

(7) Relative to their species complement, Chenopodieae I and *Atriplex* Clade 1 have a high proportion of species restricted to single land type. Those of Chenopodieae I are mostly in Riverine Desert and Mesic Plain & Range (7 of 24 species) which are inland habitats of greater moisture and lower salinity. Those of *Atriplex* Clade 1 (4 of 8 species) include the Coast obligate *A. isatidea*, *A. incrassata* in Stony Desert, *A. cephalantha* in Desert Lake and *A. rhagodioides* in Riverine Desert.

Habitats of coastal chenopods

Coast obligate and facultative types

Habitat occupancy profiles of Coast obligate and Coast facultative species are shown respectively in figures 3.4 and 3.5. Species in figure 3.5 are from clades of terrestrial habitats as the coastal and inland habitats of coastal *Tecticornia* are very prominently marshy. Three Coast obligate subspecies *Rhagodia baccata* ssp. *dioica*, *R. preissii* ssp. *obovata* and *Atriplex paludosa* ssp. *paludosa* provide comparative interest, given the paucity of Coast obligate species. Similarly, the coastal occupancy profile of Inland facultative *Rhagodia preissii* is compared with Coast facultative species, as the coastal range largely comprises a single subspecies.

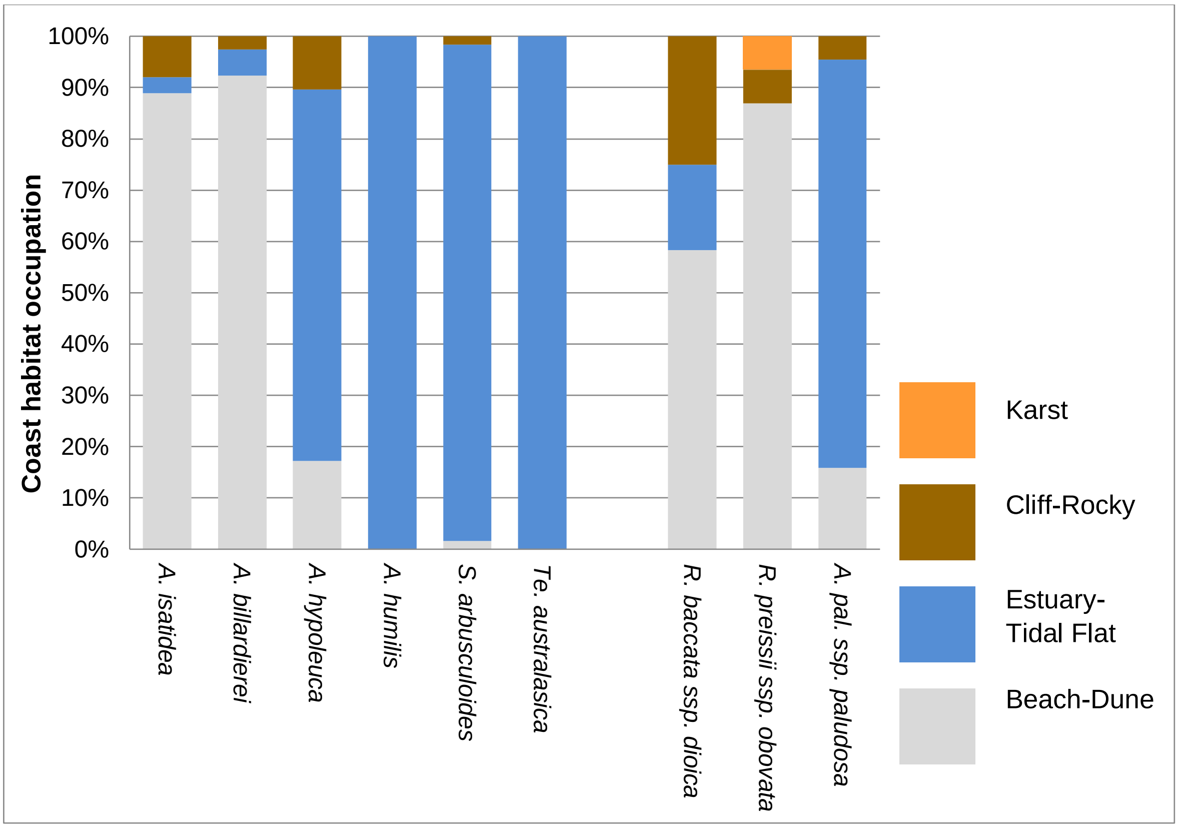


Fig 3.4: Habitat mix for coast obligate species. Coast obligate subspecies of Coast facultative species are included for comparison. The habitat key also applies to figure 3.5.

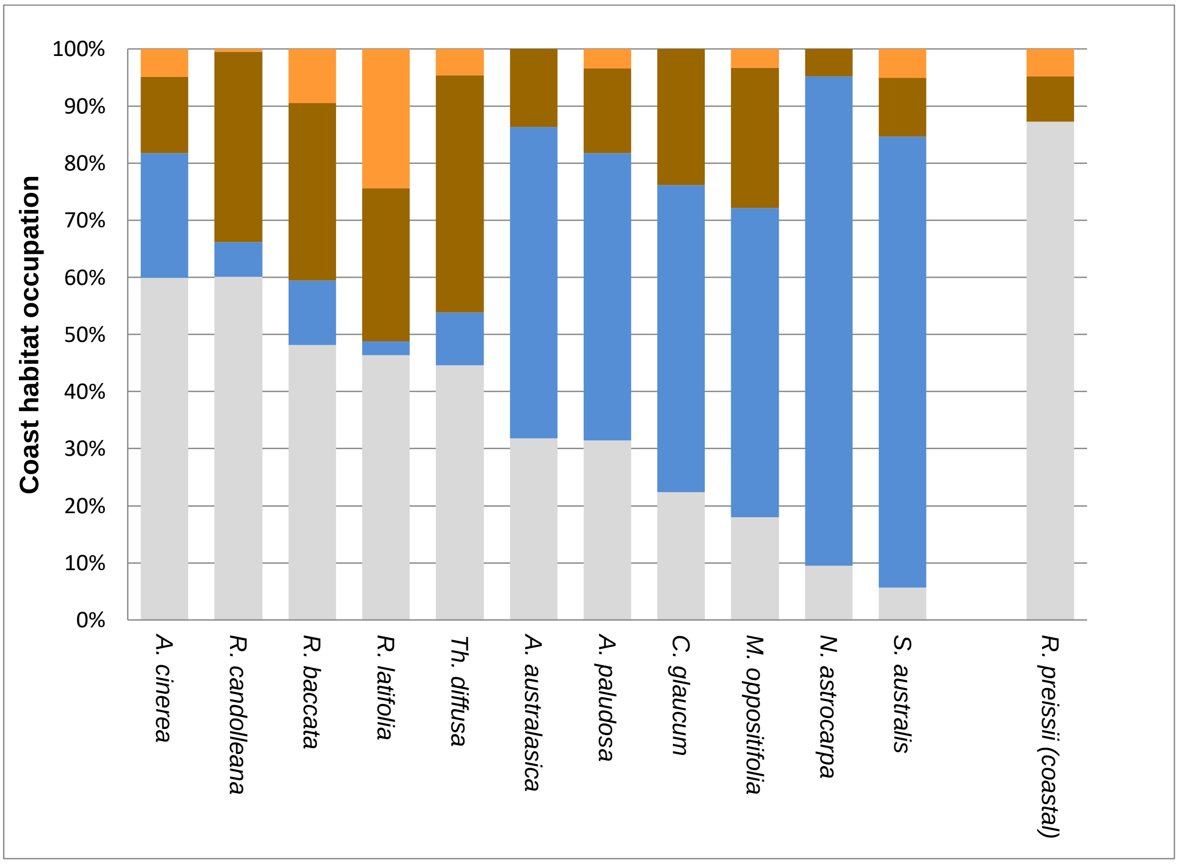


Fig 3.5: Habitat mix for Coast facultative species of Chenopodioideae, Camphorosmoideae and *Suaeda australis*. Coastal occurrences of Inland facultative *R. preissii* are included for comparison.

Coast obligate species prefer a single habitat type. Occupation frequency is generally above 89%. Two *Atriplex* species of Beach-Dune habitats, are on high energy shorelines, frequently and specifically identified as upper beach, foredune or coastal primary dune. Four species prefer Estuary-Tidal Flat habitats. *Tecticornia australasica*, *Atriplex humilis* and *Suaeda arbusculoides* very strongly show their estuarine preference. The broad habitat of *Atriplex hypoleuca* is estuarine bays and inlets of south west Western Australia, such as at Wilson Inlet (pers. obs.) where the shoreline rocks and sand sheets are not typical Beach-Dune or Cliff-Rocky systems.

The occupancy profile of two Coast obligate subspecies resembles Coast obligate species. *Atriplex paludosa* ssp. *paludosa* is prominently Estuary-Tidal Flat habitats, similar to the estuarine *A. hypoleuca*, with similar issue of inhabiting the sandy shores of estuaries. The occupancy profile of *R. preissii* ssp. *obovata* resembles that of *Atriplex isatidea*, strongly preferring Beach-Dune habitats and a minor presence on rocky shorelines that may be limestone substrates. *Rhagodia preissii* is an Inland facultative species and most of its coastal range is sympatric with *A. isatidea*.

Rhagodia baccata ssp. *dioica* though exclusively coastal, has an occupancy profile resembling Coast facultative types; the species is Coast facultative. Both species and subspecies prefer Beach-Dune habitats but are also on rocky and estuarine coasts. Within the subspecies range, shoreline forms include sand-covered, rocky limestone. Cliff-Rocky occupancy may include Karst and sand over rock may be as much a preferred habitat as deep sand.

Habitats of Coast facultative species are generally more diverse. Eight of eleven species are in all four coastal habitats. Again, Beach-Dune (5 species) and Estuary-Tidal Flat (6 species) are preferred having occupation frequency of 50%-60%. The frequency of eight species in Cliff-Rocky habitats exceeds 15%. Combined with the strong preference of seven Coast facultative species in Salicornioideae, Estuary-Tidal Flat is the dominant habitat of Coast facultative types. *Neobassia astrocarpa* and *Suaeda australis* strongly prefer Estuary-Tidal Flat with occupancy at 80-85%, very similar to Coast obligate species, especially the estuarine *Atriplex hypoleuca*.

There is a weak pattern of secondary preferences. Those primarily of Beach-Dune habitat prefer Cliff-Rocky over Estuary-Tidal flat. Coast facultative taxa preferring Estuary-Tidal Flat overall exhibit equal preference for Beach-Dune or Cliff-Rocky types.

Occupancy profiles of the three *Rhagodia* have some similarity but differ from *Chenopodium glaucum*. In this study all are treated as part of the Chenopodieae I clade. Main coastal ranges of the three *Rhagodia* are near allopatric, collectively extending around the southern coastline from Shark Bay to Brisbane. All are mostly of Beach-Dune habitat with lesser Cliff-Rocky presence (likely calcareous). *Chenopodium glaucum* has a range largely sympatric with coastal *Rhagodia*, but has marked preference for Estuary-Tidal Flat.

Very strong preference of coastal forms of *Rhagodia preissii* for Beach-Dune habitats, similar to Coast obligate types, contrasts with the other *Rhagodia*, which appreciably occur in Cliff-Rocky and Estuary-Tidal flat. The main coastal range of *Rhagodia preissii* is on the west coast and includes *R. preissii* ssp. *obovata* (Coast facultative subspecies), co-occurring with *R. baccata* and *R. latifolia*. Similar to *R. latifolia*, it is uncommon in marshes.

Coastal species of the Sclerolaenid clade have varied occupancy profiles. *Maireana oppositifolia* and *Neobassia astrocarpa* prefer Estuary-Tidal flat, but *M. oppositifolia* is also on sandy and rocky coasts. The ranges of these species are almost allopatric, overlapping marginally at Shark Bay. *Threlkeldia diffusa*, equally prefers Beach-Dune and Cliff-Rocky habitats, is uncommon in marsh habitats and has a coast range overlapping that of both *N. astrocarpa* and *M. oppositifolia*.

Each of the three *Atriplex* spp. is from a different clade. Occupancy profiles of *A. australasica* and *A. paludosa* are very similar. Both prefer Estuary-Tidal Flat over Beach-Dune and Cliff-Rocky habitats in similar proportion. *Atriplex cinerea* favours Beach-Dune habitats, and marginally prefers marshy over rocky habitats. *Atriplex cinerea* and *A. paludosa* span the continental southern coast. The range of *A. australasica* in south east Australia lies within that of *A. cinerea* and is parapatric with *A. paludosa*.

Coast and inland habitats of Coast facultative species

Coastal and inland habitat occupancy of Coast facultative species is compared in figure 3.6. Beach-Dune and Sand Desert, Karst and Karst Plain are directly comparable. For inland habitats, the marshy Desert Lake and Riverine Desert are combined for comparison with Estuary-Tidal Flat, but exclude collections specifically identified as lunette in Desert Lake land type. Similarly Shield Plain and Desert Upland occupation were combined for comparison with coastal Cliff-Rocky habitats.

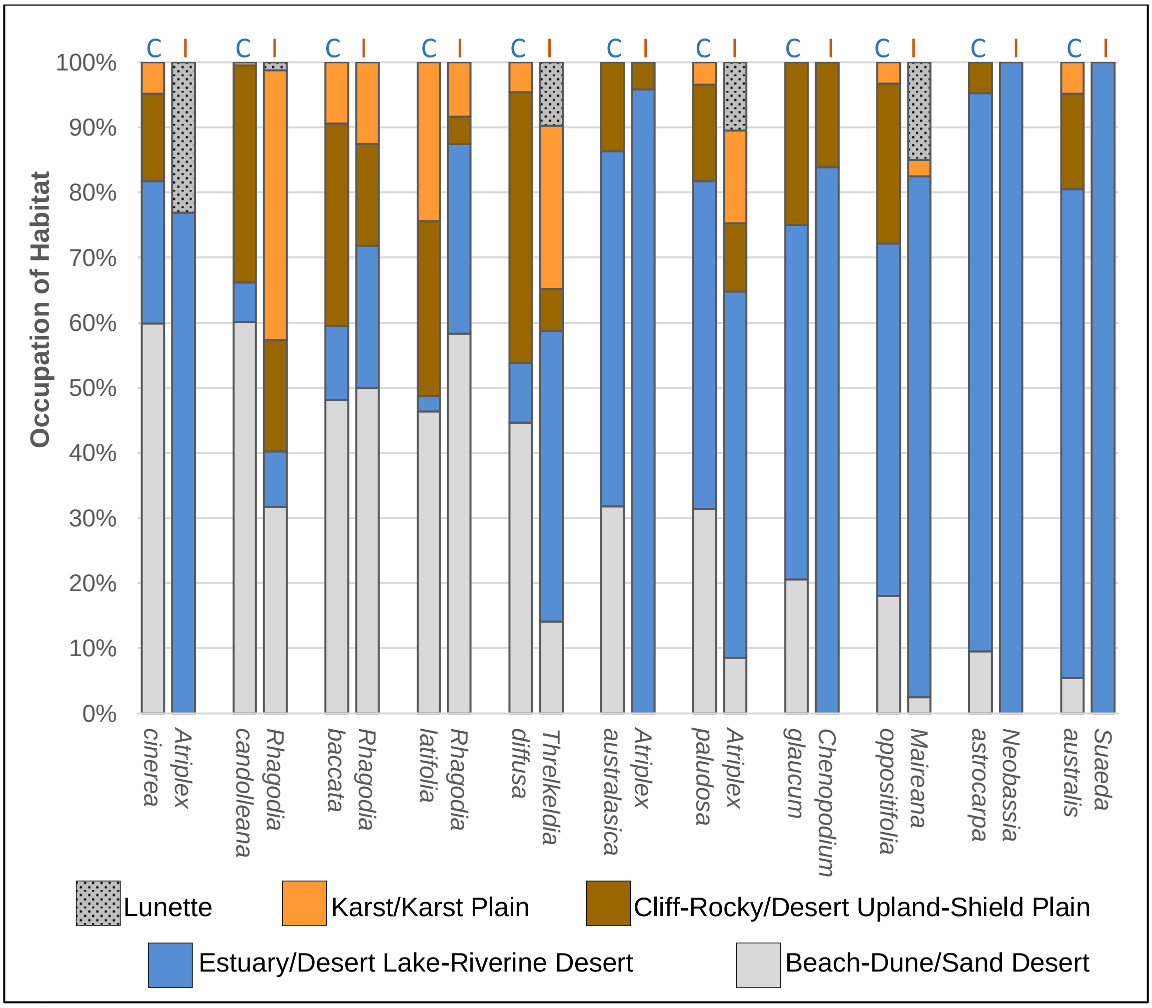


Figure 3.6: Comparison of habitat for coast facultative species in their coastal (C) and inland (I) locations. Species generally favouring coastal dunes at left and those generally favouring coastal marsh at right.

Two notable patterns of Coast facultative species are:

(1) Inland habitats are as diverse as at the coast or are largely restricted to marsh. Six species have diverse inland habitats (*Rhagodia baccata*, *R. candolleana*, *R. latifolia*, *Threlkeldia diffusa*, *Atriplex paludosa* and *Maireana oppositifolia*). Five species show a strong preference for marsh. Though coastally diverse, inland habitats of *Atriplex cinerea*, *A.*

australasica and *Chenopodium glaucum* are mainly marshy. *Neobassia astrocarpa* and *Suaeda australis* are mostly of marsh habitats both at the coast and inland.

(2) With the exception of three *Rhagodia* spp., coast species in inland habitats have greater occupancy of marsh types relative to sandy types. However, the difference varies, being marked in *Atriplex cinerea*, *A. australasica* and *Chenopodium glaucum* to marginal in *Threlkeldia diffusa*, *Atriplex paludosa* and *Maireana oppositifolia*. Reduced inland presence in sand habitats for four of the species is offset by some occupancy in lunettes, which can be dunes of deep sand but mostly are mounds or flats of gypsum “flour” with drainage and salinity different to sand dunes. Coast facultative species that strongly prefer coastal marsh are only found in inland marsh.

For inland *Atriplex cinerea*, the occupancy proportion derives from relatively few informative records, where no habitat was listed. Localities are in Desert Lake systems of lunettes and dune forms, occurring mostly in Western Australia.

The preferred occupancy of *Rhagodia baccata* and *R. latifolia* for sandy habitats is maintained rather than diminished. Inland occupation of marshy habitats is greater, but occupation of rocky habitats is notably less. *Rhagodia latifolia* has slightly increased occupancy of inland sandy habitats. *Rhagodia candolleana* occupies less sandy habitat inland, is found more in rocky and karst habitats, and unusual in coast and inland marsh.

Disjunct species

Major landforms that separate disjunct species populations at subcontinental scale are the Great Sandy and Gibson Deserts, Great Victoria Desert and Bunda Plateau (Nullarbor Plain). The Simpson-Strzelecki Desert separates disjunct populations of the Eyre-Murray Centre. Habitat occupation of 40 arid taxa in disjunct populations separated by the Great Victoria Desert and Simpson-Strzelecki Desert is shown in figure 3.7, and include species of single and multiple inland land types. All rich clades except Chenopodieae I, are represented by at least three species.

Most disjunct species are in Riverine Desert, Desert Lake, Stony Desert or Sand Desert. Riverine Desert (5 species), Desert Lake (7 species) and Stony Desert (4 species) dominate habitats of sixteen species restricted to a single inland land type; none are in Sand Desert.

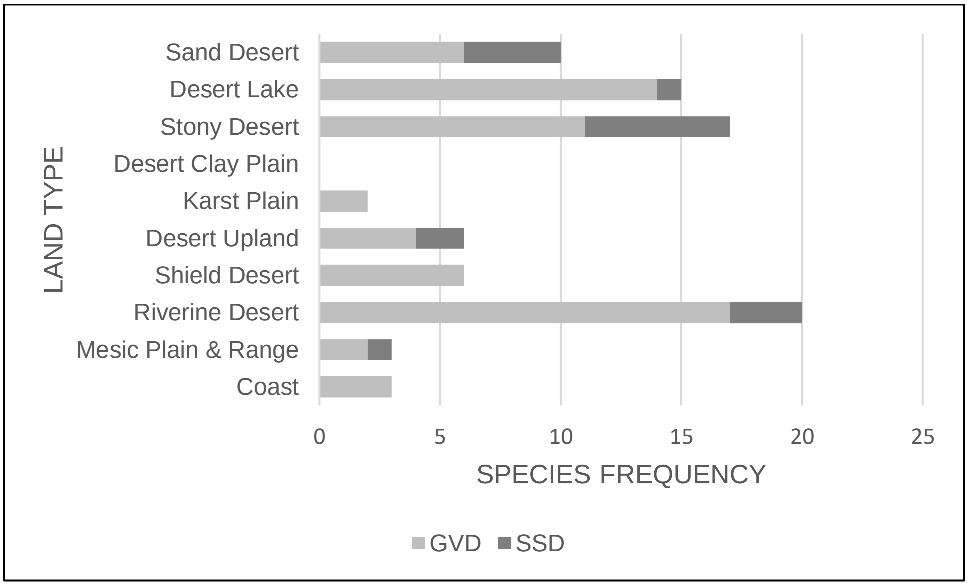


Figure 3.7: Habitat occupation of 40 disjunct chenopod species with populations separated by dune field of Great Victoria Desert (GVD) or Simpson-Strzelecki Desert (SSD). Sixteen species are restricted to a single inland land type. Twenty-three species occur in 2 or 3 land types.

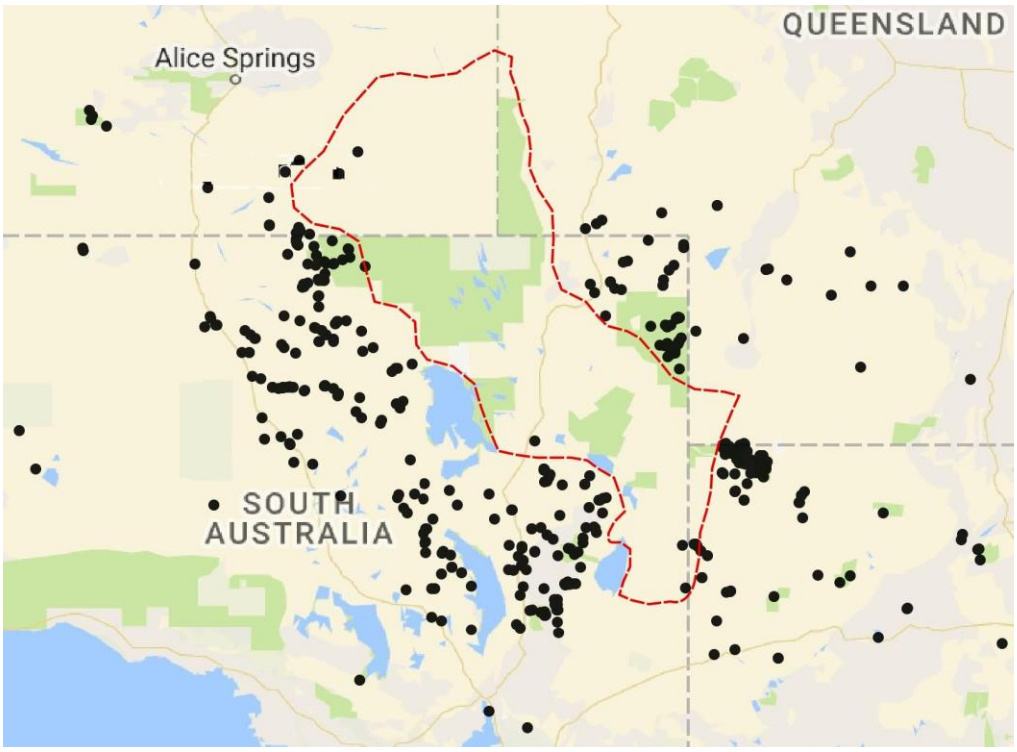


Figure 3.8: Collections of *Sclerolaena parallelicuspis* in the Simpson-Strzelecki Desert as mapped by Twidale *and Wopfner.* (1990) shown in red; *S. parallelicuspis* is mainly a Stony Desert species.

The Great Sandy and Great Victoria Deserts are extensive dune fields and sandplain, partly covering older landscapes (Beard 1969; Callen and Benbow 1995; Hesse 2010). Low to very high linear dunes, extend for long distances. The old landscapes exposed between widely spaced dunes, are of low relief, deeply weathered with duricrust, have unconsolidated surface of alluvium and colluvium, widespread landscape salinization and extensive palaeovalley systems of Cenozoic or older history (Magee 2009). The Great Victoria Desert palaeovalley systems are part of the Eucla Basin while the Great Sandy Desert have those of the Canning Basin. The Gibson Desert is relatively sand-free, dominantly of duricrust mesa, tableland and low upland and has northern parts of the Eucla Basin catchment. Chenopod taxa of continental range, with near disjunct western and eastern populations, maintain continuity through the Gibson Desert e.g. *Dysphania kalpari*, *Maireana tomentosa*, *M. triptera*, *M. villosa, Rhagodia eremaea*, *Sclerolaena convexula* and *S. eriacantha*.

Disjunct species of the Lake Eyre Basin are also divided by dunes of Simpson-Strzelecki Desert. *Maireana carnosa* and *Atriplex quinii* are in three main populations. Central populations in the Stuart Range are separated from western populations by the Great Victoria Desert and from eastern populations by the Simpson-Strzelecki Desert. Distribution of *Sclerolaena parallelicuspis*, a species largely confined to habitats of Stony Desert, is particularly constrained by dune field boundaries (figure 3.8). Otherwise, disjunct populations approximate the dune field boundaries due to exposure of older landscapes within the discontinuous spread of the dune field.

The Simpson-Strzelecki Desert landscape, as described by Twidale and Wopfner (1990) and Callen and Benbow (1995), resembles the more complex Great Victoria and Great Sandy Deserts. The dune field has developed on an ancient, deep-weathered surface of little relief that comprises stony plains, a variably saline drainage system and minor low uplands. Extensive, long linear dunes are variably spaced and only in parts obscure the underlying landscape. Constrained to the structural Lake Eyre Basin, ancient drainage and alluvial elements are more extensive, the dune field having formed in a region that once included vast, interconnected lake systems (Callen and Benbow 1995).

DISCUSSION

That inland chenopod species are overwhelmingly of habitats similar to marshy and saline coastal ones reveals the influence of niche conservatism and suggests the nature and course of invasive stages. The poverty of sandy habitats is at odds with a littoral connection given coastal taxa have dune habitats.

Coastal Colonization and Establishment

Coast facultative is the type for coastal taxa, outnumbering Coast obligate types by ratio of 3:1, occurring in more clades and characterising the coastal taxa of young clades. Most are on the coasts of high chenopod diversity. To these attributes can be added the capacity to survive diverse coastal habitats, further raising questions of ecological attributes superior to Coastal obligates, such as greater seed production or germination survival.

Coast facultative types in diverse coastal habitats reflects an ancestral capacity to readily colonize and rapidly establish on coastlines. Such capacity ensures persistence in stressful conditions with secondary succession restoring local losses after disturbance. Marshes have saturated soils, variably immersed in hypersaline pools and are subject to tidal scour. Seasonally very dry dunes are disrupted by storm surges, blasted with salt-spray and covered by blown sand. Exposed rocky slopes have thin, dry soils blasted by salt-laden winds. Seral succession ensures a presence when tectonic or eustatic events shift coastlines laterally. Despite frequent, extensive shifts of Late Pleistocene shorelines that stabilised *ca.* 6000 years ago, the western and southern coastlines of Australia have a near continuous distribution of chenopods.

Coastal populations can build quickly. Local dispersal consolidating neighbouring populations into continuous stands makes for successful colonization (Theoharides and Dukes 2007). Such consolidation occurred in populations of *Atriplex stipitata* returning after grazing, in Brookfield Conservation Park and Gawler Ranges National Park in South Australia (*pers. obs.*). Dioecious taxa producing sufficient, viable seed is problematic (Stott 1981; Cronk and Fuller 1995), but occasional reversion to monoecy, likely explains trans-Tasman populations of the dioecious *Atriplex cinerea* (de Lange *et al.* 1998, 2000; Heyligers 2001).

Landscape spread and Diversification

Coastal and continental Landscape Spread and Diversification would be separate processes.

Coastal range extension and Diversification

Landscape Spread begins with substantial coastal range extension. Dispersal capacity and Coast facultative character permits any coastal habitat distant from initial landfall to be colonized. Chenopod seeds are dispersed by wind, water and animals (Kuhn 1993). De Lange *et al.* (1998, 2000) and Heyligers (2001) demonstrate viable connections between shoreline populations of *Atriplex cinerea* (*Atriplex* Clade 1) and *A. billardierei* (*Atriplex* Clade 2) in Australia and New Zealand, citing factors of seed buoyancy, dormancy and a tolerance of burial. Additional local dispersal by wind would enlarge colonizing populations at initial landfall and colonies spreading along and from coastlines.

Substantial coastal movement prolongs the Transport stage of invasion. The global distribution of higher chenopod ranks shows great capacity for inter-continental dispersal. The family is one of only two found in all the world's deserts (Shmida 1985), with the main chenopod lineages diverging after Gondwanaland fragmented (Kadereit *et al.* 2003, 2005). West Wind Drift and oceanic dispersal of the southern latitudes (Munoz *et al.* 2004; Sanmartin *et al.* 2007) link the dry southern margins of South America, Africa and Australia, where chenopods occur.

The relative poverty of coastal species stems from few habitats, wide ranges of species tolerance, ready dispersal and intra-chenopod competition affecting coastal richness of all clades. Beach-Dune and Estuary-Tidal flats have chenopods as dominant species, and species unique to them, but none are unique to coastal Cliff-Rocky. Established coastal species must compete with new immigrants. Extinction is suspected in coastal *Scleroblitum* as ancestors were coastal, but modern taxa are not. Under a littoral connection, coastal extinctions must be assumed in the Sclerolaenid Clade, as its modern coastal taxa appear to be derived. The *Dysphania* Clade also lacks prominent coastal taxa. Of the modern coastal taxa, the most dominant and wide-ranging species are not from the three oldest clades suggesting replacement by younger clades. The low diversity of older genera in

Salicornioideae may result from their replacement with more efficient adaptations in modern lineages (Kadereit *et al.* 2006).

Subspecies of coastal taxa have particular habitats, but the influence on coastal speciation is unclear. Some are Coast obligate, but not restricted to a habitat. Some are Coast Facultative with contrasting coast-inland habitats. Species with coastal subspecies are Coast or Inland facultative types. For net gain to coastal species richness, coastal taxa would probably need two coastal subspecies, known only in *Atriplex paludosa*. Curiously this species has Coast obligate subspecies in estuarine habitats at opposite ends of the continent.

The return of inland lineages to coastlines, as postulated by Shmida (1985), adds coastal species. The three coastal taxa of the Sclerolaenid clade are derived members of inland lineages (Cabrera *et al.* 2009). *Atriplex humilis*, a Coast obligate in *Atriplex* Clade 2, is on the north coast after a continental migration. However, competition from new forms may threaten older coastal forms.

A major question is whether the extensive ranges of coastal taxa ever allowed for separate inland departures, generating lineages in different regions. And how often? *Threlkeldia diffusa* is derived within the Sclerolaenid clade, having the largest coastal range. At least one cycle has occurred, beginning another with a substantial coast migration.

Inland Landscape Spread

Palaeogeographic comparison shows inland range extensions to be of the latest Late Miocene-Early Pliocene. They were very extensive, relatively rapid, directed toward Central Australia and possibly preceded formation of desert vegetation. Most rich clades migrated soon after arrival, but that in Sclerolaenid and possibly *Dysphania* clades was delayed.

Coast facultative species show capacity for shoreline-inland exchange through marshy habitats. Their inland range comprises more marsh than sand habitats. Five of 19 Coast facultative species are exclusively in marsh. In contrast, Coastal *Rhagodia* are strongly associated with sandy and rocky (possibly calcareous) habitats. *Neobassia astrocarpa* is a marginal Coast facultative of saltmarsh from the Sclerolaenid clade. Part of a near basal

Eremophea subclade (Cabrera *et al.* 2009), it is distinct from *Maireana*. Marshy systems could also allow coast returns.

Estuaries and their connected drainage networks are the routes of inland migration, as proposed by Burbidge (1960). Coast facultative species with a capacity for water borne dispersal and marshy occupation of their inland range, indicate means of departure. The substantial occupation of marshy habitats by inland taxa, exclusively for many species, and the species poverty of sandy habitats indicates areas to which chenopods were restricted. Such migration is essential in *Tecticornia*.

Riverine Desert connects coasts to the distant interior of both centres of chenopod diversity. Figures 3.9, based on Magee (2009), and 3.10, based on Hou *et al.* (2007); Hou *et al.* (2012), map palaeodrainage systems of Western and South Australia in relation to provinces richest in chenopods. Though now also comprising Desert Lake, and much interrupted by Pleistocene sand movement, geological history shows continental palaeodrainage comprised continuous lengthy reaches of Riverine Desert from the later Miocene into the earlier Pleistocene (Clarke 1994a, 1994b; Alley *et al.* 1999; Hou *et al.* 2003).

Major divides in the Yilgarn Centre directed drainage to the Indian and Southern Oceans through the Tertiary (van de Graaff *et al.* 1977; Beard 2002). That to the Indian Ocean, is either directly west or northeast through the Canning Basin. The Eucla Basin catchment includes the south-eastern Yilgarn Centre. Drainage channels from current and former coasts extend more than 500 km inland into the Centre. Neogene continental tilting and warping has changed drainage directions near catchment divides between the Canning and Eucla Basin, but timing is not precisely known (Beard 2002).

Riverine coastal connections in the Eyre-Murray Centre are limited. The River Murray flowed into the Southern Ocean from the Murray Lowlands throughout the Tertiary (Brown and Stephenson 1991). Eucla Basin palaeodrainage extends marginally into the southwestern Eyre-Murray Centre, with rivers draining Central Australian Ranges, the western Stuart Range and northwest Eyre Peninsula.

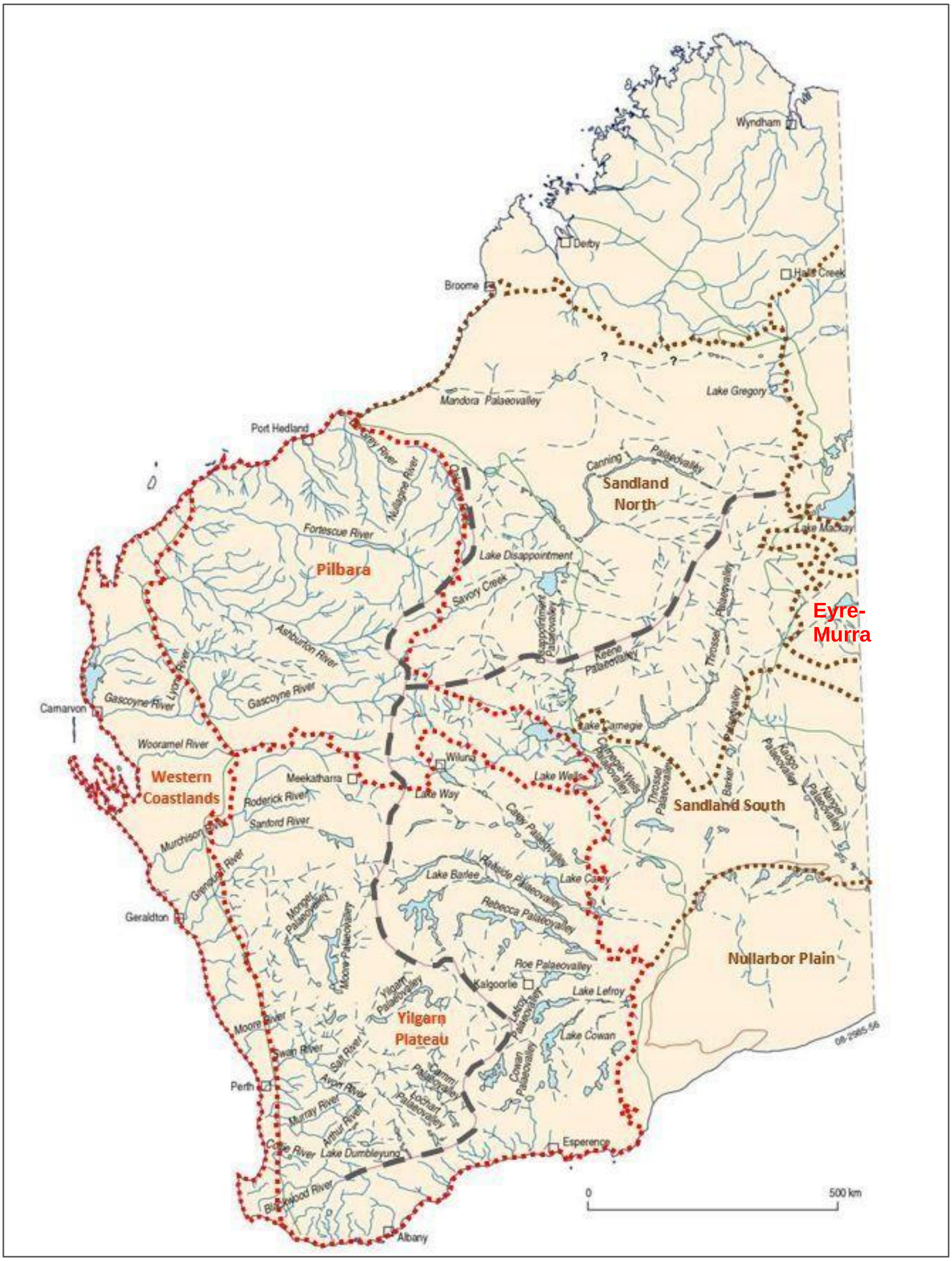


Figure 3.9: Western Australian palaeodrainage in provinces of the Yilgarn Centre of Diversity (Yilgarn Plateau, Pilbara, Western Coastlands). The ancient system also drained Sandland North and South Provinces, and western margins of the Eyre-Murray Centre. Dashed grey lines are drainage divides for Indian Ocean and Southern Ocean. Forming at the end of regular palaeodrainage flow, the Nullarbor Plain is largely devoid of palaeovalleys and channels. From Magee (2009).

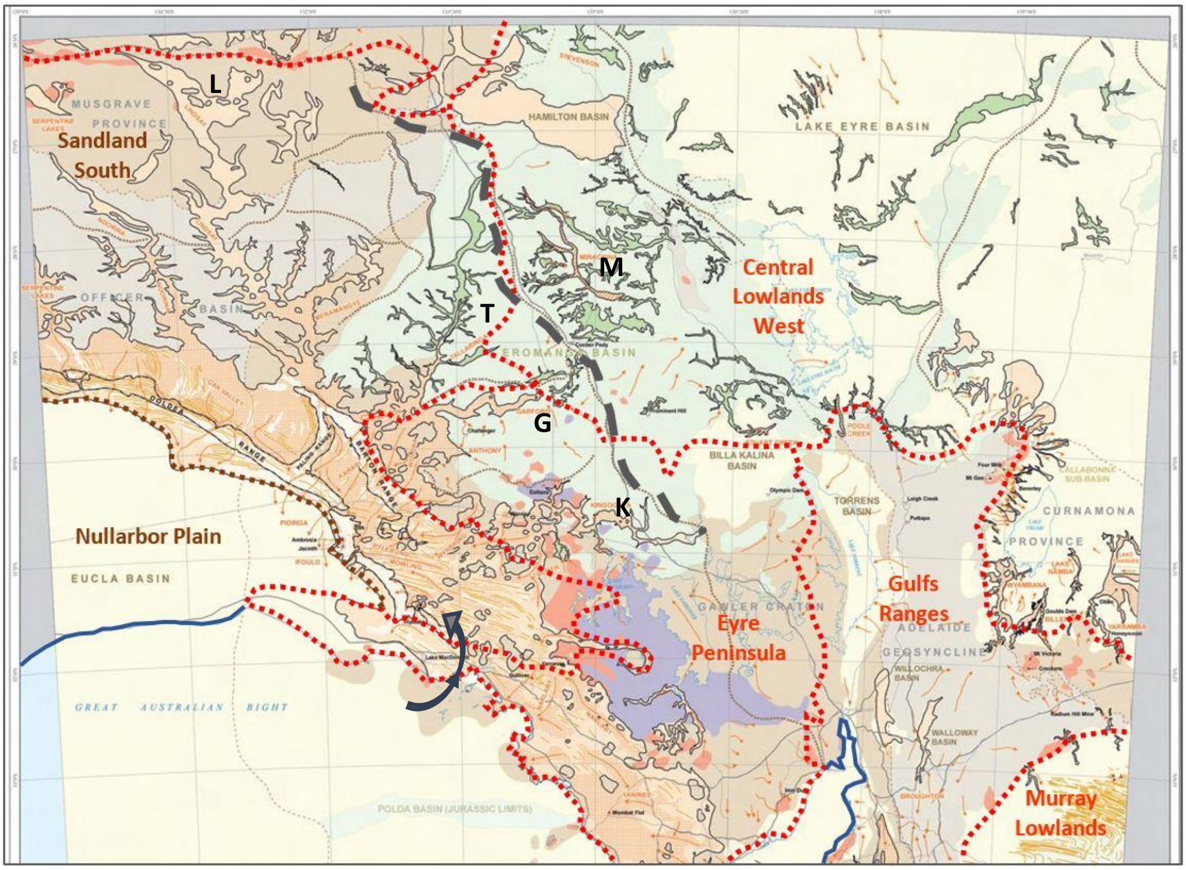


Figure 3.10: Palaeodrainage systems of South Australia in relation to richer provinces of Eyre-Murray Centre (outlined in red) and based on Hou *et al.* (2007, 2012). Grey dashed lines indicates catchment divide incorporating the Stuart Range. The Kingoonya (**K**), Garford (**G**) and Tallaringa (**T**) Palaeochannels closely approach the divide near the Mirackina system (**M**) in the Lake Eyre Basin. The Lindsay (**L**) Palaeochannel extends to the borders of Central Australian Ranges Province. The curved arrow suggests possible opening to open sea at the time of rich chenopod clade arrivals (Late Miocene-Early Pliocene) based on marginal marine to estuarine nature of sediments in the Kingoonya Palaeochannel (Stoian 2004; Hou *et al.* 2008).

The northern Eyre Murray Centre is in the endorheic Lake Eyre Basin. Dolphin fossils suggest marine connections of the Late Oligocene to Middle Miocene (Benbow *et al.* 1995a), the time of the earliest chenopod arrivals. No connection locale is identified, but the Murray Basin is more likely, because the Stuart Range separated the Lake Eyre and Eucla Basins throughout the Neogene (Krieg *et al.* 1990; Callen *et al.* 1995). The Stuart Range is a subdued, narrow watershed where headwaters of each basins' drainage systems closely approach. In the south-west Central Australian Ranges Province, Miocene drainage flowed into the northern Eucla Basin, but adjoining catchments drained to Lake Eyre (Edgoose and Ahmad 2013).

In neither Centre of Diversity is there a coast to desert climatic transition of chenopod taxa through sandy substrates. In the Yilgarn Centre, the very rich Sclerolaenid clade and ubiquitous *Salsola* are near absent from the coastal sandplain of Western Coastlands

Province, which separates coastal chenopods from the species rich Yilgarn Plateau Province. A similar climate gradient over a sandplain in the Murray Lowlands Province of the Eyre Murray Centre, links the Coorong coast with the southern Mallee Dune Field; the chenopod flora of the coastal dunes (*Atriplex* spp., *Rhagodia* spp., *Salsola* sp.) is similar to Western Australia. Away from the coast, chenopod taxa present on loam and clay of alluvial plains contrast with absence on adjoining sandplain.

Dune system age post-dates initial migrations of the Late Miocene-Pliocene. Central arid dune forms are *ca.* 1 Ma at most and developed toward the coast (Sheard *et. al.* 2006; Fujioka *et al.* 2009; Fujioka and Chappell 2010). Maximum extent was attained in the last 0.3 Ma, when dune fields of south-eastern Australia were active (Bowler 1976; Hesse 2010). Sandy transitions may be facilitating modern movement, as coastal *Rhagodia* occur on sandplains of the immediate coastal hinterland. Direct edaphic transitions for chenopod origins (Barlow 1981, 1994) would have to exclude dune-dune shifts, while youth also contributes to low chenopod occupancy.

The eco-geochronology of Riverine Desert best fits initial chenopod occupancy, but migration opportunities for immigrant clades were not equal. Clade arrivals in the Late Miocene coincide with expansions of Riverine Desert. Regional waterways are the source of Neogene chenopod pollen in northwest Australia (Martin 1994) being northern parts of the western palaeodrainage systems (van de Graaff *et al.* 1977). As Riverine Desert becomes Desert Lake under declining rainfall, no flow reaches the coast. Initially linear lakes form in the regionally flat landscapes, more easily facilitating upstream dispersal. The longer-term trend is reduced continuity and extent of marsh and increased area of saline flats. Fewer estuaries reduces opportunity for new arrivals dependent on hydrochory to leave coastlines with less marsh in drainage systems slowing migration. Desert Lake began forming in the Pliocene in Western Australia and in the later Pleistocene in Central Australia. *Sarcocornia* missed these ideal conditions, severely limiting its inland range compared with *Tecticornia*, which arrived at optimum time.

Such process explains correspondence of high species richness and diversity of coastal chenopods with arid coast of Davies (1977, 1986). Arid coast is defined by river discharge to the sea and has fewer, smaller estuaries. It adjoins the greatest continental extent of flat and low elevation with drainage catchments stretching into the continental interior.

Inland Diversification

The diversification of Australian chenopods is predominantly an inland phenomenon. Opportunities for adaptive radiations arise in a subcontinental area where a drying climate alters the nature and extent and of nine land types, but it is largely confined to Riverine Desert and Desert Lake. Coastal diversity exceeds that of Sand Desert, Shield Plain, Desert Upland or Karst Plain. Exaptation for drought-tolerance may have initially emerged in Riverine Desert.

Broad tolerances of Coast facultative species reduces a need for adaptation to occupy similar habitats of Riverine Desert. Some differentiation occurs with departures from the coast as shown by differing coast disposition, habitats and ranges of subspecies of some Coast Facultative species and an Inland Facultative species. Such differentiation is most evident in the Chenopodieae I clade, but associated with occupancy of sandy and rocky/karst habitats, not marsh habitats.

Riverine Desert and Desert Lake also have the most species restricted to a single land type. This suggests species shared with other land types originated in these habitats. Species richness relates to time and area (Wiens 2012; Lomolino *et al.* 2010) and being a more extensive and older landscape, Riverine Desert should have species richness greater than Desert Lake.

The initial pool of species is important. Coast, Riverine Desert and Desert Lake all have habitats that flood and that become disconnected under intensifying aridity. Coastal diversity is the initial, but limited, pool of species for Riverine Desert. Drying mesic conditions, increases the reliance on drought-tolerance exaptation for survival, giving rise to Desert Lake as aridity increased the ratio of evaporation to precipitation, concentrating surface salinity. The pool of Riverine Desert species provides the initial diversity of Desert Lake. Globally the main inland communities of *Atriplex* are halophyte communities of drainage systems and shrub-steppe vegetation (Osmond *et al.* 1980). In Australia both occur in Riverine Desert, associated with ancient drainage systems of the Yilgarn and Eyre-Murray Centres.

Stony Desert is also diverse with species, consistent with mapping as distinctively chenopodiaceous region (Leigh 1972, 1981 and 1988). This inhospitable habitat is the driest land of hot deserts, due to the stony surface, soil texture and chemistry (Zohary 1962; Walter and Stadelman 1968; Laity 2008). Soils are dominantly Red Vertosols or Red Sodosols (Stace *et al.* 1968; McKenzie *et al.* 2004). Salt toxicity, alkalinity and lack of soil moisture for lengthy periods, severely limits plant growth and diversity. The greatest extent is the gibber plains of the Lake Eyre Basin, in Australia's driest region.

Stony Desert features in evolution of the SclerolaenAff subgroup (Sclerolaenid clade) along with Riverine Desert. The subgroup dominates species composition of these land types, both generally and for species restricted to them. Restricted species of Stony Desert includes *Sclerolaena longicuspis* that has the longest, most rigid spines in the genus (Cunningham *et al.* 1992). Furthermore, 54 % of subgroup species are in these two habitats only, dominating groundcovers with common species such *S. anisacanthoides*, *S. divaricata* and *S. intricata*. Extensive alluvial plains of open low vegetation in Riverine Desert have Red Vertosols and Red Sodosols too, but also Grey and Brown Vertosols, of similar low soil moisture and salt-toxicity to Red Vertosols.

Chenopod species of coast and desert share particular life forms. *Sclerolaena* spp. of Stony and Riverine Desert have a "cushion" plant form when mature (figures 3.11 and 3.12). The spherical, hemispherical and round plant perimeters are mainly exhibited by perennial chamaephytes and near the soil surface protect against heat, aridity and radiation on exposed, rocky slopes and plains (Hegazy and Lovett-Doust 2016). Such form is typical of Stony Desert as it minimises the proportion of foliage exposed to direct sun, moderates diurnal extremes by keeping the interior humid and relatively shaded and traps fine matter and coarse soil particles moved by wind or run-off. *Sclerolaena* utilise the form in dispersal. Commonly named roly-poly, both *Sclerolaena birchii* and *S. muricata* break from their taproot when mature, rolling before the wind and spreading seed distantly as it does not readily detach from stems (Cunningham *et al.* 1992; Auld and Johnson 2011).

Other chenopod species have cushion forms. The shrubs *Atriplex incrassata* and *Maireana aphylla* that dominate Stony Desert plant communities (Brandle 1998) have this form in dry seasons (*pers. obs.*). *Atriplex incrassata* is part of an *A. nummularia* complex (Wilson 1984) and along with *M. aphylla*, typifies riverine plant communities on heavy soils (Leigh and Mulham 1965; Cunningham *et al.* 1992).

Cushion forms are also on coastal cliffs e.g. *Leucophyta brownii* "coastal cushion bush" in South Australia (Specht 1972; Opperman 1999). Coastal rocky cliffs and slopes, share extreme conditions of salt and exposure with Stony Desert, suggesting extreme exposure (wind, radiation, heat and dry) may have driven the emergence of *Sclerolaena*.

Stony Desert is habitat drier than Shield Plain, Desert Upland and Sand Desert (Walter and Stadelmann 1974; Kovda *et al.* 1979; Ayyad 1981; Laity 2008). It occurs in the driest part of Australia. Lack of infiltration creates very high surface run-off, generating dense networks of drainage channels in the low relief topography, and providing connection with Riverine Desert land types. Stony Desert soils have clay layers that hold water very tightly but also contain various salts, especially lime and gypsum, providing a source of cations for xerohalophytic functions.

Figure 3.11: The compact cushion form of *Sclerolaena* ssp. on stony plain of the Arcoona Tableland near Woomera, South Australia.

Figure 3.12: Cushion forms of *Atriplex incrassata* and *Sclerolaena* spp. on undulating stony plain of Witjera National Park, South Australia showing new shoots after rain.

Chenopods in Stony Desert exhibit patterns similar to other rich land types. Species are not distributed uniformly (Brandle 1998); nor are immigrant clades. Perennial species cluster in or around the gilgai that hold water after rain (e.g. *Maireana aphylla*) and a luxuriant and enduring growth of annual species. In the water-shedding shelves between gilgai, *Sclerolaena* are prominent survivors of dry conditions and *Atriplex* species are short-lived. Annual *Atriplex* contrast with the persistence and longevity of *A. incrassata* and *A. vesicaria* which are “drought-deciduous”. *Dysphania* are absent and Chenopodieae I is relatively rare, though the shrub *Rhagodia spinescens* is uncommonly around gilgai. Further indicative of links to Riverine Desert, three species of *Tecticornia* are in Stony Desert with the uncommon *T. papillata* peculiar to it (Shepherd 2008). Niche conservatism largely restricts inland occurrences to saline or brackish marsh, but Stony Desert has provided the *Tecticornia* clade with a means of escape.

The least occupied land types are Sand Desert, Desert Upland, Shield Plain, Desert Clay Plain and Karst Plain. Sand Desert is the most unusual, being 40% of the arid zone (Mabbutt 1988; Anand 2005), and the expectation in a littoral connection that it should harbour chenopod species; chenopod occupancy is only comparable to three dissimilar land types.

Species poor habitats are barriers to occupation. Sand Desert has barriers of youth and competition with xerophytes e.g. *Acacia*, *Triodia*. The other types are modified land types, forming with intensifying aridity. Desert Upland and Shield Plain have non-saline habitats with diverse xerophytic taxa similar to Sand Desert and largely derived from resident taxa, which being glycophytes, are a barrier to chenopod presence with their competitive advantage. Chenopod occupation of Desert Clay Plain is uncertain, but eco-physiological similarity to Stony Desert and clay floodplains of Riverine Desert, suggests more species may be noted with closer scrutiny.

Migration barriers or edaphic differences between coast and desert dunes do not explain species poverty of desert dunes. Australian sandy habitats include taxa of 5 chenopod clades (figure 3.2). Sand plains with dune forms adjoin coastal dunes with chenopods in regions of South of Western Australia under Mediterranean climates. Overseas, diverse chenopod genera occur on sand dunes of the Middle East (Zohary 1973, Danin 1996) and Central Asia (Grubov 2000).

The relative species poverty of Karst Plain and the Nullarbor Plain, results from topographic and edaphic uniformity. Waddell *et al.* (2010) map and describe 54 land systems on the plain in Western Australia, ranging in size from Lefroy (9 km^2) to Nyanga (12 990 km^2). Of the total area of 118 358 km^2, more than 84% is of land units noted as stony limestone or calcrete plain with *Maireana sedifolia*, *Atriplex vesicaria* and *Sclerolaena* spp.

Numerous chenopod taxa peculiar to limestone habitats suggests adaptation, but this is not straightforward. Limestone specialists are from Chenopodieae I (*Chenopodium curvispicatum*, *Rhagodia ulicina*), *Atriplex* Clade 2 (*Atriplex acutibractea* and the near endemic *A. cryptocarpa*) and the Sclerolaenid Clade (*Maireana sedifolia*, *M. trichoptera*, *Sclerolaena obliquicuspis* and *Eriochiton sclerolaenoides*). However, species that prefer calcareous sands e.g. *Atriplex stipitata*, *Maireana pentatropis*, *M. radiata* and *Sclerolaena parviflora*, while common in adjoining provinces, are not on the plain. Other prominent inhabitants are widespread species of diverse habitats (e.g. *Atriplex vesicaria*, *Maireana georgei* and *Sclerolaena diacantha*).

The suggestion of Specht (1981b) that lime tolerance facilitated coast to inland movement may apply to some taxa. That feature may have aided expansion in the clades listed immediately, but not in *Dysphania* and *Tecticornia* clades which are uncommon on limestone and on the Nullarbor Plain. Such influence may be strongest in the Chenopodieae I clade, with additional species *Rhagodia crassifolia* and *R. preissii* being mostly of Karst Plain and Coast land types, and *R. candolleana* largely of coast and mesic karst forms. *Maireana erioclada* and *M. pentatropis* in the Sclerolaenid clade strongly associate with limey soils. *Maireana erioclada* is on coastal Nullarbor Plain and adjoining Eyre Peninsula but *M. pentatropis* is very the scarce on the Plain. The two species form a distinct basal clade (Cabrera *et al.* 2009) of age contemporary with emergence of the Nullarbor Plain.

Adaptation in Australian Chenopods – a response to habitat occupation?

The expectation of notable adaptation being required to occupy very dissimilar habitats is yet to be realized. The poverty of species in dissimilar habitats prompts questions of adaptation that can be attributed to habitat, but adaptation trends are poorly known. Morphology of the mature reproductive elements taxonomically distinguish genera and species, along with floral structure for *Dysphania* (Wilson 1984). Adaptation may relate more to reproduction and dispersal, rather than to tolerance of habitat.

Flower Period	*Atriplex* Clade 1	*Atriplex* Clade 2
All year	1	14
All year (Winter-Spring peak)		2
Winter-Spring	1	8
Spring		1
Spring-Summer		1
Summer	1	1
Summer-Autumn		1
Autumn	1	2
Autumn-Spring		2
Winter		3
Not given		1

Table 3.5: Flower periods of South Australian *Atriplex*, from monthly flowering in Wilson (1986). The state has 4 of 8 species from Clade 1 and 36 of 52 species from Clade 2. Two months of a season qualifies as seasonal e.g. Aug-Oct is Spring; July to Oct is Winter-Spring. *A. acutiloba* given Aug-Sep, treated as Winter-Spring.

Marked morphological variation in the Sclerolaenid clade is consistent with richness and age. Two main characters of the fruiting perianth are wings or spines, which with their architecture, largely distinguishes the genera (Wilson 1984). The species differentiate on character states, e.g. the *Maireana* wing is glabrous or woolly, entire or in five segments;

Sclerolaena has 2, 3, 4 or 5 spines. The derivation of *Sclerolaena* may be an adaptation trend toward animal dispersal (Cabrera *et al.* 2009) but this is unclear. Many spines are small, smooth and brittle with no barbs or hooks. The perianth with two spines tends to lay flat on the ground (*pers. obs.*), so that attachment to passing animals seems ineffectual. Also spines restricted to the perianth do not protect foliage from herbivores; selection for defence won't explain this adaptation trend.

Morphological variation in *Atriplex* clades 1 and 2 is mainly in the fruiting bracteoles, but of sufficient similarity to being long thought a single clade. Table 3.5 shows phenological variation in South Australian *Atriplex* that inhabit coastal and inland areas of the Eyre-Murray Centre. Species from *Atriplex* Clade 1 have different flowering periods. Most species in *Atriplex* Clade 2 flower any time of year. Several species flower over winter and spring, but eleven species flower either over a shorter or different season.

Habitat has some influence on lifeform. Rich clades prominent in drylands habitats, have coastal taxa that are mainly shrubs. The inland species include annual and biennial forms. *Sclerolaena* are annual, biennial or triennial species, relatively richer in driest regions. Being derived from *Maireana*, which has many shrub species, indicates an evolutionary trend toward shorter-lived species – drought evasion rather than drought tolerance. Similarly, of ten species from *Atriplex* Clade 2 that grow in Stony Desert land type, one is a shrub and nine are annual/biennial herbaceous forms.

Succulent fruit is a significant dispersal adaptation. Berry or berry-like fruit is rare in chenopods, and though not unique to Australia, is notably developed here (Kuhn 1993; Kadereit *et al*. 2010), aiding dispersal by birds (Wood 1937; Lang *et al.* 2003; Brown 2014). Eighteen of 24 species from the Chenopodieae I clade have a succulent pericarp, that in 13 species swells into a small berry. It is the youngest rich clade, has continental and coastal ranges matching that of older clades, and a presence in drier woodlands of the Eastern Highlands, greater than the Sclerolaenid or *Atriplex* clades. *Atriplex semibaccata*, also found in dry woodlands, has a semi-succulent fruit. The most widespread species of the Sclerolaenid clade is *Enchylaena tomentosa*, which also has a berry fruit.

Speciation in Australian chenopods, may be stabilising traits that are somewhat plastic. The epidermal character of leaf, stem or perianth can be glabrous, scaly, mealy, tomentose or woolly. Such coating deflects radiation or retards moisture loss, as does the thickened cuticle of xerophytes. It can develop from cells that regulate salt content in plants (Kuhn 1993). These character states distinguish species, especially in the Sclerolaenid and *Atriplex* clades, and would be ancestral, being observed also in overseas taxa.

More taxon explicit and quantitative treatment of traits, is needed to fully understand evolution in each clade and especially trait variations with difference in habitat. Of some interest would be the traits allowing closely related species to occupy very different habitats especially for habitats similar and dissimilar to coastal ones.

Land types and habitats within Centres of Diversity

The land types richest in species are of varied extent within the Centres of Diversity. The richest provinces have land types poor in chenopods, so that species richness is also locally concentrated.

The centres have similar physiography, despite different underlying geological structure. Landscapes are subdued topography at low elevation, with ancient and modern drainage systems of seasonal, irregular or no flow, in vast catchments reaching from coasts into the central interior. Climatic gradients range from coastal Mediterranean and temperate to arid.

The Yilgarn Centre is predominantly an igneous and metamorphic platform with fold ranges. It comprises a transition from coastal Mesic Plain & Range to arid inland Shield Plain in the Yilgarn Plateau, with Pilbara Desert Upland in the north. The Yilgarn Plateau has a sandplain mantle (Sand Desert in dry regions, Mesic Plain in wetter) derived locally from wind-affected soils in the drier Quaternary (Mabbutt 1988; Hesse 2010). Vegetation of the sandplain, valleys and rocky hills is part of the SouthWest Global Biodiversity centre (Lambers 2014) that extends into drier regions.

Chenopod taxa mainly occupy Desert Lake and Riverine Desert of palaeodrainage in drier regions. Beard (1974, 1975, 1976b) maps chenopod formations in linear, arcuate areas of Riverine Desert and Desert Lake aligned to palaeodrainage axes. The broad, low drainage divides have *Acacia* scrub with some Eucalypts over xerophytic shrub and grass on Sand Desert and Shield Plain, but with chenopods of non-saline habitats e.g. *Maireana melanocoma*, *M. murrayana*, *M. thesioides* in mulga scrubs. Riverine Desert is mostly in valleys of regular seasonal flow with chenopod shrub-steppe vegetation. Flow channels are sandy, rocky or cut into shallow alluvium Western Australia Department of Water (2014) and once were predominantly alluvial Morgan (1993) and Clarke (1994a, 1994b). There are no vast clay floodplains or broad, alluvial plains as found in central and eastern Australia.

The Eyre-Murray Centre is set in sedimentary basins with Desert Upland, Shield Plain and Mesic Plain and Range on its periphery. River flows in this centre are generally more active than the Yilgarn Centre, with seasonal monsoon or alpine sources to the east, north and south, and irregular pluvial events of Central Australia. The species rich Central Lowlands West province, includes the Simpson Desert dune field, extensive Riverine Desert and Stony Desert and the salina of Lake Eyre. Riverine Desert and Stony Desert with chenopod shrub formations extend north and east into adjoining provinces. Chenopod formations within Riverine Desert include shrub-steppe of broad alluvial plains (e.g. *Maireana astrotricha-Atriplex vesicaria*) and halophytic marsh of floodplain, swamp or watercourse e.g. *Atriplex nummularia*, *Maireana aphylla* (Eldridge 1988; Brandle 1998).

Simpson Desert dunes have *Acacia* scrub with xerophytic grasses, similar to sandplain mantles of the Yilgarn Centre. The major landscapes of the Simpson Desert are Dune Fields, Rivers and Floodplains, Gibber Plains and Residuals and Sandplains (Purdie 1984). The main chenopod habitat in eleven dune field land systems, is the older land surfaces exposed between dunes. Systematic surveys in the Eyre-Murray Centre record few chenopod taxa on the siliceous dune sands, with *Salsola australis*, *Enchylaena tomentosa* and *Rhagodia spinescens* mainly noted (Hyde and Playfair 1997; Brandle 1998; Neagle 2010), being widespread species tolerant of several habitat types.

Chenopod poverty of Sand Desert, Shield Plain and Desert Upland indicates occupation barriers. The extent of the land types means species richness in Yilgarn and Eyre-Murray Centres has marked local variation in the richest provinces. In the Yilgarn Centre, local richness is in drainage systems. In the Eyre Murray Centre, drainage and gibber plains provide local richness. Non-saline soils are common to Sand Desert, Shield Plain and Desert Upland. The principal source of inland salt is cyclic, not parent material (Chivas *et al.* 1991; George *et al.* 2008; English *et al.* 2013). In arid areas, surface salt is removed by rainfall to lower elevations or deeper layers of sand (Walter and Stadelman 1974; Laity 2008). As landscapes are transformed under aridity, the more competitive glycophytes occupy elevated land units, retarding but not preventing chenopod occupation. In lower lying land units, halophytes have free rein because soil conditions are lethal to glycophytes.

Disjunct distributions and dune field disruption

Continental disjunction of arid taxa is associated with dune fields. Most clades and derived lineages such as *Sclerolaena* are affected. Other disjunctions of mesic-arid taxa relate in part to dune fields. Dune field landscapes date to *ca*. 1 Ma at most, achieving greatest activity and extent in the last 0.3 Ma. Wet/dry oscillations of the last 0.1 Ma influenced arid flora evolution, generating dune fields in the dry cycles, with their own adapted plant associations, and initiating disjunction in many taxa (Barlow 1981, 1994). With a recent age of disjunction there may be few chenopod sister taxa pairs resulting from range fragmentation.

Dune fields are not unsuitable habitat. Low chenopod occupancy comes from their youth and competition with other plant taxa. Other chenopod species have continuous range through dune field regions. A quarter of disjunct chenopod species grow in Sand Desert habitats. Some species are locally or temporarily dominant (*pers. obs.*; also Floristic Groups 5 and 23 in Hyde and Playfair 1997). These include *Maireana pyramidata* (a disjunct species) and *Rhagodia spinescens* on low dunes respectively south and west of Lake Frome. *Atriplex velutinella* and *Salsola australis* dominate dunes after rain in the southern Strzelecki Desert.

Chenopods adopt both avoidance and tolerance strategies for desert conditions. Avoidance includes annual or biennial life cycles as noted among *Sclerolaena* and *Atriplex*. Tolerance can involve defoliation of perennial species (“drought-deciduous”) or deeper roots into subsoil moisture (Hall *et al.* 1964). Such adaptations are oriented to eventual return of mesic conditions before loss of seed viability and or of plant reserves prevent regeneration. Salt-tolerance enabling greater capture of soil moisture, is of no use in the absence of moisture.

The disruption of dune field formation has strong potential for extinction. Widespread disruption and prominent disjunction of other taxa underlies the “Great Arid Period” from which the arid flora emerged after destruction of an ancient mesic one (Crocker and Wood 1947). More recent notions (Byrne *et al.* 2008) have extinction balancing diversification in a “speciation maintenance” phase. Chenopods are not entirely immune to disruption, their disjunctions revealing regional scale of population separation, and would have some tolerance to dune expansion. Disruptive processes are the burial of older land surfaces and sandblasting in the windy conditions. Coastal dunes build through trapping sand, blown from the adjoining, exposed beach (Nichols 2009), conditions to which coastal dune taxa are well adapted (Danin 1996). The foredune that takes the brunt of impact is where chenopods of Beach-Dune systems are commonly abundant (Clarke 1994c).

The most exacting disruption is in dune origin; disjunction and dune formation result from a climate event. Formation requires a denuded land surface (Twidale 1976; Laity 2008; Nichols 2009). In the absence of vegetation, soil surfaces are exposed to wind drag, dust is winnowed and removed and sand locally accumulates (Krieg *et al.* 1990, Twidale and Wopfner 1990). Lunette systems are similarly affected (Twidale and Wopfner 1990).

Where dune fields form, influences species richness through both speciation and extinction. Dune fields generally develop where sufficient mixed alluvium is exposed (Laity 2008, Nichols 2009), which is mainly in riverine systems of sedimentary basins (Mabbutt 1977a, 1988) e.g. the Simpson Desert in the Lake Eyre Basin (Twidale and Wopfner 1990), where species richness is high. Sand sheets develop where mixed alluvium is of insufficient quantity, such as sandy soils of the Yilgarn Plateau. Blown sand trapped in palaeovalleys aids disorganisation of drainage (van de Graaff *et al.* 1977), preventing channel throughflow, limiting water borne dispersal and isolating populations. Geographic isolation puts valley populations at some risk of extinction, but surface seepage of groundwater, common in the Yilgarn Centre, would enhance survival of fragmented populations, especially taxa tolerant of high salt content such as *Tecticornia*. Both extinction and speciation could result from the extended droughts denuding alluvial plains where dune fields form and especially in the Eyre-Murray Centre. Perennial chenopods needing inundation to restore plant biomass would face extinction, while selection for shorter life cycles drives speciation and possibly explains richness of SclerolaenAff and *Atriplex* Clade 2 in this centre. The marginally greater diversity of the Eyre-Murray Centre, could arise from combination of youth and having endured greater net extinction.

CONCLUSION

Chenopods fit the habitat element of a littoral connection, showing the strong influence of niche conservatism on chenopod evolution. All chenopod clades occur in the dominantly occupied Riverine Desert or Desert Lake which are most similar to common coastal habitats. Sandy substrates are not a shared habitat defining a littoral connection, due to age and plant competition, but a capacity to share may be emerging. Sharing of limestone habitats occurs to small degree.

The ancestral character of chenopod arrival is broad ecological tolerances allowing occupation of any coastal habitat, facilitating expansion along regional coastlines and maintaining presence despite shoreline change under eustasy or tectonism.

Riverine Desert has had a substantial role in migration and diversification. Desert Lake also produced marked speciation from the species pool in Riverine Desert. Desert Upland and Shield Plain are the main barriers to occupation. The low occupancy of Karst Plain, arises from its homogeneity, and includes a small suite of limestone taxa.

Riverine Desert facilitated initial departures from the coast, effectively extending species ranges from coasts into and throughout both Centres of Diversity. Salt-tolerance enabled desert occupation, assisted by flood-tolerance and exaptation for drought-tolerance. Other notable factors include dispersal over low watersheds into the Central Lowlands of the Eyre-Murray Centre and glycophytic taxa retarding occupation of Desert Upland and Shield Plain.

Coast to inland transitions through sandy substrates are uncommon. The limited transitions of *Rhagodia* (Chenopodieae I Clade) relate to Pleistocene formation of sand landscapes adjoining coastlines, representing recent shift only.

Diversification in Riverine Desert arises from age, its vast size and changing flow regime. Drainage decline effected geographic isolation and selection for drought-evasion life strategies, resulting in halophytes confined to drainage axes and xerohalophytes on surrounding plains increasingly reliant on rainfall for moisture. Desert Lake speciation results in part from its fragmented distribution.

Dune fields are associated with subcontinental disjunction of arid taxa. Conditions of dune field formation, more than nature of habitat were instrumental in forming disjunct taxa. Conditions of formation may have induced species extinctions of the mid-late Pleistocene.

CHAPTER 4. PHYLOGENY OF AUSTRALIAN *ATRIPLEX* – SPECIATION AND LANDSCAPE FORMATION

INTRODUCTION

Speciation is a major factor in the modern distribution of plant taxa (Cox and Moore 2010; Lomolino *et al.* 2010). For Australian chenopods, diversification is predominantly an inland phenomenon with ancestral species that are migrants from the coast or from a Centre of Diversity. Numerous chenopod taxa restricted to either the Yilgarn or Eyre-Murray Centres of Diversity suggest that phylogenetic lineages are likely restricted to those centres. However, the shared taxa are indicative of migration between Centres, possibly of exchange.

Major temporal factors in speciation patterns are clade arrival and emergence of arid landscapes. Speciation either accompanies landscape formation or occurs later. Initial inland range expansions are of extensive scale, through drying riparian habitats (Chapter 3). Many species are restricted to such habitats and although many occur also in two or three habitats, it is likely that species emerge in one land type, before colonising another. For many Australian arid taxa, adaptive radiations occurred as the arid landscapes developed (Byrne *et al.* 2008).

Coastal taxa are important to interpreting speciation pattern in littoral connections. They are potentially the oldest species in any clade, with an ecology reflecting the traits of ancestral colonizers. Taxon cycling (Shmida 1985) could explain youthful coastal species, whereas an absence of coastal taxa suggests extinction or lack of support for a littoral connection.

From a comprehensive phylogeny, the patterns of a clade's migration and diversification will be evident in the relationship of its lineages to the regions and land types of its constituent species (Lomolino *et al.* 2010; Wiley and Lieberman 2011). With the order of species and lineage emergence and the formation of land types, a clade history can be constructed, especially knowing the phylogenetic position of coastal taxa. The aggregation of all chenopod clade histories then provides the course of evolution in Australia, with pattern congruency showing principal influences and unique patterns revealing important variations.

However, analyses of all clades is beyond the scope of this study. Instead focus will be on the two C_4 *Atriplex* clades, which provide a comparative study of patterns in range extension and diversification and because only molecular analyses can determine their membership.

PHYLOGENY AND LANDSCAPE CHANGE

Phylogenetic pattern and range expansion

Phylogeny is the evolutionary relationship of an ancestor with descendant species (Lomolino *et al*. 2010) – a pattern of the order of divergence of related organisms. Of specific interest here, is the divergence in lineages arising from a common coastal ancestor. The number of lineages, their species membership and ranges, order (and age) of emergence are the patterns of expansion and diversification (Morrone 2009; Heads 2012, 2014). A lineage of species restricted to a centre of diversity identifies evolution confined to it. Lineages with shared species indicate migrations between centres. A comprehensive phylogeny could suggest the direction of migration.

The phylogenetic position of coastal species is informative of a clade’s littoral connection. Extant coastal species in basal phylogenetic position strengthen the assumption of littoral connection. The relationship of coastal taxa to one another potentially reveals coastal lineages, or episodes of inland migration and Taxon Cycling (Shmida 1985), as seems evident with *Threlkeldia* in the Sclerolaenid Clade. If none are basal, either extinction has occurred, or a littoral connection is doubtful.

Within a clade (or subclades), under a littoral connection, allowing for possibility of extinctions:

(1) The number of lineages is the minimum number of migrations, unless all lineage members are coastal and occur in a single province. Clades diverging very early indicate the number of ancestral coastal departures, especially for coastal species in basal position. See figure 4.1a and 4.1b.

(2) Lineages comprising species unique to a Centre and spread through more than one province indicate range expansion within that Centre. If clade age is comparable to arrival estimate, and the clade lacks coastal species, extinction has occurred. Coastal species in a lineage, where inland species formed through earlier divergence, are derived and may constitute return to coast, especially if closest relatives are remote from shorelines. See figures 4.1a and 4.1c.

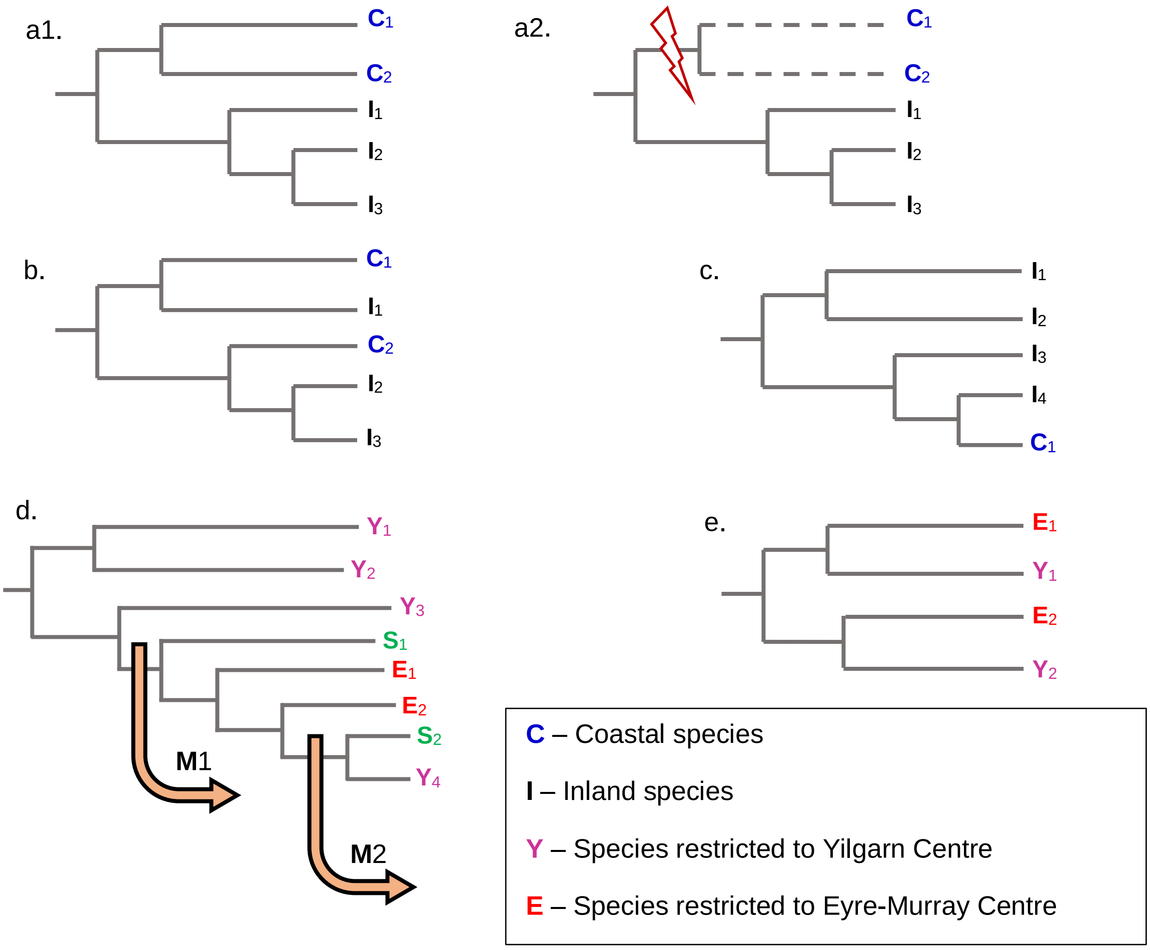


Figure 4.1: Interpretive phylogenetic patterns under littoral connection for species of particular distributions; a: coastal species in basal position within radiation of a single clade; coastal origins can be obscured by extinctions as in a2. b: coastal species of separate lineages in near basal positions indicate separate expansions inland. c: coastal species in a derived position i.e. emerging later than some inland species, and more likely if also fitting pattern (a1) and I_3 and I_4 occur remote from coastlines. d: from a lineage originating in the Yilgarn, an immediate ancestor of shared species S_1, expands range into Eyre-Murray Centre (M1), from which a lineage develops where immediate ancestor to shared species S_2 extends range into the Yilgarn Centre.

(3) Clades comprising species unique to one Centre and shared by both, indicate complexity of diversification in that centre and range expansion from one centre to another. The position of the shared species in relation to unique species within that clade, determines the order of diversification and range expansion. If the shared species is basal then widespread range expansion occurred early in lineage history. If the shared species is derived, broad range expansion occurred after initial diversification; the centre of diversity in which the unique species lie is the origin of the expansion. If a shared species is derived, a source of the expansion may be identified, when unique species emerging before the shared species belong to a single centre. See figure 4.1d

(4) Clades comprising species that vary little in their habitat of occupation indicate where niche conservatism strongly operates within a lineage. Clades with species that vary greatly

in their habitat, show niche differentiation influenced speciation, especially if adaptations enabling such shifts are identifiable. However, a mix of habitats may also show that an exaptation of salt tolerance, for tolerance of aridity, enables shifts to differing habitats where other species struggle to survive in changing circumstances.

(5) Clades of species unique to both centres, indicate either vicariance events or long-distance dispersal (see Chapter 2). In a rich clade, the more lineages exhibiting such a pattern, would favour vicariance scenarios (Lomolino *et al.* 2010). Vicariance events are especially likely where similar patterns are seen in different groups of taxa that have different ecology and dispersal means (Heads 2014), a situation possibly visible in some of 11 chenopods clades. See figure 4.1e.

The older a clade is, the more complex can be the patterns arising from several departures from the coast, multiple exchanges between centres, lineages confined to each centre or having sub-lineages from different centres. Congruency of pattern could confirm a general control of expansion and diversification e.g. if the west to east speciation pattern of the Sclerolaenid Clade (Cabrera *et al.* 2011) occurs in other clades.

Phylogeny and landscape formation

Emergence of species or lineages in landscapes is temporally constrained by the age of landscape formation. Occupation occurs as the landscape forms, as suggested for Australian desert taxa (Byrne *et al.* 2008), or after a significant lag time.

Synchronous occupation or very short time lags could be expected for Australian chenopods. With exaptation for arid conditions, adaptation is minimal or unnecessary for inland occupation, as typified by Coast facultative species and early migrations being through palaeodrainage systems of Riverine Desert. The earliest chenopod presence in the Australian interior approximates arrival times of older clades. Adaptive radiations closely followed arrival in *Tecticornia* (Shepherd *et al.* 2004) and *Atriplex* (Kadereit *et al.* 2010). Thus emergence of lineages should approximately coincide with geochronological estimates of landscape formation. Land types such as Desert Lake, Sand Desert, Karst Plain and Stony Desert are dated landscapes (Fujioka and Chappell 2010).

In contrast, occupation can be delayed. In South America, Guerrero *et al.* (2013) found significant time lags within three plant clades and one animal clade, between creation of desert habitats and emergence of arid-adapted species. However, this divergence is from mesic sister species, emphasising adaptation to novel ecological conditions, and which in Australia would relate to taxa present before the onset of aridity e.g. *Acacias*. All desert land types are climatically novel but chenopod habitat is edaphically novel. Salt tolerance enabling occupation of saline desert landscapes, is a relatively rare adaptation in plants (Flowers *et al.* 2010; Flowers and Colmer 2015).

Phylogeny of all rich immigrant clades matching species or lineages to landscape of occupation would reveal how landscapes controlled diversification and distribution. Systematic surveys show common floristic association of chenopod species from various immigrant clades (e.g. Brandle 1998; Hyde and Playfair *et al.* 1997; Waddell *et al.* 2010). Such investigations are a desired search for congruence in the relative timing of biotic and abiotic events (Byrne *et al.* 2008), at least among chenopod immigrants within the arid flora.

Molecular clock analyses may confirm near coincidence where taxa are pre-adapted, or reveal time lags required for development of adaptations. However, time lags can also point to cycles of occupation in a given land type as outlined immediately below.

The likelihood of regions reflecting origins or migration routes that derives modern distribution is best seen in a congruency of distribution pattern for several distantly related taxa e.g. plant and insect groups (Cox and Moore 2010; Lomolino *et al.* 2010; Wiley and Lieberman 2011). Elements of congruency relate to space and time (simultaneity of co-location past and present), ecology (tolerance of same environmental conditions) and include adaptation trends e.g. to drying climate. Where times of diversification coincide, events critical to chenopod evolution are identified e.g. two clades occupying a novel landscape simultaneously. In contrast, a singular event noted prominently in only one clade, relates to a critical time in that landscape or its regional location or adaptation peculiar to that clade.

At the least, such patterns can be described relative to their order of emergence. Occupation of older land types is likely to occur earlier in a clade that is present in Australia before that landscape formed, compared with one arriving after or during formation. Thus synchronous occupation is more likely in older clades, especially in the very rich and very extensive Sclerolaenid Clade, which should provide a useful comparison with speciation-landscape patterns of *Atriplex* (using Cabrera *et al.* 2011).

Species emergence could also identify undated, critical events in modified land types. Land types like Desert Upland, Shield Plain, Karst Plain, mainly became drier, whereas others such as Riverine Desert became saline as well as drier. Emergence of species restricted to modified types may point to critical climatic rather than edaphic changes.

In particular, for eleven immigrant chenopod clades of similar but varied ecology, and of different arrival date and landfall, similar events may occur at different times and repeatedly in a single clade. Occupation lags may be cyclic as shown by the co-occurrence of *Maireana sedifolia*, *Eriochiton sclerolaenoides* and *Sclerolaena obliquicuspis*, emerging in the Sclerolaenid Clade at different times. These sympatric species are restricted to karst landscapes that developed and expanded through diverse processes during the Neogene (Sheard 1995; Sheard and Smith 1995). The emergence of each species possibly relates to a different stage, with subsequent range expansion forging similar species ranges. *Atriplex acutibractea* and *Chenopodium curvispicatum* are also restricted to karst land types and have similar species ranges.

Phylogenetic position of coastal taxa is also informative. In a littoral connection, modern coastal species indicative of ancestors would appear in basal position. Though occurring at different times, crown ages of such species (or stem ages where they form a lineage) should be among the oldest in the clade i.e. the first to emerge. Extinction remains a problem in isolating the coastal ancestor, but such a pattern of firsts, is as important as those reflecting coincidence in adaptation to or occupation of drying landscapes.

Existing phylogenies and biogeography

Molecular analyses of rich immigrant chenopod clades have mostly investigated global chenopod relationships using species subsets. Though sufficiently large to suggest clade structure, phylogeny of *Tecticornia* (Shepherd *et al.* 2004), *Atriplex* (Kadereit *et. al.* 2010) and Camphorosmoideae (Cabrera *et al.* 2009, 2011) are each obscured by basal polytomy, interpreted as rapid radiation over the Late Miocene-Pliocene. All species in a clade are needed to ascertain patterns of regional speciation within centres, exchange between them and relationships of coastal taxa. Cabrera *et al.* (2009) confirm generic groupings of small lineages within the Sclerolaenid clade restricted to the Yilgarn Centre e.g. *Roycea*, *Didymanthus*, or largely confined to the Eyre-Murray Centre e.g. *Malacocera*.

Generic groupings within the Sclerolaenid Clade currently provide the best indication of migrations within the Australian continent. Combined with species distributions, Cabrera *et al.* (2011) broadly discern a west-to-east speciation pattern, beginning in south-west Australia. Species in these genera are mostly of inland habitats, with initial terrestrial expansions in the Yilgarn Centre, then toward the Eyre-Murray Centre. Ten of twelve genera are shared, so most genera have also migrated from one centre to another. Such a recurrent pattern of expansions, is indicative of mobilism with differentiation (Heads 2012, 2014).

However, the phylogeny of the species subset indicates a general trend only. A westerly expansion of at least one lineage is possible. Also, with three species in three shared genera being Coast facultative, range expansions prior to diversification may not all be terrestrial.

Genera of the Sclerolaenid clade suggest regional lineages are uncommon. *Roycea*, with three species in a near basal clade, is restricted to the Yilgarn Centre. So is the monotypic *Didymanthus*, part of *Dissocarpus* clade that spans both centres. All genera in the Eyre-Murray Centre are shared genera. *Malacocera* is largely confined to it, but has outliers of one species in the Yilgarn Centre.

Understanding chenopod diversification requires comprehensive, resolved phylogeny for the six rich clades, which is beyond the scope of this study. However, resolving a comprehensive tree for a single, rich taxon may reveal patterns for comparison and aggregation with other immigrant clades.

The genus *Atriplex* is an ideal subject to examine migration and diversification patterns. Molecular analyses are needed to determine membership of the two C_4 *Atriplex* clades, as the clades are not differentiated taxonomically. Both have relatively abundant coastal taxa, of obligate and facultative type. Both have inland species of substantial inland range, and species restricted to each centre as well as shared between them. Species of Clade 2 are found in all land types, while Clade 1 has a high proportion of species restricted to a single land type. The richer *Atriplex* Clade 2 is of subcontinental range, and species commonly co-occur with those of the Sclerolaenid and Chenopodieae I clades. Both clades have shrub forms, but Clade 2 has annual and biennial forms lacking in Clade 1. Comprehensive and resolved phylogeny will assist revision of Australian *Atriplex* taxonomy.

Molecular phylogeny of *Atriplex* reported in Kadereit *et al.* (2010) has expanded to an unpublished phylogeny of Krieg (Kadereit *pers. comm.* 2014). This includes all but 15 *Atriplex* species and shows several lineages of moderate to good support with two prominent subclades identified in each clade. However, resolution issues include species sample replicates in equivocal (conflicting) positions. Also, analyses derive from collection and sequencing protocols prior to 2005.

AIMS, OBJECTIVES AND METHODS

The principal aim of this chapter is to identify diversification patterns within *Atriplex* Clades 1 and 2 that relate to coast and inland migrations and to formation of arid landscapes in the Yilgarn and Eyre-Murray Centres of Diversity. Subsidiary aims are to define clade membership and briefly compare with diversification in the Sclerolaenid Clade.

The major objective is to resolve, complete phylogenetic trees for *Atriplex* Clades 1 and 2, to:

- identify lineages confined to either the Yilgarn or Eyre-Murray Centre that reflect internal range expansions and diversification peculiar to their landscapes
- identify the shared species in lineages and their relationship to restricted species, to determine the number and direction of exchanges between centres
- identify those lineages solely comprising restricted species to identify vicariance or long distance dispersal events
- set clade formation or divergence within geochronology of Australian landscapes, identifying possible correlations with taxa in other chenopod clades
- determine if lineages comprise a dominant landscape type or a mix of habitat types
- assign each species to *Atriplex* Clade 1 or Clade 2
- briefly compare results the Sclerolaenid Clade (Cabrera *et al.* 2011)

Methods

Species sampling

Atriplex material was obtained through field collection and herbarium specimens. Field collection included fresh foliage samples, immediately stored in desiccant silica along with a plant voucher specimen. Priority of field collection was for species not yet sequenced, along with replicates for single species samples. Herbarium species were obtained from Queensland Herbarium (Brisbane – BRI), National Herbarium of Victoria (Melbourne – MEL), Western Australian Herbarium (Perth – PER) and the State Herbarium of South Australia (Adelaide – AD) including several unnamed *Atriplex*. DNA extraction and sequencing was done at Johannes Gutenberg University in Mainz, Germany.

All collected specimens were field identified. Peter Lang (Senior Botanist) and Robert Chinnock (Senior Botanist - Retired) from the State Herbarium of South Australia (**AD**) in Adelaide assisted with formal identification. Identity was confirmed through plant vouchers lodged with the MJG Herbarium at Johannes Gutenberg University (through Institut fur Spezielle Botanik). Duplicate specimens are to be lodged with State Herbarium of South Australia, Western Australian Herbarium in Perth and other Australian Herbaria.

Recent field collection and sampling of Herbarium specimens realised a comprehensive sampling of *Atriplex*. Sample content, source and use in analysis is detailed in Appendix XIV. Samples included all but one species of *Atriplex*, most of which had a single replicate, and some subspecies. However, samples yielding insufficient quantity or quality of DNA limited some analyses and which unfortunately related most to species restricted to the Yilgarn Centre. Eventually ETS/ITS analyses involved 15 samples of 8 species from *Atriplex* Clade 1 and 104 samples of 51 species, along with four unnamed species, from *Atriplex* Clade 2. Genotyping-by-Sequencing analyses used 47 samples of 43 species.

The Outgroup for the ITS/ETS analyses was drawn from Central Asian species of *A. centralasiatica*, *A. glauca* and *A. sphaeromorpha*. Species from one Australian clade are a useful outgroup for the other, but Clade 2 is more closely related to the Central Asian species. For the Genotyping-by-Sequencing analyses, two species from *Atriplex* Clade 1 (*A. amnicola* and *A. incrassata*) were used as outgroup, because none of the Central Asian species produced suitable DNA for Genotyping-by-Sequencing. *Atriplex australasica* was not included in analyses being phylogenetically remote from the C_4 *Atriplex* Clade.

Overall, ITS/ETS markers resolved membership of the two clades. Phylogenetic structure of *Atriplex* Clade 1 is clearer, but ITS/ETS markers again revealed a near-basal polytomy in *Atriplex* Clade 2, similar to previous analyses, despite fresh, added samples. Some structure is apparent, with good support for lineages of few species and same species clusters, as also found in the Krieg phylogeny.

In the Genotyping-by-Sequencing analysis, DNA samples from 8 species proved inadequate (*A. billardierei* and *A. cornigera* from the Eyre-Murray Centre; *A. elachophylla* that is mostly in Eyre-Murray; and *A. eremitis*, *A. exilifolia*, *A. flabelliformis*, *A. hymenotheca* and *A. spinulosa* from the Yilgarn Centre). These were replaced by additional samples of other species. *Atriplex stipitata* appears in robust and gracile forms that may be subspecies (*pers. obs.*, N. Walsh *pers. comm.* 2016). Two subspecies of *A. lindleyi*, were included as *A. lindleyi* ssp. *conduplicata*, is treated as *A. conduplicata* in Jacobs (2000), along with an additional sample of *A. leptocarpa*.

Atriplex australasica, readily distinct from other Australian *Atriplex* on taxonomic and molecular bases (Kadereit *et al.* 2010), is not part of this analysis.

Molecular analyses

Two types of molecular analysis were used to generate phylogenetic trees. Following procedures of Kadereit *et al.* (2003, 2005, 2010), ITS1/2 markers were sequenced in the additional *Atriplex* species and samples. Derivation of the Krieg Phylogeny indicated such approach to be potentially fruitful. Further analysis included the closely related ETS region, which produced best resolution for a phylogenetic tree of the Sclerolaenid Clade (Cabrera *et al.* 2009). An eventual inability to produce a well resolved tree for *Atriplex* Clade 2, led to a belated attempt at Genotyping-by-Sequencing (GBS), prompted by both quality and quantity of DNA extracted from fresh material.

For Genotyping-by-Sequencing, sample preparation and DNA sequencing followed procedures of Elshire *et al.* (2011) with slight modification (Kadereit *pers. comm.* 2016). Detailed procedures are outlined in Appendix XV and were carried out at University of Mainz in June 2016. For ITS/ETS markers additional samples were analysed over later 2015. Source and identity of all samples used in analyses are identified in Appendix XIV, which includes a sample number suffix (Chen number) issued by the Botanical Museum at the Johannes Gutenberg University of Mainz (MJG herbarium code).

Phylogenetic trees

Data assembly for tree generation using ITS/ETS markers followed procedures of Cabrera, *et al.* (2009) and Kadereit *et al*. (2010). For each region, multiple sequence alignment was performed with the Muscle (Edgar 2004) plug-in for Geneious (Kearse *et al.* 2012) using the default parameters and adjusted visually on screen. Separate phylogenetic analyses (see below) of each of the ETS and ITS regions were visually examined for congruence between each marker (determining concurrence or conflict of well-supported branches in topologies) prior to analysing combined data.

To assemble the Genotyping-by-Sequencing data, the *ipyrad* (v.0.4.2) software (Eaton 2014) and the ‘de novo’ method was used. First, similar clusters of reads for each individual were identified using a threshold of 85% similarity and aligning them. This clustering threshold is moderately conservative and avoids over-splitting of loci (Harvey *et al.* 2015). The next step of joint estimation of heterozygosity and error rate (Lynch 2008) was based on a diploid model, assuming a maximum of 2 consensus alleles per individual. The parameters from the previous step were then used to determine consensus bases calls for each allele and removed consensus sequences with > 5 Ns per end of paired-end reads. Reads for each sample were then clustered and aligned to the consensus sequences. Finally, the data set was filtered according to maximum number of indels allowed per locus (8), maximum number of SNPs per locus (20), maximum proportion of shared heterozygous sites per locus (0.5) and minimum number of samples per locus (8).

Results from Genotyping-by-Sequencing and ITS/ETS markers were variably combined to produce consensus trees for all species samples, where either ITS/ETS sequence data or Genotyping-by-Sequencing sequences were available. Genotyping-by-Sequencing analysis was restricted to 50 samples only, reducing the number of samples with both ITS/ETS and Genotyping-by-Sequencing sequences available. To increase sampling size for analysis, species where ITS/ETS and Genotyping-by-Sequencing data derives from separate samples were treated as a single sample where:

(1) three or more species samples were available and there was no conflict of position with tree derived solely from ITS/ETS or GBS data (*A. bunburyana* was included; one *A. quadrivalvata* omitted)

(2) two samples separately provide ITS/ETS and GBS sequences: species are widespread and abundant and recognised stable forms; or there is no known hybridisation or common

intergrades with other species (*A. cordifolia*, *A. humifusa*, *A. infrequens*, *A. nana*, *A. pseudocampanulata*, *A. pumilio* and *A. semilunaris* included, but *A. crassipes* not)

Phylogenetic relationships were inferred under Maximum Likelihood (ML) from PhyML (Stamatakis 2006; Guindon *et al.* 2010) and Bayesian Inference (BI) from MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) optimality criteria using Geneious plug-ins. Topologies for the ITS/ETS data sets were estimated with PhyML; RAxML approach was used for larger data of Genotyping-by-Sequencing and combined ITS/ETS-GBS data sets. A GTR+I+G model of sequence evolution, with model parameters estimated from the data, was used in all analyses. For the ML analyses, branch support was assessed using 200 non-parametric bootstrap replicates (ML-BS) with values ≥ 80% considered robust. For the BI, using uninformative priors on model parameters, two independent runs each of 5 million steps comprising 4 chains (1 cold, 3 heated) were performed, sampling trees and parameter values every 1000 steps. Convergence was assessed from the post-run output, after excluding the appropriate burn-in fraction (10% in this instance), generating a majority rule consensus topology. For these analyses branches receiving posterior probability (BI-PP) of ≥ 0.95 are considered well supported.

Molecular clock, geochronology and correlates with other taxa

Determination of phylogenetic ages follows procedure used in Kadereit *et al.* (2010) for global *Atriplex*, also applied to Camphorosmoideae (Cabrera *et al.* 2011). Geochronology of Australian arid landscapes is largely covered in (Fujioka and Chappell 2010), with further references to specific landscape studies therein, especially Stony Desert (Fujioka *et al.* 2005), Sand Desert (Sheard *et al.* 2006, Fujioka *et al.* 2009). History of Riverine Desert and Desert Lake could be referenced from studies of the palaeodrainage systems including van de Graaff (1977), Clarke (1994a, 1994b), Benbow *et al.* (1995a, 1995b), Alley (1998), Alley *et al.* (1999), Stoian (2004), Bowler *et al.* (2006) and Hou *et al.* (2008). Appendix X details landscape formation through regions of Australia.

Geochronological estimates are not without hazard, being particularly reliant on assumptions for stratigraphic correlation and sedimentation processes. Estimates can be simply relative (e.g. is no older than 10 Ma). A principal controversy is dating aridity in south Western

Australia based on saline evaporitic deposits; Clarke and Pillans (2002) and Zheng *et al.* (2002) respectively support either Early Pliocene or Middle Pleistocene age estimates.

Potential correlates with other chenopod taxa were identified through range distribution maps for chenopod taxa (as in Chapter 2) emphasising similarity in range extent and location, and main habitats of occupation (from Chapter 3) and published phylogeny. Cabrera *et al.* (2009, 2011) provide phylogeny and dates for Sclerolaenid clade. As such analyses largely depend on definitions of “similarity” in distribution, and an exhaustive study over all Australian chenopod taxa would be a major study in itself, identification of potential correlates is mainly confined to species within the Eyre-Murray Centre. This region has the greatest diversity of *Atriplex* species, includes a novel land type (Stony Desert) and an expanding one (Karst Plain) and is familiar to the author.

RESULTS

Clade membership

Eight species resolve to *Atriplex* Clade 1 and forty-nine species to *Atriplex* Clade 2. The membership of *Atriplex humilis* is uncertain, but treated as Clade 2 in distribution and habitat analyses, as its species range is proximate to Clade 2 and it is placed in Section: Semibaccatae (Wilson 1984) which is all Clade 2 species. *Atriplex hypoleuca* and *A. eremitis* were inadvertently omitted from Genotyping-by-Sequencing as taxonomy and range initially suggested they are part of Clade 1.

Phylogenetic structure of Australian *Atriplex*

The phylogenetic relationship of Australian *Atriplex* Clades 1 and 2 from ITS/ETS markers and Genotyping-by-Sequencing, is illustrated in figures 4.2a and 4.2b. For descriptions, lineages are named after the most widespread and shared species of apparent early emergence. Description of clade topology follows Hallinan (2011); branch support is interpreted similarly to Kadereit *et al.* (2003). Highly supported clades, lineages or same species clusters have posterior probability [PP] ≥ 0.95 and bootstrap value [BS] ≥ 80. Moderate support is PP < 0.95 and BS ≥ 80 or PP ≥ 0.95 but BS < 80. Support is considered weak where BS ≥ 50, and non-existent where BS < 50. Values given below are denoted as [PP:BS]. Sympatric and allopatric species ranges are as defined in Chapter 2.

The clades separately resolve with good support in both trees. Under ITS/ETS only, *Atriplex* Clade 1 [1:99] is distinct from the *A. sphaeromorpha-Atriplex* Clade 2 group [0.9:91]. *Atriplex* Clade 2 species separate from their Eurasian sister with high support [1:94]. Support values are also high in the ITS/ETS-GBS concatenation, but with *Atriplex* Clade 2 [1:98] including *A. sphaeromorpha*. In the ITS/ETS tree, Clade 1 has two supported lineages, but internal structure of *Atriplex* Clade 2 is unclear. With lack of resolution in *Atriplex* Clade 2 precluding exhaustive correlation with landscape geochronology, molecular clock analyses were used to suggest order of lineage emergence as in Cabrera *et al.* (2011).

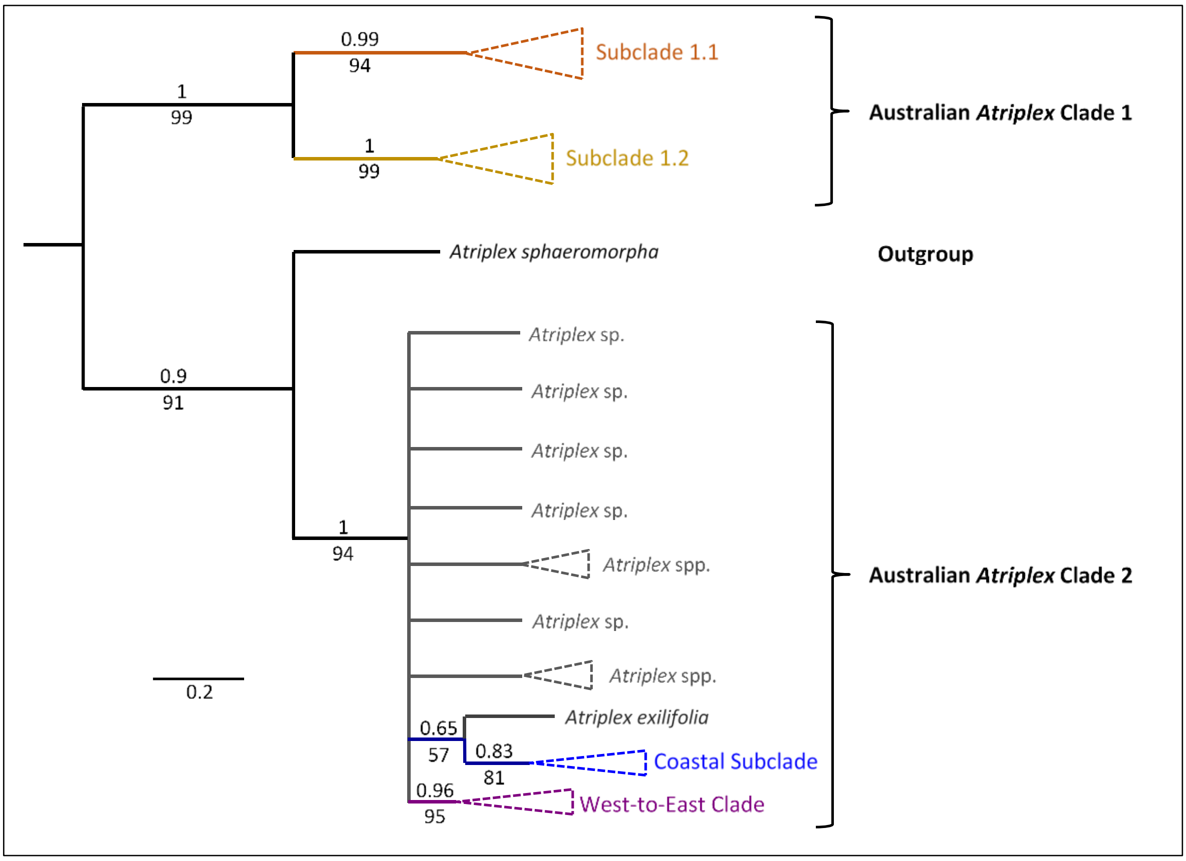


Figure 4.2a: Broad phylogenetic structure of Australian *Atriplex* Clades 1 and 2 based on ITS/ETS markers. A reduced polytomy for *Atriplex* Clade 2 is shown schematically in lighter grey; all other branches are of proportionate length. Posterior probability (Bayesian Inference) shown above the branch line with bootstrap values (Maximum Likelihood) given below the line.

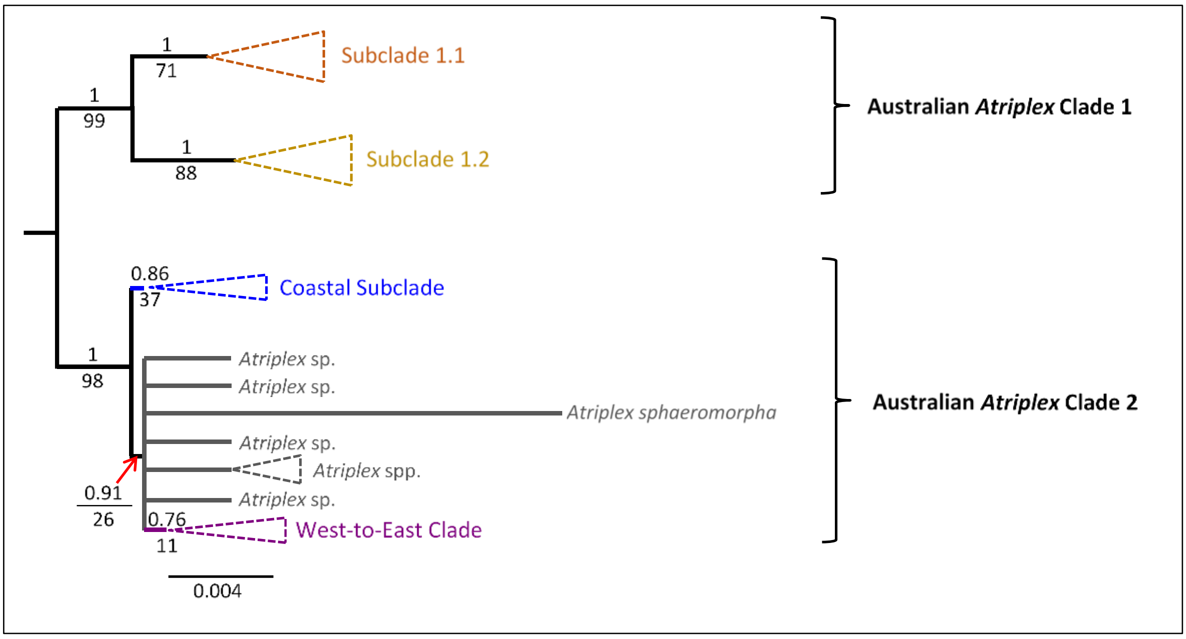


Figure 4.2b: Broad phylogenetic structure of Australian *Atriplex* Clades 1 and 2 based on ITS/ETS markers and Genotyping-by-Sequencing. The reduced polytomy for *Atriplex* Clade 2 is shown schematically in lighter grey; all other branches are of proportionate length. Posterior probability (Bayesian Inference) shown above the branch line with bootstrap values (Maximum Likelihood) given below the line.

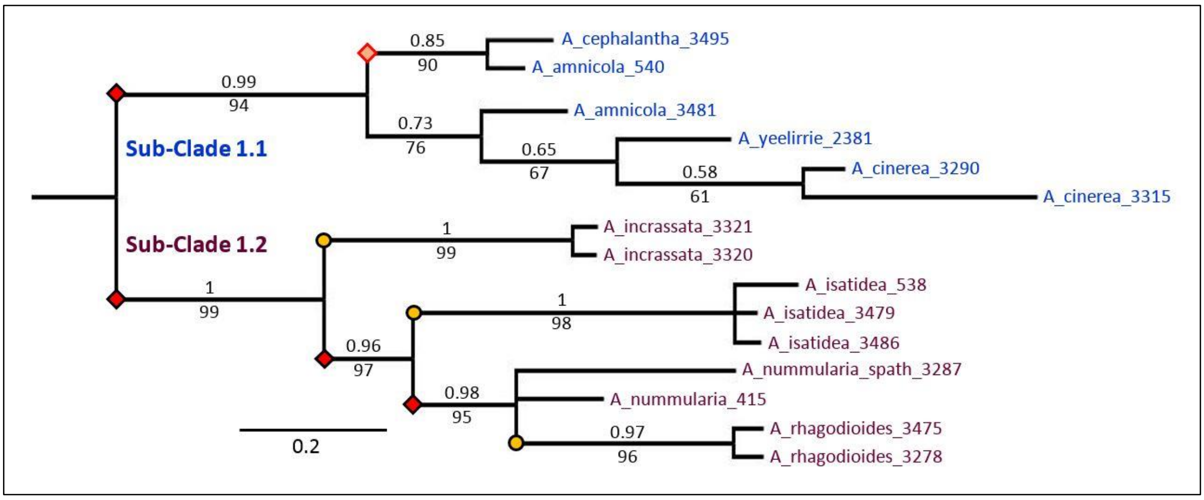


Figure 4.3: Phylogenetic tree for *Atriplex* Clade 1 based on ITS/ETS markers showing subclades 1.1 (*Atriplex cinerea* lineage) and 1.2 (*Atriplex nummularia* lineage). Diamonds indicate lineages of two or more species with moderate to high support. Circles are same species clusters of high support (see figure 4.5 for key). Number suffixes to species names are a unique number (Chen No) used in molecular analyses at MJG.

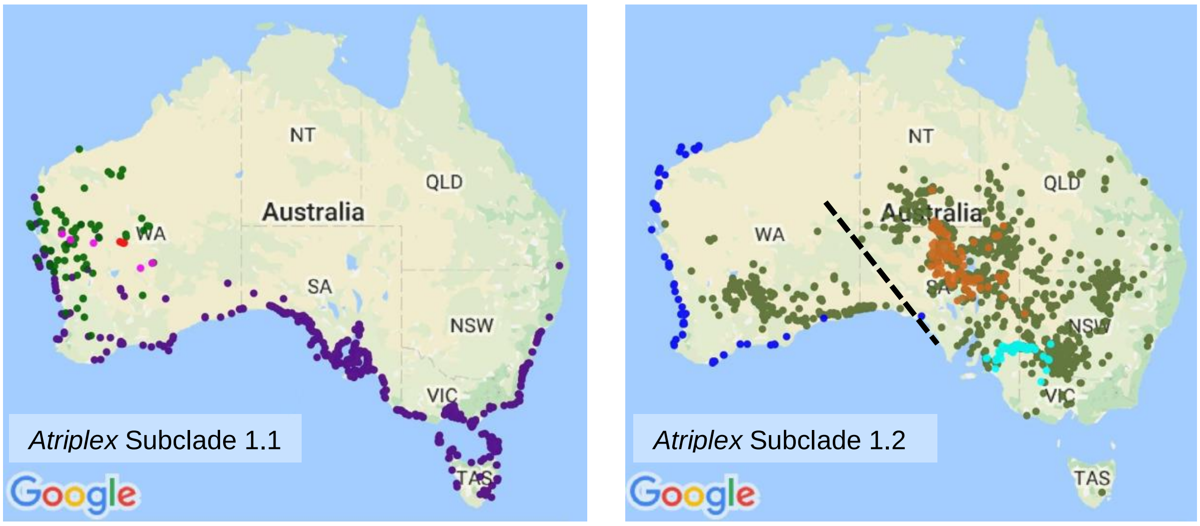


Figure 4.4: Distribution of species in *Atriplex* Clade 1. Subclade 1.1 has *A. cinerea* (purple), *A. amnicola* (green), *A. cephalantha* (pink) and *A. yeelirrie* (red). Subclade 1.2 has *A. isatidea* (royal blue), *A. nummularia* (olive-green), *A. incrassata* (orange-brown) and *A. rhagodioides* (sky blue). *A. nummularia* ssp. *spathulata* occurs west of the broken black line, while ssp. *nummularia* and ssp. *omissa* occur to the east.

Australian *Atriplex* Clade 1

The phylogenetic tree for *Atriplex* Clade 1 based on ITS/ETS markers, is a balanced topology of two well-supported lineages of 4 species each (figure 4.3). Subclade 1.1 (*A. cinerea* lineage) has an imbalanced topology. Branch bootstrap support is poor to moderate and *A. amnicola* samples are in equivocal (conflicting) positions. Subclade 1.2 (*A. nummularia*) lineage has an imbalanced topology, resolving throughout with high support (PP > 0.96 and BS > 95 for all branches). The same species cluster into pairs or triplets at adjoining branch-tips. Distribution and habitat of Clade 1 species are listed in Table 4.1. The subclades are parapatric with overlapping range on western coastlines and the southern Yilgarn Plateau. See figure 4.4.

Habitat		**Subclade 1.1**		**Subclade 1.2**	
General	**Specific**	**Species**	**Distribution**	**Species**	**Distribution**
Coast	Beach/Dune	*A. cinerea*	Continental	*A. isatidea*	West Aust
	Tidal marsh	[*A. amnicola*]	West Aust		
Riverine Desert	Watercourse/Floodplain	*A. amnicola*	West Aust	*A. rhagodioides*	South Aust
				A. nummularia *	Cent/East Aust
Desert Lake	Gypsum Rise/Lunette	*A. yeelirrie*	West Aust		
	Salt flat	*A. cephalantha*	West Aust		
	Lunette/Salt flat	[*A. cinerea*]	West Aust		
Stony Desert	Gibber plain/tableland			*A. incrassata*	Cent Aust
Karst	Sandy calcareous plain			*A. nummularia* *	West Aust

Table 4.1: Common habitats and distribution of species from Australian *Atriplex* Clade 1. Brackets indicate population subsets; * different subspecies.

Subclade 1.1 has three species restricted to the Yilgarn Centre. *Atriplex amnicola* is a relatively widespread, Inland facultative, commonly in Riverine Desert, also of Desert Lake and in sandy marsh on coastlines. *Atriplex cephalantha* and *A. yeelirrie* are Desert Lake species, relatively restricted in range. The species range of Coast facultative *A. cinerea* spans the southern coast, and extends to New Zealand (de Lange 1998; Heyligers 2001).

The inland range of the subclade comprises all species, with inland populations of *A. cinerea* in Desert Lake. *Atriplex amnicola* extends across northern Yilgarn Plateau and Pilbara provinces encompassing species ranges of *A. cephalantha* and *A. yeelirrie*. It is allopatric to *A. cinerea* with small overlap across the central Yilgarn Plateau. Initial divergence has moderate to strong bootstrap support (BS 76 for *A. cinerea* lineage; BS 90 for *A. cephalantha-A. amnicola* sister pair), but no accompanying support from posterior probability. Initial divergence, the emergence of the riverine *A. amnicola*, occurred at similar time to initial divergence in subclade 1.2.

Subclade 1.2 is also in both centres (see figure 4.4). *Atriplex incrassata* and *A. rhagodioides* are restricted to the Eyre-Murray Centre and *A. isatidea* to the Yilgarn Centre. The subcontinental *A. nummularia* has three subspecies. *Atriplex nummularia ssp. spathulata* is on sandy calcareous plains of the Yilgarn Centre and across the Nullarbor Plain, and is narrowly disjunct from the other subspecies, which are restricted to the Eyre-Murray Centre. *Atriplex nummularia* ssp. *omissa* in Central Australia is sympatric with *Atriplex incrassata*, which is restricted to Stony Desert. The more widespread *A. nummularia ssp. nummularia* is characteristic of watercourses and alluvial plains of heavy soils (Moore 1953; Beadle 1981b; Mollenmans *et al.* 1984; Cunningham *et al.* 1992), now much less abundant after long term grazing (Beadle 1948; Moore 1953). The coast obligate *A. isatidea* is narrowly disjunct from western *A. nummularia* populations. The riparian *A. rhagodioides* is near allopatric with eastern *A. nummularia*, on floodplain and terraces of the River Murray below Mildura (Wilson 1984; Stewart and Brandle 2010).

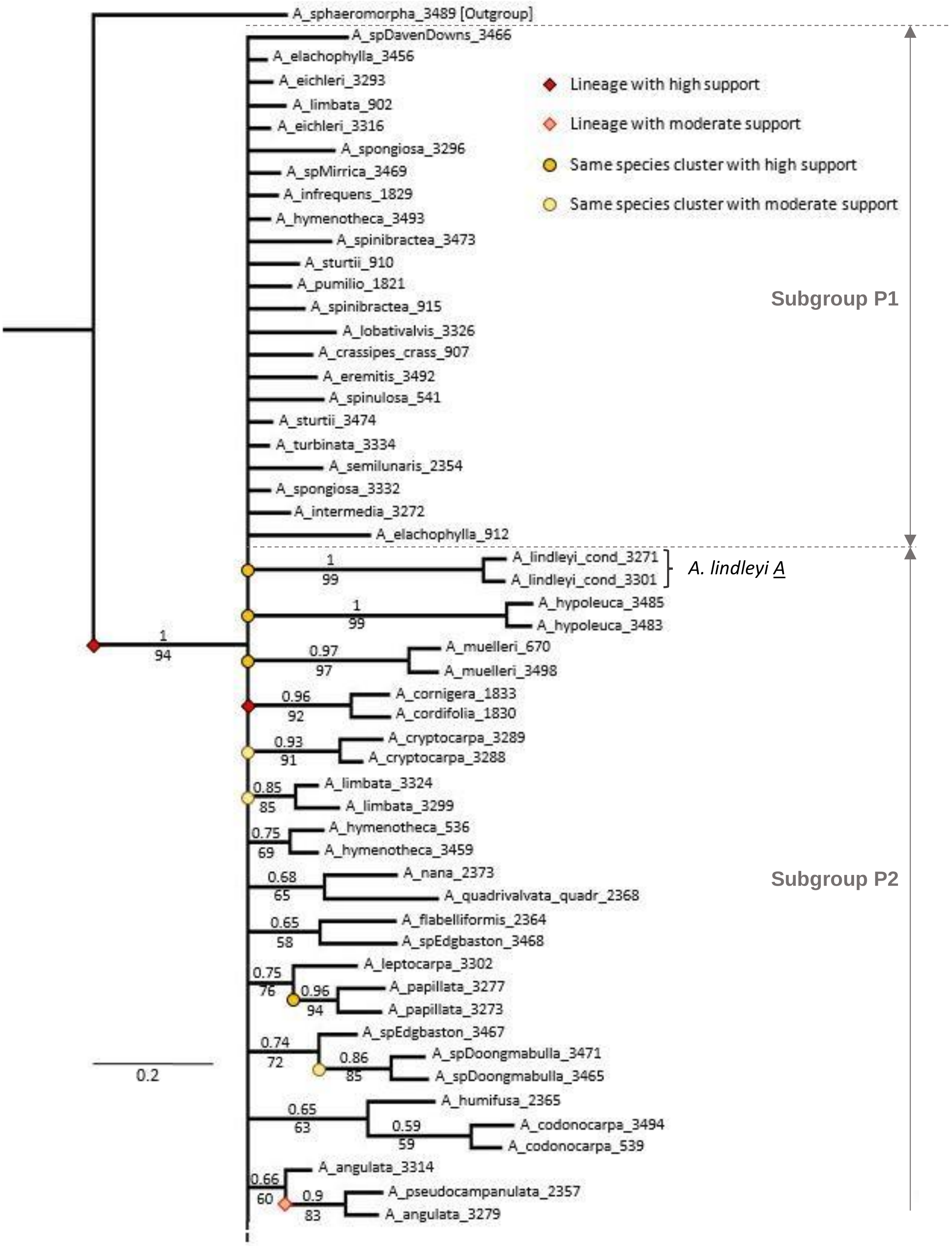
Australian *Atriplex* Clade 2

Phylogenetic trees for this clade show little evolutionary structure, but reveal some species associations. Figure 4.5 shows combined Bayesian inference and Maximum Likelihood for ITS/ETS markers. Figure 4.7 presents a Genotyping-by-Sequencing tree of Maximum Likelihood. Figure 4.8 is a consensus tree for species with both ITS/ETS and GBS data, while figure 4.9 is a consensus tree encompassing species with both or either of ITS/ETS and GBS sequences.

ITS/ETS Markers

The phylogenetic tree for *Atriplex* Clade 2 based on ITS/ETS markers has a broad, basal polytomy (figure 4.5). Three subgroups are arbitrarily defined. Subgroup P is the basal polytomy, divided into emergent single species (P1) and same species clusters or lineages of two or more species, including sister species pairs (P2). Subgroup C is a coastal lineage of four species. Subgroup I is a rich lineage of twelve species. Equivocal (conflicting) species presence confounds identification of distinct lineages. The outgroup *Atriplex sphaeromorpha* maps distantly to this clade.

Same species clusters are common to subgroup P2 and also in subgroups C and I. Separate clusters with high support [PP>0.95 and BS>97] in subgroup P2 are *A. lindleyi* A, *Atriplex muelleri*, *A. hypoleuca* and *A. vesicaria*; those of moderate support include *A. cryptocarpa* [0.93:91] and *A. limbata* [0.85:85]. Other same species clusters occurring within lineages of subgroup P2 and with high support include *A. papillata* in an *A. leptocarpa* lineage, *A. obconica* and *A. lindleyi* in an *A. lindleyi* B lineage. Those of moderate support are *Atriplex* sp. “Doongmabulla” [0.86:85] in a lineage of unnamed Queensland species and *A. kochiana* [0.93:92] in an *A. quinii* lineage.


A_sphaeromorpha_3489 [Outgroup]
A_spDavenDowns_3466
A_elachophylla_3456
A_eichleri_3293
A_limbata_902
A_eichleri_3316
A_spongiosa_3296
A_spMirrica_3469
A_infrequens_1829
A_hymenotheca_3493
A_spinibractea_3473
A_sturtii_910
A_pumilio_1821
A_spinibractea_915
A_lobativalvis_3326
A_crassipes_crass_907
A_eremitis_3492
A_spinulosa_541
A_sturtii_3474
A_turbinata_3334
A_semilunaris_2354
A_spongiosa_3332
A_intermedia_3272
A_elachophylla_912
◆ Lineage with high support
◇ Lineage with moderate support
● Same species cluster with high support
○ Same species cluster with moderate support
Subgroup P1
1
99
A_lindleyi_cond_3271
A_lindleyi_cond_3301
A. lindleyi A
1
99
A_hypoleuca_3485
A_hypoleuca_3483
1
94
0.97
97
A_muelleri_670
A_muelleri_3498
0.96
92
A_cornigera_1833
A_cordifolia_1830
0.93
91
A_cryptocarpa_3289
A_cryptocarpa_3288
0.85
85
A_limbata_3324
A_limbata_3299
0.75
69
A_hymenotheca_536
A_hymenotheca_3459
0.68
65
A_nana_2373
A_quadrivalvata_quadr_2368
Subgroup P2
0.65
58
A_flabelliformis_2364
A_spEdgbaston_3468
0.75
76
A_leptocarpa_3302
0.96
94
A_papillata_3277
A_papillata_3273
0.74
72
A_spEdgbaston_3467
0.86
85
A_spDoongmabulla_3471
A_spDoongmabulla_3465
0.2
0.65
63
A_humifusa_2365
0.59
59
A_codonocarpa_3494
A_codonocarpa_539
0.66
60
A_angulata_3314
0.9
83
A_pseudocampanulata_2357
A_angulata_3279

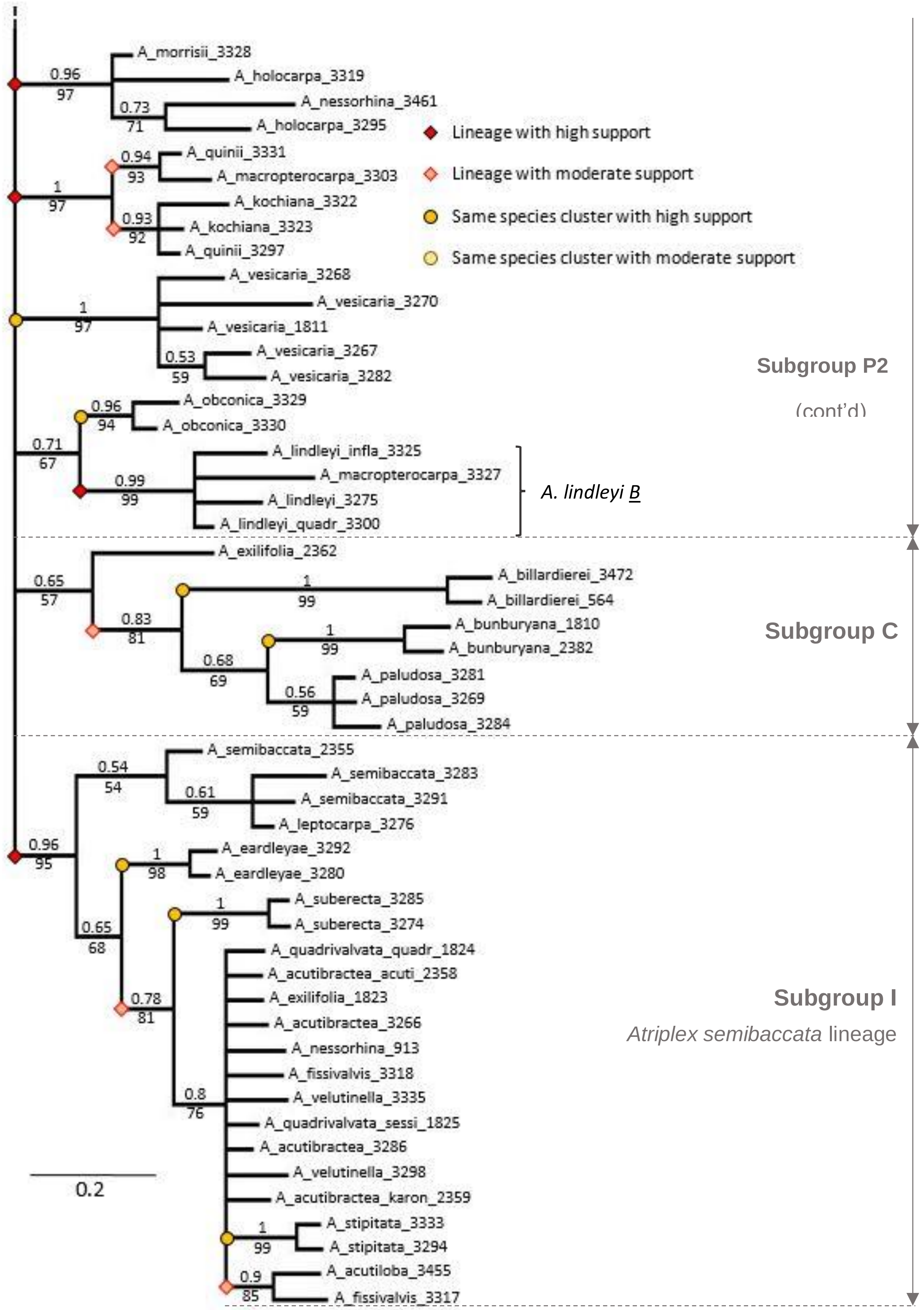


Figure 4.5: Phylogenetic tree for *Atriplex* Clade 2 based on ITS/ETS markers selectively emphasising support for lineages or species sample pairs. Posterior probabilities for Bayesian inference above branch lines with bootstrap values for Maximum Likelihood below.

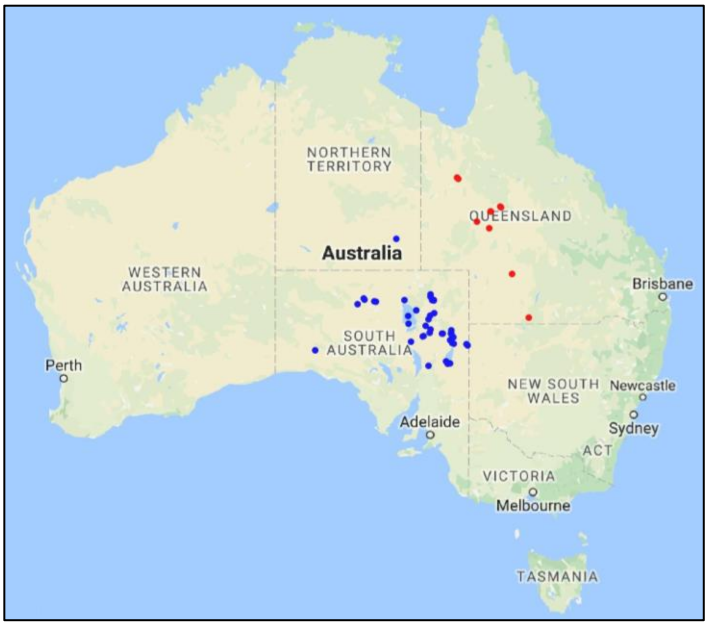


Fig 4.6a: Distribution of *Atriplex cordifolia* (blue) and *A. cornigera* (red) – disjunct species pair of central and north-eastern Australia within the Eyre-Murray Centre of Diversity.

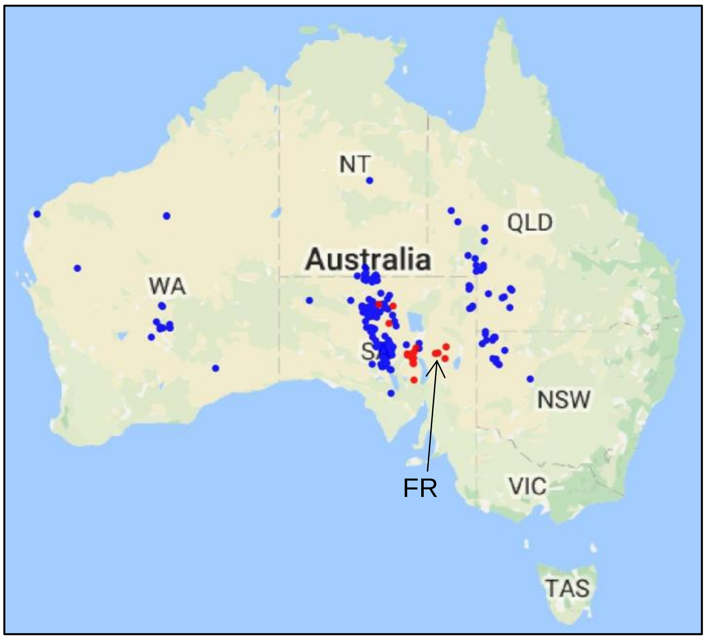


Fig 4.6b: Distribution of *Atriplex quinii* (blue) and *A. kochiana* (red). The shared *Atriplex quinii* occurs in 3 disjunct populations across Australia. Its close relative *A. kochiana* is sympatric with the range of the central population of *A. quinii*. Records of *A. kochiana* from the Flinders Ranges (FR) are considered to represent residence of the collector (M. Koch). Note similar overlaps and disjunction in ranges of *A. obconica* and *A. macropterocarpa* (figure 4.6c). *Maireana carnosa* shows a triple disjunction of populations similar to *A. quinii*, though is more widely distributed in the Yilgarn Centre.

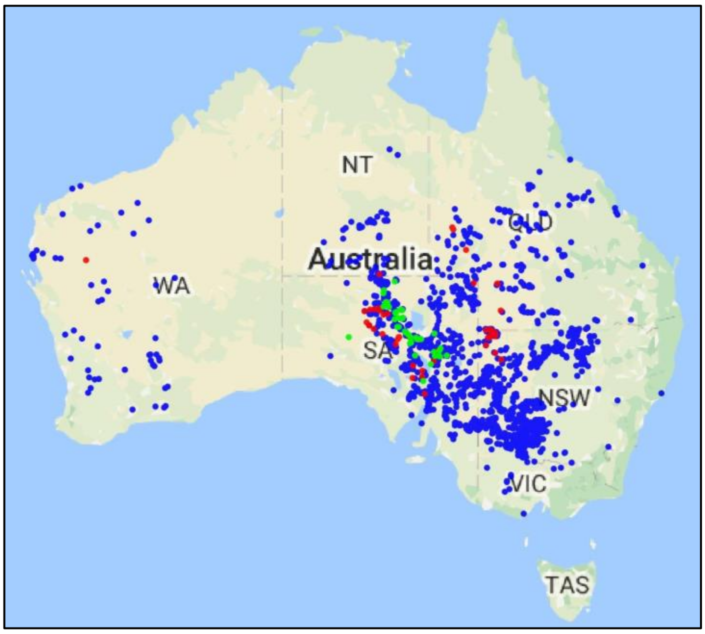


Fig 4.6c: Distribution of *Atriplex lindleyi* (blue) and *A. macropterocarpa* (red) and *A. obconica* (green). *A. lindleyi* is a continentally disjunct species, with *A. macropterocarpa* and *A. obconica* sympatric with the more extensive occurrences of eastern Australia. Note: congruent ranges/disjunct patterns with *A. quinii* and *A. kochiana* (fig 4.5b) – all are species associated with Stony Desert. Similar patterns are observed in species ranges of *Maireana schistocarpa* and *M. campanulata* in the Sclerolaenid clade.

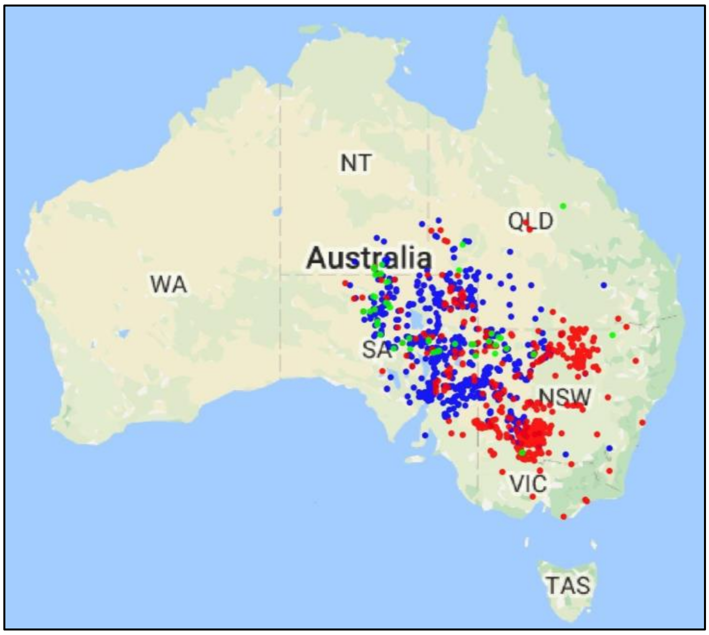


Fig 4.6d: Distribution of 3 closely related, sympatric species of the Eyre-Murray Centre – *Atriplex angulata* (blue), *A. pseudocampanulata* (red) and *A. turbinata* (green). All are associated with Riverine Desert.

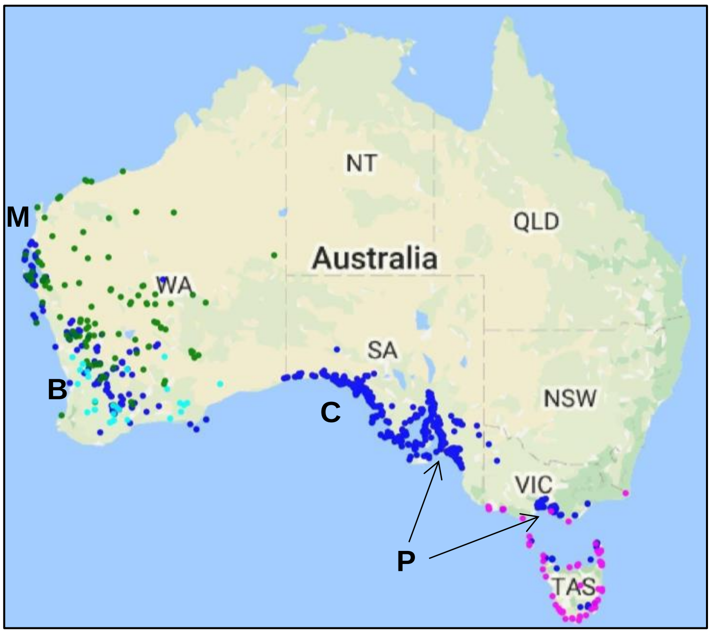


Fig 4.6e: Distribution of species in a basal subclade of *Atriplex* Clade 2 – *Atriplex paludosa* (royal blue), *A. bunburyana* (green), *A. exilifolia* (light blue) and *A. billardierei* (pink). The largely coastal *Atriplex paludosa* is the only shared species. In the Yilgarn Centre, *A. paludosa* occurs coastally or in Desert Lake, *A. exilifolia* in Desert Lake and *A. bunburyana* in Riverine Desert. In Eyre-Murray, subclade species are mostly coastal. Subspecies ranges of *A. paludosa* form a near congruent pattern (M – ssp. *moquiniana* Coastal; B – ssp. *baudinii* Desert Lake; C – ssp. *cordifolia*; P – ssp. *paludosa*)

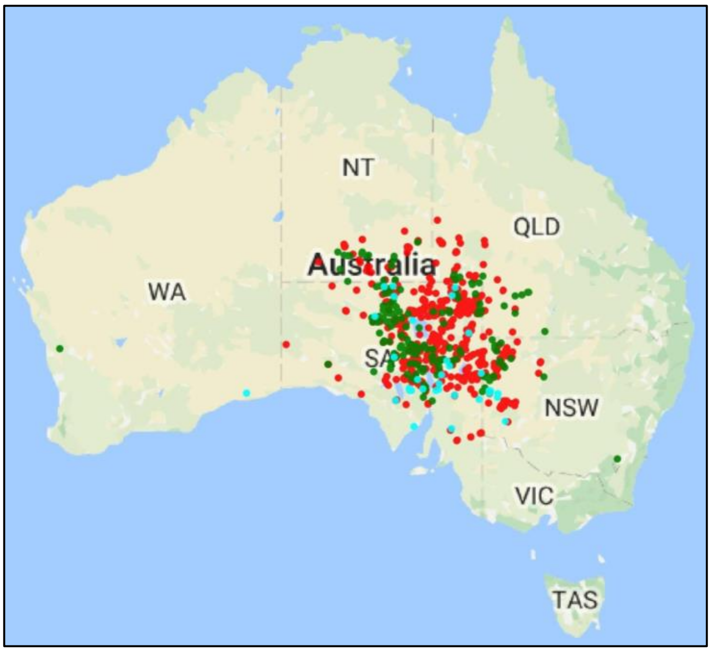


Fig 4.6f: Distribution of three closely related sympatric species of the Eyre-Murray Centre – *Atriplex velutinella* (red), *A. fissivalvis* (green) and *A. acutiloba* (light blue). Each is associated with different land type: *A. velutinella* is mostly Desert Lake, with occurrences on dunes of Sand Desert; *A. fissivalvis* is Stony Desert, while *A. acutiloba* is associated with alluvial plains of Riverine Desert. Note the similarity with distribution of *Atriplex angulata* in figure 4.6d above.

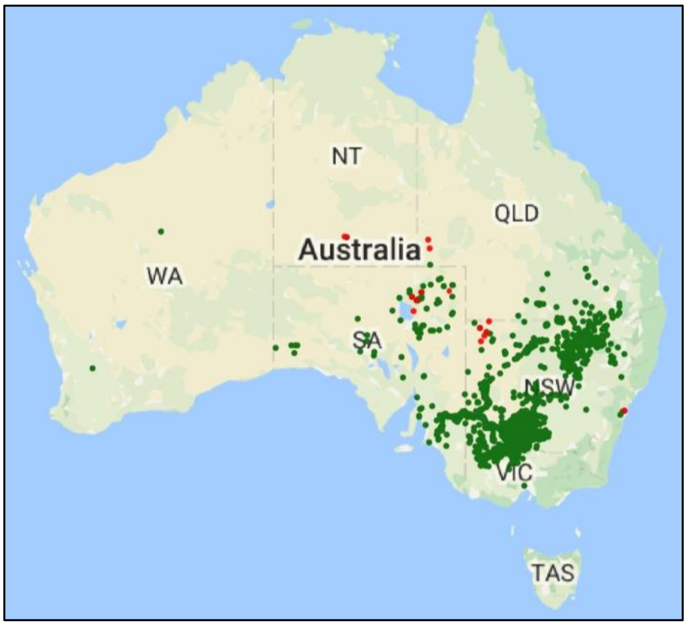


Fig 4.6g: Distribution of two closely related species in the Eyre-Murray Centre – *Atriplex leptocarpa* (green) and *A. sturtii* (red). Each is associated with Riverine Desert and largely restricted to such land type. *A. sturtii* may be a dryland phenotype of *A. leptocarpa*.

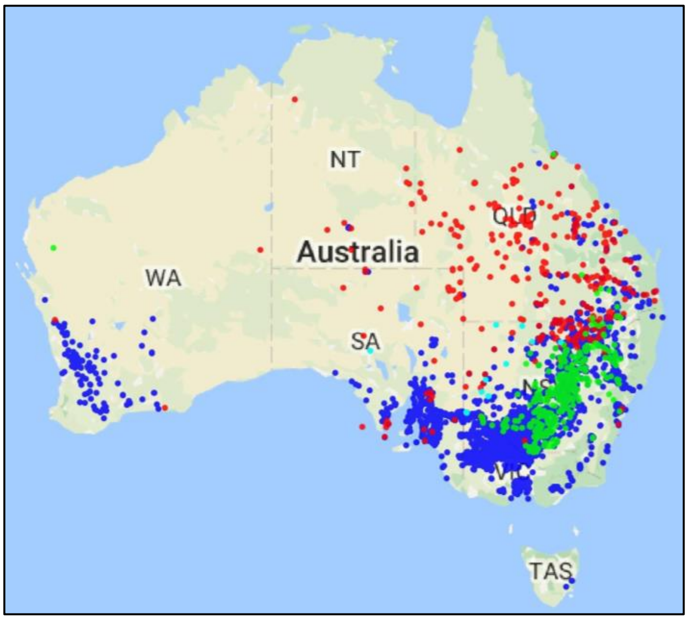


Fig 4.6h: Distribution of *Atriplex* species in the most easterly clade known in Australia – *Atriplex semibaccata* (royal blue), *A. spinibractea* (green), *A. muelleri* (red) and *A. infrequens* (light blue). *A. semibaccata*, a species of mesic habitats, is the only species shared across the centres. Wilson and Chinnock (2013) describe *A. muelleri* occurrences in South Australia only in the Far North East of the State. *A. infrequens* appears allopatric to *A. spinibractea*, but other species express degrees of sympatry.

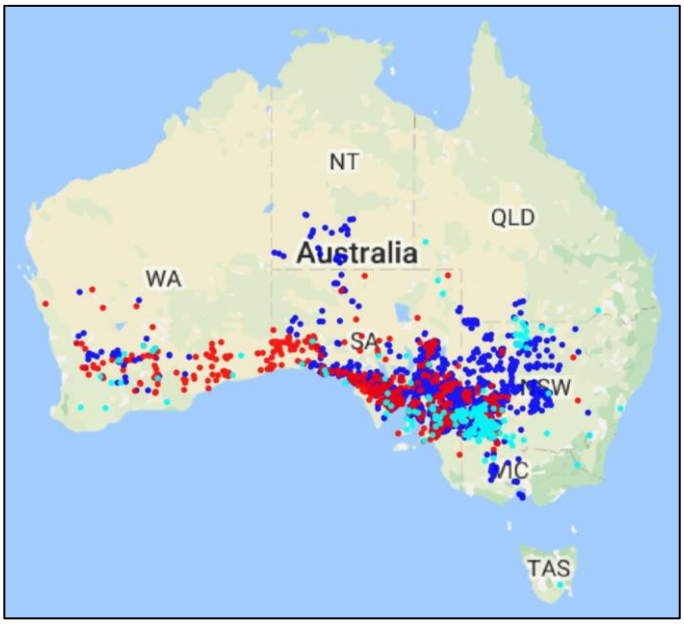


Fig 4.6i: Distribution of *Atriplex* species associated with Karst Plain – limestone plains and calcareous soils. *Atriplex stipitata* (royal blue) and *A. acutibractea* (red) map into a large derived, subclade, [Subgroup I]. Exact relationship is unknown, as is that with *A. pumilio* (light blue) which is similarly distributed. Species from other immigrant clades are similar distributed. See figure 4.6j.

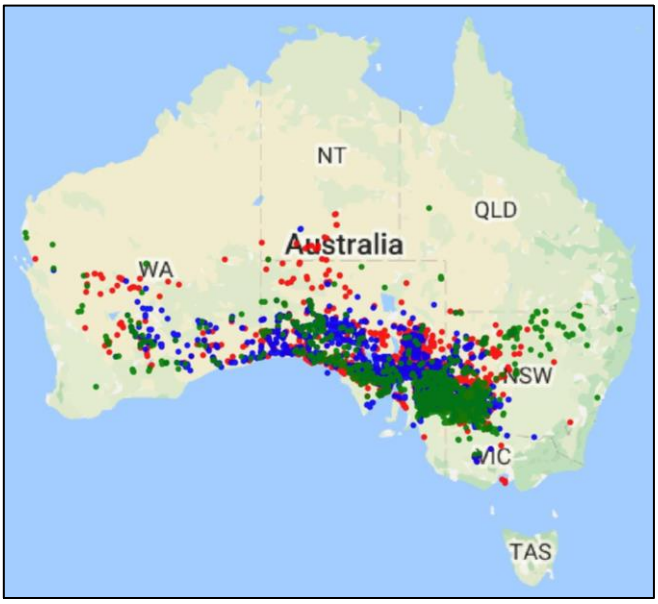


Fig 4.6j: Distribution of species from other immigrant clades associated with Karst land type – limestone plains and calcareous soils. *Sclerolaena obliquicuspis* (red), *Maireana sedifolia* (blue) and *Chenopodium curvispicatum* (green) are some of the species of similar distribution to *Atriplex* species shown in figure 4.6i.

Some are near identical e.g. *Sclerolaena obliquicuspis* and *Atriplex acutibractea*. Calcareous landscapes contribute to number of species shared by both Centres.

These same species clusters are diversely distributed. *Atriplex lindleyi* and *A. vesicaria* are shared species, usually abundant and of diverse habitats. *Atriplex limbata* is also a shared species, though scant in the Yilgarn Centre, and associated with alluvial plains of light topsoil (*pers. obs.*). *Atriplex muelleri* is a prominent annual of north-eastern subtropical Australia. Restricted in range and habitat are *A. cryptocarpa* to hollows of the Nullarbor Plain, *A. papillata* to saline flats of the western Murray Basin and *A. hypoleuca* to sandy estuaries in the south-western Yilgarn Centre.

Five lineages of moderate support or better in subgroup P2 are:

(1) *Atriplex cordifolia-A. cornigera* [0.96:92]: allopatric sister species respectively of south-western and northern-eastern parts of the Lake Eyre Basin. See figure 4.6a. Principal habitats are *A. cordifolia* in Desert Lake and *A. cornigera* in Desert Upland, but both also are in Riverine Desert.

(2) *Atriplex holocarpa* with *A. morrisii*/*A. nessorhina* [0.96:97]: *A. holocarpa* is a shared species and *A. morrisii* and *A. nessorhina* are uncommon species of the Eyre-Murray Centre. The abundant *A. holocarpa* is from Riverine Desert, Stony Desert and Desert Lake; *A. morrisii* is of Riverine Desert. *A. nessorhina* has three distinct populations in Queensland, New South Wales and South Australia; mostly of Desert Lake, and on dunes of Sand Desert. *A. nessorhina* also appears in subgroup I.

(3) *Atriplex quinii* with *A. kochiana*/*A. macropterocarpa* [1:97]: has two sub-lineages of moderate support, but each has *A. quinii*. *Atriplex quinii* occurs in three disjunct populations across Australia. *Atriplex kochiana* and *A. macropterocarpa* are Eyre-Murray species. See figure 4.6b. Records of *A. kochiana* in the Northern Flinders Ranges, likely refer to the residence of peripatetic collector M. Koch prior to 1900 (P. Lang, *pers. comm.*, State Herbarium of South Australia). *Atriplex kochiana* seems mainly sympatric with the central-southern population of *A. quinii*. *Atriplex macropterocarpa* also appears in the *A. lindleyi* B lineage.

(4) *Atriplex lindleyi* B-*A. macropterocarpa* [0.99:99]: *Atriplex lindleyi* B has subspecies *lindleyi*, *inflata* and *quadripartita*. The same species pair of *A. lindleyi* A are subspecies *conduplicata*. *Atriplex lindleyi* is a shared species of strongly disjunct subcontinental populations, with *A. macropterocarpa* from the Eyre-Murray Centre. See Figure 4.6c. *Atriplex lindleyi* is a common species of Riverine and Stony Desert and clay soils of Desert Lake. *Atriplex obconica* of the Eyre Murray Centre and of Riverine Desert is sister to this lineage, together in a clade of weak support.

(5) *Atriplex angulata*-*A. pseudocampanulata* [0.9:83]: sympatric species of the Eyre-Murray Centre, commonly of Riverine Desert and abundant. See figure 4.6d. *Atriplex angulata* is also common in Stony Desert gilgai after rain.

Subgroup C is a lineage of weak support, where *A. exilifolia* is sister to a coastal lineage of moderate support [0.83:81] and that includes same species pairs of *A. billardierei* and *A. bunburyana* with high support [1:99]. *A. billardierei* is sister to a lineage of weak support comprising a cluster of *A. paludosa* and the *A. bunburyana* pair. Notable coastal species are the shared *A. paludosa* and restricted *A. billardierei* of Bass Strait. *Atriplex bunburyana* from the Yilgarn Centre is mostly riparian, but with some coast populations. *Atriplex paludosa* range variably overlaps that of all other species, which are largely allopatric. See Figure 4.6e. *Atriplex exilifolia* also appears in Subgroup I.

Subgroup I is the *Atriplex semibaccata* lineage, of strong support [0.96:0.95] and with a sub-lineage of moderate support. Clusters of same species include *A. eardleyae* [1:98], *A.*

suberecta [1:99] and *A. stipitata* [1:99]. A derived polytomy of eight species with sister species *Atriplex suberecta* forms a sub-lineage of moderate support [0.78:81]. Except for *A. exilifolia*, all subgroup species are either shared species or restricted to Eyre-Murray Centre. The lineage *Atriplex fissivalvis* and *A. acutiloba* [0.9:85] are sympatric species of western Eyre-Murray Centre. See figure 4.6f. Replicates of four species map outside the subgroup, while three are in the derived polytomy, including *A. exilifolia*.

Species unique to subgroup I are of diverse habitats and generally have very large species ranges. The shared species *Atriplex semibaccata*, *A. suberecta*, *A. stipitata*, *A. eardleyae* and *A. acutibractea*, are sympatric or parapatric, being found in or extending from dry regions into Mesic Plain & Range. *A. semibaccata*, *A. suberecta* and *A. stipitata* have strongly disjunct eastern and western populations. *Atriplex stipitata* and *A. acutibractea* grow on calcareous soils of southern Australia, and *A. eardleyae* occurs on alluvial plains. *Atriplex velutinella*, *A. fissivalvis* and *A. acutiloba* are sympatric species of drier parts of the Eyre-Murray Centre (figure 4.6f), with species ranges allopatric or parapatric to the mesic species. *Atriplex fissivalvis* (gibber saltbush) is abundant and widespread in Stony Desert, while *A. velutinella* (sandhill saltbush), widespread and abundant in Desert Lake, is also on dunes of Sand Desert. *Atriplex acutiloba* is an uncommon species of Desert Lake and Riverine Desert.

GBS and ITS/ETS-GBS

Phylogenetic trees for *Atriplex* Clade 2 from Genotyping-by-Sequencing only and consensus tree for ITS/ETS-GBS concatenation of select species, exhibit similar results (figures 4.7 and 4.8). Both trees also show a broad polytomy, but the consensus tree suggests early phylogenetic structure. The Genotyping-by-Sequencing and consensus trees also show strong support for several lineages, some of which are sister species pairs. Support values given below are [GBS(BS):Consensus(PP,BS)]. For Genotyping-by-Sequencing analysis, only Maximum Likelihood bootstrap values are reported.

Both analyses are limited by omission of nine species, mostly from the Yilgarn Centre due to poor DNA quality and by few species replicates, but are a substantial sampling of the clade. In the following description, lifeform is as given in Wilson (1984) and Jacobs (2000).

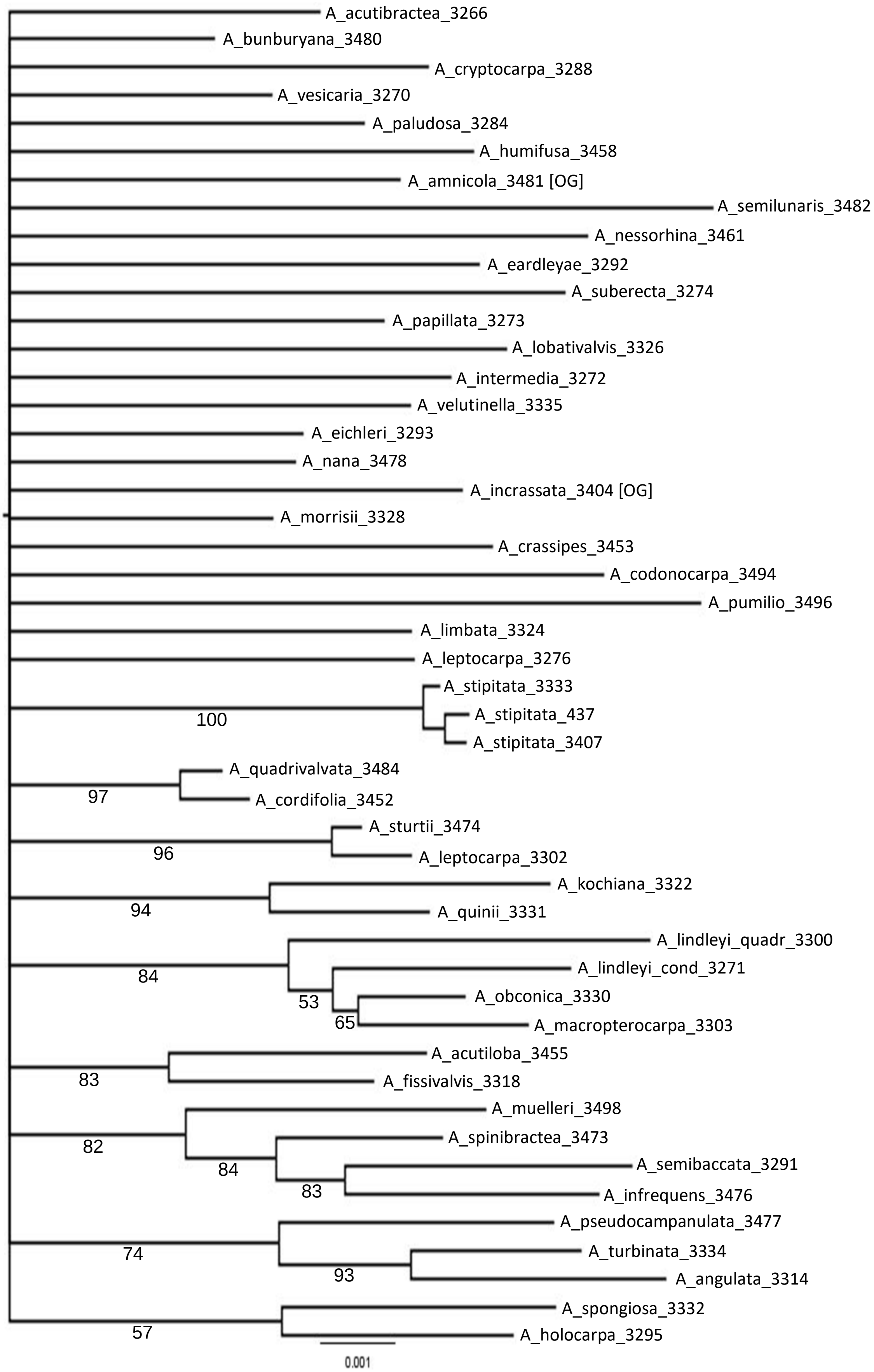


Figure 4.7: Phylogenetic tree of *Atriplex* Clade 2 based on Genotyping-by-Sequencing data set and Maximum Likelihood analysis. Higher Bootstrap Values below branch lines.

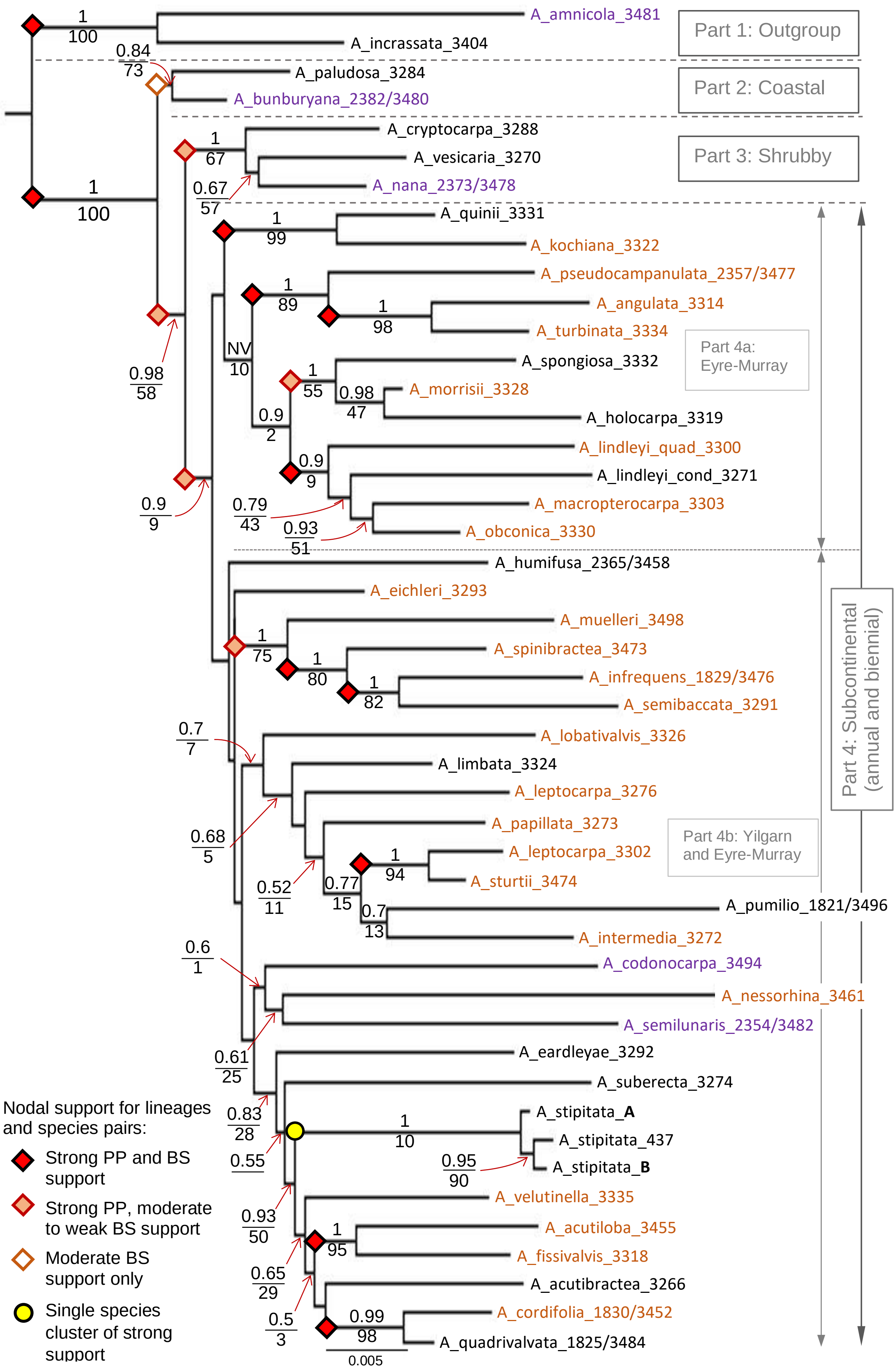


Figure 4.8: Consensus tree for *Atriplex* Clade 2 - select species samples with both ITS/ETS and GbS sequence data. Posterior Probability (Bayesian Inference) above and Bootstrap Values (Maximum Likelihood) below branch lines. Taxa restricted to Yilgarn Centre in purple; restricted to Eyre-Murray Centre in orange. Unique identity of *A. stipitata* samples was lost during processing, but are the same as in the GbS tree.

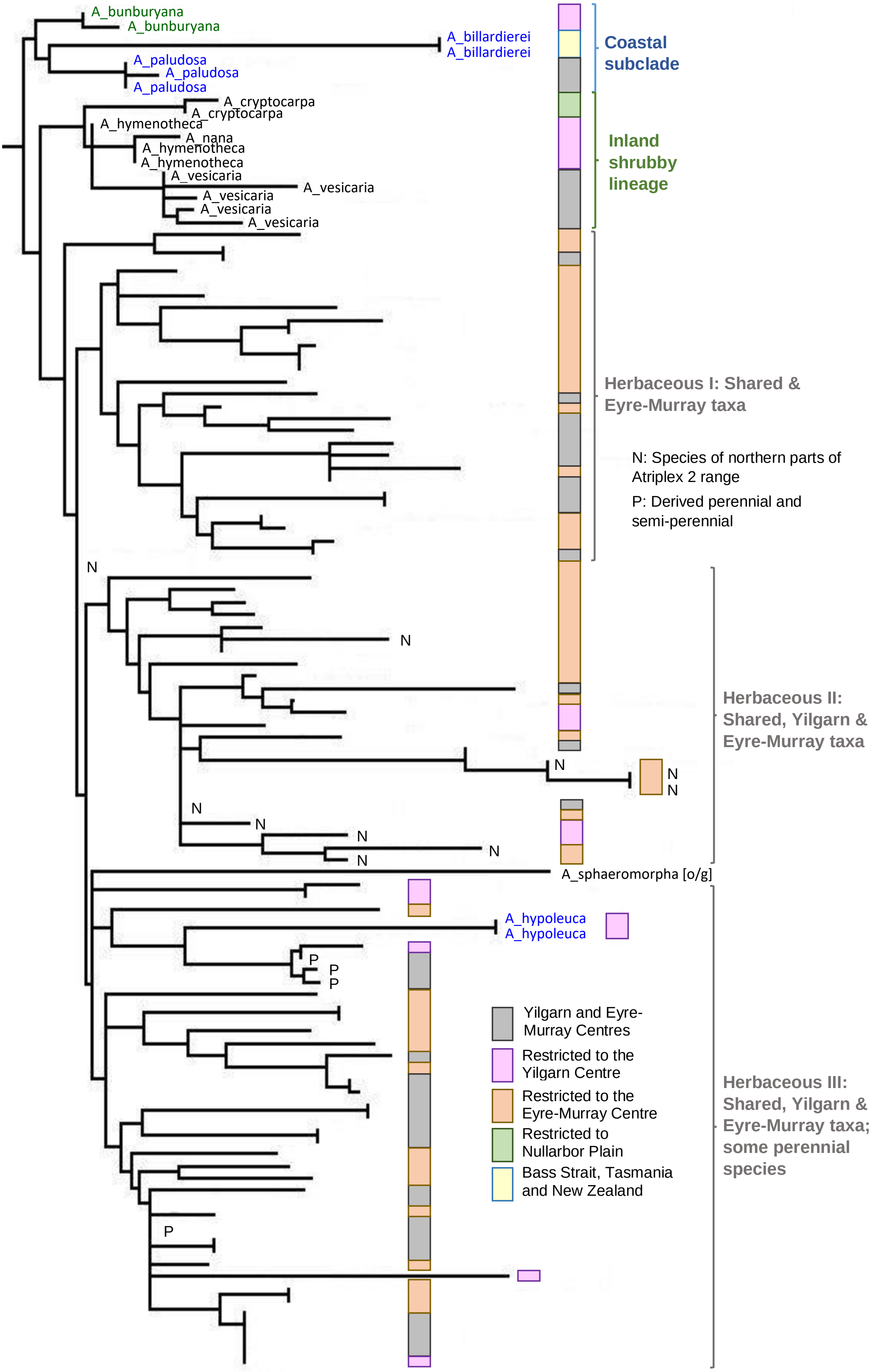


Figure 4.9: Consensus tree for *Atriplex* 2 Clade based on all available ITS/ETS and Genotyping-by-Sequencing data for all species samples, as related to Centres of Diversity.

The Genotyping-by-Sequencing tree (figure 4.7) lacks phylogenetic structure. From a basal polytomy, emerges 25 single species stems (including outgroup) and eight lineages of 2-4 species. Seven lineages have good bootstrap support. The consensus tree (figure 4.8) is treated in four parts.

Part 1 is the outlier group of 2 species from *Atriplex* Clade 1, distinct with very high support [1:100].

Part 2 is a basal *Atriplex paludosa* lineage of moderate bootstrap support [0.84:73]. A relationship to *A. bunburyana* is partly recovered in the ITS/ETS tree (figure 4.5: subgroup C), but not in the Genotyping-by-Sequencing tree. The Coast facultative *A. paludosa* has coastal range from Shark Bay to Tasmania. *Atriplex bunburyana* is an Inland facultative of the Yilgarn Centre in Riverine Desert and Desert Lake. The inland *A. paludosa ssp. baudinii* is sympatric with *A. bunburyana*. Coastal populations of *A. paludosa* have small overlap with *A. bunburyana*. Both are shrubs to 1m tall, and generally of erect habit. The *Atriplex paludosa* lineage is sister to a rich clade dominated by species of the interior (Parts 3 & 4).

Parts 3 and 4 are sister lineages of high posterior probability but low bootstrap support. A sister relationship with the coastal lineage similarly has mixed support [0.98:58].

Part 3 is an *A. vesicaria* subclade of three species, with high posterior probability and weak bootstrap support [1:67]. Relationships of the three species are not clear. *Atriplex vesicaria* is the most widespread species of Clade 2 and occupies diverse land types. It is an erect to decumbent shrub to 1 m tall, commonly of 50-70 cm height (*pers. obs.*). *Atriplex nana* is a low, erect shrub to 20 cm, endemic to central-southern Yilgarn Centre, and associated mostly with Desert Lake. *Atriplex cryptocarpa* is a shrub to 50 cm, generally of erect habit (*pers. obs.*) and confined to depressions on the Nullarbor Plain. Linear channels are interpreted as former watercourses (Benbow *et al.* 1995a; Webb and James 2006; Hou *et al.* 2008). No similar relationship is revealed in ITS/ETS or Genotyping-by-Sequencing trees.

Part 4 is the remainder of *Atriplex* Clade 2. It is a subcontinental lineage of 36 species with high posterior probability but weak bootstrap support [0.99:55] comprising sister lineages (Parts 4a/4b) that are poorly differentiated. All species emerge from a broad polytomy, as single species stems or lineages of varied support. All species are of terrestrial habitat, though *A. codonocarpa*, *A. holocarpa*, *A. lindleyi*, *A. semibaccata*, *A. semilunaris* and *A. suberecta* occur in coastal habitats. Most species are either annual or perennial herbs or annual to short-lived perennials, generally up to 30 cm in height and of diverse habit. Exceptions are *A. stipitata* (erect shrub to 1m), *A. velutinella* (erect subshrub to 1m) and *A. acutibractea* (erect subshrub to 50 cm).

Part 4a is an *Atriplex lindleyi* subclade of 11 species that are shared or restricted to the Eyre-Murray Centre, with elements of subgroup P2 on the ITS/ETS tree. The richer *A. semibaccata* subclade (P4b), comprises shared taxa and species restricted to the Yilgarn or Eyre-Murray Centre and is similar to subgroup I in the ITS/ETS tree. Both subclades have well supported lineages of few species similar to those of ITS/ETS and Genotyping-by-Sequencing trees.

In the *Atriplex lindleyi* clade:

(1) *Atriplex quinii* lineage, with *A. kochiana* [G94:C1,99]: Lineage of high support, corresponding in part to the *A. quinii* lineage of ITS/ETS tree (subgroup P2), which also has *A. macropterocarpa*. Distribution and range as previously described; also see figure 4.6b.

(2) *Atriplex angulata* lineage with *A. pseudocampanulata*, *A. turbinata* [G74:C1,89]: An Eyre-Murray Centre lineage of moderate support in Genotyping-by-Sequencing Tree and high support in the consensus tree. A corresponding lineage in the ITS/ETS tree (subgroup P2) has weaker support and excludes *A. turbinata*. The Genotyping-by-Sequencing and Consensus trees have *A. angulata* and *A. turbinata* as sister species with high support [G93:C1,89]. *Atriplex pseudocampanulata* diverged earlier. All species commonly occur in Riverine Desert. *A. turbinata* is sympatric with *A. angulata*, both being more common in the centre’s dry northern and western regions. *Atriplex pseudocampanulata* is parapatric to *A. angulata* with large overlap and is more common to mesic southern and eastern regions. See figure 4.6d.

(3) *Atriplex holocarpa* lineage with *A. spongiosa*, *A. morrisii* [G57:C1,55]: Lineage with weak bootstrap support, but very high posterior probability in the Consensus tree. A corresponding

lineage of the ITS/ETS tree (subgroup P2) has high support but excludes *A. spongiosa* and includes equivocal *A. nessorhina*. The sister pair of *Atriplex holocarpa and A. morrisii* and *A. holocarpa* of high posterior probability [0.98,47] in the consensus tree is not observed in the Genotyping-by-Sequencing tree,. In the ITS/ETS tree the close relationship is obscured by the equivocal *A. nessorhina*. *Atriplex spongiosa* and *A. holocarpa* are of subcontinental distribution, and abundantly found in Riverine Desert and Stony Desert habitats. *Atriplex morrisii* is an uncommon species of the Eyre-Murray Centre and associated with flats, pans and channels of Riverine Desert and Desert Lake.

(4) *Atriplex lindleyi* lineage with *A. macropterocarpa*/*A. obconica* [G84:C0.99,86]: This lineage of high support, has unclear species relationships. It resembles the *A. lindleyi* B lineage (subgroup P2) of the ITS/ETS tree. However, that lineage excludes *A. lindleyi* ssp. *conduplicata* and has equivocal *A. macropterocarpa* species samples (*A. macropterocarpa*_3303 maps to an *A. quinii* lineage of subgroup P2 in the ITS/ETS tree). Distribution and habitat are described previously. See figure 4.6c. *Atriplex holocarpa* and *A. lindleyi* lineages are sister lineages of weak support. Member species have fruiting bracteoles of spongy masses respectively of ovoid or tetrahedral form, distinct from planar/tubular forms of most other species in Part 4.

The well-defined lineages and clusters of the *Atriplex semibaccata* subclade are:

(1) *Atriplex semibaccata* lineage with *A. muelleri*, *A. infrequens* and *A. spinibractea* [G82:C1,75]: This well supported lineage has subsequent divergence of high support with *A. muelleri*, then *A. spinibractea* [G84:C1,80] diverging from the sister species pair of *A. semibaccata* and *A. infrequens* [G83:C1,82]. The ITS/ETS tree has no equivalent lineage. Three species are restricted to the Eyre-Murray Centre as seen in figure 4.6h. The subcontinental *Atriplex semibaccata* is climatically disjunct, with an eastern population of much greater range. In the parapatric pair of *A. semibaccata* and *A. infrequens*, the latter occurs on the drier margins of the *A. semibaccata* range. *Atriplex spinibractea* is sympatric with *A. semibaccata*, but allopatric with *A. infrequens*. *Atriplex muelleri* and *A. semibaccata* are parapatric, with the former also in northern subtropical regions.

(2) *Atriplex leptocarpa* lineage with *A. sturtii* [G96:C1,94]: A species pair with strong support in Genotyping-by-Sequencing and Consensus trees. No similar relationship is evident in ITS/ETS tree and a replicate sample of *A. leptocarpa* is distant to this pair. Both are Eyre-Murray species (figure 4.6g). The range of *A. sturtii* is entirely within the north-western (drier) range of *A. leptocarpa*. Wilson and Chinnock (2013) treat the species names synonymously.

(3) *Atriplex stipitata* species cluster [G100:C1,100]. This species cluster of high support is also recovered in subgroup I of the ITS/ETS tree. The unique sample identities were lost in processing for the consensus tree, but are the same samples as in the Genotyping-by-Sequencing tree.

(4) *Atriplex fissivalvis* lineage with *A. acutiloba* [G83:C1:95]: A species pair of high support, also noted in the ITS/ETS tree (subgroup I), with distribution and habitat described earlier (figure 4.6f).

(5) *Atriplex quadrivalvata* lineage with *A. cordifolia* [G97:C0.99,98]: a sister species pair with strong support in Genotyping-by-Sequencing and Consensus trees. It is not recognised in the ITS/ETS tree where *Atriplex quadrivalvata* is equivocal and *A. cordifolia* forms a well-supported sister pair with *A. cornigera*. *A. quadrivalvata* is a shared species of disjunct populations. *A. cordifolia* is an Eyre-Murray species, allopatric to the eastern population of *A. quadrivalvata*.

Concatenation of all available ITS/ETS and Genotyping-by-Sequencing data

Figure 4.9 is a consensus tree for *Atriplex* Clade 2 from concatenation of ITS/ETS and Genotyping-by-Sequencing data from all available species samples. The imbalanced tree resembles that of select species samples (figure 4.8) but branch support is low throughout, species are in equivocal positions and the Central Asian *A. sphaeromorpha* sits within Clade 2. Most species names are omitted and emphasis placed on coastal taxa, early emergence and species relationships to the Yilgarn and Eyre-Murray Centres.

A basal lineage is a coastal subclade being sister to a very large lineage dominated by all the inland species. The coastal *A. billardierei* is shown as distant sister species to *A. paludosa*, whereas in the ITS/ETS tree, it is sister to an *A. paludosa-A. bunburyana* ancestor. The coastal *A. hypoleuca* is not part of this basal clade.

The very large lineage broadly comprises four major sub-lineages, of imbalanced topology and progressively derived. One is a lineage of low shrub species, affiliated with southwest Australia. *Atriplex nana* (which has equivocal samples) and *A. hymenotheca* are Desert Lake species of the southern Yilgarn Centre. *Atriplex cryptocarpa* is a Nullarbor Plain endemic, growing in channels thought to be palaeodrainage remnants (Benbow 1995a; Webb and James 2006; Hou *et al.* 2008). *Atriplex vesicaria* is the most ubiquitous species of *Atriplex* Clade 2.

The remaining three major sub-lineages are of mostly herbaceous species. Herbaceous I is the oldest, with species that are shared or restricted to the Eyre-Murray Centre. Species are dominantly from Riverine Desert and Stony Desert and it includes the well-supported lineages of *Atriplex angulata*, *Atriplex lindleyi* and *Atriplex quinii*.

Herbaceous II and III are rich sister lineages with species that are shared, or restricted to either Centre. Herbaceous II species are prominently from Riverine Desert and Desert Lake and include species of the northern most range of *Atriplex* Clade 2, including *A. flabelliformis* and *A. elachophylla*, all the unnamed Queensland species and *Atriplex eremitis* from the Pilbara. Species in Herbaceous III are from diverse land types of Desert Lake, Karst Plain, Riverine Desert, Mesic Plain & Range (subtropical and temperate) and Stony Desert. Well supported lineages recovered in other analyses include *A. semibaccata*, *A. fissivalvis* and *A. cordifolia*. Two species of Sand Desert (*A. velutinella* and *A. nessorhina*) are in the youngest branches, though Desert Lake is their more common habitat. Calciphiles include the shrub *A. stipitata* and subshrub *A. acutibractea*, but species samples appear in equivocal positions. The Coast obligate *Atriplex hypoleuca* from southwest Australia and the Eurasian outgroup species *A. sphaeromorpha* also map to Herbaceous III.

Figure 4.10: Chronograms of Sclerolaenid (left) and *Atriplex* (right) clades relating species emergence to landscape geochronology. Outgroup species indicated by **o/g**. Coastal species or lineages in **blue**. Species restricted to Stony Desert in **red** bold, to Karst Plain in **orange** bold, to Desert Lake in purple. Species of Stony Desert/Riverine Desert in lighter red and those prominently of, but not restricted to, Karst Plain in orange.

Sclerolaenid Clade clock based on Cabrera, Jacobs & Kadereit (2011).

Atriplex

Green Boxes indicate clade arrival estimated in Kadereit *et al.* (2010) for clades 1 & 2.

Atriplex Clade 1

1.1 *Atriplex cinerea* lineage

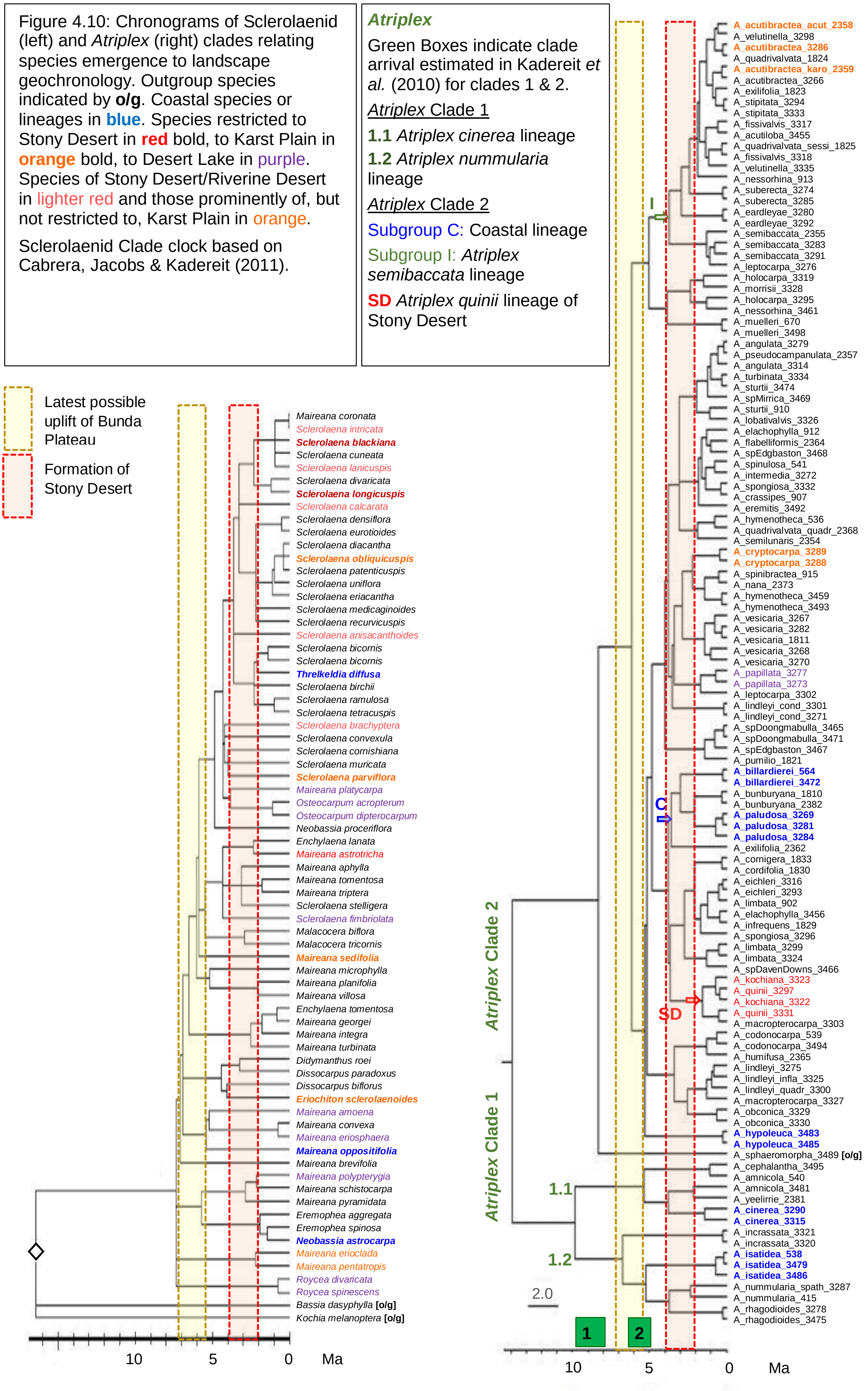
1.2 *Atriplex nummularia* lineage

Atriplex Clade 2

Subgroup C: Coastal lineage

Subgroup I: *Atriplex semibaccata* lineage

SD *Atriplex quinii* lineage of Stony Desert



Diversification correlation with landscape and other immigrant clades

Figure 4.10 compares emergence of lineages in the Sclerolaenid Clade with those of the two *Atriplex* Clades. The Sclerolaenid clade chronogram shows the relative minimum ages of lineages following molecular analysis (ETS markers) of 69 species, based on Cabrera *et al.* (2009, 2011 Figure 1). That for *Atriplex* derives from molecular clock analysis of ITS/ETS sequences adopting calibration points, protocols and settings progressively applied to chenopods (Kadereit *et al.* 2005, 2010; Cabrera *et al.* 2009, 2011). A calibration date of 14 Ma, for emergence of the Atriplex C_4 clade (Kadereit *et al.* 2010) was used to include both *Atriplex* clades in a single analysis. Incomplete sampling of the Sclerolaenid clade and lack of resolution in both, precludes clear identification of lineages and association with their landscape patterns. Confidence limits for nodal age estimates were not included in Cabrera *et al.* (2011). In both instances they are quite broad due to the low resolution in both clades. Nodal ages listed are median estimates. Interpretation of the Clade 2 chronogram is also confounded by equivocal position of numerous species.

Uplift of the Nullarbor Plain and formation of Stony Desert are included in figure 4.10 as useful time references. Uplift of the Nullarbor Plain is variably given as Middle-Late Miocene (Benbow LA 1995; Hou *et al.* 2008), Late Miocene (Benbow 1995a, 1995b) or end of Late Miocene (Webb and James 2006). The period indicated represents the last half of the Late Miocene, by when uplift would have been completed. The period of Stony Desert formation from 4-2 Ma (Fujioka *et al.* 2005; Fujioka and Chappell 2010) represents the period over which Central Australian gibber plains emerged.

Atriplex Clades 1 and 2

The chronogram for Atriplex topologically resembles the phylogeny in figures 4.2, 4.3 and 4.5. It differs primarily in displaying all bifurcations, rather than collapsing to the near basal polytomy and presenting older lineages at the base, similar to the Sclerolaenid presentation.

Crown age of *Atriplex* Clade 1 (10.4 Ma) predates the stem age of Clade 2 (8.22 Ma), both of which marginally predate their arrival estimated by Kadereit *et al.* (2010). Subsequent divergence in the two lineages of Clade 1 is initially in the *Atriplex nummularia* lineage (6.9 Ma) and later in the *Atriplex cinerea* lineage (5.5 Ma). The well-resolved *A. nummularia* lineage has further divergence of the coastal *A. isatidea* (5.4 Ma) and lastly the riverine *A. rhagodioides* (3.1 Ma). Diversification in each lineage coincides with uplift of the Bunda Plateau. Nearly all Clade 1 species, but *A. cephalantha*, had emerged by the end of Stony Desert formation. The equivocal position of *A. amnicola* precludes establishing order of diversification in the *A. cinerea* lineage.

Clade 2 has a Crown age of (6.1 Ma), coincident with the Bunda Plateau uplift. Five major lineages rapidly follow, each with Crown ages exceeding 5.6 Ma. This includes the Coastal group (Subgroup C of figure 4.5) with stem age of 5.7 Ma and a Stony Deserts *Atriplex quinii* lineage with stem age of 5.1 Ma. Differentiation within the *A. quinii* lineage occurs after Stony Desert formation.

The coastal clade (Subgroup C figure 4.5) with an equivocal sister *A. exilifolia*, dates to the basal polytomy (5.7 Ma). Order of divergence appears to be an initial separation of *A. billardierei* at 3.1 Ma, a Coast facultative of Bass Strait and Tasmania, then divergence of the shared coastal *A. paludosa* and the Yilgarn restricted *A. bunburyana* at 2.5 Ma.

The distinct *Atriplex semibaccata* lineage (Subgroup I of figure 4.5) has a sub-lineage of moderate support with a derived polytomy at age 1.8-1.6 Ma. It includes common to abundant species restricted to some habitats that appear in no other lineage such as *A. velutinella* (Desert Lake and Sand Desert), *A. acutibractea* (Karst Plain) and *A. fissivalvis* (Stony Desert).

Other lineages with some support include *Atriplex holocarpa*, *A. angulata* and *A. cordifolia* lineages. The sister species pair of *A. cordifolia* and *A. cornigera* diverged late at 0.5 Ma. Divergence in the other clades is confounded by equivocal position of species samples, either within or outside the lineage, however a divergence of the predominantly Riverine Desert species of *A. angulata* and *A. pseudocampanulata* in the Eyre-Murray Centre, dates relatively late to between 0.8 and 0.2 Ma.

Sclerolaenid Clade

The clade's three coastal species are in the chronogram. *Maireana* is the basal genus of the Sclerolaenid Clade (Cabrera *et al.* 2009). *Maireana oppositifolia* is in a basal grade and in a lineage of high PP support with three Yilgarn Plateau endemic species. It is a shared species of southern Australia, including the Nullarbor Plain coast, with an isolated population around Shark Bay. Inland populations include the Yilgarn Plateau, eastern Sandland South, Eyre Peninsula and the western Murray Basin. *Neobassia astrocarpa* is in the near-basal *Eremophea* subclade, being coastal in north-west Australia, where inland populations extend distantly into Northern Territory. *Threlkeldia diffusa* is derived and coastally extensive ranging from the Pilbara to eastern Bass Strait, enveloping the coastal range of *Maireana oppositifolia* and parapatric with that of *Neobassia astrocarpa*.

Four basal lineages of good support, predate uplift of the Bunda Plateau. These include the *Roycea* clade, which is restricted to Desert Lake habitats of south-west Australia and the *Eremophea* clade (which includes *Neobassia astrocarpa*) of north-west Australia. *Maireana pyramidata* and a *M. erioclada-pentatropis* lineages are also included, which span continental Australia. In the *M. pyramidata* lineage, *M. polypterygia* is restricted to the Yilgarn Centre and *M. schistocarpa* to the Eyre Murray Centre, but this divergence is relatively late.

At least eleven lineages in the Sclerolaenid Clade were in place prior to the development of Stony Desert. This includes five of the generic clades including *Sclerolaena*. A weakly supported *S. intricata* lineage has stem and crown node ages within age of formation of Stony Desert. The five species are commonly associated with Stony and Riverine Desert; *Sclerolaena blackiana* and *S. longicuspis* are restricted to Stony Desert in the Eyre-Murray Centre. *Maireana campanulata* and *Maireana eriantha*, which are also restricted to Stony Desert, were not included in the phylogeny. *Maireana astrotricha*, another species associated with Stony and Riverine Desert, diverged at this time. The well-supported *M. georgei* lineage has 4 species, including the two most widespread species of the Sclerolaenid clade. Though with stem age older than the Stony Plains, crown age is contemporary with it. Of all species sampled, *Sclerolaena brachyptera* is the Eyre-Murray species longest in isolation with stem age almost 5 Ma.

Species restricted to Karst Plain are also noteworthy. The basal *M. erioclada-M. pentatropis* lineage is associated with limestone soils. The emergence of *Maireana sedifolia* coincides with uplift of the Bunda Plateau, but *Eriochiton sclerolaenoides* emerges much later and *Sclerolaena obliquicuspis* only more recently.

Tecticornia Clade

A phylogeny of *Tecticornia* from ITS and *trn*L markers (Shepherd *et al.* 2004) comprises a basal polytomy from which Sister species pairs and lineages emerge with varied branch support. Parsimony analysis of ITS identifies *T. flabelliformis* as basal and a similar analysis of concatenated data suggests *T. halocnemoides* is basal. *Tecticornia flabelliformis* is coastal only in South Australia while *Tecticornia halocnemoides* is largely absent from the south-east coast. The coastally widespread *T. pergranulata* and *T. indica* were included in analyses.

DISCUSSION

The context of a littoral connection applying to chenopod species permits several interpretations of a phylogenetic tree. Coastal species in a basal phylogenetic position are surviving ancestors. Coastal species in derived positions demonstrate taxon cycling in the sense of Shmida (1985). In clades with none of the coastal species in basal position, the coastal ancestor has become extinct. Lineages deeply rooted within a clade can be explained as migrations from near a coastline.

Coastal species in basal phylogenetic positions can also demonstrate the validity of the assumption. However, coastal species in derived positions, can be explained by extinction of a coastal ancestor. Only in one Atriplex phylogeny is an extant species identified as basal, with support being moderate at best – *Atriplex paludosa* in *Atriplex* Clade 2. Clear interpretations remain hampered by the overall lack of resolution. In the clearer tree of *Atriplex* Clade 1, no species is definitively basal.

Certainly *A. paludosa* and *A. cinerea* (from Clade 1) exhibit qualities expected of a coastal ancestor. Both occur abundantly and extensively along coastlines and are Coast Facultative types. Both readily disperse along shorelines due to having buoyant propagules. Other coastal species of Clade 2 are more restricted in range and are Coast Obligate, though *A. billardierei* may be an ancestral candidate. It appears to be near basal, readily dispersive, and its presumed extinction in Victoria, possibly indicative of what may have happened farther west in the very remote past.

***Atriplex* diversity and richness**

Membership of the two Australian C_4 clades of *Atriplex* is largely resolved through phylogenetic analysis, though uncertainty in clade richness and phylogeny remains.

Atriplex Clade 1 has eight species in two lineages of four species. Only subclade 1.2 fully resolves to species level. Molecular analyses confirm suspected taxonomic relationships. Wilson (1984) suggested *A. rhagodioides* be treated as part of the *A. nummularia* complex, not as part of the *A. cinerea* complex. Wilson and Chinnock (2013) note close relationship of *A. nummularia*, *A. rhagodioides* and *A. incrassata*. *Atriplex amnicola* and *A. rhagodioides* are distinct western and eastern species, needing clearer taxonomic differentiation. The Yilgarn endemics *A. cephalantha* and *A. yeelirrie* are not described in Wilson (1984). Molecular analysis confirms taxonomic affinity of *A. yeelirrie* to *A. cinerea* (Clarke *et al.* 2012; Shepherd *et al.* 2015).

Membership of *Atriplex* Clade 2 is clear, but richness is uncertain and phylogeny unresolved. Uncertainty lies mainly in molecular analyses failing to fully resolve the member species. Several *Atriplex* sp. *Nov.* from Queensland and the robust and gracile forms of *A. stipitata* await taxonomic clarification, and problems of circumscription issues raised by (Wilson 1984) remain. Kadereit *et al.* (2010) attributed the basal polytomy of the clade, in part, to incomplete differentiation of forms. Current species descriptions, at least, recognize the variety of forms within *Atriplex* Clade 2. Same species clusters indicate stabilisation of some species. Future taxonomic revision that reduces species richness is recognition of greater morphological variation within species and future habitat studies would have to accommodate phenotypic and genotypic aspects.

Some of the defined lineages relate to hybridising or intergrading noted by Wilson (1984). He suspects *Atriplex obconica* to be a stabilised hybrid of *A. lindleyi* and *A. macropterocarpa*, and a close relationship is evident in the ITS/ETS and ITS/ETS-GBS concatenation. Similarly intergrades between *A. angulata*, *A. pseudocampanulata* and *A. turbinata*, as well as between *A. semibaccata* and *A. spinibractea* are consistent with being part of well-supported lineages. For the *A. leptocarpa-A. sturtii* species pair, Wilson and Chinnock (2013) treats the names as synonyms. Intergrades of *A. crassipes*, *A. eardleyae and A. humifusa* with species above are not apparent here. Taxonomic revision subsequently treating hybridising or intergrading species as synonymous would notably reduce species richness in the Eyre-Murray Centre.

Atriplex humilis lacks firm assignation to a clade and is assumed part of Clade 2. Molecular analyses of *A. humilis* is currently difficult. The last of only five herbarium specimens was collected in 1922 and extraction of suitable DNA is unlikely. Its persistence is also uncertain. Enquiries at the Queensland Herbarium revealed no recent, specific searches. *Atriplex humilis* was previously collected in the vicinity of Karumba, where taxonomist and chenopod authority S.W.L. Jacobs, collected *Sclerolaena bicornis* (1974) and *S. cuneata* (2005). It is inconceivable no search for *A. humilis* was attempted at these times. Assignation to *Atriplex* Clade 2 stems from parsimonious preference for membership of Clade 1 or 2 rather than being separate immigrant clade, its herbaceous lifeform and proximity to the taxon range of Clade 2. Coastal habitat makes it of prime interest in littoral origins of chenopods.

Molecular clock and geochronology

Molecular clock analyses are hampered by the broad range of the confidence limits for age estimates in both the Sclerolaenid and *Atriplex* clades. They indicate an order of divergence, at least within each immigrant Clade, even though the ancestral forms diverging are difficult to identify. Emergence of some species and lineages within Sclerolaenid clade exhibit some correspondence with emergence of landforms, but there is very poor correspondence of species emergence with landform origin in both *Atriplex* clades.

Of particular interest are lineages and species of Stony Desert, because geochronological ages indicate these emerged much later than estimated by molecular clock analyses. Divergence of *Atriplex incrassata* in Clade 1 and emergence of *A. quinii* lineage in Clade 2 date prior to the habitats to which they are restricted. Similarly, from the *A. nummularia* lineage in Clade 1, the emergence of *A. rhagodioides* at 3.1 Ma contrasts with habitat age of 0.7 Ma.

Assuming similar substitution rates within each clade, revising lineage and species emergence to age of landscape formation, has several outcomes for both clades. Clade 1 arrival would better align with the later estimate of Kadereit *et al.* (2010) and possibly predate Nullarbor Plain formation. Diversification into the two main lineages would approximate formation of the Nullarbor Plain. Initial diversification within each lineage would be contemporary or post-date formation of Stony Desert. Similarly, Clade 2 arrival would better align with the estimate of Kadereit *et al.* (2010), and which would coincide with the latest possible uplift of the Nullarbor Plain. The basal polytomy of Clade 2 would date to the Early Pliocene, between uplift of the Nullarbor Plain and formation of Stony Desert.

Estimated dates of late emerging species would also shift closer to their landscape formation times, including lineages of moderate support or better. Both *A. yeelirrie* and *A. cephalantha* from the *A. cinerea* lineage in Clade 1, are Desert Lake species of the Yilgarn Plateau. Though their habitat was present at estimated emergence, a later date may better fit their uncommon and rare status. A later divergence of *A. cornigera* and *A. cordifolia*, separated in part by the Simpson Desert, could identify these as a sister species pair derived through dune field disjunction. Though in a lineage of weak support, later emergence of *A. papillata* from *A. leptocarpa* would better align with the earliest emergence of Desert Lake habitats from Riverine Desert at 0.7 Ma in the western Murray Basin.

Atriplex Clade 1

The clade has two distinct lineages, each with coastal, riverine and terrestrial species. Together with lineage parapatry of relatively small overlap, they represent separate migrations from the coast and across the continent but through different routes. Divergence order, species ranges, littoral connections and West Wind Drift strongly suggest a western landfall. See figure 4.11.

The *Atriplex cinerea* lineage (Subclade 1.1) is largely of the coast and Yilgarn Centre drainage. The inland species are restricted to Riverine Desert and Desert Lake habitats of the Yilgarn Centre. Desert Lake habitats first formed there in the Pliocene (Clarke 1994a, 1994b; Alley 1999).The order of divergence is uncertain, but *Atriplex amnicola* likely emerged early. It occurs principally in catchments draining toward the Indian Ocean and occupies habitats similar to *A. cinerea*. Inland populations of *A. cinerea* are mainly south of the range of *A. amnicola* and in channels that drain to the south. An ancestral *A*. *cinerea*/*amnicola*, once widespread along the western coastline, left the Indian Ocean along drainage lines, but remained in the west. Expansion across Australia is an easterly migration along the southern coastline that in later stages includes northerly movement along the east coast and dispersal to New Zealand. See figure 4.11a.

The *Atriplex nummularia* lineage (Subclade 1.2) is in inland habitats of both Centres and has a clear order of species divergence tied to specific landscapes. First divergence is *A. incrassata*, restricted to gibber plains of Central Australia, which formed 4-2 Ma (Fujioka *et al.* 2005; Fujioka and Chappell 2010) in the later Pliocene. The coastal *A. isatidea* is restricted to the Yilgarn Centre. Commonly of calcareous coastal sands, it is disjunct from *A.*

nummularia ssp. *spathulata*, a species of sandy, calcareous soils (Waddell *et al.* 2010). Except in the endorheic Lake Eyre Basin, *Atriplex nummularia* is predominantly of catchments currently or previously draining toward the southern coast. The lineage ancestor would be a Coast or Inland facultative of inland species range over both centres. *A. isatidea*, also occurring along the south-west coast, involves northward range expansion along the west coast, or a coastal hinterland vicariance event. Date of this divergence, would not be reliable guide to the event initiating disjunction. See figure 4.11b.

The late divergence of *A. rhagodioides* and *A. nummularia* relates to Lake Bungunnia. The current range of *A. rhagodioides* in the lower reaches of the River Murray, was covered by this vast lake from 2.6–0.7 Ma. Though predominantly freshwater, the lake became alkaline and evaporitic in its final stages (Bowler *et al.* 2006; McLaren *et al.* 2011). Shoreline retreat from upstream, combined with river floodplain and terrace habitat would suggest downstream expansion of *A. rhagodioides*. A migration route from coast to inland through the Murray Basin is extremely unlikely.

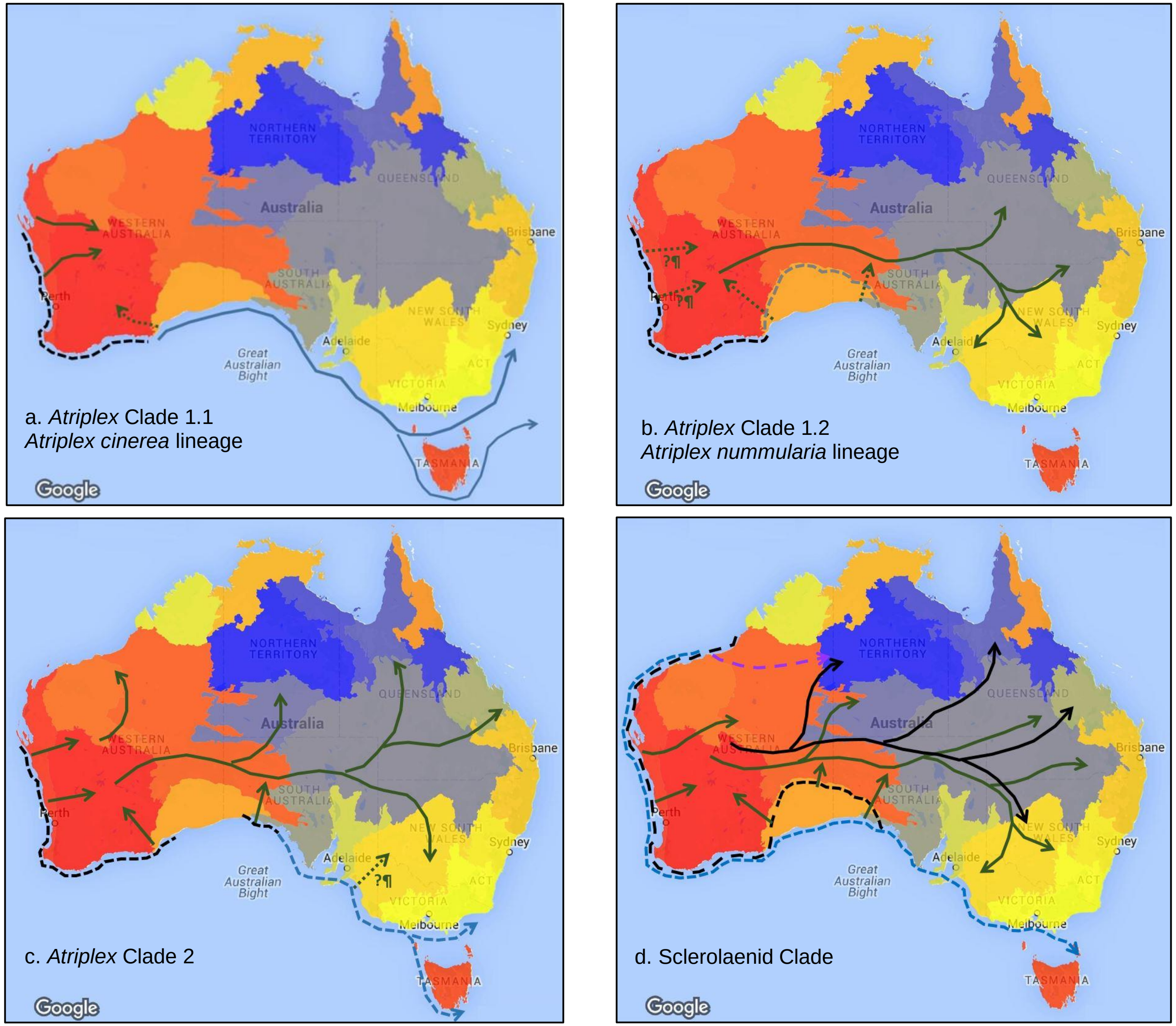
Significant salinization of western palaeodrainage occurred over the Pliocene, continuing into Pleistocene (Clarke 1994a, 1994b; Alley *et al.* 1999). Predominant substrates are gypsiferous muds forming under prevailing evaporitic conditions that previously created alkaline substrates. The palaeodrainage-controlled diversification in the *Atriplex cinerea* lineage corresponds with the rich diversification of *Tecticornia* (Shepherd *et al.* 2004) and early emergence of *Roycea* in the Sclerolaenid clade (Cabrera *et al.* 2011), which are Desert Lake genera. This is later than the initial Late Miocene diversification suggested by Cabrera *et al.* (2009, 2011).

The Coast facultative, *A. cinerea*, may best represent a coastal ancestor. It has a species range larger than the Coast obligate *A. isatidea*, which appears derived, emerging after near-continental expansion inland, and after separation from an *A. nummularia* ancestor. If so, the association of the *A. cinerea* lineage (subclade 1.1) with westerly flowing drainage, indicates the west coast of Australia as the likely landfall of the coastal ancestor.

Dispersal could explain the difference in subclade ranges. To extend its inland range farther east, the *A. nummularia* lineage must have breached the drainage divide between the Eucla and Lake Eyre Basins, and possibly watersheds of the Yilgarn Plateau. The fruiting bracteole of all species in the *A. cinerea* lineage is 10 mm or smaller and thick near the hard or corky bases (Wilson 1984). They readily float on water (Heyligers 2000) restricting presence to coastlines and inland drainage. The papery, laminar bracteole up to 15 mm size in *A. nummularia* and *A. incrassata* (Wilson 1984) is more susceptible to wind dispersal, though also buoyant in water. The small corky fruit of *A. isatidea* and *A. rhagodioides* in the *A. nummularia* lineage, would then be a reversion to an ancestral trait, suited to their coastal and riparian habitats. Atmospheric circulation prevalent over southern Australia in the later Miocene was an easterly movement (Kemp 1978).

Atriplex Clade 2

The order of diversification in Clade 2 is uncertain. At least, several migrations are likely as noted in the Sclerolaenid clade (Cabrera *et al.* 2009) and *Tecticornia* (Shepherd *et al.* 2004), but not specifically identifiable. Most would be internal, between the centres, but two coastal migrations occurred. No sister species resulting from continental disjunction could be identified, but a pair in the Eyre-Murray Centre are possible provincial candidates. See figure 4.11c.



a. *Atriplex* Clade 1.1
Atriplex cinerea lineage

b. *Atriplex* Clade 1.2
Atriplex nummularia lineage

c. *Atriplex* Clade 2

d. Sclerolaenid Clade

Figure 4.11: Main migrations in *Atriplex* Clades 1 & 2 and the Sclerolaenid Clade.

<u>*Atriplex* Clade 1</u>: Initial landfall is on the Yilgarn Centre coastline (a) The *Atriplex cinerea* lineage is mainly in the Yilgarn Centre, with continental migration along the south coast. (b) The *Atriplex nummularia* lineage migrates from the Yilgarn Centre to the Eyre-Murray Centre. Initial movement inland could be through Eucla Basin palaeodrainage.

<u>*Atriplex* Clade 2</u>: Initial landfall on the Yilgarn Centre coast. Inland movement from west coast, and maybe eastern and western Eucla Basin, prior to several waves of easterly migration. *Atriplex paludosa* may have completed a late coastal migration. Inland movement along the River Murray is unlikely, but possible.

<u>Sclerolaenid Clade</u>: Initial landfall is over a much longer coastline than for *Atriplex*. Initial coastal migration through Yilgarn, Eucla Basin and Canning Basin drainage (purple). *Maireana* (green) and *Sclerolaena* (black) would have separately migrated east. *Threlkeldia diffusa* migrated coastally south then east in more recent times (dashed blue).

Migrations also occurred across the Nullarbor Plain in *Atriplex* Clade 2 and Sclerolaenid Clade.

- - - - Landfall coastlines
→ Coastal migrations
→ Inland migrations

The Coast facultative *A. paludosa* could represent an ancestral coastal form. It is part of a coastal lineage in the ITS/ETS tree, which maps basally in an ITS/ETS-GBS concatenation though with moderate support. The species has the largest coastal range in the clade and is of diverse coastal habitats. The inland populations most distant from shorelines are in Western Australia where saline palaeodrainage developed early and extensively.

Close relationships within this coastal clade point to separate migrations and adaptation. Sister relationship with *A. bunburyana* indicates migration into the Yilgarn Centre. *Atriplex paludosa* ssp. *baudinii* is an inland form parapatric with the southern range of *A. bunburyana* (figure 4.6e). Both species are dioecious shrubs with paniculate inflorescence, whereas other shrubs of Clade 2 have axillary or spiked inflorescences. Close relationship to Coast obligate *A. billardierei* represents an easterly coastal migration with marked changes. *A. billardierei* is a monoecious herb of beaches. The laminar fruiting bracteoles of *Atriplex paludosa* and *A. bunburyana* have seed parallel to them, but in the axillary inflorescence of *A. billardierei*, the urceolate fruiting bracteoles have seed aligned at right angles. This unusual orientation in *Atriplex*, prompted Wilson (1984) to place the species in a distinct subgenus, but an adaptive function is not understood. Phylogenetic position of the coastal *A. hypoleuca* in southwest Australia is uncertain.

The relationship with New Zealand taxa has implication for adaptation and migration within this coastal clade. In New Zealand, *Atriplex billardierei* is closely related to the endemic *A. hollowayi* sp. Nov, and these herbaceous lifeforms are well adapted to high energy, sandy beaches (de Lange 2000). Given a tolerance of diverse coastal habitats, the coastal absence of *A. paludosa* in New Zealand and eastern Australia (where *Atriplex cinerea* occurs), suggests current populations of *A. paludosa* in Bass Strait are recent regional arrivals. Forming 6000 years ago (Blewett *et al.* 2012), all coastal species have shifted range in Bass Strait, but older coastlines of the region lack *A. paludosa* too. *Atriplex billardierei* would be a disjunct sister species arising after long distance dispersal early in Clade 2 history.

The broad polytomy, also noted by Kadereit *et al.* (2010), is a sizeable lineage of herbaceous species that is sister to an *Atriplex vesicaria* lineage of shrub species. Both derive from inland ancestors of the basal coastal clade, exhibit continental migrations and represent a separation of shrub and herbaceous forms. The *Atriplex vesicaria* lineage has the ubiquitous saltbush of Clade 2, along with a Yilgarn species (*A. nana*) and an endemic of the Nullarbor Plain (*A. cryptocarpa*), both of which are in habitats related to palaeodrainage systems. This strongly suggests that inland speciation occurs first in Western Australia, as Cabrera *et al.* (2011) determined for the Sclerolaenid Clade.

The large herbaceous clade has four defined lineages indicative of five interior migrations between the Centres of Diversity. The migrations relate chiefly to range expansions of five species, shared between the centres. Defined lineages also reveal limited speciation restricted to the Eyre-Murray Centre. The broad polytomy prevents identifying substantial lineages restricted to a single centre.

Habitats and taxon ranges of the lineages and their species indicate constraints to evolutionary events. Most relate to climatic trend toward aridity and some have geochronological constraints. The *Atriplex quinii* lineage comprises species of Stony Desert, and divergence of *A. kochiana* cannot precede the estimated formation date of 4-2 Ma (Fujioka *et al.* 2005; Fujioka and Chappell 2010). Of similar origin could be the *A. fissivalvis*-*A. acutiloba* sister pair of the Eyre-Murray Centre. *Atriplex fissivalvis* is also a Stony Desert species, but the range of *A. acutiloba* suggests the divergence may relate to formation of stony pavements around Flinders and Barrier Ranges, which date to 3-1 Ma (Krieg 1990; Callen *et al.* 1995). Species of the *A. angulata* lineage are predominantly of Riverine Desert in the Eyre-Murray Centre; the two main species are overlapping populations of the drier north-western (*A. angulata*) and mesic south-eastern regions (*A. pseudocampanulata*).

The *Atriplex semibaccata* lineage reflects a drying eastern Australia, but event times are not currently dated. It has four species tied to changing mesic habitats in the central and eastern Eyre-Murray Centre. *Atriplex semibaccata* inhabits southern, temperate Mesic Plain & Range and is the only shared species. The early divergence of *A. muelleri* relates to developing subtropical Mesic Plain & Range habitats. From the temperate mesic ancestor, emerged allopatric Riverine Desert forms under seasonal flow (*A. spinibractea*) and infrequent flow (*A. infrequens*). Shmida (1985) termed this eco-geographic pattern as Boyko's Rule – a species distributed along a mesic and xeric gradient, occupies the moist habitats of drier areas, along with any arid adapted close relatives. In such circumstances, desert elements do not expand into mesic habitats because they are outcompeted (Ward 2009).

Such diversification pattern seems contrary to speciation trend of transition from coast into riverine systems with adjustment to xeric conditions as riverine systems decline. However, this is a trend of early clade history. Adjustment to increasingly xeric conditions, after expansion along river systems, may include adaptation to climates becoming highly seasonal with increasing intensity and duration of dry season – such as may apply to eastern Australia, west of the Eastern Highlands. Chenopods globally have strong association with highly seasonal Mediterranean climates (Kuhn 1993). The Australian chenopods occurring with some diversity (especially *Sclerolaena*) in strongly seasonal subtropical regions appear to emerge later in clade history.

Comparison of *Atriplex* Clades 1 and 2

The younger *Atriplex* Clade 2 seems a more successful immigrant than the older *Atriplex* Clade 1. Atriplex Clade 2 has five times the species richness over a greater taxon range and in more diverse habitats. Clade 1 species are absent from Desert Upland, Shield Desert and Sand Desert, but the few Clade 2 species found there, are more characteristic of other land types. The uncommon *Atriplex spinulosa* in Desert Upland is an exception. However Clade 1 species are ecologically prominent in vegetation communities, including *A. incrassata* in the exceptionally dry Stony Desert, where the other prominent perennials are mainly the shrubs *A. vesicaria* (Clade 2) and *Maireana aphylla* and the grasses *Astrebla* spp. (Brandle 1998).

A significant difference between the *Atriplex* clades is in life-form. Short-lived forms never arose in Clade 1, and mostly emerged in Clade 2 during the initial continental expansion. Some reversion to shrub forms came with later emergence of *A. stipitata* and *A. acutibractea*. Emergence of herbaceous annuals or biennials from perennial shrubs reflects a shift in strategies from drought tolerance to drought evasion. Parr-Smith (1982) suggested *Atriplex* evolution in Australia began with divergence of shrub forms in western parts of the continent and short-lived forms emerged later.

In contrast, *Atriplex* in North America, which are closely related to Clade 1 (Kadereit *et. al.* 2010), exhibit rapid evolution of forms and frequent hybridization (Stutz 1978, 1984). Here diversification links to a geomorphic dynamism in landscapes that promoted alternating periods of mixing and isolation of species populations. *Atriplex* migrated northward into the western United States from hot, dry deserts and gypsiferous soils of northern Mexico. Expansion was facilitated by pre-adaptation to saline and alkaline clay soils, forming as evaporites under hot and dry climates of the Pleistocene and adaptation to dry, seasonally freezing conditions of northerly regions. Topographic isolation of long valleys, effected by mountain ranges and vast lakes that separated opposite ends of the valleys initiated speciation. Pluvial variation induced great fluctuation in lake size, allowing temporary mixing of once isolated populations in drier times. With desiccation and evaporation of lakes after the final pluvial phase, range expansion of formerly isolated species into common alluvial areas, enabled hybridization, some of which stabilised quickly into new species forms.

The scenario in Stutz (1978, 1984) compares with Australian circumstances, but with some notable differences. Conditions involve changing riverine and lacustrine systems with shifting shorelines and an overall drying trend that produced alkaline and saline soils of heavy texture. Initial migrations proceed with the onset of aridity, rather than with its attainment, accompanied by pre-adaptation. However, these Late Pleistocene events are much younger than Late Miocene–Pliocene events in Australia. Stutz (1984) considered the North American environment more disruptive than the more quiescent history of Australian saline plains.

The most rapid and diverse evolution of *Atriplex* in Australia is in Clade 2, but the stable *Atriplex* Clade 1 is derived from the fast evolving North American stock (Kadereit *et al.* 2010). Australian continental topography may explain this. Lacking mountain ranges, regional or local isolation is difficult to achieve. The same, relative flatness can facilitate range expansion of vast areas, but under long-term drying trend driving a shift to annual and biennial lifeforms, which come and go with rainfall, isolation is possibly effected by variably interrupted gene flow due to extended regional droughts.

Atriplex, Sclerolaenid and *Tecticornia* clades

Tecticornia clade

Tecticornia species diversity is highest in the Yilgarn Plateau (Chapter 2) similar to *Atriplex* Clade 1. Regional lineages are suspected but not yet confirmed. *Tecticornia halocnemoides* may best represent the coastal *Tecticornia* ancestor. It is widespread coastally, including the northern coast where landfall is suspected (Kadereit *et al.* 2005, 2006). However, its basal phylogenetic position is very tentative. Bridgewater and Cresswell (2003) suggested saltmarsh colonisation from central southern and central western coastal systems. After arrival on the north coast, western coasts would be the most likely entry to the interior.

Sclerolaenid clade

The Sclerolaenid phylogeny suggests no substantial lineages restricted to either centre, though some limited diversification of sub-lineages is evident in both centres. Larger sampling and resolved phylogeny are required to confirm. But for *Roycea*, the taxon ranges of genera show them to be shared lineages, as appears to be numerous lineages within the basal *Maireana* e.g. *Maireana georgei* and *Maireana pyramidata* lineages. Most of the main lineages in the Sclerolaenid clade were in place prior to the development of Stony Desert.

The clade’s coastal taxa have evolutionary significance for origin and migration. A coastal ancestor is not readily identifiable in the modern taxa. If *M. oppositifolia* is not basal, the coastal ancestor is now extinct, or a littoral connection doesn’t apply to the clade. Its current inland range is consistent with access to the interior limited to the eastern and western margins of the Eucla Basin. Taxon cycles of differing periodicity are indicated by phylogenetic position. The derived *N. astrocarpa* and *T. diffusa* both emerged about 2 Ma, but the former is part of a near-basal subclade, while the latter is related to the later emerging *Sclerolaena* genus. The range of the derived *Threlkeldia diffusa* resembles distributions of coastal *Atriplex*. It is not yet present in Tasmania, nor on the east coast or in New Zealand, suggesting arrival in Bass Strait is very recent, as suspected for *A. paludosa*.

The taxon range of the *Eremophea* subclade could represent a taxon cycle restricted to the Yilgarn Centre.

The Sclerolaenid and *Atriplex* clades have species peculiar to Stony Desert. Occupation of this habitat occurred relatively early in *Atriplex* clades but appears late in the Sclerolaenid Clade. However *Maireana* spp. restricted to Stony Desert are not included in the phylogeny. The other species are also prominent Riverine Desert species (e.g. *S. intricata*, *S. cuneata*, *S. divaricata*), resembling relationships in *Atriplex* Clade 1 (e.g. *A. nummularia-A. incrassata*) and Clade 2 (e.g. *A. lindleyi-A. macropterocarpa*).

Sympatric species of Karst Plain habitats emerged early and late in the histories of the Sclerolaenid Clade and *Atriplex* Clade 2. They also appear in other immigrant clades, especially Chenopodieae I. Though not as strong a link between the Yilgarn and Eyre-Murray centres as Sandland South province, the Nullarbor Plain nevertheless is an evolutionary connection, discussed further below.

Sympatry in the ranges of some species that are of similar habitats suggest additional congruency of emergence in the Sclerolaenid and *Atriplex* clades. *Maireana enchylaenoides*, *M. brevifolia* and *A. semibaccata* are continentally disjunct species of Mesic Plain & Range. In south-eastern Australia, sympatric and parapatric *Maireana* species of similar habitat include *M. decalvans*, *M. excavata* and *M. humillima*, along with the riparian *M. microphylla*. If these species are identified in a single lineage the processes likely mirrors divergence within the *Atriplex semibaccata* lineage.

Karst Plain species and the Nullarbor anomalies

Specht (1981b) suggested calcareous substrates facilitated migrations from the coast and across the interior. Though a link between the Yilgarn and Eyre-Murray Centres through Sandland South province is stronger, the Nullarbor Plain also links the centres through species of Karst Plain land types. This includes species of widespread range and diverse habitats (i.e. also in Sandland South) and species restricted to Karst Plain Land types. The link is more evident in the Sclerolaenid Clade than in other immigrant clades, as seen in Table 4.2 which lists species tolerant of limestone soils. This includes widespread taxa broadly tolerant of diverse habitats and those peculiar to limestone soils, many of which are from the Sclerolaenid Clade.

Widespread Species		**Calciphiles**	
Present	**Absent-Rare**	**Present**	**Absent-Rare**
Atriplex vesicaria		*Atriplex nummularia* ssp. *spathulata* *A. acutibractea* *A. cryptocarpa* #	*Atriplex pumilio* *A. stipitata*
Rhagodia spinescens	*Chenopodium desertorum* *Einadia nutans*	*Chenopodium curvispicatum* *Rhagodia crassifolia* *R. ulicina*	*Chenopodium gaudichaudianum* *Rhagodia candolleana* *R. preissii*
Maireana georgei *Enchylaena tomentosa*	*Maireana integra*	*Maireana erioclada* *M. sedifolia* *M. trichoptera* *M. turbinata* *Eriochiton sclerolaenoides*	*Maireana pentatropis* *M. radiata*
Sclerolaena diacantha		*Sclerolaena brevifolia* *S. obliquicuspis* *S. patenticuspis* *S. uniflora*	*Sclerolaena parviflora*

Table 4.2: Presence of chenopod species from *Atriplex*, Chenopodieae I and Sclerolaenid clades on Nullarbor Plain. # Endemic to the Nullarbor.

This minor link through Nullarbor Plain and Karst Plain land types has three significant aspects for chenopod evolution.

First, clades arriving before uplift of the Bunda Plateau, would have migrated along a coastline that was once the southern margin of Sandland South province. Migrants could establish on the coastal barrier dune of the Ooldea Sand similar to their modern presence on Younghusband Peninsula at the Coorong Coast. Direct entry to coastal marshes and lagoons would only occur at each end of the barrier dune on western and eastern margins of the Eucla Basin. There is no evidence of the dune breached by outlets to the ocean, except at these ends (Benbow 1990; Benbow *et al.* 1995b; Hou *et al.* 2008). Later migrations bypassed the Bunda Cliffs that formed with uplift. Coastal species like *Maireana oppositifolia* are uncommon cliff-top species, but coastal *Atriplex* are absent.

Second, species restricted to Karst Plain emerged at different times, possibly in relation to formation of varied types of Karst Plain. The formation of the Nullarbor Plain, aeolian calcarenites and pedogenic and phreatic calcretes are Late Miocene to Late Pleistocene events (Phillips and Milnes 1988; Sheard 1995; Sheard and Smith 1995; Anand and Paine 2002; Bowler *et al.* 2006; Webb and James 2006; Hou *et al.* 2008) that developed progressively in an easterly expansion. This eventually realised a near continuous habitat from the eastern Yilgarn Plateau to the western Murray Lowlands, which is the common range of calciphile species found on the Nullarbor Plain. Species ranges may extend west to limestone plains along the west coast (Hocking and Preston 1998) or north into Central

Australia where Miocene limestones have been exposed and calcretes have formed through the Pliocene and Pleistocene (Edgoose and Ahmad 2013). See figures 4.6i and 4.6j.

Karst Plain species emerged at different times in the Sclerolaenid and *Atriplex* clades. Emergence associated with a particular stages of Karst Plain development is uncertain, but divergence occurred early and late in both clades, with possibly up to four distinct episodes in the Sclerolaenid Clade. Emergence of *Maireana erioclada* and *M. pentatropis* in a near-basal lineage approximates formation of the Bunda Plateau, and possibly predates arrival of *Atriplex* Clade 2. The Nullarbor Plain endemic *Atriplex cryptocarpa* (Clade 2) is from a near-basal shrub lineage, differentiating early in the initial inland migration, an event comparable to emergence of *M. sedifolia* even if not contemporary. Emergence post-dates formation of the Nullarbor Plain and emergence of the calciphile *Eriochiton*. Late emergent species include *Sclerolaena obliquicuspis*, *Atriplex acutibractea* and *Atriplex stipitata*.

Commonly co-occurring, the relative presence of the species is varied. Those from the Sclerolaenid clade, particularly *Maireana sedifolia*, *M. erioclada*, *Sclerolaena obliquicuspis* and *S. patenticuspis*, occur abundantly and help define shrubland floristic elements of the regions (Hudspith *et al.* 2001; Kenny and Thompson 2008; Waddell *et al.* 2010). *Rhagodia ulicina* and *Chenopodium curvispicatum* from Chenopodieae I, and the *Atriplex* spp., are generally less significant, the most notable *Atriplex* being the generalist *A. vesicaria*.

Third, some species notably associated with calcareous soils avoid the Nullarbor Plain, but are related to its inhabitants. See figure 4.6i. The avoiders are listed in Table 4.2. These are species of calcareous sands with pedogenic calcrete at depth growing in mixed woodlands of *Eucalyptus*, *Casuarina* and *Myoporum*. They occur in sandy landscape elements west, north and east of the Nullarbor Plain, including the Sandland South province (Great Victoria Desert) immediately to the north. Of the near-basal *Maireana erioclada-M. pentatropis* lineage, *Maireana pentatropis* is near absent from the plain. The age of the lineage is estimated at 7-7.5 Ma, but divergence occurred about 2 Ma. Similarly, *Atriplex stipitata* and *A. acutibractea*, both of which belong to a late emerging clade are closely related species. *A. stipitata* is relatively abundant on calcareous sandy soils in mallee woodlands and *A. acutibractea* occurs on calcareous loamy soils in low shrubland of the Nullarbor Plain.

Avoiders also include widespread species that are found in diverse habitats e.g. *Chenopodium desertorum* and *Einadia nutans*. Occurrences in Sandland South Province (Great Victoria Desert) to the north, sharply delineate margins of the Plain e.g. *Sclerolaena parviflora*.

Karst Plain has generally accepted species from lineages associated with other habitats. Only the *M. erioclada-M. pentatropis* lineage seems uniquely associated with Karst Plain, but neither is exclusive to the Nullarbor Plain. Species of Karst Plain habitats did not all emerge simultaneously.

CONCLUSION

Atriplex Clade 1 comprises eight species arising through separate migrations from a coast ancestor. *Atriplex* Clade 2 comprises 52 species and is likely one major migration from coastal areas traversing the contienent, but includes several migrations from each Centre.

Transition from coast species to species of drainage elements are evident in the *Atriplex* Clade 1 subclades, representing an influence of niche conservatism on speciation. However, *Atriplex* subclade 1.2 also adapted early to Stony Desert, which is a habitat of high exposure, similar to coastal cliffs. Niche conservatism likely also operated similarly in early stages of *Atriplex* Clade 2, though early emergence of the widespread *A. vesicaria* could suggest a growing influence of niche differentiation.

Of available molecular phylogeny, strongest evidence for coastal species in basal position is in both *Atriplex* Clades. *Tecticornia* and Sclerolaenid clades have little evidence for such. The Sclerolaenid Clade evinces derivation of coastal species, but extinction of coastal ancestors is also possible.

Several similar patterns of distribution, habitat and phylogeny, resembling congruencies, are apparent in *Atriplex* clades, and have some parallels in Sclerolaenid Clade and possibly in Chenopodieae I. Patterns are interpretable as a process varying in time e.g. episodic adaptation to and range expansion through Karst Plain, or near simultaneous event e.g. adaptation to and range expansion through Stony Desert. The broad pattern of easterly expansion from Yilgarn to Eyre-Murray has elements of both.

Diversification patterns suggested in phylogenetic trees are credible in the context of a littoral connection, but poor resolution of the trees indicate detail of the course of evolution is yet to be firmly established.

CHAPTER 5. DISCUSSION AND CONCLUSION

On the premise of a littoral connection, chenopod evolution in Australia is interpreted as a Neogene serial invasion, driven by niche conservatism, through continental drainage systems. Its course does not exactly fit current notions of development of the arid biota, due to the youth and salt-based ecology of chenopod taxa.

PHYTOGEOGRAPHY, HABITAT, PHYLOGENY AND LITTORAL CONNECTIONS

The Yilgarn and Eyre-Murray centres delineate the main evolutionary space of range expansion and diversification of chenopod taxa. Together they have 97% of Australian species and occupy most of the arid zone but are not confined to it. These centres share 43% of all species, reflecting widespread initial colonisation from coastlines and multiple migrations across them. Additional diversification has also occurred with 23.2% of species restricted to the Yilgarn Centre and 31.8% to the Eyre-Murray Centre. The inland province of Sandland South (Great Victoria Desert) is the strongest link between the centres, not the coastal Nullarbor Plain though it is dominated by chenopod vegetation.

The evolutionary process is a Neogene serial invasion of eleven immigrant clades, where range expansion and diversification is strongly influenced by niche conservatism. Initial stages of Transport, Colonisation and Establishment are associated with oceans and shorelines. Later stages of Landscape Spread and Diversification are most prominently inland processes. The richer clades ultimately achieved similar widespread distributions. Though with a high degree of co-occurrence of taxa, distribution is not uniform because *Tecticornia* and *Atriplex* Clade 1 are richer in the Yilgarn and *Atriplex* Clade 2 is richer in Eyre-Murray. Variations in distribution reflect clade ecology, the location and time of landfall and the course of range expansions.

Chenopod abundance in Riverine Desert and Desert Lake shows the influence of niche conservatism. The main inland habitat of chenopods is drainage systems with critical elements of salinity and flooding. Palaeodrainage networks initially facilitated migrations to distant inland regions and hosted the early species radiations within extensive novel habitats. The size and low relief of both centres would also have enhanced diversity through effecting reproductive isolation of species strongly tied to drainage elements. The minor occupation of

Stony Desert can be related to harsh conditions of exposed coastal cliffs. The influence of niche conservatism does not include dune forms. Sand Desert contributes little to chenopod diversity, nothing to initial range expansions and curiously is associated with extinction. It is a very young habitat, largely occupied by glycophytic taxa, which are much more competitive in the absence of soil salt.

Chenopod clades generally observe the taxon, habitat and trait elements, as shown in Table 5.1. In the taxon element, sister species do not form separate and distinct coast and inland suites. Species of distinctive coastal ecology also extend inland, while inland species appear on the coast. *Dysphania* lacks distinctive coastal taxa. In young clades, coastal species are prominent and typically have inland populations of small range proximate to coasts. The exceptional *Scleroblitum*, now with no coastal taxa but having a coastal ancestor, indicates the taxon element has a time dimension.

The phylogenetic position of coastal taxa is significant in the taxon element. A basal position suggests an ancestral arrival and is expected in young clades of few species, but not necessarily in older clades. *Atriplex paludosa* in *Atriplex* Clade 2 is possibly basal. The coastal species of Clade 1 are near basal, as are *Maireana oppositifolia* and *Neobassia astrocarpa* in the Sclerolaenid Clade. *Dysphania* and Chenopodieae I need further sampling to determine position of coastal taxa. Coastal species not in basal phylogenetic position, point to taxon cycling in the manner of Shmida (1985).

Extinction can modify taxon element patterns. In order to discount littoral origins, absence of coastal taxa would have to occur in most clades, and especially in younger clades. Coastal taxa of older clades, competing with newer arrivals, would be at greatest risk of extinction. A combination of competition and shoreline retreat may explain loss of coastal populations of *Scleroblitum*.

All chenopod clades satisfy the habitat and trait elements, particularly through sharing saline and marshy habitats. It also suggests how chenopod taxa adjusted to inland habitats (see below). Traits largely relate to facets of salt-tolerance and its exaptation for drought-tolerance. Any detailed clade studies should identify the specific physiological and morphological traits for tolerance of salt, flooding and drought, but trait sharing is most evident in stem or leaf succulence in all clades but *Dysphania*.

Subfamily/Clade	**Nº of Species**	**Age (Ma)**	**Littoral Connection Element**			**Basal Coast Taxa**	**Taxon Cycle**	**Coast Facultat. Species**
			Taxon	**Habitat**	**Trait**			
Chenopodioideae								
Scleroblitum	1	42.2-26	No	Yes	Yes	No	No	No
Dysphania	16	16.1-9.9	Yes*	Yes	Yes	K	K	No
Atriplex Clade 1	8	9.8-7.8	Yes	Yes	Yes	Yes	No	Yes
Atriplex Clade 2	52	6.3-4.8	Yes	Yes	Yes	Yes	Yes	Yes
Chenopodieae I	24	4.2-2.9	Yes	Yes	Yes	K	K	Yes
Atriplex australasica	1	2.4-0.1	Yes	Yes	Yes	Yes	-	Yes
Camphorosmoideae								
Sclerolaenid	150	16.4-10.3	Yes	Yes	Yes	No[#]	Yes	Yes
Salicornioideae								
Tecticornia	44	10.9-4.8	Yes	Yes	Yes	K	K	Yes
Sarcocornia	3	4-1.8	Yes	Yes	Yes	Yes	K	Yes
Suaedoideae								
Suaeda	2	K	Yes	Yes	Yes	Yes	K	Yes
Salsoloideae								
Salsola	1	K	Yes*	Yes	Yes	Yes	-	No[@]

Table 5.1: Chenopod clade characteristics of a littoral connection and other noteworthy evolutionary considerations [K – not known; *taxon element observed in absence of coast obligate or coast facultative species; [#] near basal coastal taxa known; [@] can be regionally coast facultative].

NEOGENE INVASION AND MIGRATION

Transport

Long distance, oceanic dispersal brought chenopods to Australia. West Wind Drift carried ancestral *Scleroblitum*, Sclerolaenid Clade, *Atriplex* Clades 1 and 2, *Sarcocornia* and *Atriplex australasica*. It extended *Atriplex* Clades 1 and 2 and Chenopodieae I to New Zealand. *Tecticornia* most likely stepped through islands of South East Asia. Sources of *Dysphania* and Chenopodieae I are unclear.

Colonisation and Establishment

Landfall was mainly on western and southern coasts, except *Tecticornia* which likely arrived on the north coast. *Scleroblitum* and *Atriplex australasica* have the most easterly landfall. Every clade has a current or past association with coastlines. The Coast facultative character assists ready colonisation of shorelines and rapid establishment of bridgehead populations.

Landscape Spread

Landscape spread at continental scale comprises migrations along coastlines, from coast to inland and between inland regions.

Coastal range expansion

Coastal species range expands immediately on arrival. West Wind Drift assisted easterly extensions along the south coast in all clades. The younger *Sarcocornia* and *Suaeda* clades show the relative rapidity of coastal expansions, while the older *Tecticornia* now occupies almost the entire coastline.

Current range extensions include *Suaeda* and *Sarcocornia* on the northern coast, and *Atriplex* Clade 1, Chenopodieae I and *A. australasica* north along the eastern seaboard. *Atriplex paludosa* and *Threlkeldia diffusa* have likely only recently reached Bass Strait and could in future appear in New Zealand, similar to other *Atriplex* and the Chenopodieae I clade. Absence of the Sclerolaenid Clade there is a curiosity. Absence of the Sclerolaenid Clade and clades of the Chenopodioideae from northern coast, reflects ecological barriers.

Inland range extension

Inland migration must precede radiation and can quickly follow landfall. Pollen presence inland matches estimated clade arrivals, though the clades are not identifiable. Chenopods can be present under seasonal climates before regional vegetation is dominantly xeric (Martin 1979) as seen in subtropical Queensland. Diversification closely follows arrival of *Atriplex* Clades 1 and 2, but at least 3 million years separates arrival and earliest diversification in the older Sclerolaenid Clade (Kadereit and Freitag 2011). Chenopodieae I probably extended inland on arrival, in order to achieve continental distribution in relatively short time. *Tecticornia* migrated from the north coast before finding pathways inland, but *Sarcocornia* arrived when estuarine-riverine connections on western and southern coasts were in decline. Lack of suitable inland habitat inhibited expansion of the oldest clades, but drainage no longer reaching coastlines inhibits expansion of the youngest. Coast facultative capacity that enhances coastline departure, likely also allowed occupation of diverse Riverine Desert mesohabitats, promoting distant extension across a flat, low continent.

Migrations from coastlines seem few, with the western and southern coastline from Broome (WA) to Portland (Vic) providing best opportunity. Two such migrations are observed in *Atriplex* Clade 1. Taxon ranges of the two subgenera in *Dysphania* (recently confirmed with molecular analyses: Kadereit *pers*. *comm*.) suggest two migrations, though relationships with coastal ancestors are uncertain. The Sclerolaenid and *Atriplex* 2 clades seem to comprise a single migration from the coast that multiplied only with diversification of inland taxa. Where Tertiary basins adjoin shorelines, large catchments of low relief with continuity of drainage habitat allowed distant and rapid range expansion along drainage axes. Past coastlines were located similarly to the present, except for a marked ingress of the Murray and Eucla Basins.

The most common form of inland range extension is from one inland centre to another with a common route through the Great Victoria Desert. Incomplete or unresolved phylogeny prevents identifying the lineages. Distribution of genera in the Sclerolaenid clade suggests six major internal movements between centres, with a similar number in the recognized lineages of *Atriplex* Clade 2.

Major barriers to internal migration are mesic tropical and temperate regions, though coastal migration could circumvent them. Range extension principally followed their respective movements north and east over the Neogene as aridity intensified, with some contraction and expansion under climatic oscillations of the Pleistocene.

These barriers are near impervious to chenopod clades. The cool, mesic regions are strong and sharp barriers, though a little permeable to *Dysphania* and Chenopodieae I clades. The northern arid provinces are a diffuse barrier where outlying populations of 17% of chenopod species are scattered along a broad arid to tropical gradient. This barrier shifted northward during the Neogene. Tropical monsoon savannah, similar to that now in northern Australia, existed in Central Australia in the Miocene (Alley *et al.* 1999). Similarly, Central Lowlands East province is a diffuse barrier across an arid to seasonally subtropical gradient, the latter conditions of which prevailed over much of Australia during the Neogene (Martin 2006). The main barrier to *Tecticornia* is the dynamics of freshwater flows in arid river systems with monsoon sources. Population dynamics at range edges of the modern species of these regions could be indicative of past barriers to chenopod expansion.

Range contraction and shift

Species range contractions are evident in the fragmented species populations of mesic and arid chenopod taxa in diverse clades. Each major sandy desert has associated disjunct species populations, with a Great Victoria–Great Sandy Deserts divide separating the two main centres. The Simpson–Strzelecki Deserts divide has the only currently recognized sister species pair. Disjunction results from extensive denudation of alluvial plains that is a pre-condition to dune formation, not because dune fields are unsuitable habitat.

Disjunction of mesic and coastal species populations is complex vicariance of disruption through the Neogene. Events include emergence of the Nullarbor Plain, formation of Lake Bungunnia, expansion of arid zone to coastlines, shoreline retreat and advance on southern and northern coastlines and dune field formation in southeast Australia. The greatest range shift of recent times would be of coastal taxa over the substantial distances covered by oscillating northern and southern shorelines.

Diversification

With 81.5% of chenopod taxa being dissociated from coastlines, diversification is largely an inland phenomenon. Earliest diversification of major clades broadly coincides with emerging aridity in the Late Miocene to Early Pliocene. The delay after arrival, in the Sclerolaenid clade, may also have occurred in *Dysphania*, given their similar age and the fewer species. Diversification closely following arrival, strongly implies common location of emerging aridity, landfall and initial migration.

Coastal diversification

Coastal diversity is relatively low, being 0.08% of species overall. Coastal richness is highest on the west and south coasts with most being perennials. Coastal richness relates mainly to the number of immigrant clades, as each has a similar number of coastal species. Low diversity could stem from ready dispersal facilitating gene flow, few coastal habitats and interspecific competition among chenopod taxa. A few coastal species result from a littoral Evolutionary Taxon Cycle (Shmida 1985), occurring twice in the Sclerolaenid Clade. *Neobassia astrocarpa* emerged early and *Threlkeldia diffusa* later. *Atriplex humilis* and *A. hypoleuca* may represent separate cycles in *Atriplex* Clade 2.

Inland diversification

The Yilgarn and Eyre-Murray Centres largely result from inland processes. The interplay of migration and diversification awaits resolved phylogenetic analyses. West to east trends probably dominate, especially for coastal migrations, but a degree of inland exchange between centres remains possible. Regional lineages of substantial size seem unlikely, except perhaps for *Tecticornia* in the Yilgarn Centre. Small lineages are identified, but whether they precede migration or end with it is unclear. Both relationships are apparent in *Atriplex* Clade 1.

Similar capacity for facultative occupation of habitat, as at the coast, would also offer initial opportunity for adjusting to dry habitats, aided by the exaptation for drought-tolerance (as outlined below).

The size and low relief of both centres would also have enhanced diversity through effecting reproductive isolation of species strongly tied to drainage elements. Size may also have effected isolation in widespread populations not tied to drainage elements, especially during the Pleistocene. Australian Deserts have high spatio-temporal variability of rainfall (Dunkerley 2010) and river flow (Brock *et al.* 2006) raising questions of gene flow through populations of the shared taxa and impact on isolation of populations.

A major morphological adaptation to aridity involved shift from perennial to annual and biennial forms, most notable in the derivation of *Sclerolaena* and likely occurring in *Atriplex* Clade 2. Desert chenopods are mainly xerohalophytes, occupying saline landscapes in very dry regions; none have become genuine xerophytes.

Extinction

Chenopod populations have disappeared and species extinction is suspected. Vicariant disjunction of arid and mesic taxa extinguished local populations. Coastal populations of *Scleroblitum* have disappeared or been simply abandoned by a retreating coastline.

Extreme events can cause extinction. A Wet Reversal in the Early Pliocene briefly interrupted the long term Neogene drying trend (Martin 2006; Webb and James 2006; Fujioka and Chappell 2010; Sniderman *et al.* 2016). Rainforest taxa returned to eastern Australia (Martin

2006) and mesic *Eucalypt* forest replaced semi-arid vegetation in the Nullarbor region (Sniderman *et al.* 2016). Extinctions at this time possibly eliminated early migrations from the coast. A pre-condition to dune field formation is removal of vegetation in Riverine Desert landscapes which are diverse with chenopod taxa. Occupation of similar habitats by different clades with interspecific competition brings chance of competitive exclusion.

Major migrations deriving the modern distribution

The geography of chenopod evolution in Australia is dominantly the development of the Yilgarn and Eyre-Murray Centres. Given their coastlines, habitat and species complements, alternative scenarios that are not mutually exclusive, and have the same first stage, were open to immigrant clades, or lineages within them (see figure 5.1). During or before the Early Pliocene, chenopod clades established along what is now the western and southern coasts. Inland incursion was limited to estuarine tidal regime and coastal seral communities. *Scleroblitum*, Sclerolaenid and *Atriplex* Clades 1 and 2 made landfall along this coast, but *Tecticornia* migrated into it from the north. Chenopodieae I, *Sarcocornia* and *Atriplex australasica* clades arrived in the Late Pliocene and Pleistocene.

Fragmentation scenario

(1) Colonisation/Establishment stage: coastal bridgeheads form and expand.

(2) Landscape Spread stage: Range extension distributes chenopods through catchments that drain to the west and south coasts. Aridity develops earlier in the west, extension is faster, taxon ranges are larger, but western and eastern regions are linked through ancestral Great Victoria Desert. Differentiation from coastal species generates the taxa shared by both centres of diversity.

(3) Diversification stage 1: Broad expansion to current limits of Subcontinental Arid–Mediterranean Group, especially in central-eastern interior. Speciation increases with expansion of new and existing arid habitats, deriving more shared taxa and early emergence of restricted taxa.

(4) Diversification stage 2: The incipient Subcontinental Arid–Mediterranean Group fragments into western Yilgarn and central-eastern Eyre-Murray Centres of Diversity,

generating lineages restricted to each centre. The dune field disjunction of arid taxa, is a final stage of climatic disjunction of mesic and semi-arid taxa.

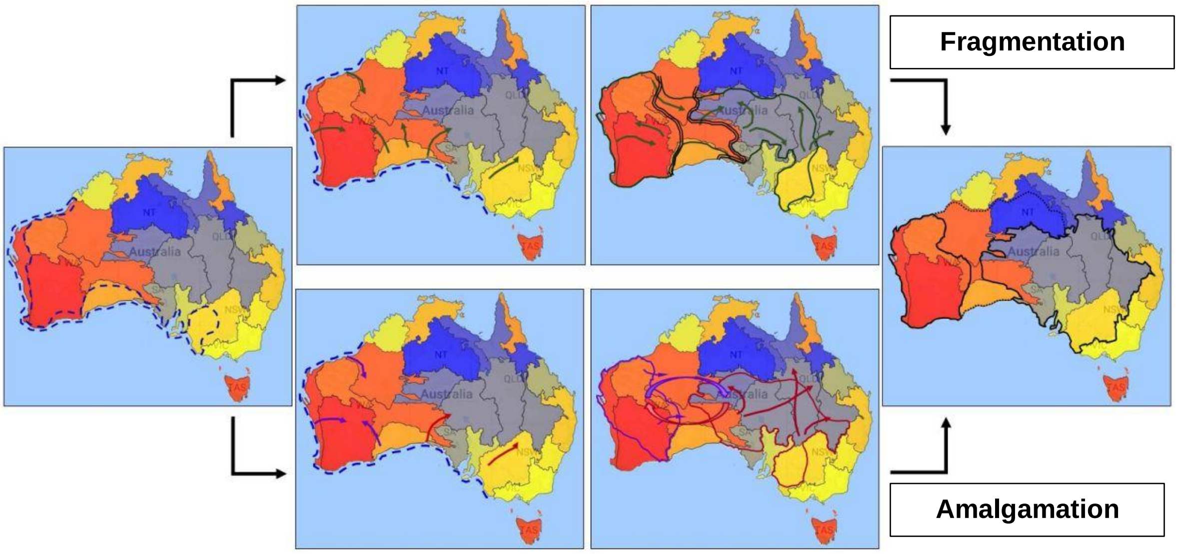


Figure 5.1: Options of development for the Yilgarn and Eyre-Murray Centres.

<u>Amalgamation scenario</u>

(1) Colonisation/Establishment stage: coastal bridgeheads form and expand.

(2) Landscape Spread/Diversification stage 1: Range extension produces separate western and eastern provincial fronts through catchments that drain to the western and southern coasts. Diversification starts with differentiation from coastal species and separation of the western and eastern expansions that form ancestral lineages in each centre. Taxa restricted to each Centre begin to emerge in developing arid habitats, especially in the Yilgarn Centre.

(3) Landscape Spread/Diversification stage 2: As the subcontinent becomes very dry, the Centres merge. Range expansion through the Great Victoria Desert, possibly an exchange of species, derives the shared taxa.

(4) Landscape Spread: Northerly range extension in both centres forms the Subcontinental Arid–Mediterranean Group.

A resolved phylogeny would help determine the degree each scenario plays in each clade. Existing clade phylogenies and distribution patterns favour the fragmentation scenario, but the phylogenies are incomplete. *Atriplex* Clade 1 shows elements of both scenarios. Emergence of the very widespread *Atriplex nummularia* lineage fits an initial common development of the centres, whereas the *A. cinerea* lineage differentiated only in the Yilgarn.

The relationships of the many species of *Atriplex* Clade 2 in the Eyre-Murray Centre, to each other and shared taxa are unclear.

Landscape speciation and aridity

Palaeodrainage decline also suggests the nature of diversification, and particularly the role of Riverine Desert in acclimatising to aridity and in population isolation.

Figure 5.2 is a geomorphic palaeodrainage model based on the Yilgarn Centre (Magee 2009) that relates land types and their chenopod diversity to drainage topography. Eyre-Murray landscapes are hydrologically similar (Magee 2009), but valleys are 2-5 times broader and clay floodplains much more extensive. Karst Plain only occurs as pedogenic calcretes in this model.

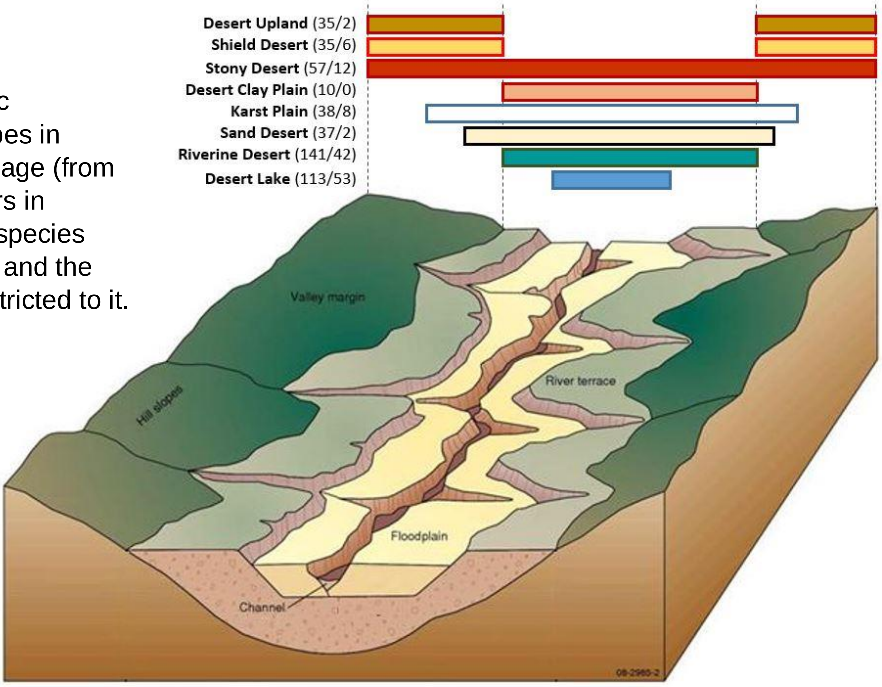


Figure 5.2: Geographic relationship of land types in relation to palaeodrainage (from Magee 2009). Numbers in brackets refer to total species recorded for land type and the number of species restricted to it.

The richest land types (Riverine Desert, Desert Lake and Stony Desert) share palaeodrainage space, their areal proportions differing over time. The older, migration conduit of Riverine Desert provides the initial pool of species that occupies Desert Lake and Stony Desert and possibly of Sand Desert in future. Rainfall decrease with intensifying aridity, subsequently reduces water availability and increases salinity. Being salt-tolerant, chenopods have competitive advantage and also adjust to aridity, but face geographic isolation of species populations where dispersal is water dependent.

Such development proceeds through the following phases:

(1) Drainage of the mesic past is high volume, frequent flow under abundant rainfall, lasting until the mid-Miocene in the Yilgarn Centre; to the Late Pliocene-Pleistocene in Eyre-Murray.

(2) Channel migration across the valley ceases as rainfall declines with the onset of aridity and elevated terraces no longer flood. Contiguous linear lakes form along drainage floors, maintained by a limited flow. Rainfall variation and shallow valley gradients cause much lateral shifting of fluctuating shorelines. Alkaline lake deposits produced under strong seasonality are exposed in drier periods. Chenopods dispersing along drainage axes establish halophytic formations on shifting shorelines and drying lake beds.

(3) With further rainfall decrease, lake size diminishes, overbank flows cease and water flow is restricted to channels. Vegetation on higher plains distant from channels, becomes more dependent on rainfall for moisture. Pedogenic carbonates form in alluvial soils. Hydrologic systems begin to disconnect. Chenopods are halophytic communities in drainage with erratic flow and dominate shrub-steppe communities away from drainage systems. Selection favours short-lived forms. Stony Desert develops on valley margins in the driest regions.

(4) At certain rainfall thresholds, cyclic salt is not flushed from the landscape and accumulates in lowland terminals. Evaporation matches then exceeds precipitation; evaporites form in channel terminals and at groundwater surface seepages, with gypsum preceding sodium salts. Alluvial soils become alkaline and saline but upland margins are salt and lime free. Chenopods diversify in disconnected saline drainage.

(5) Aridity attains maximum intensity, denuding floodplains and alluvial plains. Lunettes form marginal to salinas and playa lakes. Dust is winnowed from exposed valley surfaces and sand blown into mounds then dunes. Chenopods are largely restricted to extensive saline landscapes, continuing to diversify under strong selection for annual and biennial forms.

Four landscape influences on speciation work in combination:

<u>Requirements of new habitats</u>: Salt-tolerance is a rare adaptation (Flowers and Colmer 2015) and deserts are novel habitats. Saline landscapes are more opportune for invading salt-

tolerant taxa, than for the long resident taxa. With exaptation of drought-tolerance, taxa of Riverine Desert readily occupy drier plains. Also the novel landscapes of Stony Desert and Desert Lake, that form in or adjacent to Riverine Desert. Desert Upland, Shield Desert and Sand Desert are the main arid land types open to taxa that are not salt tolerant.

Selection for aridity: Selection under a gradually emerging arid climate would be strong in valleys as flood flows decreased. Elevated plains distant from channels are no longer flooded. Increasing reliance on diminishing, erratic rainfall, favours annual and biennial forms. The shrub-steppe, dryland taxa differentiates from halophytic, marshy types especially within the vast, alluvial plains of the Eyre-Murray Centre, the exaptation of salt-tolerance for drought-tolerance proceeds in the presence of salt, inducing xero-halophytism. Though having xerophytic traits such as C_4 photosynthesis and epidermal protection, low chenopod occupancy of Desert Upland, Shield Plain and Sand Desert, indicates plant competition as a barrier to their occupation, along with combination of mobility, lack of soil moisture for extended periods and of salts to enhance drought tolerance of dune systems.

Geographic isolation in a vast, flat landscape: Increasing disconnection of drainage channels, isolates species populations, especially plants reliant on water borne dispersal, disrupting gene flow patterns (e.g. *Tecticornia*: Shepherd *et al.* 2004). Earlier onset of aridity in the Yilgarn Centre would explain the greater richness of that clade. Such isolation would apply generally to halophytic marshy taxa, especially to those restricted to channel habitats.

Hybridisation: Hybridization between genetically distinct populations occurs in disturbed and extreme environments, in expanding and contracting species ranges (especially invasive species) and can promote adaptive divergence (Gross and Rieseberg 2005; Abbott *et al.* 2013). Rapid diversification of *Atriplex* forms in western North America is attributed to cycles of lake formation (isolation) and evaporation (mixing) in basin and range topography (Stutz 1978, 1984). In Australia, a similar isolation and mixing may arise from drainage disorganization and renewal in a vast, flat landscape, under climatic and hydrologic oscillations of emerging aridity (Fujioka and Chappell 2010).

Geographic isolation and selection for aridity work within landscape processes, somewhat peculiar to Australia. Brock *et al.* (2006) allude to such influences in desert river systems while Dunkerley (2010) describes that of rainfall. Effects of infrequent flooding and declining rainfall on the land surface emulate coastal processes of tidal and wave scour and strandline deposition, further reinforcing the influence of niche conservatism, but more importantly, suggesting a significant difference in coast and inland speciation. Microhabitat availability at the coast may be similar to that in Riverine Desert, but in the linearity of coastal habitats, competitive exclusion keeps coastal diversity low. In inland areas, the extent of Riverine Desert arising from the subdued continental topography may dilute its influence.

Desert river floodplains are a transition from mesic channels to xeric uplands where spatial variability of water influences plant presence (Brock *et al.* 2006). The main water sources are floods and rainfall. Flooding affects only the low-lying parts of the floodplain and varies markedly in frequency, duration, depth, flow velocity, nutrient and sediment load. Rainfall is rarely uniform where floodplains are extensive and it concentrates run-off on plains marginal to uplands. The net evolutionary effect is lifeform strategies for surviving both water shortage and disturbance broadly categorised as endurers, resisters, invaders and avoiders, depending on adaptive traits.

Transitions from semi-arid to arid climates change partitions in the soil-water balance significantly altering the eco-geomorphology of landscapes (Dunkerley 2010). Lower rainfall supports less vegetation, reducing plant interception and increasing surface run-off. Surface erosion consequently increases, sections of soil become bare while others accumulate litter in shallow banks, reaching heights of 50-60 mm. Preferential germination of seeds and growth of plants contributes to formation of banded vegetation common in the Australian inland (e.g. Stony Desert), particularly because of its low and relatively flat topography.

Rain event structure is significant at low rainfall levels, in the extensive, flat Australian landscape (Dunkerley 2010). Change in other variables (e.g. the number of rain days, amount delivered per rain event) alters surface processes, even if mean annual rainfall changes little. Falls of less than 6 mm of rain are very frequent and useful to annuals but not to perennials, due to ready evaporation. The morphological trend from low shrub forms to annual and biennial forms notably occurs in *Atriplex* Clade 2 and the Sclerolaenid Clade, which have their most species in Australia's driest region.

Chenopods and development of the arid biota

Occupation of novel saline habitats, virtually unavailable to long resident taxa, distinguishes chenopods from other arid plant taxa. Barlow (1981, 1994) considers chenopods exceptional, their evolution not exactly fitting modern notions of development of the arid biota, and presumes other plant taxa with a littoral connection would be similar.

Chenopod evolution only loosely fits the development phases as outlined by Byrne *et al.* (2008). It more likely is a process of continuous speciation, rather than distinct assembly and maintenance phases defined on speciation rates (though phylogeny of all clades is required to determine speciation rate). Byrne *et al.* (2008) describe a pre-Miocene biota adapting from mesic to xeric conditions, but with plant taxa largely unable to adjust to saline habitats. Chenopods arrived serially from the Late Miocene onwards, already adapted to saline habitats, and with exaptation for tolerating xeric conditions.

Certainly two stages with similar time frames can be identified but these relate to landscape development, not a slowing of speciation rate. Chenopod lineages did assemble contemporary with other arid taxa in the Late Miocene-Pliocene as Riverine Desert emerged with the onset of aridity. Speciation continued through the Pleistocene with the formation of Desert Lake and the expansion of Riverine and Stony Desert in eastern Australia, where both land types are most extensive. While disorganised drainage, salt-lakes and desert dune fields arising in the most arid periods was severe on long resident taxa, chenopod species continued to emerge, largely through the subcontinental area that provided suitable habitat and isolation effected by discontinuous salt-lakes. Drastic conditions of the Pleistocene did adversely affect chenopod evolution. Disjunct taxa show local species populations became extinct. Desert dune formation possibly induced species extinction in Riverine Desert, but did not reduce net speciation rate to zero.

Previous notions of chenopod origin are in part vindicated. Beadle (1981a, 1981b) correctly identified a Late Miocene time and saline habitats of southern Australia as instrumental in their evolution. Specht (1972, 1981b) alluded similarly to the location and time, but migration through calcareous habitats relates to relatively few taxa. Barlow (1981, 1994) also recognized the Late Miocene timeframe and the marshy connection of coast and inland, but connecting dune habitats played no part and inland migrations probably began under highly seasonal climates rather than arid ones.

The model of Burbidge (1960) is largely correct, but for two issues. A Cretaceous origin and application to the entire arid flora is inappropriate. However, progressive stages of migration through estuaries into drainage systems, habitation of inland lake shores and alluvial plains as shorelines fluctuate, occupation of deflating inland lakes and adaptation to dune fields (but with little speciation) in the final stage is essentially the most likely process.

KEY ISSUES, ALTERNATIVES AND REPRERESENTATION

Dispersal

Dispersal is key to understanding chenopod evolution because it underpins migration and speciation likely relates to differing dispersal mechanisms. Movement along coastlines, through drainage systems over watersheds and open plains employs varied dispersal mechanisms. Those of Australian chenopods are poorly understood. Much is assumed from the morphology of the fruiting perianth (Kuhn 1993).

Water and wind assisted dispersal are common and result in extensive taxon ranges (Kuhn 1993). Numerous chenopod genera are of cosmopolitan distribution (Ridley 1930; van der Pijl 1972; Osmond *et al.* 1980; Kuhn 1993; Shepherd *et al.* 2004; Kadereit *et al.* 2006). Buoyant and small seed or fruit are easily carried on floating debris. Coastal forms most readily exhibit features of water borne dispersal e.g. corky or inflated fruits. *Sclerolaena muricata* is a tumbleweed (Cunningham *et al.* 1992) similar to *Salsola* and *Suaeda* (Kuhn 1993). The perianth of *Atriplex* dryland species is a papery wing or inflated bladder (Osmond *et al.* 1980; Kuhn 1993) especially on *Atriplex vesicaria* (van der Pijl 1982). *Kochia* and *Salsola* fruit roll over the ground driven by the wind (van der Pijl 1982). The *Maireana* perianth is similar, with the abundant *M. sedifolia* (Hall *et al.* 1964; Wotton 1993) and the rare and low growing *M. cheelii* (Anon 2009) being wind-dispersed. The largest wing (to 20 mm) is on the very widespread *Maireana georgei*.

A combination of water and wind dispersal facilitates migration through drainage systems. Wind and water dispersal are the physics of propagule weight and surface area under fluid dynamics (Van der Pijl 1982:71). Most propagules adapted for wind dispersal also float and can be widely distributed by floods in heavy rushes of water (Ridley 1930:193). Under regular and voluminous river flow, upstream dispersal is slow. With declining discharge, surface wind currents push buoyant propagules upstream over the long, linear lakes in the low gradient landscapes. Westerly airflows prevailed over much of southern Australia from the early Miocene onward (Kemp 1978; Barlow 1981), assisting easterly movement from western landfalls. Widespread species of papery or inflated perianth with larger surface area that move with wind or water include *Atriplex nummularia* and *A. vesicaria*.

Wind dispersal better promotes range expansion. Vegetation of dry, saline and alkaline valleys is open and low, reducing the traps for dispersing propagules. Water-borne dispersal confines range extension to water features. Wind dispersal breaches catchment interfluves and watershed boundaries. Entry to the Lake Eyre Basin, which is thought endorheic through the Tertiary, was likely achieved in this way. The Billa Kalina Basin, between the Eucla and Lake Eyre basins, has Miocene aeolian sediments that formed under strong south westerlies (Callen and Cowley 1995).

Transport by birds, mammals and arthropods also disperses chenopods (Ridley 1930; van der Pijl 1982; Kuhn 1993). Berry-like fruit occur unusually in four subfamilies (Kuhn 1993; Sukhorukov and Zhang 2013; Sukhorukov *et al.* 2015). Small birds of woodland and shrublands disperse *Enchylaena tomentosa* (the second most widespread species), *Rhagodia* and *Einadia* (Chenopodieae I clade) within Australia (Wood 1937; Lang *et al.* 2003; Brown 2014). The younger Chenopodieae I clade is as widespread as older clades, probably in part due to dispersal capacity. *Atriplex semibaccata* (*Atriplex* Clade 2) has a semi-succulent fruit and is a species of dry woodlands. *Sclerolaena* spines may make it a trample burr, attaching to the underside of animal feet (van der Pijl 1982).

Alternatives and representation

A re-examination of littoral connections requires brief consideration of two matters. The premise of a littoral connection is coastal arrival after intercontinental oceanic transport and alternatives must involve inland landfall. Curiously, the most likely alternative is a littoral connection by different means. Also, chenopods are not the only plant taxon presumed to have such an origin, begging the question of whether patterns of chenopod migration and speciation are also observed in those taxa.

Alternatives to a littoral connection

Only atmospheric or zoological transport can achieve inland landfall following intercontinental travel. Atmospheric dispersal of seed bearing plants was long thought unlikely due to vast distance, indiscriminate landfall, exposure to upper atmosphere radiation and temperature and change in diaspore weight/surface area in humid air (Ridley 1930; van der Pijl 1982). Possibly excepting orchids, distance limits for wind dispersal are commonly of 15-30 km (up to 200 km at most) and over longer distances, animal dispersal more efficiently bears seed to suitable habitat (van der Pijl 1982).

However, more recent research largely using modelling and simulation, indicates intercontinental atmospheric plant dispersal is possible, though considered uncommon and difficult to precisely identify. One important factor is wind turbulence with uplift that aids propagules to reach upper atmosphere global wind streams, and which works more strongly during drier periods (Wright *et al.* 2010; Robledo-Arnuncio *et al.* 2014). Tang *et al.* (2018) notes importance of duration and frequency of desert wind turbulence in generation of global dust aerosols, which would likely affect propagules adapted to movement in wind.

Zoological transport may be more likely. Birds can effectively carry seed over intercontinental distance, but the only birds with potential to do so, are migratory shorebirds or nomadic waterfowl, also found in the habitats of a littoral connection. Australia is part of the East Asian Australasia Flyway (Bamford *et al.* 2007) that links Australia to eastern parts of the Eurasian centre of chenopod origin. Fifty-four shorebird species annually migrate, between breeding grounds, respite stops and refuges comprising saline or freshwater wetlands of the coast and inland. Most shorebirds eat invertebrates, and some eat plant seed, foraging on muddy shores (Marchant and Higgins 1993) of chenopod habitat. Small diaspores stuck to bird feet by mud, is a common means of external carriage (Ridley 1930; van der Pijl 1982). Of the 54 species listed in Bamford *et al.* (2008), the Australian range maps of Simpson and Day

(2010) show ten have coastal habitats only, five are mainly coastal or in the immediate hinterland and nineteen are of coastal and inland regions. Eight have very small, mainly coastal ranges. Ten are not in Simpson and Day (2010).

	Bird Taxa	**Food Items**
Waterbirds	*Oxyura australis*, *Chenonetta jubata*, *Malacorhynchus membranaceus*, *Anas gracilis*, *A. castanea*, *A. superciliosa*, *A. rhynchotis*, *Aythya australis; Rostratula australis*; *Cygnus atratus*	[General] Chenopodiaceae, *Atriplex* and *Chenopodium;* [Specific] *Atriplex semibaccata*, *Chenopodium nitrariaceum*, *Dysphania pumilio* and *Scleroblitum atriplicinum*
	Porphyrio porphyrio	*Chenopodium* spp.
	Tadorna tadornoides	*Tecticornia arbusculoides*, *T. halocnemoides* and *Sarcocornia quinqueflora*
Terrestrial	*Dromaius novaehollandiae*; *Ardeotis australis*; *Pedionormus torquatus*; *Charadrius australis*; *Vanellus mile*s	*Atriplex*, *Chenopodium*, *Rhagodia*, *Einadia*, *Dysphania*, *Maireana*, *Sclerolaena*, *Osteocarpum*, *Salsola*
	Cacatua spp.	*Maireana*
	Small parrots	*Sclerolaena*

Table 5.2: Food items of Australian birds as listed in Marchant and Higgins (1990, 1993); those for *Cacatua* spp. (*pers. obs.*) and small parrots (Anon 2008).

Once in Australia, water, wind and further avian dispersal could follow. Larger, nomadic waterfowl carry more seed through consumption and muddy adherence to larger feet. Table 5.2 lists bird species and chenopod food items. Water birds further disperse seed at local to continental scale, but more importantly also breach interfluves and watersheds. It may explain, how in the possibly recent inland expansion of *Sarcocornia*, its presence in unconnected inland drainage channels.

Two issues immediately arise. First, such ecological relationships must have existed in the Late Miocene-Pliocene, involving vector species arriving south of the northern tropical wetlands. Evolution can even disguise ancient patterns. The marsh bird *Rostratula australis* is endemic to Australia (Simpson and Day 2010) but the generic range through Africa, South Asia and South-East Asia, intersects the Eurasian centre of chenopod origin. Second, if geographic isolation contributes significantly to speciation, avian inland dispersal is less significant than that from wind and water.

<u>Chenopodiaceae representing a littoral connection</u>

Chenopod distribution through Yilgarn and Eyre-Murray Centres is compared with three other plant families in Table 5.3. Comparison is hampered by unknown arrival times of other taxa and whether they are a single immigrant clade or more.

FAMILY/ Subgroup	Shared: Yilgarn & Eyre-Murr	Restricted Yilgarn	Restricted Eyre-Murr	Eastern H/lands	Northern Tropical	Nullarbor Plain	Continent Sp. Pop'n Disjunct
CHENOPODIACEAE [302 species]							
Nº of Species	129	70	96	2	3	1	45
Species %	42.7	23.2	31.8	0.7	1	0.3	14.9
AIZOACEAE [45 species]							
Nº of Species	13	13	6	2	5	0	6
Species %	28.9	28.9	13.3	4.4	11.1	0	13.3
FRANKENIACEAE [47 species]							
Nº of Species	4	21	20	0	0	1	1
Species %	8.5	44.7	42.6	0	0	2.1	2.1
Frankenia Grp 1	4	14	10	0	0	0	1
Frankenia Grp 2	0	7	10	0	0	1	0
ZYGOPHYLLACEAE [62 species]							
Nº of Species	22	8	16	1	6	0	9
Species %	35.5	12.9	25.8	1.6	9.7	0	14.5
Tribulopis	1	0	0	1	4	0	0
Tribulus	5	4	5	1	2	0	4
Zygophyllum	16	4	11	0	0	0	5

Table 5.3: Distribution of taxa in four families presumed to have a littoral connection. Chenopod data omits *Tecticornia bibenda* which is endemic to Sandland North Province. Data for Aizoaceae, Frankeniaceae and Zygophyllaceae derives from native species listed respectively in Barnsley (1982); Prescott and Venning (1984); Barker (2013). More recent work identifies *Roepera* within Australian *Zygophyllum*.

(1) The Yilgarn and Eyre-Murray Centres have a large proportion of each family's species, being least in Aizoaceae at 71.1%, with 74.2 % in Zygophyllaceae and 95.7% in Frankeniaceae.

(2) Chenopodiaceae have 5-7 times as many species and more genera. The paucity of genera in Frankeniaceae and Zygophyllaceae suggests arrival later than chenopods and fewer immigrant clades. Five genera in Aizoaceae are also overseas, inferring at least five immigrant clades.

(3) A notable proportion of taxa from Aizoaceae and Zygophyllaceae is in the northern tropical provinces. *Tribulopis* (Zygophyllaceae) is notably tropical. *Trianthema* (Aizoaceae) has most coastal taxa on the north coast and its major inland occurrences are in the northern arid zone. Frankeniaceae is largely absent from Tropical Northern and Eastern Highlands areas.

(4) Aizoaceae, Zygophyllaceae and chenopods have proportionately the same number of Yilgarn – Eyre-Murray species population disjuncts, including the distinctively Australian

genus *Gunniopsis*. Vicariance events have had a proportionately similar impact on these three plant groups.

(5) The Centres share few species from Frankeniaceae suggesting distinct lineages in each centre.

Assuming a littoral connection applies to these plant taxa, there are patterns on a theme. Distributions concentrate in the Yilgarn and Eyre-Murray Centres. Considering the youth of Sand Desert and with each taxon affected by dune field disjunction, coast-desert dune migrations are unlikely. By default, marshy connections then largely explain coast to inland migration and early diversification similar to chenopods. For Aizoaceae and Zygophyllaceae, a littoral connection readily operates in tropical regions, but for Frankeniaceae and chenopods it does not. High proportion of shared species in Aizoaceae and Zygophyllaceae indicates multiple migrations from one centre to another, similar to chenopods. There may be similarities of process, but examination of the taxon and habitat elements and of phylogenetic relationships are needed to reveal them.

OVERALL SUMMARY

A littoral connection remains the most credible hypothesis for the origin of Australian chenopods, occurring as a serial invasion of immigrant clades over the later Neogene. Each clade exhibits the taxon, habitat and trait elements of a littoral connection. Modern coastal species either reflect the coastal ancestors or taxon cycling within the clade.

Chenopod species generally inhabit drier, inland areas of the Yilgarn and Eyre-Murray Centres that broadly define the common space of rich immigrant clades. Coastal occupation allows their presence in all Australian regions. Immigrant clades are differently distributed through Australia and of varied regional species richness, including within Centres.

The development of the centres intertwines migration and speciation but incomplete and unresolved phylogeny inhibits identifying the pattern detail. Shared species indicate significant migration from one centre to another, while the species restricted to either indicate significant diversification within them. The Great Victoria Desert is a stronger link between the two centres than is the Nullarbor Plain.

Chenopod taxa readily establish on arrival including some movement inland. Ancestral character includes capacity to occupy diverse coastal habitats, which also enables rapid and distant coastal expansion.

Marshy habitats of Riverine Desert connect coastal and inland areas with major inland migration through declining palaeodrainage systems. Early diversification within the drainage systems provided the pool of species that occupied and further diversified in Stony Desert and Desert Lake habitats. Further expansion of Riverine Desert and emergence of Desert Lake and Stony Desert in the Pleistocene, continued the trend of increased speciation contrary to speciation maintenance phase observed generally in the arid biota.

Dune fields are too young to have facilitated inland migration. They contribute little to diversification and their formation is implicated in the disjunction of species populations in most immigrant clades. The dune field disjunction gap is strongest across the Great Victoria Desert, the same landscape that separates the Yilgarn and Eyre-Murray centres.

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APPENDICES

Appendix I: Taxonomy of Australian Chenopodiaceae – nomenclature hierarchy, authorship and immigrant clade membership

	Clade/Subgroup Name *	Taxonomy (Wilson 1984)	Accepted Revision or Species Additions	Clade Name Source/Identity
Chenopodioideae				
	Scleroblitum	*Scleroblitum*		Kadereit *et al.* (2005); Kadereit *et al.* (2010)
	Dysphania	*Dysphania*; *Chenopodium* Subg. II Ambrosia	(Mosyakin 2013); Mosyakin and Clemants (2002, 2008); Shepherd and Wilson (2008, 2009)	Kadereit *et al.* (2005, 2010)
	Atriplex Clade 1	*Atriplex*: Subg. I Atriplex (part Sect. V Dialysex)	Shepherd *et al.* (2015)	Kadereit *et al.* (2005, 2010)
	Atriplex Clade 2	*Atriplex*: Subg. I Atriplex (Sect. III Spongiocarpus, Sect. IV Semibaccatae, part Sect. V Dialysex); Subg. II Theleophyton	Cranfield (2008)	Kadereit *et al.* (2005, 2010)
	Chenopodieae I	*Einadia*; *Rhagodia*; *Chenopodium*: Subg. I Chenopodium (Sect. I Chenopodium, Sect. III Leprophyllum, Sect. IV Desertorum, Sect. V Auricoma, Sect. VI Rhagodioides)		Kadereit *et al.* (2005, 2010)
	Atriplex australasica	*Atriplex*: Subg. I Atriplex (Sect. II Teutliopsis)		Kadereit *et al.* (2005, 2010)
Camphorosmoideae				
	Sclerolaenid [MaireanAff Subgroup]	*Maireana*, *Roycea*, *Eremophea*, *Dissocarpus*, *Eriochiton*, *Didymanthus*, *Enchylaena*, *Malacocera*; *Neobassia astrocarpa*		Cabrera *et al.* (2009) Kadereit and Freitag (2011) From Sclerolaenae – former name of Australian taxa
	Sclerolaenid [SclerolaenAff Subgroup]	*Sclerolaena*, *Osteocarpum*, *Threlkeldia*; *Neobassia proceriflora*; Sclerochlamys#, Stelligera#	[See also Jacobs (1988)]	Cabrera et al. (2009) Kadereit and Freitag (2011)
Salicornioideae				
	Tecticornia	Tegicornia#, Pachycornia#, Sclerostegia#, Halosarcia#, *Tecticornia*	Shepherd and Wilson (2007); Shepherd and Van Leeuwen (2007); Shepherd (2008)	Shepherd *et al.* (2004); Kadereit *et al.* (2006) – *Halosarcia* Clade
	Sarcocornia	*Sarcocornia*		Steffen *et al.* (2015)
Suaedoideae				
	Suaeda	*Suaeda*		Schutze *et al.* (2003) – sect. *Brezia* Clade
Salsoloideae				
	Salsola	*Salsola*	Borger *et al.* (2008); Chinnock (2010)	Akhani *et al.* (2007) – *Kali* Clade

* Except for Sclerolaenid Clade, each name could be prefixed “Australian” to specificially identify the indigenous element of a global or subglobal clade, with formal and informal use in the sources. # Later generic revision. Proposed revisions for Scleroblitum [*Blitum*] and Chenopodieae I [*Chenopodium*] are yet to be fully accepted.

Based on (Wilson 1984) and recognized in the Australian Plant Name Index of the Australian Plant Census and by Council of Heads of Australasian Herbaria at August 2014.

Australian *Atriplex* Clades 1, 2 & *A. australasica* Clade

Plant Species (Author)	CHAH-APC	Plant Species	Immigrant Clade
Atriplex acutibractea R.H.Anderson	sensu CHAH (2005)	Atriplex acutibractea	Australian Atriplex Clade 2
Atriplex acutibractea R.H.Anderson subsp. acutibractea	sensu CHAH (2005)	Atriplex acutibractea subsp. acutibractea	Australian Atriplex Clade 2
Atriplex acutibractea subsp. karoniensis Aellen	sensu CHAH (2005)	Atriplex acutibractea subsp. karoniensis	Australian Atriplex Clade 2
Atriplex acutiloba R.H.Anderson	sensu CHAH (2005)	Atriplex acutiloba	Australian Atriplex Clade 2
Atriplex amnicola Paul G.Wilson	sensu CHAH (2005)	Atriplex amnicola	Australian Atriplex Clade 1
Atriplex angulata Benth.	sensu CHAH (2005)	Atriplex angulata	Australian Atriplex Clade 2
Atriplex australasica Moq.	sensu Wilson, P.G. (1984)	Atriplex australasica	Atriplex australasica Clade
Atriplex billardierei (Moq.) Hook.f.	sensu CHAH (2005)	Atriplex billardierei	Australian Atriplex Clade 2
Atriplex bunburyana F.Muell.	sensu CHAH (2005)	Atriplex bunburyana	Australian Atriplex Clade 2
Atriplex cephalantha Aellen	sensu CHAH (2005)	Atriplex cephalantha	Australian Atriplex Clade 1
Atriplex cinerea Poir.	sensu CHAH (2005)	Atriplex cinerea	Australian Atriplex Clade 1
Atriplex codonocarpa Paul G.Wilson	sensu CHAH (2005)	Atriplex codonocarpa	Australian Atriplex Clade 2
Atriplex cordifolia J.M.Black	sensu Wilson, P.G. (1984)	Atriplex cordifolia	Australian Atriplex Clade 2
Atriplex cornigera Domin	sensu Wilson, P.G. (1984)	Atriplex cornigera	Australian Atriplex Clade 2
Atriplex crassipes J.M.Black	sensu Wilson, P.G. (1984)	Atriplex crassipes	Australian Atriplex Clade 2
Atriplex crassipes var. appendiculata Aellen	sensu Wilson, P.G. (1984)	Atriplex crassipes var. appendiculata	Australian Atriplex Clade 2
Atriplex crassipes J.M.Black var. crassipes	sensu CHAH (2005)	Atriplex crassipes var. crassipes	Australian Atriplex Clade 2
Atriplex cryptocarpa Aellen	sensu Wilson, P.G. (1984)	Atriplex cryptocarpa	Australian Atriplex Clade 2
Atriplex eardleyae Aellen	sensu CHAH (2005)	Atriplex eardleyae	Australian Atriplex Clade 2
Atriplex eichleri Aellen	sensu CHAH (2005)	Atriplex eichleri	Australian Atriplex Clade 2
Atriplex elachophylla F.Muell.	sensu CHAH (2005)	Atriplex elachophylla	Australian Atriplex Clade 2
Atriplex eremitis Cranfield	sensu CHAH (2008)	Atriplex eremitis	Australian Atriplex Clade 2
Atriplex exilifolia F.Muell.	sensu CHAH (2005)	Atriplex exilifolia	Australian Atriplex Clade 2
Atriplex fissivalvis F.Muell.	sensu CHAH (2005)	Atriplex fissivalvis	Australian Atriplex Clade 2
Atriplex flabelliformis Paul G.Wilson	sensu Wilson, P.G. (1984)	Atriplex flabelliformis	Australian Atriplex Clade 2
Atriplex holocarpa F.Muell.	sensu CHAH (2005)	Atriplex holocarpa	Australian Atriplex Clade 2

Plant Species (Author)	CHAH-APC	Plant Species	Immigrant Clade
Atriplex humifusa Paul G.Wilson	sensu Wilson, P.G. (1984)	Atriplex humifusa	Australian Atriplex Clade 2
Atriplex humilis F.Muell.	sensu Wilson, P.G. (1984)	Atriplex humilis	Australian Atriplex Clade 2
Atriplex hymenotheca Moq.	sensu CHAH (2005)	Atriplex hymenotheca	Australian Atriplex Clade 2
Atriplex hypoleuca Nees	sensu CHAH (2005)	Atriplex hypoleuca	Australian Atriplex Clade 2
Atriplex incrassata F.Muell.	sensu CHAH (2005)	Atriplex incrassata	Australian Atriplex Clade 1
Atriplex infrequens Paul G.Wilson	sensu CHAH (2005)	Atriplex infrequens	Australian Atriplex Clade 2
Atriplex intermedia R.H.Anderson	sensu CHAH (2005)	Atriplex intermedia	Australian Atriplex Clade 2
Atriplex isatidea Moq.	sensu CHAH (2005)	Atriplex isatidea	Australian Atriplex Clade 1
Atriplex kochiana Maiden	sensu Wilson, P.G. (1984)	Atriplex kochiana	Australian Atriplex Clade 2
Atriplex leptocarpa F.Muell.	sensu CHAH (2005)	Atriplex leptocarpa	Australian Atriplex Clade 2
Atriplex limbata Benth.	sensu CHAH (2005)	Atriplex limbata	Australian Atriplex Clade 2
Atriplex lindleyi Moq.	sensu CHAH (2005)	Atriplex lindleyi	Australian Atriplex Clade 2
Atriplex lindleyi subsp. conduplicata (F.Muell.) Paul G.Wilson	sensu CHAH (2005)	Atriplex lindleyi subsp. conduplicata	Australian Atriplex Clade 2
Atriplex lindleyi subsp. inflata (F.Muell.) Paul G.Wilson	sensu CHAH (2005)	Atriplex lindleyi subsp. inflata	Australian Atriplex Clade 2
Atriplex lindleyi Moq. subsp. lindleyi	sensu Wilson, P.G. (1984)	Atriplex lindleyi subsp. lindleyi	Australian Atriplex Clade 2
Atriplex lindleyi subsp. quadripartita Paul G.Wilson	sensu Wilson, P.G. (1984)	Atriplex lindleyi subsp. quadripartita	Australian Atriplex Clade 2
Atriplex lobativalvis F.Muell.	sensu CHAH (2005)	Atriplex lobativalvis	Australian Atriplex Clade 2
Atriplex macropterocarpa (Aellen) H.Eichler	sensu Wilson, P.G. (1984)	Atriplex macropterocarpa	Australian Atriplex Clade 2
Atriplex morrisii R.H.Anderson	sensu Wilson, P.G. (1984)	Atriplex morrisii	Australian Atriplex Clade 2
Atriplex muelleri Benth.	sensu CHAH (2005)	Atriplex muelleri	Australian Atriplex Clade 2
Atriplex nana Parr-Sm.	sensu Wilson, P.G. (1984)	Atriplex nana	Australian Atriplex Clade 2
Atriplex nessorhina S.W.L.Jacobs	sensu Wilson, P.G. (1984)	Atriplex nessorhina	Australian Atriplex Clade 2
Atriplex nummularia Lindl.	sensu Wilson, P.G. (1984)	Atriplex nummularia	Australian Atriplex Clade 1
Atriplex nummularia Lindl. subsp. nummularia	sensu CHAH (2005)	Atriplex nummularia subsp. nummularia	Australian Atriplex Clade 2
Atriplex nummularia subsp. omissa Aellen	sensu Wilson, P.G. (1984)	Atriplex nummularia subsp. omissa	Australian Atriplex Clade 2
Atriplex nummularia subsp. spathulata Aellen	sensu Wilson, P.G. (1984)	Atriplex nummularia subsp. spathulata	Australian Atriplex Clade 2
Atriplex obconica Paul G.Wilson	sensu Wilson, P.G. (1984)	Atriplex obconica	Australian Atriplex Clade 2

Plant Species (Author)	**CHAH-APC**	**Plant Species**	**Immigrant Clade**
Atriplex paludosa R.Br.	sensu Wilson, P.G. (1984)	Atriplex paludosa	Australian Atriplex Clade 2
Atriplex paludosa subsp. baudinii (Moq.) Aellen	sensu CHAH (2005)	Atriplex paludosa subsp. baudinii	Australian Atriplex Clade 2
Atriplex paludosa subsp. cordata (Benth.) Aellen	sensu Wilson, P.G. (1984)	Atriplex paludosa subsp. cordata	Australian Atriplex Clade 2
Atriplex paludosa subsp. moquiniana (Webb ex Moq.) Parr-Sm.	sensu Wilson, P.G. (1984)	Atriplex paludosa subsp. moquiniana	Australian Atriplex Clade 2
Atriplex paludosa R.Br. subsp. paludosa	sensu CHAH (2005)	Atriplex paludosa subsp. paludosa	Australian Atriplex Clade 2
Atriplex papillata J.H.Willis	sensu Wilson, P.G. (1984)	Atriplex papillata	Australian Atriplex Clade 2
Atriplex pseudocampanulata Aellen	sensu CHAH (2005)	Atriplex pseudocampanulata	Australian Atriplex Clade 2
Atriplex pumilio R.Br.	sensu CHAH (2005)	Atriplex pumilio	Australian Atriplex Clade 2
Atriplex quadrivalvata Diels	sensu CHAH (2005)	Atriplex quadrivalvata	Australian Atriplex Clade 2
Atriplex quadrivalvata Diels var. quadrivalvata	sensu Wilson, P.G. (1984)	Atriplex quadrivalvata var. quadrivalvata	Australian Atriplex Clade 2
Atriplex quadrivalvata var. sessilifolia (Ising) Ising	sensu Wilson, P.G. (1984)	Atriplex quadrivalvata var. sessilifolia	Australian Atriplex Clade 2
Atriplex quinii F.Muell.	sensu Wilson, P.G. (1984)	Atriplex quinii	Australian Atriplex Clade 2
Atriplex rhagodioides F.Muell.	sensu Wilson, P.G. (1984)	Atriplex rhagodioides	Australian Atriplex Clade 1
Atriplex semibaccata R.Br.	sensu CHAH (2005)	Atriplex semibaccata	Australian Atriplex Clade 2
Atriplex semilunaris Aellen	sensu Wilson, P.G. (1984)	Atriplex semilunaris	Australian Atriplex Clade 2
Atriplex spinibractea R.H.Anderson	sensu CHAH (2005)	Atriplex spinibractea	Australian Atriplex Clade 2
Atriplex spinulosa Paul G.Wilson	sensu Wilson, P.G. (1984)	Atriplex spinulosa	Australian Atriplex Clade 2
Atriplex spongiosa F.Muell.	sensu CHAH (2005)	Atriplex spongiosa	Australian Atriplex Clade 2
Atriplex stipitata Benth.	sensu Wilson, P.G. (1984)	Atriplex stipitata	Australian Atriplex Clade 2
Atriplex sturtii S.W.L.Jacobs	sensu CHAH (2005)	Atriplex sturtii	Australian Atriplex Clade 2
Atriplex suberecta I.Verd.	sensu CHAH (2005)	Atriplex suberecta	Australian Atriplex Clade 2
Atriplex turbinata (R.H.Anderson) Aellen	sensu CHAH (2005)	Atriplex turbinata	Australian Atriplex Clade 2
Atriplex velutinella F.Muell.	sensu CHAH (2005)	Atriplex velutinella	Australian Atriplex Clade 2
Atriplex vesicaria Heward ex Benth. #	sensu CHAH (2006)	Atriplex vesicaria #	Australian Atriplex Clade 2
Atriplex yeelirrie K.A.Sheph.&K.R.Thiele	Shepherd et al (2015) *	Atriplex yeelirrie	Australian Atriplex Clade 1

* Shepherd KA, Thiele KR, Sampson J, Coates D & M. Byrne (2015) *Australian Systematic Botany* **28** 240-243

Subspecific notations of *Atriplex vesicaria* are not used in this study.

(Australian) Chenopodieae I Clade

Plant Species (Author)	CHAH-APC	Plant Species
Chenopodium auricomiforme Murr & Thell.	sensu Wilson, P.G. (1984)	Chenopodium auricomiforme
Chenopodium auricomum Lindl.	sensu CHAH (2005)	Chenopodium auricomum
Chenopodium curvispicatum Paul G.Wilson	sensu CHAH (2005)	Chenopodium curvispicatum
Chenopodium desertorum (J.M.Black) J.M.Black	sensu Wilson, P.G. (1984	Chenopodium desertorum
Chenopodium desertorum subsp. anidiophyllum (Aellen) Paul G.Wilson	sensu Wilson, P.G. (1984)	Chenopodium desertorum subsp. anidiophyllum
Chenopodium desertorum (J.M.Black) J.M.Black subsp. desertorum	sensu Wilson, P.G. (1984	Chenopodium desertorum subsp. desertorum
Chenopodium desertorum subsp. microphyllum Paul G.Wilson	sensu CHAH (2005)	Chenopodium desertorum subsp. microphyllum
Chenopodium desertorum subsp. rectum Paul G.Wilson	sensu Wilson, P.G. (1984)	Chenopodium desertorum subsp. rectum
Chenopodium desertorum subsp. virosum Paul G.Wilson	sensu Wilson, P.G. (1984)	Chenopodium desertorum subsp. virosum
Chenopodium erosum R.Br.	sensu CHAH (2014)	Chenopodium erosum
Chenopodium gaudichaudianum (Moq.) Paul G.Wilson	sensu Wilson, P.G. (1984	Chenopodium gaudichaudianum
Chenopodium glaucum L.	sensu CHAH (2014)	Chenopodium glaucum
Chenopodium hubbardii Aellen	sensu Wilson, P.G. (1984)	Chenopodium hubbardii
Chenopodium nitrariaceum (F.Muell.) F.Muell. ex Benth.	sensu CHAH (2014)	Chenopodium nitrariaceum
Einadia hastata (R.Br.) A.J.Scott	sensu CHAH (2014)	Einadia hastata
Einadia nutans (R.Br.) A.J.Scott	sensu CHAH (2014)	Einadia nutans
Einadia nutans subsp. eremaea Paul G.Wilson	sensu CHAH (2014)	Einadia nutans subsp. eremaea
Einadia nutans subsp. linifolia (R.Br.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Einadia nutans subsp. linifolia
Einadia nutans (R.Br.) A.J.Scott subsp. nutans	sensu CHAH (2005)	Einadia nutans subsp. nutans
Einadia nutans subsp. oxycarpa (Gauba) Paul G.Wilson	sensu CHAH (2014)	Einadia nutans subsp. oxycarpa
Einadia polygonoides (Murr) Paul G.Wilson	sensu Wilson, P.G. (1984)	Einadia polygonoides
Einadia trigonos (Schult.) Paul G.Wilson	sensu CHAH (2005)	Einadia trigonos
Einadia trigonos subsp. leiocarpa Paul G.Wilson	sensu CHAH (2014)	Einadia trigonos subsp. leiocarpa
Einadia trigonos subsp. stellulata (Benth.) Paul G.Wilson	sensu CHAH (2014)	Einadia trigonos subsp. stellulata
Einadia trigonos (Schult.) Paul G.Wilson subsp. trigonos	sensu CHAH (2014)	Einadia trigonos subsp. trigonos
Rhagodia acicularis Paul G.Wilson	sensu CHAH (2014)	Rhagodia acicularis

Plant Species (Author)	CHAH-APC	Plant Species
Rhagodia baccata (Labill.) Moq.	sensu Wilson, P.G. (1984)	Rhagodia baccata
Rhagodia baccata (Labill.) Moq. subsp. baccata	sensu CHAH (2014)	Rhagodia baccata subsp. baccata
Rhagodia baccata subsp. dioica (Nees) Paul G.Wilson	sensu CHAH (2014)	Rhagodia baccata subsp. dioica
Rhagodia candolleana Moq.	sensu CHAH (2014)	Rhagodia candolleana
Rhagodia candolleana subsp. argentea Paul G.Wilson	sensu CHAH (2014)	Rhagodia candolleana subsp. argentea
Rhagodia candolleana Moq. subsp. candolleana	sensu CHAH (2014)	Rhagodia candolleana subsp. candolleana
Rhagodia crassifolia R.Br.	sensu CHAH (2014)	Rhagodia crassifolia
Rhagodia drummondii Moq.	sensu CHAH (2014)	Rhagodia drummondii
Rhagodia eremaea Paul G.Wilson	sensu CHAH (2014)	Rhagodia eremaea
Rhagodia latifolia (Benth.) Paul G.Wilson	sensu CHAH (2014)	Rhagodia latifolia
Rhagodia latifolia (Benth.) Paul G.Wilson subsp. latifolia	sensu CHAH (2014)	Rhagodia latifolia subsp. latifolia
Rhagodia latifolia subsp. recta Paul G.Wilson	sensu CHAH (2014)	Rhagodia latifolia subsp. recta
Rhagodia parabolica R.Br.	sensu CHAH (2014)	Rhagodia parabolica
Rhagodia preissii Moq.	sensu Wilson, P.G. (1984)	Rhagodia preissii
Rhagodia preissii subsp. obovata (Moq.) Paul G.Wilson	sensu CHAH (2014)	Rhagodia preissii subsp. obovata
Rhagodia preissii Moq. subsp. preissii	sensu CHAH (2014)	Rhagodia preissii subsp. preissii
Rhagodia spinescens R.Br.	sensu CHAH (2014)	Rhagodia spinescens
Rhagodia ulicina (Gand.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Rhagodia ulicina

Scleroblitum Clade

Plant Species (Author)	CHAH-APC	Plant Species
Chenopodium atriplicinum (F.Muell.) F.Muell.	sensu CHAH (2014)	Scleroblitum atriplicinum

Dysphania Clade

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species Name
Dysphania carinata (R.Br.) Mosyakin & Clemants	sensu CHAH (2008)	Dysphania carinata
Dysphania cristata (F.Muell.) Mosyakin & Clemants	sensu CHAH (2008)	Dysphania cristata
Dysphania glandulosa Paul G.Wilson	sensu Wilson, P.G. (1984)	Dysphania glandulosa
Dysphania glomulifera (Nees) Paul G.Wilson	sensu CHAH (2005)	Dysphania glomulifera
Dysphania glomulifera subsp. eremaea Paul G.Wilson	sensu CHAH (2005)	Dysphania glomulifera subsp. eremaea
Dysphania glomulifera (Nees) Paul G.Wilson subsp. glomulifera	sensu CHAH (2005)	Dysphania glomulifera subsp. glomulifera
Dysphania kalpari Paul G.Wilson	sensu Wilson, P.G. (1984)	Dysphania kalpari
Dysphania littoralis R.Br.	sensu Wilson, P.G. (1984	Dysphania littoralis
Dysphania melanocarpa (J.M.Black) Mosyakin & Clemants	sensu CHAH (2008)	Dysphania melanocarpa
Dysphania plantaginella F.Muell.	sensu Wilson, P.G. (1984)	Dysphania plantaginella
Dysphania platycarpa Paul G.Wilson	sensu Wilson, P.G. (1984)	Dysphania platycarpa
Dysphania pumilio (R.Br.) Mosyakin & Clemants	sensu CHAH (2008)	Dysphania pumilio
Dysphania rhadinostachya (F.Muell.) A.J.Scott	sensu Wilson, P.G. (1984)	Dysphania rhadinostachya
Dysphania rhadinostachya subsp. inflata (Aellen) Paul G.Wilson	sensu Wilson, P.G. (1984)	Dysphania rhadinostachya subsp. inflata
Dysphania rhadinostachya (F.Muell.) A.J.Scott subsp. rhadinostachya	sensu Wilson, P.G. (1984)	Dysphania rhadinostachya subsp. rhadinostachya
Dysphania saxatilis (Paul G. Wilson) Mosyakin & Clemants	sensu CHAH (2008)	Dysphania saxatilis
Dysphania simulans F.Muell. & Tate	sensu Wilson, P.G. (1984)	Dysphania simulans
Dysphania sphaerosperma Paul G.Wilson	sensu Wilson, P.G. (1984)	Dysphania sphaerosperma
Dysphania truncata (Paul G. Wilson) Mosyakin & Clemants	sensu CHAH (2008)	Dysphania truncata
Dysphania valida Paul G.Wilson	sensu Wilson, P.G. (1984)	Dysphania valida

Salsola Clade

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species
Salsola australis R.Br.	sensu CHAH (2011)	Salsola australis
Salsola tragus L	sensu CHAH (2005)	Salsola australis

Sclerolaenid Clade

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species
Didymanthus roei Endl.	sensu Wilson, P.G. (1984)	Didymanthus roei
Dissocarpus biflorus (R.Br.) F.Muell.	sensu CHAH (2005)	Dissocarpus biflorus
Dissocarpus biflorus (R.Br.) F.Muell. var. biflorus	sensu CHAH (2005)	Dissocarpus biflorus var. biflorus
Dissocarpus biflorus var. cephalocarpus (F.Muell.) A.J.Scott	sensu Wilson, P.G. (1984)	Dissocarpus biflorus var. cephalocarpus
Dissocarpus biflorus var. villosus (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Dissocarpus biflorus var. villosus
Dissocarpus fontinalis Paul G.Wilson	sensu Wilson, P.G. (1984)	Dissocarpus fontinalis
Dissocarpus latifolius (J.M.Black) Paul G.Wilson	sensu Wilson, P.G. (1984)	Dissocarpus latifolius
Dissocarpus paradoxus (R.Br.) Ulbr.	sensu CHAH (2005)	Dissocarpus paradoxus
Enchylaena tomentosa R.Br.	sensu Wilson, P.G. (1984)	Enchylaena tomentosa
Enchylaena tomentosa var. glabra Benth.	sensu Wilson, P.G. (1984)	Enchylaena tomentosa var. glabra
Enchylaena tomentosa R.Br. var. tomentosa	sensu CHAH (2005)	Enchylaena tomentosa var. tomentosa
Eremophea aggregata Paul G.Wilson	sensu Wilson, P.G. (1984)	Eremophea aggregata
Eremophea spinosa (Ewart & O.B.Davies) Paul G.Wilson	sensu Wilson, P.G. (1984)	Eremophea spinosa
Eriochiton sclerolaenoides (F.Muell.) A.J.Scott	sensu Wilson, P.G. (1984)	Eriochiton sclerolaenoides
Maireana amoena (Diels) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana amoena
Maireana aphylla (R.Br.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana aphylla
Maireana appressa (Benth.) Paul G.Wilson	sensu CHAH (2005)	Maireana appressa
Maireana astrotricha (L.A.S.Johnson) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana astrotricha
Maireana atkinsiana (W.Fitzg.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana atkinsiana
Maireana brevifolia (R.Br.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana brevifolia
Maireana campanulata Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana campanulata
Maireana cannonii (J.M.Black) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana cannonii
Maireana carnosa (Moq.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana carnosa
Maireana cheelii (R.H.Anderson) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana cheelii
Maireana ciliata (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana ciliata
Maireana convexa Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana convexa

Plant Species Name (CHAH-APC)	**CHAH-APC**	**Plant Species**
Maireana coronata (J.M.Black) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana coronata
Maireana decalvans (Gand.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana decalvans
Maireana dichoptera (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana dichoptera
Maireana diffusa Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana diffusa
Maireana enchylaenoides (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana enchylaenoides
Maireana eriantha (F.Muell.) Paul G.Wilson	sensu CHAH (2005)	Maireana eriantha
Maireana erioclada (Benth.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana erioclada
Maireana eriosphaera Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana eriosphaera
Maireana excavata (J.M.Black) Paul G.Wilson	sensu CHAH (2005)	Maireana excavata
Maireana georgei (Diels) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana georgei
Maireana glomerifolia (F.Muell. & Tate) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana glomerifolia
Maireana humillima (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana humillima
Maireana integra (Paul G.Wilson) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana integra
Maireana lanosa (Lindl.) Paul G.Wilson	sensu CHAH (2005)	Maireana lanosa
Maireana lobiflora (Benth.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana lobiflora
Maireana luehmannii (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana luehmannii
Maireana marginata (Benth.) Paul G.Wilson	sensu CHAH (2005)	Maireana marginata
Maireana melanocarpa Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana melanocarpa
Maireana melanocoma (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana melanocoma
Maireana microcarpa (Benth.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana microcarpa
Maireana microphylla (Moq.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana microphylla
Maireana murrayana (Ewart & B.Rees) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana murrayana
Maireana oppositifolia (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana oppositifolia
Maireana ovata (Ising) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana ovata
Maireana pentagona (R.H.Anderson) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana pentagona
Maireana pentatropis (Tate) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana pentatropis
Maireana planifolia (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana planifolia

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species
Maireana platycarpa Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana platycarpa
Maireana polypterygia (Diels) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana polypterygia
Maireana prosthecochaeta (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana prosthecochaeta
Maireana pyramidata (Benth.) Paul G.Wilson	sensu CHAH (2005)	Maireana pyramidata
Maireana radiata (Paul G.Wilson) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana radiata
Maireana rohrlachii (Paul G.Wilson) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana rohrlachii
Maireana schistocarpa Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana schistocarpa
Maireana scleroptera (J.M.Black) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana scleroptera
Maireana sedifolia (F.Muell.) Paul G.Wilson	sensu CHAH (2005)	Maireana sedifolia
Maireana spongiocarpa (F.Muell.) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana spongiocarpa
Maireana stipitata Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana stipitata
Maireana suaedifolia (Paul G.Wilson) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana suaedifolia
Maireana thesioides (C.A.Gardner) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana thesioides
Maireana tomentosa Moq.	sensu Wilson, P.G. (1984)	Maireana tomentosa
Maireana tomentosa Moq. subsp. tomentosa	sensu CHAH (2005)	Maireana tomentosa subsp. tomentosa
Maireana tomentosa subsp. urceolata Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana tomentosa subsp. urceolata
Maireana trichoptera (J.M.Black) Paul G.Wilson	sensu Wilson, P.G. (1984)	Maireana trichoptera
Maireana triptera (Benth.) Paul G.Wilson	sensu CHAH (2005)	Maireana triptera
Maireana turbinata Paul G.Wilson	sensu CHAH (2005)	Maireana turbinata
Maireana villosa (Lindl.) Paul G.Wilson	sensu CHAH (2005)	Maireana villosa
Malacocera albolanata (Ising) Chinnock	sensu Wilson, P.G. (1984)	Malacocera albolanata
Malacocera biflora Ising	sensu Wilson, P.G. (1984)	Malacocera biflora
Malacocera gracilis Chinnock	sensu Wilson, P.G. (1984)	Malacocera gracilis
Malacocera tricornis (Benth.) R.H.Anderson	sensu Wilson, P.G. (1984)	Malacocera tricornis
Neobassia astrocarpa (F.Muell.) A.J.Scott	sensu CHAH (2005)	Neobassia astrocarpa
Neobassia proceriflora (F.Muell.) A.J.Scott	sensu Wilson, P.G. (1984)	Neobassia proceriflora
Osteocarpum acropterum (F.Muell. & Tate) Volkens	sensu Wilson, P.G. (1984)	Osteocarpum acropterum

Plant Species Name (CHAH-APC)	**CHAH-APC**	**Plant Species**
Osteocarpum acropterum (F.Muell. & Tate) Volkens var. acropterum	sensu Wilson, P.G. (1984)	Osteocarpum acropterum var. acropterum
Osteocarpum acropterum var. deminutum (J.M.Black) Paul G.Wilson	sensu Wilson, P.G. (1984)	Osteocarpum acropterum var. deminutum
Osteocarpum dipterocarpum (F.Muell.) Volkens	sensu Wilson, P.G. (1984)	Osteocarpum dipterocarpum
Osteocarpum pentapterum (F.Muell. & Tate) Volkens	sensu Wilson, P.G. (1984)	Osteocarpum pentapterum
Osteocarpum salsuginosum F.Muell.	sensu Wilson, P.G. (1984)	Osteocarpum salsuginosum
Osteocarpum X scleropterum (F.Muell.) Volkens	sensu Wilson, P.G. (1984)	Osteocarpum scleropterum
Roycea divaricata Paul G.Wilson	sensu Wilson, P.G. (1984)	Roycea divaricata
Roycea pycnophylloides C.A.Gardner	sensu Wilson, P.G. (1984)	Roycea pycnophylloides
Roycea spinescens C.A.Gardner	sensu Wilson, P.G. (1984)	Roycea spinescens
Sclerolaena alata Paul G.Wilson	sensu Wilson, P.G. (1984)	Sclerolaena alata
Sclerolaena anisacanthoides (F.Muell.) Domin	sensu CHAH (2005)	Sclerolaena anisacanthoides
Sclerolaena articulata (J.M.Black) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena articulata
Sclerolaena beaugleholei (Ising) A.J.Scott	sensu CHAH (2005)	Sclerolaena beaugleholei
Sclerolaena bicornis Lindl.	sensu Wilson, P.G. (1984)	Sclerolaena bicornis
Sclerolaena bicornis Lindl. var. bicornis	sensu CHAH (2005)	Sclerolaena bicornis var. bicornis
Sclerolaena bicornis var. horrida Domin	sensu Wilson, P.G. (1984)	Sclerolaena bicornis var. horrida
Sclerolaena bicuspis (F.Muell.) Domin	sensu Wilson, P.G. (1984)	Sclerolaena bicuspis
Sclerolaena birchii (F.Muell.) Domin	sensu CHAH (2005)	Sclerolaena birchii
Sclerolaena blackiana (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena blackiana
Sclerolaena blakei (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena blakei
Sclerolaena brachyptera (F.Muell.) S.W.L.Jacobs	sensu CHAH (2005)	Sclerolaena brachyptera
Sclerolaena brevifolia (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena brevifolia
Sclerolaena burbidgeae (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena burbidgeae
Sclerolaena calcarata (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena calcarata
Sclerolaena clelandii (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena clelandii
Sclerolaena constricta (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena constricta
Sclerolaena convexula (R.H.Anderson) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena convexula

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species
Sclerolaena cornishiana (F.Muell.) A.J.Scott	sensu CHAH (2005)	Sclerolaena cornishiana
Sclerolaena costata (R.H.Anderson) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena costata
Sclerolaena crenata (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena crenata
Sclerolaena cuneata Paul G.Wilson	sensu Wilson, P.G. (1984)	Sclerolaena cuneata
Sclerolaena decurrens (J.M.Black) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena decurrens
Sclerolaena densiflora (W.Fitzg.) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena densiflora
Sclerolaena deserticola Paul G.Wilson	sensu CHAH (2005)	Sclerolaena deserticola
Sclerolaena diacantha (Nees) Benth.	sensu CHAH (2005)	Sclerolaena diacantha
Sclerolaena divaricata (R.Br.) Sm.	sensu CHAH (2005)	Sclerolaena divaricata
Sclerolaena drummondii (Benth.) Domin	sensu CHAH (2005)	Sclerolaena drummondii
Sclerolaena eriacantha (F.Muell.) Ulbr.	sensu Wilson, P.G. (1984)	Sclerolaena eriacantha
Sclerolaena eurotioides (F.Muell.) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena eurotioides
Sclerolaena everistiana (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena everistiana
Sclerolaena fimbriolata (F.Muell.) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena fimbriolata
Sclerolaena fontinalis Paul G.Wilson	sensu CHAH (2005)	Sclerolaena fontinalis
Sclerolaena forrestiana (F.Muell.) Domin	sensu CHAH (2005)	Sclerolaena forrestiana
Sclerolaena fusiformis Paul G.Wilson	sensu Wilson, P.G. (1984)	Sclerolaena fusiformis
Sclerolaena gardneri (Ising) A.J.Scott	sensu CHAH (2005)	Sclerolaena gardneri
Sclerolaena glabra (F.Muell.) Domin	sensu Wilson, P.G. (1984)	Sclerolaena glabra
Sclerolaena holtiana (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena holtiana
Sclerolaena hostilis (Diels) Domin	sensu Wilson, P.G. (1984)	Sclerolaena hostilis
Sclerolaena intricata (R.H.Anderson) A.J.Scott	sensu CHAH (2005)	Sclerolaena intricata
Sclerolaena johnsonii (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena johnsonii
Sclerolaena lanicuspis (F.Muell.) F.Muell. ex Benth.	sensu Wilson, P.G. (1984)	Sclerolaena lanicuspis
Sclerolaena limbata (J.M.Black) Ulbr.	sensu Wilson, P.G. (1984)	Sclerolaena limbata
Sclerolaena longicuspis (F.Muell.) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena longicuspis
Sclerolaena medicaginoides Paul G.Wilson	sensu Wilson, P.G. (1984)	Sclerolaena medicaginoides

Plant Species Name (CHAH-APC)	**CHAH-APC**	**Plant Species**
Sclerolaena microcarpa (R.H.Anderson) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena microcarpa
Sclerolaena minuta (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena minuta
Sclerolaena muelleri (Benth.) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena muelleri
Sclerolaena muricata (Moq.) Domin	sensu CHAH (2005)	Sclerolaena muricata
Sclerolaena muricata (Moq.) Domin var. muricata	sensu CHAH (2005)	Sclerolaena muricata var. muricata
Sclerolaena muricata var. semiglabra (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena muricata var. semiglabra
Sclerolaena muricata var. villosa (Benth.) Ulbr.	sensu CHAH (2005)	Sclerolaena muricata var. villosa
Sclerolaena napiformis Paul G.Wilson	sensu Wilson, P.G. (1984)	Sclerolaena napiformis
Sclerolaena obliquicuspis (R.H.Anderson) Ulbr.	sensu Wilson, P.G. (1984)	Sclerolaena obliquicuspis
Sclerolaena parallelicuspis (R.H.Anderson) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena parallelicuspis
Sclerolaena parviflora (R.H.Anderson) A.J.Scott	sensu CHAH (2005)	Sclerolaena parviflora
Sclerolaena patenticuspis (R.H.Anderson) Ulbr.	sensu Wilson, P.G. (1984)	Sclerolaena patenticuspis
Sclerolaena ramulosa (C.T.White) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena ramulosa
Sclerolaena recurvicuspis (W.Fitzg.) Domin	sensu Wilson, P.G. (1984)	Sclerolaena recurvicuspis
Sclerolaena stelligera (F.Muell.) S.W.L.Jacobs	sensu CHAH (2005)	Sclerolaena stelligera
Sclerolaena stylosa (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena stylosa
Sclerolaena symoniana (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena symoniana
Sclerolaena tatei (F.Muell.) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena tatei
Sclerolaena tetracuspis (C.T.White) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena tetracuspis
Sclerolaena tetragona Paul G.Wilson	sensu Wilson, P.G. (1984)	Sclerolaena tetragona
Sclerolaena tricuspis (F.Muell.) Ulbr.	sensu Wilson, P.G. (1984)	Sclerolaena tricuspis
Sclerolaena tridens (F.Muell.) Domin	sensu CHAH (2005)	Sclerolaena tridens
Sclerolaena tubata (R.H.Anderson) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena tubata
Sclerolaena uniflora R.Br.	sensu CHAH (2005)	Sclerolaena uniflora
Sclerolaena urceolata (Ising) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena urceolata
Sclerolaena ventricosa (J.M.Black) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena ventricosa
Sclerolaena walkeri (C.T.White) A.J.Scott	sensu Wilson, P.G. (1984)	Sclerolaena walkeri

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species
Threlkeldia diffusa R.Br.	sensu CHAH (2005)	Threlkeldia diffusa
Threlkeldia inchoata (J.M.Black) J.M.Black	sensu Wilson, P.G. (1984)	Threlkeldia inchoata

Tecticornia Clade

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species
Tecticornia annelida K.A.Sheph. & M.Lyons	sensu Shepherd, K.A. & Lyons, M.N. (2009)	Tecticornia annelida
Tecticornia arborea Paul G.Wilson	sensu CHAH (2008)	Tecticornia arborea
Tecticornia arbuscula (R.Br.) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia arbuscula
Tecticornia auriculata (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia auriculata
Tecticornia australasica (Moq.) Paul G.Wilson	sensu CHAH (2005)	Tecticornia australasica
Tecticornia bibenda K.A.Sheph. & S.J.van Leeuwen	sensu Shepherd, K.A. & van Leeuwen, S.J. (2007)	Tecticornia bibenda
Tecticornia bulbosa (Paul G.Wilson) K.A.Sheph. & PaulG.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia bulbosa
Tecticornia calyptrata (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia calyptrata
Tecticornia chartacea (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia chartacea
Tecticornia cupuliformis (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia cupuliformis
Tecticornia cymbiformis K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. (2007)	Tecticornia cymbiformis
Tecticornia disarticulata (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia disarticulata
Tecticornia doleiformis (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia doleiformis
Tecticornia entrichoma (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia entrichoma
Tecticornia fimbriata (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia fimbriata
Tecticornia flabelliformis (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia flabelliformis
Tecticornia fontinalis (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia fontinalis
Tecticornia globulifera K.A.Sheph	sensu Shepherd, K.A. & van Leeuwen, S.J. (2011)	Tecticornia globulifera
Tecticornia halocnemoides (Nees) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia halocnemoides
Tecticornia halocnemoides subsp. catenulata (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia halocnemoides subsp. catenulata
Tecticornia halocnemoides subsp. caudata (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia halocnemoides subsp. caudata

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species
Tecticornia halocnemoides (Nees) K.A.Sheph. & Paul G.Wilson subsp. halocnemoides	sensu CHAH (2008)	Tecticornia halocnemoides subsp. halocnemoides
Tecticornia halocnemoides subsp. longispicata (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia halocnemoides subsp. longispicata
Tecticornia halocnemoides subsp. tenuis (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia halocnemoides subsp. tenuis
Tecticornia indefessa K.A.Sheph.	sensu Shepherd, K.A. (2007)	Tecticornia indefessa
Tecticornia indica (Willd.) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia indica
Tecticornia indica subsp. bidens (Nees) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia indica subsp. bidens
Tecticornia indica (Willd.) K.A.Sheph. & Paul G.Wilson subsp. indica	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia indica subsp. indica
Tecticornia indica subsp. julacea (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia indica subsp. julacea
Tecticornia indica subsp. leiostachya (Benth.) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia indica subsp. leiostachya
Tecticornia laevigata K.A.Sheph.	sensu Shepherd, K.A. (2007)	Tecticornia laevigata
Tecticornia lepidosperma (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia lepidosperma
Tecticornia leptoclada (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia leptoclada
Tecticornia leptoclada subsp. inclusa (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia leptoclada subsp. inclusa
Tecticornia leptoclada (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson subsp. leptoclada	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia leptoclada subsp. leptoclada
Tecticornia loriae K.A.Sheph. & M.Lyons	sensu Shepherd, K.A. & Lyons, M.N. (2009)	Tecticornia loriae
Tecticornia lylei (Ewart & Jean White) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia lylei
Tecticornia medullosa (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia medullosa
Tecticornia medusa K.A.Sheph	sensu Shepherd, K.A. & van Leeuwen, S.J. (2011)	Tecticornia medusa
Tecticornia mellaria K.A.Sheph	sensu Shepherd, K.A. (2007)	Tecticornia mellaria
Tecticornia moniliformis (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia moniliformis
Tecticornia nitida (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia nitida
Tecticornia papillata K.A.Sheph	sensu Shepherd, K.A. (2008)	Tecticornia papillata
Tecticornia peltata (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia peltata
Tecticornia pergranulata (J.M.Black) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia pergranulata
Tecticornia pergranulata subsp. divaricata (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia pergranulata subsp. divaricata

Plant Species Name (CHAH-APC)	CHAH-APC	Plant Species
Tecticornia pergranulata subsp. elongata (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia pergranulata subsp. elongata
Tecticornia pergranulata (J.M.Black) K.A.Sheph. & Paul G.Wilson subsp. pergranulata	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia pergranulata subsp. pergranulata
Tecticornia pergranulata subsp. queenslandica (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia pergranulata subsp. queenslandica
Tecticornia pluriflora (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia pluriflora
Tecticornia pruinosa (Paulsen) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia pruinosa
Tecticornia pterygosperma (J.M.Black) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia pterygosperma
Tecticornia pterygosperma subsp. denticulata (Paul G. Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia pterygosperma subsp. denticulata
Tecticornia pterygosperma (J.M.Black) K.A.Sheph. & Paul G.Wilson subsp. pterygosperma	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia pterygosperma subsp. pterygosperma
Tecticornia sparagosa K.A.Sheph. & M.Lyons	sensu Shepherd, K.A. & Lyons, M.N. (2009)	Tecticornia sparagosa
Tecticornia syncarpa (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia syncarpa
Tecticornia tenuis (Benth.) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia tenuis
Tecticornia triandra (F.Muell.) K.A.Sheph. & Paul G.Wilson	sensu CHAH (2008)	Tecticornia triandra
Tecticornia undulata (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia undulata
Tecticornia uniflora (Paul G.Wilson) K.A.Sheph. & Paul G.Wilson	sensu Shepherd, K.A. & Wilson, Paul G. (2007)	Tecticornia uniflora
Tecticornia verrucosa Paul G.Wilson	sensu Wilson, P.G. (1984)	Tecticornia verrucosa

Sarcocornia Clade

Plant Species Name (CHAH-APC)	CHAH-APCSuff	Plant Name
Sarcocornia blackiana (Ulbr.) A.J.Scott	sensu Wilson, P.G. (1984)	Sarcocornia blackiana
Sarcocornia globosa Paul G.Wilson	sensu Wilson, P.G. (1984)	Sarcocornia globosa
Sarcocornia quinqueflora (Bunge ex Ung.-Sternb.) A.J.Scott	sensu Wilson, P.G. (1984)	Sarcocornia quinqueflora
Sarcocornia quinqueflora (Bunge ex Ung.-Sternb.) A.J.Scott subsp. quinqueflora	sensu Wilson, P.G. (1984)	Sarcocornia quinqueflora subsp. quinqueflora
Sarcocornia quinqueflora subsp. tasmanica Paul G.Wilson	sensu Wilson, P.G. (1984)	Sarcocornia quinqueflora subsp. tasmanica

Suaeda Clade

Plant Species Name (CHAH-APC)	**CHAH-APCSuff**	**Plant Name**
Suaeda arbusculoides L.S.Sm.	sensu Wilson, P.G. (1984)	Suaeda arbusculoides
Suaeda australis (R.Br.) Moq.	sensu Wilson, P.G. (1984)	Suaeda australis

Nomenclatural change in Australian Salicornioideae (Shepherd and Wilson 2007) affecting saltmarsh floristic nomenclature (Bridgewater and Cresswell 2003).

Revised Taxon Name (2007)	Floristic Taxon Name (2003)
Tecticornia arbuscula	Sclerostegia arbuscula
Tecticornia doleiformis	Halosarcia doleiformis
Tecticornia halocnemoides	Halosarcia halocnemoides
Tecticornia indica	Halosarcia indica
Tecticornia leptoclada	Halosarcia leptoclada
Tecticornia pergranulata	Halosarcia pergranulata
Tecticornia tenuis	Sclerostegia tenuis

Appendix II: Issues of chenopod distribution in Australia – current description, coast disposition, species richness and assembly

Existing descriptions of distribution

Distribution of chenopod taxa as currently described is exceptionally general, hampered by taxonomic issues and skewed by ecological and economic perceptions.

Inadequacy of existing descriptions

Existing description of chenopod distribution is simplistic and deficient, being largely based on climatic generalizations for select species. Emphasis is on dominant arid taxa with no provision at genus or subfamily rank. Climatic description includes variations on arid and semi-arid Australia, the winter rainfall zone of southern Australia, southern semi-arid areas and south of the Tropic of Capricorn (Osborn *et al.* 1935; Burbidge 1960; Hall *et al.* 1964; Wilson 1966, 1994; Leigh 1972, 1981, 1994; Williams 1979; Graetz and Wilson 1984). Specific landscape and climatic limits for some perennial species of pastoral and ecological importance e.g. Hall *et al.* (1964); Leigh (1972, 1981, 1994); Graetz and Wilson (1984), would be uncertainly applied to related taxa. Regional flora descriptions e.g. Leigh and Mulham (1965); Cunningham *et al.* (1992); Kutsche and Lay (2003); Moore (2005), have species ranges, habitat and regional occurrence for select species. Arid and coastal chenopods are treated separately in context of respective ecology e.g. Specht (1972); Beadle (1981); Groves (1981, 1994).

Distribution mapping of species is coarse, incomplete or inconsistent. Focus is on chenopod formations or dominant species in only part of their entire range. Mapping of chenopod shrubland at continental scale in Leigh (1972, 1981, 1994), Graetz and Wilson (1984) and Carnahan (1986) does not distinguish taxa. Western and southern species, with varied floristic and habitat analyses, are mapped at regional scale e.g. Beard (1974, 1975, 1976), in Technical Bulletins e.g Curry *et al.* (1994) and in South Australian Biological Surveys e.g. Brandle (1998); Kenny and Thompson (2008). Eastern chenopods are covered in Regional Ecosystem Description Database (Queensland Herbarium 2018), the Western Arid Regional Land Use Studies (Queensland Department of Primary Industry 1974, 1978, 1979, 1990a, 1990b, 1993) and Walker (1991) for New South Wales. Emphasis is on vegetation community and type, listing the more common chenopod species. However, chenopod taxa are much more widespread, occurring prominently in mallee woodland (Parsons 1981, 1994; Noble 1984), semi-arid woodland (Harrington *et al.* 1984), *Acacia* woodland (Johnson and Burrows 1981, 1994; Morrissey 1984) and arid grasslands (Brandle 1998).

Existing species level mapping is not readily quantifiable. National and state floras either portray species ranges on small national or state maps, or note presence in collection districts. Such representations limit capability for aggregation to quantify patterns above species rank or at continental scale (Gaston 2003).

Problems of existing taxonomy

Constructing distributions through aggregation of individual species ranges to depict course of evolution, requires exact knowledge of constituent taxa and their relationships. However, chenopod taxonomy and phylogeny is appreciably uncertain. Considerable polymorphism and hybridisation makes ‘circumscription of some taxa arbitrary and identification difficult’ in respect of *Atriplex* (Wilson 1984: 85). Hybridization is suspected within genus *Sclerolaena* and related genera (Wilson 1984: 238) as is greater diversity in *Salsola* and *Tecticornia* (see Introduction).

Circumscription problems effectively preclude cladistic analyses based on phylogenetic constructions of identified primitive or modern characters in the sense of Hennig (1965). Wilson (1984) assigns *Atriplex* species to Sections and *Chenopodium* species to Subgenera, on criteria derived from global treatments, which would suggest complex origins within each genus. Parr-Smith (1982) proposed an early evolutionary sequence for *Atriplex* species within Section *Dialysex*. Kadereit *et al.* (2010) showed the section to be paraphyletic, demonstrating *Atriplex* origins are complex, but not in the manner taxonomy suggests. The molecular phylogeny of Cabrera *et al.* (2009) seems the first attempt at understanding emergence of genera and species in the very rich Sclerolaenid clade.

Resolution of issues in coastal disposition, species richness and assembly analyses

Identifying and classifying coastal disposition

Disposition classes are coarsely and quickly determined from broad-scale appraisal of shoreline presence (or absence) and relative size of inland and coastal distributions. Obligate types are more readily identified than Facultative types. In such a coarse appraisal, the eye attempts comparison of linear coastal and areal inland ranges of a species. Problems included species being transitional between classes, as well as sources lacking information or not easily interpreted in shoreline context. Ultimate resort was to sampling collection records through Australasian Virtual Herbarium and compiling location and habitat notes, to determine coastal disposition. Many records of coastal proximity could not be confirmed as a shoreline location. Coastal location e.g. West Beach, was only considered indicative with accompanying notes e.g. along shoreline, above high water mark. *Dysphania melanocarpa* plots coastal, but no collection records confirmed shoreline presence.

For species ranges comprising few collection plot points, all AVH records were examined to classify coastal disposition and habitat type (for Chapter 3 analyses). For species abundantly collected, the entire range was evenly sampled until an arbitrary, sufficient number was examined. Collection records examined are summarised in Appendix XII. Several collections at a site are a single observation, unless recorded habitats are different.

At continental scale, coastal proximity does not reflect shoreline influence, even allowing for plot point accuracy. Inland salinity gradients are very steep on the high rainfall, southern coasts. Near-shoreline heath or sclerophyll formations are not regarded as salt-tolerant but have chenopods within them. Conversely, chenopods are diverse around Shark Bay where gentle salinity gradients arise from salt spray extending some distance inland over the low-lying landscape. An estuary layer on ALA assisted resolution where estuarine channels extend some distance from a coastline, but were not portrayed on available mapping (See Chapter 3).

Specific issues of taxonomic status and the gradational nature of coastal disposition were resolved as follows: (1) *Chenopodium glaucum* (Chenopodieae I) is Coast facultative based on range and habitat of the species complex which likely includes exotic taxa, (2) All *Salsola* records were treated as a single, indigenous species and regarded as Inland facultative, (3) *Rhagodia baccata* (Chenopodieae I) is Coast facultative, because Wheeler *et al.* (2002) and collection records confirm it occurs away from shorelines, contrary to Wilson (1984), (4) *Atriplex cinerea* is Coast facultative having numerous inland occurrences, (5) The widespread *Tecticornia australasica* is Coast obligate despite two inland collections from very restricted locations.

Neobassia astrocarpa and *Rhagodia preissii* seem equally prominent in coastal and inland habitats and lie in the Coast-Inland transition of facultative types. The inland range of *N. astrocarpa* is mainly within the inaccessible Great Sandy Desert and adjoining Tanami Desert and is possibly of greater area than its coastal range. Classification as Coast facultative is, in part, a deliberate addition to the few coastal taxa of the very rich Sclerolaenid clade. The species range of Inland facultative *Rhagodia preissii* has a subcontinental span. In its north-western range subspecies *R. preissii* ssp. *obovata* is almost Coast obligate but subspecies *R. preissii* ssp. *preissii* is near Inland obligate through the major part of its range across southern Australia. Until March 2018 *Atriplex eremitis* was regarded as Coast Facultative, also seeming equally prominent in very restricted coastal and inland habitats of the Pilbara coast. However, in December 2017, five collections from the region, previously determined as *A. elachophylla*, were revised to *A. eremitis* (PERTH: 2380307, 2381315, 2380323, 2380412, 7167989) and the species accordingly classed as Inland Facultative.

Most uncertainty with disposition class is in distinguishing the two inland classes. A degree of subjective assessment arose through uncertain coastal proximity, lack of specific description and multiple collections from the same coastal sites. For these taxa, Inland obligate was set as a default class in absence of evidence of coastal presence. As these two classes are not a focus of analyses, the issue is of little consequence, but the following specific classifications should be noted. Inland facultative includes *Dysphania plantaginella*, *Rhagodia eremaea* and *R. parabolica*, *Maireana rohrlachii* and *Dissocarpus biflorus*, *Sclerolaena bicornis*, *S. diacantha and S. uniflora*. Through having too few coastal populations, *Atriplex holocarpa*, *A. lindleyi* and *A. muelleri*, *Dysphania glomulifera*, *Sclerolaena brevifolia* and *S. tricuspis* are classed as Inland obligate. *Malacocera gracilis*, an uncommon species with small range adjoining northern Spencer Gulf in South Australia, is arbitrarily classed as Inland obligate. *Dysphania pumilio*, is classed as an Inland facultative, but its many coastal collection records lack a habitat description. The locality information of recent collections, often more accurately noted or plotted, suggests the species is proximate to coastlines, rather than on shorelines.

Improving differentiation of coastal and inland taxa

To better distinguish Coast and Inland facultative classes, comparison of ecological fitness of coast and inland populations of species (e.g. abundance, meta-population dynamics, productivity, growth rate, germination etc.) may be more exacting. Species with coast populations of habitat fitness superior or equal to inland ones would class as Coast facultative. The strongest expression of the taxon element would be each clade with at least one species classed Coast facultative or Coast obligate.

In such case, the disposition of *Salsola* and possibly *Dysphania*, may become coastal, strengthening expression of the taxon element. *Salsola australis* was classed as Inland facultative because its inland range greatly exceeds coastal range. However, *Salsola* is a common component various coastal habitats and plant communities on temperate and tropical coastlines. It is functionally important (along with *Cakile* and *Euphorbia*) in colonizing the upper beach of coastal dune systems, where coastal species of other clades (e.g. *Atriplex cinerea*) are also found, and it exhibits a similar ecological role in inland dunefields (*pers. obs.*). *Salsola australis* also has the habitat characteristics of a Coast facultative type.

No *Dysphania* seems prominently coastal and the taxon element is broadly expressed as terrestrial species with some coastal presence. *Dysphania littoralis* is named for the shoreline habitat of initial collection, but it is classed here as marginal Inland facultative. A greater coastal prominence based on ecological fitness could classify the species as Coast facultative, strengthening expression of the taxon element. Conversely, there is further doubt over a littoral origin or increased suspicion of local coastal extinctions in creating sister taxa patterns.

Compiling richness counts and provincial composition

In general, provincial presence/absence is readily tallied for the 302 species on the ALA platform. Plot points of collections remote from a common range could be quickly validated or disregarded as an introduction, unreliable or incorrect plot. Misinterpreted locality names (usually an archaic spelling or unclear handwriting) when correctly recognised, fell within the main range. Remote collection plots also arise from coordinates that are incorrectly calculated, misrepresented or a best guess for a vague locality. To resolve inconsistency of location information with plot point coordinates, written locality information was preferred.

The principal area where province boundaries affected presence scoring was the Central Lowlands, especially with Sandland South and Barkly-Tanami, where encroaching sands unevenly covering older landscapes make boundary delineation imprecise (*pers. obs.*).

Appendix III: Summary of the general ecology of Australian chenopod immigrant clades

Atriplex clades

For Osmond *et al.* (1980) communities of cosmopolitan *Atriplex* include arid shrublands, littoral-maritime formations and weedy-ruderal types. Continental interiors of the world's semi-arid regions have a substantial richness of *Atriplex* of shrub-steppe and halophytic communities. Shrub-steppe includes perennial *Atriplex* spp. that dominate extensive formations. Halophytic vegetation of mixed annual and perennial species, is associated with saline soils, scalds, washes or sinks. Coastal communities have fewer, but more widespread *Atriplex* species, subject to disruptive disturbance regimes on foredunes under beach-dune dynamic or in salt marsh under tidal-riverine dynamic.

Chenopodieae I clade

Little is known of habitat ecology of this clade which includes annual herbs and shrubs. Kuhn (1993) suggested development of the succulent berry in *Rhagodia* relates directly to dispersal. *Einadia* and some *Chenopodium* also possess a semi-succulent berry. Wood (1937) and Lang *et al.* (2003) refer to their occurrence beneath bird perches, especially trees. Increased growth beneath trees follows reductions in stocking pressure (*pers. obs*.). Chapter 2 indicates a presence of the clade in mesic regions, especially *Einadia* in Eastern Highlands, in association with woodland habitats, so that the clade may have a shade-tolerance unusual for chenopods.

Dysphania clade

Little is known of evolutionary ecology. All species are annual herbs with very small flowers (Wilson 1984). Grozeva and Cvetanova (2013) and Sukhorukov and Zhang (2013) note the most indicative trait to be glands, simple hairs or glandular hairs imparting an aromatic smell. The cosmopolitan genus comprises species of restricted range or weedy types of subtropical regions, and generative organs generally are very small, with Australian taxa having minute fruit, unlike any other species within subfamily Chenopodioideae. Some species temporarily dominate open, sunlit areas of regular disturbance (Grozeva and Cvetanova 2013). Pollination is very likely wind-driven, while the fruits which stick to animal fur, due to perianth lobes and glands, can be carried distantly, because of their small size (Grozeva and Cvetanova 2013).

Scleroblitum clade

In proposing to place *Scleroblitum* within *Blitum*, Mosyakin (2013) also observed that species aggregates of the genus occur in mountainous terrain. Current range and estimated arrival time of *S. atriplicinum* includes the earliest palynological evidence of chenopods in Australia (Kershaw *et al.* 1994) with pollen traces found throughout the entire core of the estuarine Late Oligocene-Miocene Geera Clay in the Murray Basin (Truswell *et al.* 1985).

Salsola clade

Salsola are characteristic of more extreme deserts, particularly sandy ecosystems; Tribe Salsolae are mostly of halophytic, xerohalophytic, xerophytic and ruderal character (Akhani *et al.* 2007). The subfamily has many taxa with C_4 photosynthesis (Kadereit *et al.* 2012).

Sclerolaenid clade

Taxa within subfamily Camphorosmoideae are mainly confined to arid, saline or disturbed environments (Kadereit and Freitag 2011). Australian ancestors arrived by long-distance dispersal from semi-arid/arid parts of Eurasia and were present in Australia before the onset of aridity, in coastal and inland disturbed or saline habitats (Cabrera *et al.* 2011), though earliest evidence for inland saline habitats is mainly Pliocene (Alley *et al.* 1999; Clarke 1994b, 1994a). Strong selective pressures of harsh environments caused high degree of morphological homoplasy (Kadereit and Freitag 2011).

Tecticornia and *Sarcocornia* clades

Habitat requirements of Salicornioideae are globally uniform and distinct (Kadereit *et al.* 2006). They are restricted to distinctly saline habitats, flooded to some degree and are highly light demanding. Consequently the taxa are present mainly in coastal salt marshes and tidal mud or sand flats which are rich in clay, organic matter and nutrients. In inland salt marshes of arid zones, they are on shores of salt-lakes, clay pans or other poorly drained heavy and saline soils, subject to varied flooding.

Suaeda clade

According to Schutze *et al*. (2003), *Suaeda* are globally distributed halophytes, especially abundant in temperate zones, in saltmarshes of semi-deserts, deserts and coastal habitats, and especially of strongly saline soils. Vegetative characters vary greatly with salinity, competition and supply of water and nutrients. Australian species have C_3 photosynthesis and belong to clade especially tolerant of immersion in water. Australian *Suaeda* has species of primitive floral character.

Appendix IV: Subgroups of the Sclerolaenid Clade

Containing 150 species, the Sclerolaenid Clade is nearly 4 times the size of the second richest clade and collective chenopod patterns could simply be patterns of this clade. Two genera *Maireana* and *Sclerolaena* equally share about 80% of clade species. *Maireana* is basal and *Sclerolaena* is derived in the clade and associated with notable adaptation of the fruiting perianth (Wilson 1984; Cabrera *et al.* 2009), where considering them distinctly could put geographic perspective on such adaptation. The fruiting perianth in *Maireana* commonly possesses a single, entire or split, membranous to crustaceous wing; several species have a wing in five segments. *Sclerolaena* have a fruiting perianth with spines of varied architecture and no wings, considered by Cabrera *et al.* (2009) as possibly related to dispersal.

In constructing two evolutionary, analytical subgroups, there two problems. The major genera are polyphyetic (Cabrera *et al.* 2009) and their relationship to the other 10 genera is not clearly understood. Despite poor phylogenetic support, Cabrera *et al.* (2009), indicate useful affiliations.

Polyphyly of *Maireana* and *Sclerolaena*

Two *Maireana* species (*M. coronata* and *M. platycarpum*) ally with *Sclerolaena*, while two *Sclerolaena* species (*S. stelligera* and *S. fimbriolata*) likely affiliate with *Maireana*. With about half the species in each genus sampled, an estimated 8 species at most may need generic revision, which will only have minor influence on analyses involving all species. Species as currently listed within *Maireana* and *Sclerolaena* are assigned respectively to subgroups MaireanAff and SclerolaenAff.

Generic Relationships

Relationships of genera to each other and to *Maireana* and *Sclerolaena* are:

The genera *Roycea*, *Eremophea*, *Dissocarpus*, *Malacocera* and *Osteocarpum* resolve as monophyletic.

Neobassia astrocarpa is sister to *Eremophea*, but *N*. *proceriflora* is sister to *Sclerolaena*. *Eriochiton* and *Didymanthus* are sister to *Dissocarpus*.

Roycea is basal and *Eremophea* near basal within *Maireana*. *Dissocarpus* occurs along a grade of basal *Maireana* clades. *Enchylaena* is polyphyletic. Species are known to hybridise with *Maireana* spp. or have a winged perianth like *Maireana*.

Sclerolaena, *Osteocarpum*, *Threlkeldia*, *Malacocera* and *Enchylaena* are derived. *Threlkeldia diffusa* and *Osteocarpum* are sister to *Sclerolaena* clades or lineages (Cabrera *et al.* 2009, Figure 1) but relationship of *T. inchoata* is uncertain. *Malacocera* is possibly sister to later lineages of *Maireana*.

Consequently composition of the subgroups is:

MaireanAff Subgroup	**SclerolaenAff Subgroup**
Maireana	*Sclerolaena*
Roycea	*Osteocarpum*
Eremophea	*Threlkeldia*
Neobassia astrocarpa	*Neobassia proceriflora*
Dissocarpus	
Didymanthus	
Eriochiton	
Enchylaena	
Malacocera	

Appendix V: The influence of outliers in chenopod species richness and assembly

Gaston (2003) describes problems of isolates (outliers) and core-periphery continuity in estimating species range areas and for delimiting the range. Isolates are few occurrences, notably separate, often distant, from a main range. Core-periphery continuity is a transition from near-continuous density in the core of a species range, to discontinuous nearer the periphery. Plot points marking observations are farther apart or distinctly clustered. Unlike isolates, peripheral stands are not remote. Isolates represent extending or contracting fronts of temporary or incipient occupation, with extension more likely under invasion. Ignoring isolates emphasises the main range, but can reduce provincial species richness, the number of provinces in which a species occurrs and can vary provincial assembly patterns.

Provincial presence is noted as Major or Minor. Major presence, by and large, includes all or part of core-periphery continuity. Minor presence relates to isolates or the sparsest peripheral. For each species over all provinces, Major and Minor presence are combined for Total species presence, for comparison with Major Presence, where outliers and some peripherals are effectively equivalent to absence.

The following criteria determine Major and Minor presence:

(1) For each species, at least one province is identified as having a Major presence.

(2) Seven or more separate collections in a province is Major, irrespective of the number of plot points defining the range. Minor provincial presence is one to six separate collection sites, relative to the collection plot points defining the species range.

(3) Where dot maps have few collection plot points over two or more provinces, the province with the most, separate collections is Major. Provinces with half this number or more are also Major. Those with less than half are considered outliers or sparse periphery and of Minor presence.

Appendix VI: Coastal disposition of Australian chenopod species

Subfamily: Chenopodioideae

Clade/Species	Coast Disp
Australian *Atriplex* Clade 1	
Atriplex amnicola	IF
Atriplex cephalantha	IO
Atriplex cinerea	CF
Atriplex incrassata	IO
Atriplex isatidea	CO
Atriplex nummularia	IO
Atriplex rhagodioides	IO
Atriplex yeelirrie	IO
Australian *Atriplex* Clade 2	
Atriplex acutibractea	IO
Atriplex acutiloba	IO
Atriplex angulata	IO
Atriplex billardierei	CO
Atriplex bunburyana	IF
Atriplex codonocarpa	IF
Atriplex cordifolia	IO
Atriplex cornigera	IO
Atriplex crassipes	IO
Atriplex cryptocarpa	IO
Atriplex eardleyae	IO
Atriplex eichleri	IO
Atriplex elachophylla	IO
Atriplex eremitis	IF
Atriplex exilifolia	IO
Atriplex fissivalvis	IO
Atriplex flabelliformis	IO
Atriplex holocarpa	IO
Atriplex humifusa	IO
Atriplex humilis	CO
Atriplex hymenotheca	IO
Atriplex hypoleuca	CO
Atriplex infrequens	IO
Atriplex intermedia	IO
Atriplex kochiana	IO
Atriplex leptocarpa	IO
Atriplex limbata	IO
Atriplex lindleyi	IO
Atriplex lobativalvis	IO
Atriplex macropterocarpa	IO
Atriplex morrisii	IO
Atriplex muelleri	IO
Atriplex nana	IO
Atriplex nessorhina	IO
Atriplex obconica	IO
Atriplex paludosa	CF
Atriplex papillata	IO
Atriplex pseudocampanulata	IO
Atriplex pumilio	IO
Atriplex quadrivalvata	IO
Atriplex hymenotheca	IO
Atriplex quinii	IF
Atriplex semibaccata	IF
Atriplex semilunaris	IO
Atriplex spinibractea	IO
Atriplex spinulosa	IO
Atriplex spongiosa	IO
Atriplex stipitata	IO
Atriplex sturtii	IO
Atriplex suberecta	IF
Atriplex turbinata	IO
Atriplex velutinella	IO
Atriplex vesicaria	IF
***Atriplex australasica* Clade**	
Atriplex australasica	CF

Clade/Species	Coast Disp
Australian Chenopodieae I Clade	
Chenopodium auricomiforme	IO
Chenopodium auricomum	IO
Chenopodium curvispicatum	IO
Chenopodium desertorum	IO
Chenopodium erosum	IO
Chenopodium gaudichaudianum	IF
Chenopodium glaucum	CF
Chenopodium hubbardii	IO
Chenopodium nitrariaceum	IO
Einadia hastata	IF
Einadia nutans	IF
Einadia polygonoides	IO
Einadia trigonos	IF
Rhagodia acicularis	IO
Rhagodia baccata	CF
Rhagodia candolleana	CF
Rhagodia crassifolia	IF
Rhagodia drummondii	IO
Rhagodia eremaea	IF
Rhagodia latifolia	CF
Rhagodia parabolica	IF
Rhagodia preissii	IF
Rhagodia spinescens	IO
Rhagodia ulicina	IO
Dysphania Clade	
Dysphania glandulosa	IO
Dysphania glomulifera	IO
Dysphania kalpari	IO
Dysphania littoralis	IF
Dysphania plantaginella	IF
Dysphania platycarpa	IO
Dysphania rhadinostachya	IO
Dysphania simulans	IO
Dysphania sphaerosperma	IO
Dysphania valida	IO
Dysphania carinata	IO
Dysphania cristata	IO
Dysphania melanocarpa	IO
Dysphania pumilio	IF
Dysphania saxatilis	IO
Dysphania truncata	IO
Scleroblitum Clade	
Scleroblitum atriplicinum	IO

Subfamily: Camphorosmoideae

Clade/Species	Coast Disp
Sclerolaenid Clade: MaireanAff Subgroup	
Maireana amoena	IO
Maireana aphylla	IO
Maireana appressa	IO
Maireana astrotricha	IO
Maireana atkinsiana	IO
Maireana brevifolia	IO
Maireana campanulata	IO
Maireana cannonii	IO
Maireana carnosa	IO
Maireana cheelii	IO
Maireana ciliata	IO
Maireana convexa	IO
Maireana coronata	IO
Maireana decalvans	IO
Maireana dichoptera	IO
Maireana diffusa	IO
Maireana enchylaenoides	IO

Clade/Species	Coast Disp
Maireana eriantha	IO
Maireana erioclada	IF
Maireana eriosphaera	IO
Maireana excavata	IO
Maireana georgei	IO
Maireana glomerifolia	IO
Maireana humillima	IO
Maireana integra	IO
Maireana lanosa	IO
Maireana lobiflora	IO
Maireana luehmannii	IO
Maireana marginata	IO
Maireana melanocarpa	IO
Maireana melanocoma	IO
Maireana microcarpa	IO
Maireana microphylla	IO
Maireana murrayana	IO
Maireana oppositifolia	CF
Maireana ovata	IO
Maireana pentagona	IO
Maireana pentatropis	IO
Maireana planifolia	IO
Maireana platycarpa	IO
Maireana polypterygia	IO
Maireana prosthecochaeta	IO
Maireana pyramidata	IO
Maireana radiata	IO
Maireana rohrlachii	IF
Maireana schistocarpa	IO
Maireana scleroptera	IO
Maireana sedifolia	IO
Maireana spongiocarpa	IO
Maireana stipitata	IO
Maireana suaedifolia	IO
Maireana thesioides	IO
Maireana tomentosa	IO
Maireana trichoptera	IO
Maireana triptera	IO
Maireana turbinata	IO
Maireana villosa	IO
Didymanthus roei	IO
Dissocarpus biflorus	IF
Dissocarpus fontinalis	IO
Dissocarpus latifolius	IO
Dissocarpus paradoxus	IO
Enchylaena lanata	IO
Enchylaena tomentosa	IF
Eremophea aggregata	IO
Eremophea spinosa	IO
Eriochiton sclerolaenoides	IO
Malacocera albolanata	IO
Malacocera biflora	IO
Malacocera gracilis	IF
Malacocera tricornis	IO
Neobassia astrocarpa	CF
Roycea divaricata	IO
Roycea pycnophylloides	IO
Roycea spinescens	IO
Sclerolaenid Clade: SclerolaenAff Subgroup	
Sclerolaena alata	IO
Sclerolaena anisacanthoides	IO
Sclerolaena articulata	IO
Sclerolaena beaugleholei	IO
Sclerolaena bicornis	IF
Sclerolaena bicuspis	IO
Sclerolaena birchii	IO
Sclerolaena blackiana	IO

Clade/Species	Coast Disp
Sclerolaena blakei	IO
Sclerolaena brachyptera	IO
Sclerolaena brevifolia	IO
Sclerolaena burbidgeae	IO
Sclerolaena calcarata	IO
Sclerolaena clelandii	IO
Sclerolaena constricta	IO
Sclerolaena convexula	IO
Sclerolaena cornishiana	IO
Sclerolaena costata	IO
Sclerolaena crenata	IO
Sclerolaena cuneata	IO
Sclerolaena decurrens	IO
Sclerolaena densiflora	IO
Sclerolaena deserticola	IO
Sclerolaena diacantha	IF
Sclerolaena divaricata	IO
Sclerolaena drummondii	IO
Sclerolaena eriacantha	IO
Sclerolaena eurotioides	IO
Sclerolaena everistiana	IO
Sclerolaena fimbriolata	IO
Sclerolaena fontinalis	IO
Sclerolaena forrestiana	IO
Sclerolaena fusiformis	IO
Sclerolaena gardneri	IO
Sclerolaena glabra	IO
Sclerolaena holtiana	IO
Sclerolaena hostilis	IO
Sclerolaena intricata	IO
Sclerolaena johnsonii	IO
Sclerolaena lanicuspis	IO
Sclerolaena limbata	IO
Sclerolaena longicuspis	IO
Sclerolaena medicaginoides	IO
Sclerolaena microcarpa	IO
Sclerolaena minuta	IO
Sclerolaena muelleri	IO
Sclerolaena muricata	IO
Sclerolaena napiformis	IO
Sclerolaena obliquicuspis	IO
Sclerolaena parallelicuspis	IO
Sclerolaena parviflora	IO
Sclerolaena patenticuspis	IO
Sclerolaena ramulosa	IO
Sclerolaena recurvicuspis	IO
Sclerolaena stelligera	IO
Sclerolaena stylosa	IO
Sclerolaena symoniana	IO
Sclerolaena tatei	IO
Sclerolaena tetracuspis	IO
Sclerolaena tetragona	IO
Sclerolaena tricuspis	IO
Sclerolaena tridens	IO
Sclerolaena tubata	IO
Sclerolaena uniflora	IF
Sclerolaena urceolata	IO
Sclerolaena ventricosa	IO
Sclerolaena walkeri	IO
Neobassia proceriflora	IO
Osteocarpum acropterum	IO
Osteocarpum dipterocarpum	IO
Osteocarpum pentapterum	IO
Osteocarpum salsuginosum	IO
Osteocarpum X scleropterum	IO
Threlkeldia diffusa	CF
Threlkeldia inchoata	IO

Subfamily: Salsoloideae

Clade/Species	Coast Disp
***Salsola* Clade**	
Salsola australis	IF

Subfamily: Suaedoideae

Clade/Species	Coast Disp
***Suaeda* Clade**	
Suaeda arbusculoides	CO
Suaeda australis	CF

Coastal taxa and subspecies

Clade/Species	Coast Disp
Australian *Atriplex* Clade 2	
Atriplex paludosa	CF
Atriplex paludosa ssp. baudinii	IO
Atriplex paludosa ssp. cordata	CF
Atriplex paludosa ssp. moquiniana	CO
Atriplex paludosa ssp. paludosa	CO
Australian Chenopodieae I	
Rhagodia baccata	CF
Rhagodia baccata ssp. baccata	CF
Rhagodia baccata ssp. dioica	CO
Rhagodia latifolia	CF
Rhagodia latifolia ssp. latifolia	CF
Rhagodia latifolia ssp. recta	CF
Rhagodia preissii	IF
Rhagodia preissii ssp. obovata	CF
Rhagodia preissii ssp. preissii	IF

KEY

Disposition Class	Abbrev
Coast Obligate	CO
Coast Facultative	CF
Inland Facultative	IF
Inland Obligate	IO

DEFINITIONS

Disposition Class
Coast Obligate
Species range restricted to coastlines, at places affected by coastal shoreline processes
Coast Facultative
Species range is coastal and inland, but largely along coastlines in places under the influence of shoreline processes; lesser inland ranges are unaffected by coastline processes
Inland Facultative
Terrestrial species of coast and inland with larger inland species range; coastal populations in places affected by coastal shoreline processes
Inland Obligate
Terrestrial species of inland range; near coast populations are in habitats not strongly affected by shoreline processes

Subfamily: Salicornioideae

Clade/Species	Coast Disp
***Tecticornia* Clade**	
Tecticornia annelida	IO
Tecticornia arborea	IO
Tecticornia arbuscula	CF
Tecticornia auriculata	CF
Tecticornia australasica	CO
Tecticornia bibenda	IO
Tecticornia bulbosa	IO
Tecticornia calyptrata	IO
Tecticornia chartacea	IO
Tecticornia cupuliformis	IO
Tecticornia cymbiformis	IO
Tecticornia disarticulata	IO
Tecticornia doleiformis	IO
Tecticornia entrichoma	IO
Tecticornia fimbriata	IO
Tecticornia flabelliformis	CF
Tecticornia fontinalis	IO
Tecticornia globulifera	IO
Tecticornia halocnemoides	CF
Tecticornia indefessa	IO
Tecticornia indica	CF
Tecticornia laevigata	IO
Tecticornia lepidosperma	IO
Tecticornia leptoclada	IO
Tecticornia loriae	IO
Tecticornia lylei	IO
Tecticornia medullosa	IO
Tecticornia medusa	IO
Tecticornia mellaria	IO
Tecticornia moniliformis	IO
Tecticornia nitida	IO
Tecticornia papillata	IO
Tecticornia peltata	IO
Tecticornia pergranulata	IF
Tecticornia pluriflora	IO
Tecticornia pruinosa	IF
Tecticornia pterygosperma	IF
Tecticornia sparagosa	IO
Tecticornia syncarpa	IF
Tecticornia tenuis	IO
Tecticornia triandra	IO
Tecticornia undulata	IO
Tecticornia uniflora	IO
Tecticornia verrucosa	IF
Tecticornia annelida	IO
Sarcocornia clade	
Sarcocornia blackiana	CF
Sarcocornia globosa	IO
Sarcocornia quinqueflora	CF

Appendix VII: Provincial richness & ranking for Total and Major Presence

Province	Total Presence		Major Presence	
	Species Richness	**Rank**	**Species Richness**	**Rank**
Yilgarn Plateau	175	1	149	1
Central Lowlands West	166	2	132	2
Murray Lowlands	158	3	128	3
Eyre Peninsula	151	4	117	5
Gulfs Ranges	149	5	127	4
Central Lowlands Central	137	6	109	6
Central Australian Ranges	137	6	94	7
Western Coastlands	123	8	75	9
Sandland South	118	9	74	10
Central Lowlands East	115	10	81	8
Pilbara	106	11	74	10
Sandland North	75	12	24	17
Nullarbor Plain	75	12	40	12
Barkly-Tanami Plain	68	14	36	13
New England-Moreton Uplands	57	15	34	16
Fitzroy Uplands	54	16	36	13
Kosciuskan Uplands	50	17	36	13
Burdekin Uplands	41	18	19	19
Macquarie Uplands	39	19	24	17
Carpentaria Fall	21	20	12	20
Kimberley	21	20	10	22
Carpentaria Lowlands	20	22	9	23
Tasmanian Uplands	20	22	12	20
North Australian Plateaus	14	24	8	24
Peninsula Upland	13	25	5	25
Great Barrier Reef	2	26	1	26

Appendix VIII: Chenopod species presence in Australian Physiographic Provinces

Subfamily Chenopodioideae

Plant Species	Western Coastlds	Pilbara	Yilgarn Plateau	Kimberley	Sandland North	Sandland South	Nullarbor Plain	North Aust. Plateaus	Carpentaria Fall	Barkly-Tanami Plains	Central Aust. Ranges	Central Lowlands West	Eyre Peninsula	Gulfs Ranges	Carpentaria Lowlands	Centrral Lowlands Cent	Murray Lowlands	Peninsular Uplands	Great Barrier Reef	Burdekin Uplands	Fitzroy Uplands	Centrral Lowlands East	New England-Moreton Upl'ds	Macquarie Uplands	Kosciuszkan Uplands	Tasmanian Uplands	Discount	Absent	Major Pres	Total Pres
Australian *Atriplex* Clade 1																														
Atriplex amnicola	20	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	3	3
Atriplex cephalantha	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Atriplex cinerea	20	0	20	0	0	0	20	0	13	0	0	0	20	20	0	0	20	0	0	0	0	0	10	20	20	20	1	16	9	10
Atriplex incrassata	0	0	0	0	0	0	0	0	0	0	10	20	20	11	0	0	0	0	0	0	0	0	0	0	0	0	1	23	2	3
Atriplex isatidea	20	10	20	0	0	0	10	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	2	5
Atriplex nummularia	10	0	20	0	10	10	20	0	0	11	20	20	20	20	0	20	20	0	0	0	10	20	10	13	10	13	3	11	9	15
Atriplex rhagodioides	0	0	0	0	0	0	0	0	0	0	0	12	12	14	0	0	20	0	0	0	0	0	0	0	0	0	3	25	1	1
Atriplex yeelirrie	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Australian *Atriplex* Clade 2																														
Atriplex acutibractea	10	0	20	0	0	10	20	0	0	0	0	10	20	20	0	0	20	0	0	0	0	0	0	0	0	0	0	18	5	8
Atriplex acutiloba	0	0	0	0	0	0	13	0	0	0	0	20	20	20	0	0	10	0	0	0	0	0	0	0	0	0	1	22	3	4
Atriplex angulata	0	0	0	0	0	11	0	0	0	11	10	20	20	20	0	20	20	0	0	0	0	10	0	0	0	0	2	19	5	7
Atriplex billardierei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	20	0	24	2	2
Atriplex bunburyana	20	20	20	0	10	11	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	21	3	5
Atriplex codonocarpa	20	20	20	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	3	5
Atriplex cordifolia	0	0	0	0	0	0	12	0	0	0	0	20	0	10	0	0	0	0	0	0	0	0	0	0	0	0	1	24	1	2
Atriplex cornigera	0	0	0	0	0	0	0	0	11	0	10	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	1	24	1	2
Atriplex crassipes	0	0	0	0	0	11	13	0	0	10	10	20	20	10	0	20	10	0	0	0	0	20	0	0	0	0	2	18	4	8
Atriplex cryptocarpa	0	0	0	0	0	0	20	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Atriplex eardleyae	0	0	20	0	0	11	20	0	11	12	0	20	20	20	0	20	20	0	0	0	0	20	0	0	14	0	4	18	8	8
Atriplex eichleri	0	0	0	0	0	0	0	0	0	0	0	20	11	20	0	0	0	0	0	0	0	0	0	0	0	0	1	24	2	2
Atriplex elachophylla	10	0	0	0	20	20	0	0	11	20	20	20	12	11	0	20	0	0	0	0	10	20	11	14	0	0	5	17	7	9
Atriplex eremitis	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Atriplex exilifolia	11	0	20	0	0	0	10	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	2	24	1	2
Atriplex fissivalvis	13	0	0	0	0	0	12	0	0	0	20	20	20	20	0	20	10	0	0	0	0	0	0	0	14	0	3	20	5	6
Atriplex flabelliformis	10	20	10	0	10	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	1	21	1	5
Atriplex holocarpa	20	12	20	0	0	20	20	0	0	0	20	20	20	20	0	20	20	0	0	0	0	20	12	10	14	0	3	14	11	12
Atriplex humifusa	0	0	0	0	0	0	0	0	11	20	20	20	0	0	0	20	0	0	0	0	0	10	0	0	0	0	1	21	4	5
Atriplex humilis	0	0	0	0	0	0	0	0	20	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	24	2	2
Atriplex hymenotheca	11	0	20	0	10	0	10	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	22	1	4
Atriplex hypoleuca	20	0	20	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	24	2	2
Atriplex infrequens	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	10	20	0	0	0	0	10	0	0	0	0	0	22	1	4
Atriplex intermedia	0	0	0	0	0	0	0	0	0	0	0	20	11	20	0	20	20	0	0	0	0	0	0	0	0	0	1	22	4	4

Plant Species	**Western Coastlds**	**Pilbara**	**Yilgarn Plateau**	**Kimberley**	**Sandland North**	**Sandland South**	**Nullarbor Plain**	**North Aust. Plateaus**	**Carpentaria Fall**	**Barkly-Tanami Plains**	**Central Aust. Ranges**	**Central Lowlands West**	**Eyre Peninsula**	**Gulfs Ranges**	**Carpentaria Lowlands**	**Centrral Lowlands Cent**	**Murray Lowlands**	**Peninsular Uplands**	**Great Barrier Reef**	**Burdekin Uplands**	**Fitzroy Uplands**	**Centrral Lowlands East**	**New England-Moreton Upl'ds**	**Macquarie Uplands**	**Kosciuszkan Uplands**	**Tasmanian Uplands**	**Discount**	**Absent**	**Major Pres**	**Total Pres**
Atriplex kochiana	0	0	0	0	0	0	0	0	0	0	0	20	10	11	0	0	0	0	0	0	0	0	0	0	0	0	1	24	1	2
Atriplex leptocarpa	0	0	13	0	12	0	10	0	0	0	13	20	10	20	0	20	20	0	0	0	0	20	10	10	11	0	4	17	5	9
Atriplex limbata	10	0	10	0	10	10	10	0	0	11	20	20	20	20	0	20	20	0	0	0	0	20	12	0	11	0	3	14	7	12
Atriplex lindleyi	20	20	20	0	0	11	10	0	0	10	20	20	20	20	0	20	20	0	0	12	20	20	10	11	11	0	4	12	11	14
Atriplex lobativalvis	0	0	0	0	0	11	0	0	0	11	10	20	20	11	0	20	0	0	0	0	0	0	0	0	0	0	3	22	3	4
Atriplex macropterocarpa	0	10	0	0	0	11	0	0	0	0	0	20	10	10	0	10	0	0	0	0	0	0	0	0	0	0	1	21	1	5
Atriplex morrisii	0	0	0	0	0	0	10	0	0	11	0	20	0	11	0	10	10	0	0	0	0	0	0	0	0	0	2	22	1	4
Atriplex muelleri	13	0	12	0	0	11	0	12	0	20	10	20	10	20	10	20	20	0	0	10	20	20	20	13	0	0	5	14	8	12
Atriplex nana	0	0	20	0	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	1	3
Atriplex nessorhina	0	0	0	0	0	0	0	0	0	0	0	10	20	0	0	20	0	0	0	0	0	0	0	0	0	0	0	23	2	3
Atriplex obconica	0	0	0	0	0	10	0	0	0	0	0	20	11	20	0	0	0	0	0	0	0	0	0	0	0	0	1	23	2	3
Atriplex paludosa	20	11	20	0	0	10	20	0	0	0	0	0	20	20	0	0	20	0	0	0	0	0	0	0	20	20	1	17	8	9
Atriplex papillata	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	24	1	2
Atriplex pseudocampanulata	0	0	0	0	0	11	0	0	0	0	10	20	10	20	0	20	20	0	0	0	0	20	10	10	10	0	1	16	5	10
Atriplex pumilio	0	0	20	0	0	10	10	0	0	0	0	10	20	20	0	20	20	0	0	0	0	10	0	13	0	0	1	17	5	9
Atriplex quadrivalvata	0	10	20	0	0	11	0	0	0	0	10	20	20	11	0	0	0	0	0	0	0	0	0	0	0	0	2	21	3	5
Atriplex quinii	10	11	20	0	10	10	10	0	0	10	11	20	20	11	0	20	10	0	0	0	0	0	0	0	0	0	3	16	4	10
Atriplex semibaccata	10	0	20	0	0	0	0	0	0	0	10	10	20	20	0	20	20	0	0	10	20	20	20	20	20	13	1	12	10	14
Atriplex semilunaris	20	20	20	0	10	0	11	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	21	3	5
Atriplex spinibractea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	20	20	20	20	0	0	21	5	5
Atriplex spinulosa	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	1	24	1	2
Atriplex spongiosa	10	0	20	0	10	20	20	0	0	11	20	20	20	20	0	20	20	0	0	11	10	20	11	0	0	0	3	13	10	13
Atriplex stipitata	10	0	20	0	0	20	11	0	0	0	20	20	20	20	0	20	20	0	0	0	0	10	0	12	10	0	2	15	8	11
Atriplex sturtii	0	0	0	0	0	0	0	0	0	0	10	20	0	0	0	11	0	0	0	0	0	0	0	14	0	0	2	24	1	2
Atriplex suberecta	10	0	20	0	0	0	10	0	0	0	10	10	20	20	0	20	20	0	0	0	0	20	10	10	20	10	0	12	7	14
Atriplex turbinata	0	0	0	0	0	11	0	0	0	0	0	20	11	11	0	10	10	0	0	10	0	10	0	0	0	0	3	21	1	5
Atriplex velutinella	0	0	0	0	0	10	10	0	0	10	20	20	20	20	0	20	20	0	0	0	0	0	0	0	0	0	0	17	6	9
Atriplex vesicaria	20	20	20	0	20	20	20	0	0	20	20	20	20	20	0	20	20	0	0	11	0	20	0	0	10	0	1	11	14	15
***Atriplex australasica* Clade**																														
Atriplex australasica	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	20	0	0	0	0	0	10	20	20	10	0	20	4	6
***Scleroblitum* Clade**																														
Scleroblitum atriplicinum	0	0	13	0	0	0	0	0	0	0	0	20	10	20	0	11	20	0	0	0	0	20	11	11	11	0	5	21	4	5
***Dysphania* Clade**																														
Dysphania carinata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	10	0	20	20	20	20	0	0	0	0	20	5	6
Dysphania cristata	20	10	20	0	0	20	20	0	0	10	20	20	20	20	0	20	20	10	0	11	10	20	20	10	0	0	1	9	12	17
Dysphania glandulosa	10	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	1	3
Dysphania glomulifera	20	20	20	0	10	10	0	0	0	11	20	20	20	20	0	20	20	0	0	20	20	20	20	20	20	10	1	8	15	18
Dysphania kalpari	10	20	20	0	20	20	10	0	11	20	20	10	0	0	0	20	10	0	0	11	10	20	0	0	0	0	2	13	8	13

Plant Species	Western Coastlds	Pilbara	Yilgarn Plateau	Kimberley	Sandland North	Sandland South	Nullarbor Plain	North Aust. Plateaus	Carpentaria Fall	Barkly-Tanami Plains	Central Aust. Ranges	Central Lowlands West	Eyre Peninsula	Gulfs Ranges	Carpentaria Lowlands	Centrral Lowlands Cent	Murray Lowlands	Peninsular Uplands	Great Barrier Reef	Burdekin Uplands	Fitzroy Uplands	Centrral Lowlands East	New England-Moreton Upl'ds	Macquarie Uplands	Kosciuszkan Uplands	Tasmanian Uplands	Discount	Absent	Major Pres	Total Pres
Dysphania littoralis	0	0	13	0	0	0	0	0	0	0	10	0	0	0	0	20	20	0	0	20	20	10	10	10	10	0	1	17	4	9
Dysphania melanocarpa	20	20	20	0	10	20	20	0	0	10	20	20	20	20	0	20	20	0	0	10	10	20	20	20	11	0	1	8	14	18
Dysphania plantaginella	20	20	10	20	20	10	0	20	0	20	20	20	20	10	0	10	10	0	0	10	0	0	0	0	0	0	0	11	9	15
Dysphania platycarpa	10	0	10	0	11	11	0	0	0	11	20	20	10	11	0	10	10	0	0	0	0	10	0	0	0	0	4	18	2	8
Dysphania pumilio	20	10	20	0	0	10	0	0	0	10	10	20	20	20	10	20	20	10	0	10	10	20	20	20	20	20	0	6	12	20
Dysphania rhadinostachya	20	20	20	20	20	20	0	10	20	20	20	10	13	0	10	20	10	0	0	20	20	10	10	0	0	0	1	8	12	18
Dysphania saxatilis	0	20	20	0	20	20	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	2	22	4	4
Dysphania simulans	0	0	20	0	10	10	0	0	0	10	20	20	10	10	0	10	10	0	0	0	0	0	0	0	0	0	0	16	3	10
Dysphania sphaerosperma	20	20	10	0	10	0	0	0	0	10	20	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	3	7
Dysphania truncata	0	0	0	0	0	10	0	0	0	10	20	20	20	20	0	20	20	0	0	0	0	20	20	14	0	0	1	16	8	10
Dysphania valida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	10	20	11	0	0	0	1	23	1	3
Australian Chenopodieae I																														
Chenopodium auricomiforme	12	0	0	0	0	0	0	0	0	10	0	0	0	0	0	10	0	0	0	0	20	20	20	20	0	0	1	20	4	6
Chenopodium auricomum	20	20	10	10	10	0	0	20	10	20	20	20	10	20	10	20	20	0	0	10	20	20	10	0	12	0	1	7	11	19
Chenopodium curvispicatum	10	11	20	0	0	20	20	0	0	0	10	20	20	20	0	20	20	0	0	0	0	20	10	13	0	0	2	14	9	12
Chenopodium desertorum	0	0	20	0	11	20	10	0	0	11	20	10	20	20	0	20	20	0	0	0	20	20	10	20	20	0	2	12	11	14
Chenopodium erosum	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	20	10	20	10	0	21	2	5
Chenopodium gaudichaudianum	20	20	20	0	11	20	20	0	0	0	0	0	20	10	0	0	10	0	0	0	0	13	0	0	0	0	2	18	6	8
Chenopodium glaucum	20	0	20	0	0	0	0	0	0	0	0	0	10	20	0	0	20	0	0	0	0	0	20	20	20	20	0	17	8	9
Chenopodium hubbardii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	20	0	0	0	0	0	24	1	2
Chenopodium nitrariaceum	0	10	20	0	10	20	10	0	0	10	20	20	20	20	0	20	20	0	0	0	0	20	0	10	11	0	1	12	9	14
Einadia hastata	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	20	0	0	10	20	20	20	20	20	0	1	19	6	7
Einadia nutans	0	11	20	20	10	20	0	11	20	20	20	20	20	20	0	20	20	10	0	20	20	20	20	20	20	20	2	6	18	20
Einadia polygonoides	0	0	0	0	0	0	0	0	0	0	0	0	13	13	0	11	20	0	0	0	20	20	20	20	20	0	3	20	6	6
Einadia trigonos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	20	10	0	11	20	20	20	20	20	0	1	18	7	8
Rhagodia acicularis	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Rhagodia baccata	20	0	20	0	10	0	11	0	0	0	13	0	0	10	0	0	0	0	0	0	0	0	0	10	10	10	2	19	2	7
Rhagodia candolleana	20	0	20	0	0	20	20	0	0	0	0	0	20	20	0	0	20	0	0	0	0	0	20	20	20	20	0	15	11	11
Rhagodia crassifolia	0	0	20	0	0	20	20	0	0	0	0	0	20	20	0	0	20	0	0	0	0	0	0	0	0	0	0	20	6	6
Rhagodia drummondii	20	11	20	0	0	20	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	23	3	3
Rhagodia eremaea	20	20	20	0	20	20	0	11	0	20	20	20	11	0	0	0	0	0	0	0	0	0	0	0	0	0	2	18	8	8
Rhagodia latifolia	20	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Rhagodia parabolica	10	0	0	0	10	20	11	0	0	10	20	20	20	20	0	11	20	0	0	0	20	20	20	20	20	10	2	11	11	15
Rhagodia preissii	20	20	20	0	0	20	20	0	0	0	0	0	20	20	0	12	20	0	0	0	0	0	0	0	0	0	1	18	8	8
Rhagodia spinescens	0	10	10	0	0	20	20	0	0	20	20	20	20	20	0	20	20	0	0	11	20	20	20	10	20	0	1	10	13	16
Rhagodia ulicina	10	0	10	0	0	20	20	0	0	0	0	20	20	20	0	20	20	0	0	0	0	10	0	14	10	0	1	15	7	11

Subfamily Camphorosmoideae

Plant Species	Western Coastlands	Pilbara	Yilgarn Plateau	Kimberley	Sandland North	Sandland South	Nullarbor Plain	North Aust. Plateaus	Carpentaria Fall	Barkly-Tanami Plains	Central Aust. Ranges	Central Lowlands West	Eyre Peninsula	Gulfs Ranges	Carpentaria Lowlands	Central Lowlands Cent.	Murray Lowlands	Peninsular Uplands	Great Barrier Reef	Burdekin Uplands	Fitzroy Uplands	Central Lowlands East	New England-Moreton Upl'ds	Macquarie Uplands	Kosciuszkan Uplands	Tasmanian Uplands	Discount	Absent	Major Pres	Total Pres
MaireanAff Subgroup																														
Maireana amoena	10	20	20	0	10	10	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	21	2	5
Maireana aphylla	20	10	0	0	0	11	0	0	0	11	20	20	20	20	0	20	20	0	0	0	0	20	0	10	10	0	2	15	8	11
Maireana appressa	20	11	20	0	11	20	11	0	0	0	20	20	20	20	0	20	20	0	0	0	0	0	0	0	10	0	3	16	9	10
Maireana astrotricha	0	0	0	0	0	10	0	0	0	0	20	20	20	20	0	20	20	0	0	0	0	0	0	0	0	0	0	19	6	7
Maireana atkinsiana	20	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	2	2
Maireana brevifolia	20	0	20	0	0	10	0	0	10	0	10	20	20	20	0	20	20	0	0	0	0	20	10	10	10	0	0	12	8	14
Maireana campanulata	0	0	0	0	0	10	0	12	20	20	20	20	10	20	0	20	0	0	0	0	0	0	0	0	0	0	1	18	6	8
Maireana cannonii	0	0	0	0	0	0	0	0	0	0	0	0	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	24	2	2
Maireana carnosa	20	20	20	0	10	10	10	0	0	0	20	20	0	10	0	20	10	0	0	0	0	0	0	0	0	0	0	15	6	11
Maireana cheelii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	20	0	0	0	0	0	0	0	0	0	0	24	1	2
Maireana ciliata	0	0	13	0	0	11	0	0	0	0	10	20	20	20	0	0	20	0	0	0	0	10	0	0	0	0	2	20	4	6
Maireana convexa	20	20	20	0	11	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	22	3	4
Maireana coronata	0	0	0	0	0	0	0	0	0	10	20	20	10	20	0	20	20	0	0	11	10	20	11	13	0	0	3	17	6	9
Maireana decalvans	0	0	0	0	0	0	0	0	0	0	0	10	0	20	0	10	20	0	0	0	0	20	20	10	20	0	0	18	5	8
Maireana dichoptera	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	20	0	0	0	10	10	20	10	0	0	0	0	20	2	6
Maireana diffusa	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Maireana enchylaenoides	11	10	20	0	10	10	10	0	0	0	10	0	20	20	0	10	20	0	0	10	10	20	20	20	20	0	1	10	8	16
Maireana eriantha	0	0	10	0	0	10	0	0	0	0	10	20	20	20	0	20	10	0	0	0	0	0	0	0	0	0	0	18	4	8
Maireana erioclada	0	11	20	0	0	20	20	0	0	0	10	11	20	20	0	0	20	0	0	0	0	0	0	0	13	0	3	19	6	7
Maireana eriosphaera	10	20	20	0	10	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	2	6
Maireana excavata	0	0	13	0	0	0	0	0	0	0	0	11	10	20	0	0	20	0	0	0	0	0	0	0	20	0	2	22	3	4
Maireana georgei	20	20	20	10	20	20	20	10	20	20	20	20	20	20	0	20	20	0	0	11	10	10	0	0	0	0	1	8	14	18
Maireana glomerifolia	10	20	20	0	0	10	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	22	2	4
Maireana humillima	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	20	0	0	0	0	20	0	10	20	0	0	21	3	5
Maireana integra	10	10	20	0	10	20	10	0	0	10	20	20	20	20	0	20	20	0	0	0	0	20	0	0	0	0	0	12	9	14
Maireana lanosa	20	20	10	0	0	10	10	0	0	11	20	20	10	20	0	20	20	0	0	0	0	10	0	0	0	0	1	14	7	12
Maireana lobiflora	10	0	10	0	10	20	20	0	0	0	20	20	20	20	0	0	20	0	0	0	0	11	0	0	0	0	1	16	7	10
Maireana luehmannii	0	10	10	0	20	10	0	0	0	20	20	10	0	0	0	11	0	0	0	0	0	0	0	0	0	0	1	19	3	7
Maireana marginata	11	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25	1	1
Maireana melanocarpa	0	0	0	0	0	10	0	0	0	0	0	20	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2	3
Maireana melanocoma	20	20	20	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	3	4
Maireana microcarpa	0	0	0	0	0	10	0	0	0	11	0	20	20	20	0	20	20	0	0	0	0	20	20	11	0	0	2	18	7	8
Maireana microphylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	20	0	0	10	20	20	20	20	20	0	0	18	7	8
Maireana murrayana	10	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Maireana oppositifolia	10	0	20	0	0	20	20	0	0	0	0	0	20	20	0	0	20	0	0	0	0	0	0	0	0	0	0	19	6	7

Plant Species	**Western Coastlands**	**Pilbara**	**Yilgarn Plateau**	**Kimberley**	**Sandland North**	**Sandland South**	**Nullarbor Plain**	**North Aust. Plateaus**	**Carpentaria Fall**	**Barkly-Tanami Plains**	**Central Aust. Ranges**	**Central Lowlands West**	**Eyre Peninsula**	**Gulfs Ranges**	**Carpentaria Lowlands**	**Central Lowlands Cent.**	**Murray Lowlands**	**Peninsular Uplands**	**Great Barrier Reef**	**Burdekin Uplands**	**Fitzroy Uplands**	**Central Lowlands East**	**New England-Moreton Upl'ds**	**Macquarie Uplands**	**Kosciuszkan Uplands**	**Tasmanian Uplands**	**Discount**	**Absent**	**Major Pres**	**Total Pres**
Maireana ovata	0	0	0	0	0	20	0	0	0	0	11	20	11	20	0	0	10	0	0	0	0	10	0	0	0	0	2	21	3	5
Maireana pentagona	10	0	10	0	0	0	0	0	0	0	0	10	10	0	0	10	20	0	0	0	0	20	10	11	20	0	1	17	3	9
Maireana pentatropis	0	0	20	0	0	20	20	0	0	0	20	20	20	20	0	20	20	0	0	0	0	10	0	0	0	0	0	16	9	10
Maireana planifolia	20	20	20	0	20	20	11	0	0	10	20	20	20	10	0	10	10	0	0	0	0	10	0	0	0	0	1	13	8	13
Maireana platycarpa	20	20	20	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	3	4
Maireana polypterygia	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	1	25	1	1
Maireana prosthecochaeta	0	20	20	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2	3
Maireana pyramidata	10	20	20	0	10	10	10	0	0	0	10	20	20	20	0	20	20	0	0	0	0	10	0	0	12	0	1	13	7	13
Maireana radiata	0	0	20	0	0	20	20	0	0	0	10	10	20	20	0	0	20	0	0	0	0	0	0	0	0	0	0	18	6	8
Maireana rohrlachii	0	0	0	0	0	0	0	0	0	0	0	0	20	20	0	0	20	0	0	0	0	0	0	0	11	0	1	23	3	3
Maireana schistocarpa	0	0	0	0	0	10	0	0	0	0	20	10	20	11	0	20	10	0	0	0	0	20	0	0	0	0	1	19	4	7
Maireana scleroptera	0	10	10	0	10	20	0	0	0	0	20	20	0	11	0	0	10	0	0	0	0	0	0	0	0	0	1	19	3	7
Maireana sedifolia	11	0	20	0	0	20	20	0	0	0	10	20	20	20	0	20	20	0	0	0	0	0	0	0	11	0	2	17	8	9
Maireana spongiocarpa	0	0	10	12	0	0	0	0	0	0	20	20	20	20	0	20	11	0	0	0	0	0	0	0	12	0	3	20	5	6
Maireana stipitata	20	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Maireana suaedifolia	0	10	20	0	0	20	0	0	0	0	0	0	20	0	0	0	10	0	0	0	0	0	0	0	0	0	0	21	3	5
Maireana thesioides	10	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2	3
Maireana tomentosa	20	20	20	0	20	20	11	0	0	10	20	20	10	20	0	10	20	0	0	0	0	10	0	0	0	0	1	13	9	13
Maireana trichoptera	20	10	20	0	0	20	20	0	0	10	20	20	20	20	0	10	20	0	0	0	0	0	0	0	11	0	1	14	9	12
Maireana triptera	10	20	20	10	20	20	10	0	10	20	20	20	20	20	0	20	20	0	0	11	0	20	0	0	0	0	1	10	12	16
Maireana turbinata	0	13	20	0	0	20	20	0	0	0	10	20	20	20	0	20	20	0	0	0	0	10	0	0	0	14	2	16	8	10
Maireana villosa	10	20	20	0	20	20	11	0	20	20	20	20	20	10	0	20	20	0	0	20	20	20	10	0	0	0	1	9	14	17
Affiliate species																														
Roycea divaricata #	10	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2	3
Roycea pycnophylloides #	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Roycea spinescens #	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Eremophea aggregata $	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Eremophea spinose $	20	20	20	0	20	20	0	0	0	20	20	20	12	0	0	0	0	0	0	13	0	13	0	0	0	0	3	18	8	8
Neobassia astrocarpa $	20	20	0	20	20	0	0	0	0	20	10	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	1	20	5	6
Enchylaena lanata	10	11	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	24	1	2
Enchylaena tomentosa	20	20	20	20	20	20	20	13	20	20	20	20	20	20	20	20	20	10	20	20	20	20	20	20	20	0	1	2	23	24
Didymanthus roei @	20	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	2	2
Dissocarpus biflorus @	0	0	12	0	0	0	20	0	0	0	20	20	20	20	0	20	20	0	0	20	20	20	0	10	12	0	2	15	10	11
Dissocarpus fontinalis @	0	0	0	0	0	0	0	0	0	0	0	20	20	20	0	11	10	0	0	0	0	0	0	0	0	0	1	22	3	4
Dissocarpus latifolius @	0	0	0	0	0	11	0	0	0	0	0	20	10	12	0	20	13	0	0	0	0	10	0	0	0	0	3	22	2	4
Dissocarpus paradoxus @	20	20	20	0	10	20	20	0	0	10	20	20	20	20	0	20	20	0	0	10	0	20	11	13	0	0	2	11	12	15
Eriochiton sclerolaenoides @	10	0	20	0	10	20	20	0	0	0	20	20	20	20	0	20	20	0	0	0	0	10	0	13	10	0	1	13	9	13
Malacocera albolanata %	0	0	0	0	0	0	0	0	0	0	0	20	20	11	0	20	13	0	0	0	0	0	0	0	0	0	2	23	3	3

Plant Species	**Western Coastlands**	**Pilbara**	**Yilgarn Plateau**	**Kimberley**	**Sandland North**	**Sandland South**	**Nullarbor Plain**	**North Aust. Plateaus**	**Carpentaria Fall**	**Barkly-Tanami Plains**	**Central Aust. Ranges**	**Central Lowlands West**	**Eyre Peninsula**	**Gulfs Ranges**	**Carpentaria Lowlands**	**Central Lowlands Cent.**	**Murray Lowlands**	**Peninsular Uplands**	**Great Barrier Reef**	**Burdekin Uplands**	**Fitzroy Uplands**	**Central Lowlands East**	**New England-Moreton Upl'ds**	**Macquarie Uplands**	**Kosciuszkan Uplands**	**Tasmanian Uplands**	**Discount**	**Absent**	**Major Pres**	**Total Pres**
Malacocera biflora %	0	0	0	0	0	11	0	0	0	0	10	20	0	11	0	11	0	0	0	0	0	0	0	0	0	0	3	24	1	2
Malacocera gracilis %	0	0	0	0	0	0	12	0	0	0	0	20	20	20	0	0	0	0	0	0	0	0	0	0	0	0	1	23	3	3
Malacocera tricornis %	0	0	10	0	0	11	0	0	0	0	20	20	20	20	0	20	20	0	0	0	0	20	0	0	0	0	1	18	7	8
SclerolaenAff Subgroup																														
Sclerolaena alata	0	10	20	0	10	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	1	4
Sclerolaena anisacanthoides	0	0	0	0	0	0	0	0	0	0	10	10	0	11	0	20	20	0	0	20	20	20	10	0	0	0	1	18	5	8
Sclerolaena articulata	0	10	10	0	0	0	10	0	0	0	10	20	10	20	0	20	20	0	0	0	0	20	0	0	12	0	1	16	5	10
Sclerolaena beaugleholei	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Sclerolaena bicornis	10	20	10	10	10	0	0	10	20	20	20	20	20	20	20	20	20	0	0	10	20	20	11	13	11	0	3	8	12	18
Sclerolaena bicuspis	10	0	0	0	0	0	0	0	0	0	0	10	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	22	1	4
Sclerolaena birchii	0	0	0	0	0	0	0	0	10	10	20	10	0	20	0	20	20	0	0	10	20	20	20	20	20	0	0	13	9	13
Sclerolaena blackiana	0	0	0	0	0	10	0	0	0	0	0	20	0	11	0	10	11	0	0	0	0	10	0	0	0	0	2	22	1	4
Sclerolaena blakei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Sclerolaena brachyptera	0	0	0	0	10	10	0	0	0	0	20	20	20	20	0	20	20	0	0	0	0	20	0	13	11	0	2	17	7	9
Sclerolaena brevifolia	0	0	20	0	0	20	20	0	0	0	0	0	20	20	0	0	20	0	0	0	0	0	0	0	0	0	0	20	6	6
Sclerolaena burbidgeae	0	10	20	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	1	3
Sclerolaena calcarata	0	0	0	0	0	10	0	0	0	0	20	20	0	11	12	20	20	0	0	10	20	20	11	14	0	0	4	18	6	8
Sclerolaena clelandii	0	0	10	0	20	20	0	0	0	10	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	4	6
Sclerolaena constricta	0	0	0	0	0	10	0	0	0	0	10	20	10	20	0	10	10	0	0	0	0	0	0	0	0	0	0	19	2	7
Sclerolaena convexula	0	20	20	0	10	20	11	12	12	20	20	20	20	20	0	20	20	0	0	10	20	20	10	0	0	0	3	11	12	15
Sclerolaena cornishiana	10	20	11	10	20	10	0	12	20	20	20	20	0	0	10	20	0	0	0	0	10	0	0	0	0	0	2	14	7	12
Sclerolaena costata	20	20	20	0	10	10	10	0	0	10	20	10	10	10	0	10	10	0	0	0	0	0	0	0	0	0	0	13	4	13
Sclerolaena crenata	0	0	0	10	10	0	0	0	0	20	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	1	4
Sclerolaena cuneata	10	20	20	0	10	10	0	0	11	20	20	20	20	20	10	20	20	0	0	11	11	20	0	11	0	0	4	12	10	14
Sclerolaena decurrens	0	0	0	0	0	11	10	0	0	0	20	20	20	20	0	20	20	0	0	0	0	20	0	0	0	0	1	18	7	8
Sclerolaena densiflora	20	20	20	0	10	0	0	0	0	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	3	6
Sclerolaena deserticola	10	10	20	0	10	20	0	0	0	10	20	10	10	20	0	10	10	0	0	0	0	10	0	0	0	0	0	13	4	13
Sclerolaena diacantha	20	20	20	0	10	20	20	0	0	10	20	20	20	20	0	20	20	0	0	10	10	20	10	11	20	0	1	8	13	18
Sclerolaena divaricata	0	20	10	0	10	20	0	0	11	10	20	20	20	20	10	20	20	0	0	0	0	20	10	0	11	0	2	12	9	14
Sclerolaena drummondii	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Sclerolaena eriacantha	10	20	20	0	10	20	0	0	11	20	20	20	20	20	0	20	10	0	0	0	0	20	0	13	10	0	2	12	10	14
Sclerolaena eurotioides	20	10	20	0	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	3	5
Sclerolaena everistiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	13	0	0	20	11	0	0	0	0	0	2	24	1	2
Sclerolaena fimbriolata	0	11	20	0	10	10	0	0	0	0	10	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	2	22	1	4
Sclerolaena fontinalis	0	0	0	0	0	0	0	0	0	0	20	0	0	11	0	11	0	0	0	0	0	0	0	0	0	0	2	25	1	1
Sclerolaena forrestiana	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Sclerolaena fusiformis	10	11	20	0	0	10	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	22	1	4
Sclerolaena gardneri	20	20	20	0	0	10	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	3	5

Plant Species	**Western Coastlands**	**Pilbara**	**Yilgarn Plateau**	**Kimberley**	**Sandland North**	**Sandland South**	**Nullarbor Plain**	**North Aust. Plateaus**	**Carpentaria Fall**	**Barkly-Tanami Plains**	**Central Aust. Ranges**	**Central Lowlands West**	**Eyre Peninsula**	**Gulfs Ranges**	**Carpentaria Lowlands**	**Central Lowlands Cent.**	**Murray Lowlands**	**Peninsular Uplands**	**Great Barrier Reef**	**Burdekin Uplands**	**Fitzroy Uplands**	**Central Lowlands East**	**New England-Moreton Upl'ds**	**Macquarie Uplands**	**Kosciuszkan Uplands**	**Tasmanian Uplands**	**Discount**	**Absent**	**Major Pres**	**Total Pres**
Sclerolaena glabra	11	20	10	10	0	0	0	0	10	20	20	20	0	10	20	20	0	0	0	10	0	10	0	0	0	0	1	14	6	12
Sclerolaena holtiana	0	0	0	0	0	20	11	0	0	0	11	20	20	20	0	10	10	0	0	0	0	13	0	0	0	0	3	20	4	6
Sclerolaena hostilis	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Sclerolaena intricata	0	0	10	0	0	11	0	0	0	10	20	20	20	20	0	20	20	0	0	11	0	20	0	0	0	0	2	17	7	9
Sclerolaena johnsonii	0	0	10	0	0	20	0	10	0	0	20	20	0	0	0	20	11	0	0	0	10	0	0	0	0	0	1	19	4	7
Sclerolaena lanicuspis	11	20	20	10	10	20	0	0	20	20	20	20	20	20	10	20	20	0	0	20	10	20	11	0	0	0	2	9	13	17
Sclerolaena limbata	0	0	0	0	0	0	0	0	0	0	13	20	10	20	0	0	20	0	0	0	0	10	0	0	0	0	1	21	3	5
Sclerolaena longicuspis	0	0	0	0	0	0	0	0	0	0	20	20	10	20	0	20	10	0	0	11	0	0	0	0	0	0	1	20	4	6
Sclerolaena medicaginoides	11	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25	1	1
Sclerolaena microcarpa	0	11	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25	1	1
Sclerolaena minuta	0	20	0	0	0	0	0	0	10	20	20	10	0	0	0	20	0	0	0	11	0	0	0	0	0	0	1	20	4	6
Sclerolaena muelleri	0	0	0	0	10	0	0	0	0	20	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	24	1	2
Sclerolaena muricata	0	0	0	0	0	10	0	0	10	0	10	20	11	20	10	20	20	0	0	10	20	20	20	20	20	0	1	12	9	14
Sclerolaena napiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	25	1	1
Sclerolaena obliquicuspis	10	0	20	0	0	20	20	0	0	0	20	20	20	20	0	20	20	0	0	0	0	10	0	0	14	0	1	15	9	11
Sclerolaena parallelicuspis	10	0	0	0	0	10	0	0	0	10	10	20	20	20	0	20	20	0	0	0	0	10	0	0	0	0	0	16	5	10
Sclerolaena parviflora	0	0	20	0	10	20	11	0	0	0	20	10	20	10	0	0	20	0	0	0	0	0	0	0	0	0	1	18	5	8
Sclerolaena patenticuspis	0	0	20	0	11	20	0	0	0	10	20	20	20	20	0	20	20	0	0	0	0	10	0	0	14	0	2	16	8	10
Sclerolaena ramulosa	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	11	0	0	0	20	20	20	0	0	0	0	1	22	3	4
Sclerolaena recurvicuspis	20	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2	3
Sclerolaena stelligera	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	20	20	0	0	0	10	20	10	0	10	0	0	19	3	7
Sclerolaena stylosa	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Sclerolaena symoniana	0	0	10	0	11	20	11	0	0	10	20	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	2	21	2	5
Sclerolaena tatei	0	0	0	0	0	0	0	0	0	0	0	20	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2	3
Sclerolaena tetracuspis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	10	0	0	11	20	20	20	0	0	0	1	21	3	5
Sclerolaena tetragona	0	20	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Sclerolaena tricuspis	0	0	0	0	0	11	0	0	0	0	0	20	10	20	10	20	20	0	0	20	20	20	10	13	0	0	2	16	7	10
Sclerolaena tridens	20	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2	3
Sclerolaena tubata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	25	1	1
Sclerolaena uniflora	20	10	20	0	11	20	20	0	0	0	10	20	20	20	0	11	20	0	0	0	0	20	0	0	11	0	3	15	9	11
Sclerolaena urceolata	0	0	0	0	11	0	0	0	0	0	20	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	24	1	2
Sclerolaena ventricosa	0	0	0	0	0	10	0	0	0	0	13	20	20	20	0	20	20	0	0	0	0	20	0	0	11	0	2	19	6	7
Sclerolaena walkeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Affiliate species																														
Neobassia proceriflora	0	0	0	0	0	10	0	0	0	0	20	20	10	10	0	20	20	0	0	0	0	20	0	13	0	0	1	17	5	8
Threlkeldia diffusa	20	20	20	10	0	11	20	0	0	0	0	0	20	20	0	0	20	0	0	0	0	0	0	0	20	20	1	15	9	10
Threlkeldia inchoata	0	0	0	0	0	11	0	0	0	0	10	20	0	0	0	0	13	0	0	0	0	0	0	0	0	0	2	22	1	2
Osteocarpum acropterum #	20	10	0	0	11	20	10	0	0	0	20	20	20	20	0	20	20	0	0	0	0	20	0	0	11	0	2	13	9	11

Plant Species	**Western Coastlands**	**Pilbara**	**Yilgarn Plateau**	**Kimberley**	**Sandland North**	**Sandland South**	**Nullarbor Plain**	**North Aust. Plateaus**	**Carpentaria Fall**	**Barkly-Tanami Plains**	**Central Aust. Ranges**	**Central Lowlands West**	**Eyre Peninsula**	**Gulfs Ranges**	**Carpentaria Lowlands**	**Central Lowlands Cent.**	**Murray Lowlands**	**Peninsular Uplands**	**Great Barrier Reef**	**Burdekin Uplands**	**Fitzroy Uplands**	**Central Lowlands East**	**New England-Moreton Upl'ds**	**Macquarie Uplands**	**Kosciuszkan Uplands**	**Tasmanian Uplands**	**Discount**	**Absent**	**Major Pres**	**Total Pres**
Osteocarpum dipterocarpum #	0	0	0	0	0	11	0	0	0	0	20	20	20	20	0	20	11	0	0	0	0	20	0	0	0	0	2	18	6	6
Osteocarpum pentapterum #	0	0	0	0	0	0	0	0	0	11	10	20	0	10	0	10	0	0	0	0	0	0	0	0	0	0	1	21	1	4
Osteocarpum salsuginosum #	0	0	20	0	0	0	10	0	0	0	20	10	20	20	0	10	20	0	0	0	0	0	0	0	0	0	0	18	5	8
Osteocarpum scleropterum #	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	25	1	1

Subfamily Salicornioideae

Plant Species	**Western Coastlands**	**Pilbara**	**Yilgarn Plateau**	**Kimberley**	**Sandland North**	**Sandland South**	**Nullarbor Plain**	**North Aust. Plateaus**	**Carpentaria Fall**	**Barkly-Tanami Plains**	**Central Aust. Ranges**	**Central Lowlands West**	**Eyre Peninsula**	**Gulfs Ranges**	**Carpentaria Lowlands**	**Central Lowlands Cent.**	**Murray Lowlands**	**Peninsular Uplands**	**Great Barrier Reef**	**Burdekin Uplands**	**Fitzroy Uplands**	**Central Lowlands East**	**New England-Moreton Upl'ds**	**Macquarie Uplands**	**Kosciuszkan Uplands**	**Tasmanian Uplands**	**Discount**	**Absent**	**Major Pres**	**Total Pres**
***Tecticornia* Clade**																														
Tecticornia annelida	11	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25	1	1
Tecticornia arborea	10	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	1	3
Tecticornia arbuscula	0	0	20	0	0	0	11	0	0	0	0	10	20	20	0	0	20	0	0	0	0	10	0	0	0	20	1	19	5	7
Tecticornia auriculata	20	20	0	11	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	23	3	3
Tecticornia australasica	0	0	0	0	0	0	0	20	20	10	14	0	0	0	20	0	0	20	0	20	20	0	10	0	0	0	1	18	6	8
Tecticornia bibenda	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia bulbosa	10	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Tecticornia calyptrata	0	11	20	0	10	10	0	0	0	20	20	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	1	20	3	6
Tecticornia chartacea	0	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	2	2
Tecticornia cupuliformis	0	0	0	0	0	0	0	0	0	0	0	20	10	0	0	11	0	0	0	0	0	0	0	0	0	0	1	24	1	2
Tecticornia cymbiformis	0	20	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25	1	1
Tecticornia disarticulata	20	20	20	0	0	10	20	0	0	0	20	20	20	20	0	20	10	0	0	0	0	0	0	0	0	0	0	15	9	11
Tecticornia doleiformis	20	10	20	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	2	4
Tecticornia entrichoma	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia fimbriata	11	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25	1	1
Tecticornia flabelliformis	0	0	20	0	0	0	0	0	0	0	0	0	20	20	0	0	20	0	0	0	0	0	0	0	0	0	0	22	4	4
Tecticornia fontinalis	0	0	0	0	0	0	0	0	0	0	0	20	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Tecticornia globulifera	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia halocnemoides	20	20	20	20	20	20	10	20	10	20	20	20	20	20	20	20	20	20	0	10	10	10	0	0	20	0	0	4	17	22
Tecticornia indefessa	0	0	20	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	2
Tecticornia indica	20	20	20	20	20	20	10	20	20	20	20	20	20	20	20	20	20	20	0	20	20	0	20	0	0	0	0	5	20	21
Tecticornia laevigata	0	10	20	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	1	4
Tecticornia lepidosperma	20	0	20	0	0	0	0	0	0	0	0	0	20	10	0	0	10	0	0	0	0	0	0	0	0	0	0	21	3	5
Tecticornia leptoclada	20	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2	3

Plant Species	**Western Coastlands**	**Pilbara**	**Yilgarn Plateau**	**Kimberley**	**Sandland North**	**Sandland South**	**Nullarbor Plain**	**North Aust. Plateaus**	**Carpentaria Fall**	**Barkly-Tanami Plains**	**Central Aust. Ranges**	**Central Lowlands West**	**Eyre Peninsula**	**Gulfs Ranges**	**Carpentaria Lowlands**	**Central Lowlands Cent.**	**Murray Lowlands**	**Peninsular Uplands**	**Great Barrier Reef**	**Burdekin Uplands**	**Fitzroy Uplands**	**Central Lowlands East**	**New England-Moreton Upl'ds**	**Macquarie Uplands**	**Kosciuszkan Uplands**	**Tasmanian Uplands**	**Discount**	**Absent**	**Major Pres**	**Total Pres**
Tecticornia loriae	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia lylei	0	0	20	0	0	10	20	0	0	0	0	0	20	0	0	0	20	0	0	0	0	0	0	0	0	0	0	21	4	5
Tecticornia medullosa	0	0	0	0	0	0	0	0	0	11	0	20	20	10	0	10	11	0	0	0	0	0	0	0	0	0	2	22	2	4
Tecticornia medusa	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia mellaria	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia moniliformis	0	0	20	0	0	0	11	0	0	0	0	0	20	10	0	0	20	0	0	0	0	0	0	0	10	0	1	21	3	5
Tecticornia nitida	0	0	0	0	0	0	0	0	0	0	0	20	20	0	0	0	20	0	0	0	0	0	0	0	0	0	0	23	3	3
Tecticornia papillata	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia peltata	20	11	20	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	23	2	3
Tecticornia pergranulata	20	10	20	10	0	10	10	10	0	20	20	20	20	20	20	20	20	10	0	20	20	10	20	14	20	10	1	4	14	22
Tecticornia pluriflora	0	0	0	0	0	0	0	0	0	0	0	20	20	20	0	10	10	0	0	0	0	10	0	0	0	0	0	20	3	6
Tecticornia pruinosa	20	20	20	0	11	20	10	0	0	0	20	10	20	20	0	0	20	0	0	0	0	0	0	0	0	0	1	16	8	10
Tecticornia pterygosperma	20	20	20	0	10	11	20	0	0	0	0	10	20	20	0	0	20	0	0	0	0	0	0	0	0	0	1	17	7	9
Tecticornia sparagosa	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia syncarpa	20	0	20	0	0	0	11	0	0	0	0	0	10	20	0	0	20	0	0	0	0	0	0	0	0	0	1	21	4	5
Tecticornia tenuis	0	0	20	0	0	0	0	0	0	20	20	20	20	20	0	20	20	0	0	0	0	10	0	0	0	0	0	17	8	9
Tecticornia triandra	0	0	20	0	0	10	0	0	0	0	20	0	10	11	0	20	20	0	0	0	0	10	0	0	0	0	1	19	4	7
Tecticornia undulata	10	10	20	0	10	0	0	0	0	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	1	6
Tecticornia uniflora	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Tecticornia verrucosa	10	10	20	20	20	0	0	20	0	20	20	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	17	6	9
***Sarcocornia* Clade**																														
Sarcocornia blackiana	20	0	20	0	0	0	10	0	0	0	0	20	20	20	0	0	20	0	0	0	0	0	0	0	20	20	0	17	8	9
Sarcocornia globosa	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	1	1
Sarcocornia quinqueflora	20	0	20	0	0	0	0	0	0	0	0	10	20	20	0	0	20	10	0	10	20	0	20	20	20	20	0	13	10	13

Subfamilies Salsoloideae and Suaedoideae

Plant Species	Western Coastlands	Pilbara	Yilgarn Plateau	Kimberley	Sandland North	Sandland South	Nullarbor Plain	North Aust. Plateaus	Carpentaria Fall	Barkly-Tanami Plains	Central Aust. Ranges	Central Lowlands West	Eyre Peninsula	Gulfs Ranges	Carpentaria Lowlands	Central Lowlands Cent.	Murray Lowlands	Peninsular Uplands	Great Barrier Reef	Burdekin Uplands	Fitzroy Uplands	Central Lowlands East	New England-Moreton Upl'ds	Macquarie Uplands	Kosciuszkan Uplands	Tasmanian Uplands	Discount	Absent	Major Pres	Total Pres
***Salsola* (Kali) Clade**																														
Salsola australis	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	10	20	20	20	20	20	20	10	0	0	24	26
***Suaeda* (Brezia) Clade**																														
Suaeda arbusculoides	10	20	0	20	11	0	0	20	0	0	0	0	0	0	10	0	0	0	0	20	20	0	20	0	0	0	1	18	6	8
Suaeda australis	20	0	20	0	0	0	10	10	0	0	0	10	20	20	0	0	20	20	0	20	20	0	20	20	20	20	0	11	12	15

Key to tables of this Appendix

Provincial presence of collection plot points is scored as follows:

0	No plot point for a collection record in the province.
10	Minor or isolated population/outlier of species in the province, remote from greater range.
20	Major population of species in the province.
11	The only plot point for a province is located near a boundary with an adjoining province where the species is more prominently present.
12	Incorrect or unreliable position due to vague, imprecise or misinterpreted locality; or plot point coordinates inconsistent with locality information.
13	Recognized or likely introduction to province.
14	Cultivation at Research, Education or Horticultural Institution.

Sum totals for species provincial frequencies are:

Discount: Sum of provinces with discounted presence, recorded as 11, 12, 13 or 14.

Absent: Sum of provinces with presence recorded 0, 11, 12, 13 or 14.

Major presence: Sum of provinces with presence recorded 20.

Total presence: Sum of provinces with major presence (20) and with minor/outlier/isolate population (10)

#, %, @, $: In Subfamily Camphorosmoideae, symbols after species names in subgroups of affiliate genera, link taxa believed to be of the same subclade. The two *Enchylaena* spp. are now considered not closely related but are part of distinct *Maireana* lineages. Similarly *Threlkeldia* spp. are now considered, and *Neobassia* spp. determined, to be distantly related (Cabrera *et al.* 2009).

Appendix IX: Standard Distance Sorenson Dissimilarity for provincial chenopod assembly

TOTAL PRESENCE **PROVINCE**	Western Coastlands	Pilbara	Yilgarn Plateau	Kimberley	Sandland North	Sandland South	Nullarbor Plain	North Aust. Plateaus	Carpentaria Fall	Barkly-Tanami Plain	Central Aust. Ranges	Central Lowlands West	Eyre Peninsula
Western Coastlands	0.0	0.3275	0.2886	0.7778	0.4646	0.4357	0.5051	0.8248	0.8333	0.5812	0.4923	0.5225	0.4891
Pilbara	0.3275	0.0	0.3879	0.7008	0.3923	0.5	0.6133	0.8167	0.7795	0.4943	0.4979	0.5882	0.6187
Yilgarn Plateau	0.2886	0.3879	0.0	0.8265	0.472	0.3447	0.456	0.8730	0.8571	0.5885	0.3974	0.4604	0.3804
Kimberley	0.7778	0.7008	0.8265	0.0	0.6667	0.8273	0.8333	0.3714	0.3810	0.5955	0.7722	0.8396	0.8488
Sandland North	0.4646	0.3923	0.472	0.6667	0.0	0.4301	0.6533	0.7978	0.7292	0.3846	0.4340	0.5685	0.6372
Sandland South	0.4357	0.5	0.3447	0.8273	0.4301	0.0	0.4301	0.8788	0.7986	0.4946	0.3176	0.3662	0.3532
Nullarbor Plain	0.5051	0.6133	0.456	0.8333	0.6533	0.4301	0.0	0.8652	0.875	0.7063	0.5472	0.5436	0.4159
North Australian Plateaus	0.8248	0.8167	0.8730	0.3714	0.7978	0.8788	0.8652	0.0	0.5429	0.7317	0.8543	0.8778	0.8909
Carpentaria Fall	0.8333	0.7795	0.8571	0.3810	0.7292	0.7986	0.875	0.5429	0.0	0.5955	0.7595	0.7968	0.8488
Barkly-Tanami Plain	0.5812	0.4943	0.5885	0.5955	0.3846	0.4946	0.7063	0.7317	0.5955	0.0	0.3951	0.5043	0.5708
Central Australian Ranges	0.4923	0.4979	0.3974	0.7722	0.4340	0.3176	0.5472	0.8543	0.7595	0.3951	0.0	0.2145	0.3194
Central Lowlands West	0.5225	0.5882	0.4604	0.8396	0.5685	0.3662	0.5436	0.8778	0.7968	0.5043	0.2145	0.0	0.2114
Eyre Peninsula	0.4891	0.6187	0.3804	0.8488	0.6372	0.3532	0.4159	0.8909	0.8488	0.5708	0.3194	0.2114	0.0
Gulfs Ranges	0.5	0.6235	0.4198	0.8353	0.6339	0.3633	0.4375	0.8896	0.8118	0.5760	0.3357	0.2063	0.1267
Carpentaria Lowlands	0.8322	0.7619	0.8667	0.4146	0.7684	0.8261	0.8947	0.4706	0.3659	0.6364	0.7962	0.8172	0.8480
Central Lowlands Centre	0.5846	0.6214	0.5256	0.8101	0.6132	0.3961	0.5472	0.8675	0.7595	0.4829	0.2555	0.2013	0.2917
Murray Lowlands	0.4947	0.6212	0.3994	0.8436	0.6223	0.3406	0.4249	0.8837	0.8324	0.5841	0.3288	0.2346	0.1586
Peninsular Uplands	0.8676	0.8824	0.8936	0.6471	0.8864	0.8779	0.8409	0.5556	0.6471	0.7778	0.8933	0.8883	0.8780
Great Barrier Reef	0.968	0.9630	0.9774	0.8261	0.9481	0.9667	0.9481	0.875	0.8261	0.9429	0.9712	0.9762	0.9739
Burdekin Uplands	0.7561	0.7143	0.7778	0.5484	0.6897	0.7610	0.8103	0.5636	0.5484	0.5963	0.6742	0.6908	0.75
Fitzroy Uplands	0.7062	0.7125	0.7467	0.6533	0.6589	0.6744	0.7209	0.6471	0.6	0.5410	0.6021	0.6182	0.6976
Central Lowlands East	0.6050	0.6561	0.5724	0.8235	0.6316	0.4678	0.5895	0.8915	0.7794	0.5191	0.3571	0.3025	0.3684
New England-Moreton Uplands	0.7095	0.7778	0.7403	0.7922	0.7710	0.7126	0.7252	0.7714	0.7143	0.6452	0.6684	0.6486	0.6522
Macquarie Uplands	0.7778	0.8621	0.8037	0.9	0.8421	0.7962	0.7368	0.9245	0.8	0.7944	0.75	0.7659	0.7368
Koscziuskan Uplands	0.6647	0.8333	0.7156	0.8310	0.792	0.7262	0.696	0.875	0.8028	0.7966	0.7219	0.7130	0.6517
Tasmanian Uplands	0.7902	0.9206	0.8359	0.8049	0.8947	0.8841	0.8105	0.8235	0.9024	0.8864	0.9108	0.8817	0.8129

TOTAL PRESENCE **PROVINCE**	Gulfs Ranges	Carpentaria Lowlands	Central Lowlands Centr.	Murray Lowlands	Peninsular Uplands	Great Barrier Reef	Burdekin Uplands	Fitzroy Uplands	Central Lowlands East	New Engl. Moreton Uplands	Macquarie Uplands	Koscziuska n Uplands	Tasmanian Uplands
Western Coastlands	0.5	0.8322	0.5846	0.4947	0.8676	0.968	0.7561	0.7062	0.6050	0.7095	0.7778	0.6647	0.7902
Pilbara	0.6235	0.7619	0.6214	0.6212	0.8824	0.9630	0.7143	0.7125	0.6561	0.7778	0.8621	0.8333	0.9206
Yilgarn Plateau	0.4198	0.8667	0.5256	0.3994	0.8936	0.9774	0.7778	0.7467	0.5724	0.7403	0.8037	0.7156	0.8359
Kimberley	0.8353	0.4146	0.8101	0.8436	0.6471	0.8261	0.5484	0.6533	0.8235	0.7922	0.9000	0.8310	0.8049
Sandland North	0.6339	0.7684	0.6132	0.6223	0.8864	0.9481	0.6897	0.6589	0.6316	0.7710	0.8421	0.7920	0.8947
Sandland South	0.3633	0.8261	0.3961	0.3406	0.8779	0.9667	0.7610	0.6744	0.4678	0.7126	0.7962	0.7262	0.8841
Nullarbor Plain	0.4375	0.8947	0.5472	0.4249	0.8409	0.9481	0.8103	0.7209	0.5895	0.7252	0.7368	0.6960	0.8105
North Australian Plateaus	0.8896	0.4706	0.8675	0.8837	0.5556	0.875	0.5636	0.6471	0.8915	0.7714	0.9245	0.8750	0.8235
Carpentaria Fall	0.8118	0.3659	0.7595	0.8324	0.6471	0.8261	0.5484	0.6000	0.7794	0.7143	0.8	0.8028	0.9024
Barkly-Tanami Plain	0.5760	0.6364	0.4829	0.5841	0.7778	0.9429	0.5963	0.5410	0.5191	0.6452	0.7944	0.7966	0.8864
Central Australian Ranges	0.3357	0.7962	0.2555	0.3288	0.8933	0.9712	0.6742	0.6021	0.3571	0.6684	0.7500	0.7219	0.9108
Central Lowlands West	0.2063	0.8172	0.2013	0.2346	0.8883	0.9762	0.6908	0.6182	0.3025	0.6486	0.7659	0.7130	0.8817
Eyre Peninsula	0.1267	0.8480	0.2917	0.1586	0.8780	0.9739	0.75	0.6976	0.3684	0.6522	0.7368	0.6517	0.8129
Gulfs Ranges	0.0	0.8225	0.2937	0.1466	0.8765	0.9735	0.7158	0.6749	0.3485	0.6098	0.6596	0.5879	0.7751
Carpentaria Lowlands	0.8225	0.0	0.7834	0.8315	0.5758	0.8182	0.4754	0.5676	0.7778	0.6579	0.8644	0.8286	0.85
Central Lowlands Centre.	0.2937	0.7834	0.0	0.2475	0.8667	0.9712	0.6180	0.5183	0.1984	0.5544	0.7045	0.6684	0.9236
Murray Lowlands	0.1466	0.8315	0.2475	0.0	0.8713	0.975	0.6683	0.5849	0.2601	0.5327	0.6345	0.5481	0.8090
Peninsular Uplands	0.8765	0.5758	0.8667	0.8713	0.0	0.7333	0.5926	0.6119	0.8594	0.6522	0.6923	0.7143	0.6364
Great Barrier Reef	0.9735	0.8182	0.9712	0.975	0.7333	0.0	0.9070	0.9286	0.9658	0.9310	0.9024	0.9231	0.9091
Burdekin Uplands	0.7158	0.4754	0.6180	0.6683	0.5926	0.9070	0.0	0.2632	0.5769	0.4021	0.6000	0.6264	0.7705
Fitzroy Uplands	0.6749	0.5676	0.5183	0.5849	0.6119	0.9286	0.2632	0.0	0.4438	0.2727	0.5054	0.5385	0.7838
Central Lowlands East	0.3485	0.7778	0.1984	0.2601	0.8594	0.9658	0.5769	0.4438	0.0	0.4620	0.5974	0.5758	0.8815
New England-Moreton Uplands	0.6098	0.6579	0.5544	0.5327	0.6522	0.9310	0.4021	0.2727	0.4620	0.0	0.3053	0.3585	0.6316
Macquarie Uplands	0.6596	0.8644	0.7045	0.6345	0.6923	0.9024	0.6000	0.5054	0.5974	0.3053	0.0	0.2809	0.5254
Koscziuskan Uplands	0.5879	0.8286	0.6684	0.5481	0.7143	0.9231	0.6264	0.5385	0.5758	0.3585	0.2809	0.0	0.4571
Tasmanian Uplands	0.7751	0.85	0.9236	0.8090	0.6364	0.9091	0.7705	0.7838	0.8815	0.6316	0.5254	0.4571	0.0

MAJOR PRESENCE **PROVINCE**	Western Coastlands	Pilbara	Yilgarn Plateau	Kimberley	Sandland North	Sandland South	Nullarbor Plain	North Aust. Plateaus	Carpentaria Fall	Barkly-Tanami Plain	Central Aust. Ranges	Central Lowlands West	Eyre Peninsula
Western Coastlands	0.0	0.4765	0.4464	0.8353	0.7172	0.6312	0.6696	0.8795	0.8864	0.7658	0.6331	0.7005	0.6250
Pilbara	0.4765	0.0	0.5605	0.8095	0.6122	0.6429	0.7895	0.8537	0.7931	0.5818	0.5714	0.6990	0.7068
Yilgarn Plateau	0.4464	0.5605	0.0	0.9119	0.8150	0.5070	0.6296	0.9490	0.9012	0.7730	0.5802	0.6370	0.4361
Kimberley	0.8353	0.8095	0.9119	0.0	0.5294	0.8421	0.9200	0.3333	0.5652	0.6087	0.8462	0.9155	0.9055
Sandland North	0.7172	0.6122	0.8150	0.5294	0.0	0.6222	0.8750	0.6875	0.6216	0.4000	0.6610	0.7949	0.8582
Sandland South	0.6312	0.6429	0.5070	0.8421	0.6222	0.0	0.4528	0.9189	0.7975	0.6471	0.4125	0.5253	0.4426
Nullarbor Plain	0.6696	0.7895	0.6296	0.9200	0.8750	0.4528	0.0	0.9583	0.8868	0.8684	0.7164	0.7093	0.5032
North Australian Plateaus	0.8795	0.8537	0.9490	0.3333	0.6875	0.9189	0.9583	0.0	0.7143	0.7273	0.8824	0.9286	0.9360
Carpentaria Fall	0.8864	0.7931	0.9012	0.5652	0.6216	0.7975	0.8868	0.7143	0.0	0.5510	0.7944	0.8621	0.8769
Barkly-Tanami Plain	0.7658	0.5818	0.7730	0.6087	0.4000	0.6471	0.8684	0.7273	0.5510	0.0	0.5077	0.6786	0.7647
Central Australian Ranges	0.6331	0.5714	0.5802	0.8462	0.6610	0.4125	0.7164	0.8824	0.7944	0.5077	0.0	0.3363	0.4313
Central Lowlands West	0.7005	0.6990	0.6370	0.9155	0.7949	0.5253	0.7093	0.9286	0.8621	0.6786	0.3363	0.0	0.3253
Eyre Peninsula	0.6250	0.7068	0.4361	0.9055	0.8582	0.4426	0.5032	0.9360	0.8769	0.7647	0.4313	0.3253	0.0
Gulfs Ranges	0.6337	0.7313	0.5000	0.9270	0.8940	0.4922	0.5569	0.9407	0.8857	0.7669	0.4299	0.2741	0.1967
Carpentaria Lowlands	0.8810	0.8554	0.9367	0.5789	0.7576	0.8933	0.9184	0.5294	0.4545	0.6889	0.8641	0.9007	0.9048
Central Lowlands Centre	0.7391	0.6831	0.6202	0.8992	0.8195	0.5657	0.7047	0.9316	0.8197	0.6276	0.3103	0.2697	0.3540
Murray Lowlands	0.6453	0.7426	0.4874	0.9275	0.8816	0.5155	0.5595	0.9412	0.8865	0.7805	0.4595	0.3923	0.2571
Peninsular Uplands	0.9000	0.9241	0.9481	0.6000	0.7931	0.9155	0.9556	0.3846	0.6667	0.8537	0.9394	0.9562	0.9344
Great Barrier Reef	0.9737	0.9733	0.9867	0.8182	0.9200	0.9701	0.9512	1.0000	0.8571	0.9459	0.9789	0.9850	0.9831
Burdekin Upland	0.8511	0.8280	0.8810	0.5862	0.7674	0.8353	0.8983	0.7037	0.5000	0.7091	0.8230	0.8675	0.8529
Fitzroy Upland	0.8198	0.8000	0.8486	0.7391	0.8333	0.8039	0.8947	0.7727	0.6735	0.6667	0.7231	0.7857	0.7778
Central Lowland East	0.7949	0.7677	0.7304	0.9341	0.8667	0.6463	0.7521	0.9551	0.8723	0.7265	0.4971	0.4836	0.5152
New England-Moreton Uplands	0.7798	0.8889	0.8361	0.7727	0.8966	0.8200	0.8378	0.8571	0.8298	0.8000	0.8125	0.8072	0.7616
Macquarie Uplands	0.7980	0.9184	0.8382	0.8235	0.9167	0.8444	0.8438	0.9375	0.8378	0.9000	0.8644	0.8974	0.8014
Kosciuzkan Uplands	0.7297	0.8909	0.7838	0.8261	0.9000	0.8235	0.7895	0.9091	0.8776	0.8333	0.8308	0.8571	0.7255
Tasmanian Uplands	0.7931	0.9767	0.8634	0.9091	1.0000	0.9487	0.8462	1.0000	0.9200	0.9583	0.9811	0.9583	0.8450

MAJOR PRESENCE **PROVINCE**	Gulfs Ranges	Carpentaria Lowlands	Central Lowlands Centr.	Murray Lowlands	Peninsular Uplands	Great Barrier Reef	Burdekin Uplands	Fitzroy Uplands	Central Lowlands East	New Engl. Moreton Uplands	Macquarie Uplands	Koscziuskan Uplands	Tasmanian Uplands
Western Coastlands	0.6337	0.8810	0.7391	0.6453	0.9000	0.9737	0.8511	0.8198	0.7949	0.7798	0.7980	0.7297	0.7931
Pilbara	0.7313	0.8554	0.6831	0.7426	0.9241	0.9733	0.8280	0.8000	0.7677	0.8889	0.9184	0.8909	0.9767
Yilgarn Plateau	0.5000	0.9367	0.6202	0.4874	0.9481	0.9867	0.8810	0.8486	0.7304	0.8361	0.8382	0.7838	0.8634
Kimberley	0.9270	0.5789	0.8992	0.9275	0.6000	0.8182	0.5862	0.7391	0.9341	0.7727	0.8235	0.8261	0.9091
Sandland North	0.8940	0.7576	0.8195	0.8816	0.7931	0.9200	0.7674	0.8333	0.8667	0.8966	0.9167	0.9000	1.0000
Sandland South	0.4922	0.8933	0.5657	0.5155	0.9155	0.9701	0.8353	0.8039	0.6463	0.8200	0.8444	0.8235	0.9487
Nullarbor Plain	0.5569	0.9184	0.7047	0.5595	0.9556	0.9512	0.8983	0.8947	0.7521	0.8378	0.8438	0.7895	0.8462
North Australian Plateaus	0.9407	0.5294	0.9316	0.9412	0.3846	1.0000	0.7037	0.7727	0.9551	0.8571	0.9375	0.9091	1.0000
Carpentaria Fall	0.8857	0.4545	0.8197	0.8865	0.6667	0.8571	0.5000	0.6735	0.8723	0.8298	0.8378	0.8776	0.9200
Barkly-Tanami Fall	0.7669	0.6889	0.6276	0.7805	0.8537	0.9459	0.7091	0.6667	0.7265	0.8000	0.9000	0.8333	0.9583
Central Australian Ranges	0.4299	0.8641	0.3103	0.4595	0.9394	0.9789	0.8230	0.7231	0.4971	0.8125	0.8644	0.8308	0.9811
Central Lowlands West	0.2741	0.9007	0.2697	0.3923	0.9562	0.9850	0.8675	0.7857	0.4836	0.8072	0.8974	0.8571	0.9583
Eyre Peninsula	0.1967	0.9048	0.3540	0.2571	0.9344	0.9831	0.8529	0.7778	0.5152	0.7616	0.8014	0.7255	0.8450
Gulfs Ranges	0.0	0.9118	0.3305	0.1765	0.9394	0.9844	0.8630	0.7423	0.4615	0.7019	0.7616	0.6687	0.8417
Carpentaria Lowlands	0.9118	0.0	0.8814	0.9124	0.4286	0.8000	0.6429	0.7333	0.9333	0.8140	0.8788	0.8222	1.0000
Central Lowlands Central	0.3305	0.8814	0.0	0.3249	0.9474	0.9818	0.7813	0.6414	0.3263	0.7203	0.8195	0.7793	0.9669
Murray Lowlands	0.1765	0.9124	0.3249	0.0	0.9398	0.9845	0.8231	0.6463	0.3684	0.6420	0.6974	0.5854	0.8429
Peninsular Uplands	0.9394	0.4286	0.9474	0.9398	0.0	1.0000	0.6667	0.8049	0.9767	0.8462	0.8621	0.8537	0.8824
Great Barrier Reef	0.9844	0.8000	0.9818	0.9845	1.0000	0.0	0.9000	0.9459	0.9756	0.9429	0.9200	0.9459	1.0000
Burdekin Upland	0.8630	0.6429	0.7813	0.8231	0.6667	0.9000	0.0	0.3818	0.7800	0.6604	0.7674	0.7818	0.8710
Fitzroy Upland	0.7423	0.7333	0.6414	0.6463	0.8049	0.9459	0.3818	0.0	0.5214	0.3714	0.4667	0.5278	0.8750
Central Lowland East	0.4615	0.9333	0.3263	0.3684	0.9767	0.9756	0.7800	0.5214	0.0	0.5478	0.6571	0.6239	0.9570
New England-Moreton Uplands	0.7019	0.8140	0.7203	0.6420	0.8462	0.9429	0.6604	0.3714	0.5478	0.0	0.2759	0.3429	0.7391
Macquarie Uplands	0.7616	0.8788	0.8195	0.6974	0.8621	0.9200	0.7674	0.4667	0.6571	0.2759	0.0	0.2667	0.6111
Kosciuzkan Uplands	0.6687	0.8222	0.7793	0.5854	0.8537	0.9459	0.7818	0.5278	0.6239	0.3429	0.2667	0.0	0.5417
Tasmanian Uplands	0.8417	1.0000	0.9669	0.8429	0.8824	1.0000	0.8710	0.8750	0.9570	0.7391	0.6111	0.5417	0.0

Appendix X: Specific sources for age of chenopod clades and history of land types

Clade Ages

Reported data

Additional to reported estimates in Kadereit *et al.* (2005):

> Kadereit *et al.* (2010) p1680: *Atriplex* Clade 1 arrives 9.8-7.8 Ma, *Atriplex* Clade 2 arrives 6.3-4.8 Ma – *i.e.* both based on difference in Stem-Crown age
>
> Cabrera *et al.* (2011) Figure 1 & p322: Sclerolaenid Clade initially diversifies ~7.5 Ma (Late Miocene) with 70% of lineages in place by end of Pliocene.
>
> Kadereit and Freitag (2011) p69: Sclerolaenid clade with onset of rapid diversification during Late Miocene-Pliocene; long after Australian & Central Asian split.
>
> Steffen *et al.* (2015) p11: *Sarcocornia* arrived in Australia during the Pliocene

Sclerolaenid Clade

From Table 3 (Kadereit and Freitag 2011):

Node	***rbc*L**		***ndh*F**		***atp*B-*rbc*L**		**Geological Time, Events and Landscape**
	r8s-PL	**BEAST**	**r8s-PL**	**BEAST**	**r8s-PL**	**BEAST**	
Stem age: *Grubrovia* & Sclerolaenid Clade	20.3-18.6	17.7 (25.1—10.7)	23.5-17.7	22.6 (32.2-13.6)	20.9-17.3	21.38 (30.8-11.5)	Early Miocene: Oceanic Isolation of Australia; Neritic basins dominate west and south coasts; Mega-lakes of Central Australia
Stem age: Sclerolaenid Clade	15.4-14.1	10.3 (17.3—4.5)	16.3-12.1	15.3 (24.0-6.5)	16.2-13.3	16.35 (28.2-8.9)	Middle Miocene: Cessation of regular flow in Eucla Basin Palaeodrainage; Emergence of Nullarbor Plain; Diminishing mega-lakes of Central Australia
Crown age: Sclerolaenid Clade	11.5-9.2	6.3 (11—2.1)	4.8-2.6	3.9 (8.1-0.8)	2.5-2.1	5.26 (10.9-0.9)	Late Miocene-Pliocene: Alkaline/Saline forms in southwest, southern and central Australia; Murray Basin marine incursion with humid lowlands.

Age estimates in Ma (millions of years).

Other Chenopod Clades

Publish Source	**Clade**	**Clade Spp**	**Spp in Subset**	**Data Source**	**Analysis**	**Crown Age**	**Crown Age Range**	**Stem Age**	**Stem Age Range**	**Estimate Diversifying**	**Stem Notes**
Kad2010	Australian Chenopodieae I	24	4	Fig. 1	*rbc*L/BEAST	5.17	9–1	11.67	18–5.5	5.17–3.04	Crown in clade of North American/Pacific species
Kad2010	Australian Chenopodieae I	24	6	Fig. 2	*atp*B-*rbc*L /BEAST	3.16	6–1	5.2	9.5–1.5	3–1	Crown with *Chenopodium murale* sister
Kad2010	*Dysphania*	16	2	Fig. 1	*rbc*L/BEAST	6.75	1.7–2.5	13.75	20.7.7		Crown with sisters *D. ambrosioides* & *D. botrys*
Kad2010	*Dysphania*	16	2	Fig. 2	*atp*B-*rbc*L /BEAST	3.85	7.5–1	6.92	12.5–2.5		Crown with *Cycloma atriplicifolium* sister
Kad2010	Australian *Atriplex* Clade 1	8	5	Fig. 3	ITS/BEAST	7.83	11.4–4.1	9.83	13–6.5		Crown with sister American and Eurasian clades
Kad2010	Australian *Atriplex* Clade 2	52	27	Fig. 3	ITS/BEAST	4.79	6.75–2.6	6.25	8.6–3.3	Lineage crowns at 4.08, 3.96, 3.56	Crown with 4 Central Asian species
Kad2010	*Atriplex australasica*	1		Fig. 3	ITS/BEAST			1.24	2.6–0.1		Crown with *A. glabriuscula* sister
Steff2015	*Sarcocornia*	3	2	Fig. 3	*atp*B-*rbc*L:*rpL*32-*trn*L:ETS/BEAST	0.7		3.2			Crown with *S. xerophila* (South Africa)
Steff2015	*Sarcocornia*	3	3	Fig. 4	ETS/BEAST	0.6	2–0.4	2.1	4–0.6		
Steff2015	*Tecticornia*	44	2	Fig. 4	atpB-rbcL:rpL32-trnL:ETS/BEAST	6.9	15–1	20.1	25.8–14.2		
Kad2012	*Tecticornia*	44	2	Fig. 4	rbcL, atpB-rbcL/BEAST	9 (read fig)		16 (read fig)			

Publish Source key:

Kad2010: Kadereit *et al.* (2010) for Atripliceae

Kad2012: Kadereit *et al.* (2012) for Chenopodiaceae

Steff2015: Steffen *et al.* (2015) for *Sarcocornia*

Ages either noted on or read from figures indicated and given in Ma (millions of years).

Landscape Ages

These notes are not exhaustive and have some gaps especially for Desert Uplands and Shield Plain, but are sufficient to indicate landscape chronology, especially for Australia south of the Tropic of Capricorn. Square brackets contain author comments. Ma and Ka respectively refer to million and thousand years ago.

General notes and comments

Heightened aridity begins earlier in Australian centre than at periphery (Fujioka *et al.* 2009), particularly evident in dune field formation (Fujioka and Chappell 2010). In the driest period over the last 0.3 Ma, aridity in Eastern Australia moved toward the coast (Nanson *et al.* 1992).

Climatic zonation of modern Australia is evident by end of Pliocene, though not as dry as today (Martin 2006; Fujioka and Chappell 2010).

Preservation of Nullarbor Plain Surface and Ooldea Range (once a coastal dune persisting from Late Eocene to Early Miocene) indicative of marked aridity in region, though not as dry as in Quaternary (Benbow 1990). This aridity is punctuated by significant, brief returns to mesic conditions in the Pliocene (Webb and James 2006; Doerr *et al.* 2011).

Lake Eyre Basin: Middle Eocene vegetation mosaic, interpreted from palynofloras, would be similar to that in present monsoonal areas of northern Australia (Alley 1998).

Central & Southeast Australia: savannah woodland replaces forest in Early Pliocene; formerly large bodies of water here and in Murray Basin vanished by Late Pleistocene (Fujioka and Chappell 2010 citing Hope 1982).

The combination of Stony Deserts, Dune Fields & Playas that associates with arid climates is largely of Quaternary age, but an Early-Middle Miocene arid phase is marked by alkaline lakes (Fujioka and Chappell 2010). Aeolian activity is marked by dune field formation and dust deposits that travel even farther afield; luminescent dates may best indicate stabilisation or active accumulation phases; inception is best indicated by cosmogenic nuclides (Fujioka and Chappell 2010).

In dating landscapes from geologic evidence, it is not easy to distinguish incipient transformations under increasing aridity to extensive presence of the landscape. For some sedimentary units when they first become habitat can be uncertain e.g. central Australian dolomites forming in extensive lakes.

Sand Desert

Northwest Australia: first serious dust flux in glacial phase about 0.15 Ma (Fujioka and Chappell 2010).

Northern Australia, Lake Gregory (Mulan): dune fields active at 0.23 Ma, but started earlier (Bowler *et al.* 2001).

Central Australia, Strzelecki-Simpson Desert (SSD): last major dune building 13-23 Ka, with Holocene extensions; earlier phases of dune building back to 0.25 Ma (Mabbutt 1988). Western Simpson Desert began forming 1 Ma (Fujioka and Chappell 2009).

Central Australia, Lake Eyre Basin: aeolian activity from increasing aridity in Late Pleistocene and Holocene with major phase of dune building in last glacial maximum that overlie older aeolian deposits (Alley 1998).

Central Australia, Great Victoria Desert (GVD): Sand blown eastward from the Eucla Basin forms the GVD dune field in mid to late Quaternary (Lintern 2003). The measured age for the dune core at Immarna spans a time range of 215 ± 15 to 188 ± 14 Ka; similarly for Barton, age range spans 197 ± 14 to 105 ± 8 Ka (Sheard *et al.* 2006).

Central-East Australia: much dune activity in last 0.35 Ma, where most inland/arid luminescent determinations done; cosmogenic nuclide determinations give inception as old as 1 Ma in Central Australia (Fujioka and Chappell 2010).

Central-East Australia: dust origin in Lake Eyre (LEB) and Murray Darling Basins (MDB); first significant dust transport from MDB *ca*. 0.35 Ma, with larger fluxes in subsequent glacial stages;

Northwest New South Wales dust accumulations at least by 0.5 Ma, possibly as old as 1 Ma (Fujioka and Chappell 2010).

Western Australia, Yilgarn Platform: aeolian forms are mostly sandplain of the Quaternary (Glassford and Semeniuk 1995). Form shallow cover to Shield Plain (Mabbutt 1988).

Southern Australia: extensive development of clay lunettes in playa systems at end of Pleistocene in areas currently arid (Mabbutt 1988).

Southeast Australia: earliest arid land forms (dunes, lunettes etc.) at 0.3 Ma (Bowler 1976). Aeolian forms no earlier than 0.45 Ma, peaking at 0.35 Ma (Fujioka and Chappell 2009, citing Hesse 2004). Aeolian forms of west Murray Basin Woorinen Formation, Molineaux Sand, Bunyip Sand are Middle Pleistocene to Holocene (Brown and Stephenson 1991; Rogers 1995).

Southeast Australia, western Murray Basin: dune fields (Big Desert, Sunset, Little Desert, 90 Mile Desert) initiated about 0.5 Ma; origin from Loxton-Parilla sands that formed in last Major retreat of Murray Basin coastline; dunes also associated with coastal-inland Bridgewater Formation at 1.3 Ma (Bowler *et al.* 2006).

Stony Desert

Central Australia (Coober Pedy-Oodnadatta): stripping of soil mantles from table lands begins 4 Ma, and Stony Desert actively forming 3 Ma; rate of formation slowed after 2 Ma (Fujioka *et al.* 2005; Fujioka and Chappell 2010). Stony Desert surfaces would be younger than older “lateritic profiles” of probable Neogene age (Mabbut 1988).

Southern Australia, North Flinders Ranges: Late Tertiary to Holocene age Willawortina Formation flanks these ranges, the flanking fans form in Late Pliocene onwards (Alley 1998 [Stony Desert pavements form on these flanking deposits]). Much of Willawortina Formation is older than 0.78 Ma; is also found on northern Olary Ranges; and fans around the Flinders Ra, began building in Late Miocene and Pliocene (Callen *et al.* 1995b).

Karst Plain

Central Australia, Lake Eyre Basin: Oligocene to Pliocene Etadunna & Namba Formation dolomites now overlain by Quaternary sediments or exposed at the surface; were exposed when Wipajiri Formation laid down but no known date for this, maybe Pliocene; extensive lakes deriving Etadunna/Namba formations began drying in Middle Miocene [assume exposed under warm strongly seasonal climate]; also Cadelga Limestone of Late Miocene to Quaternary age; dense calcrete horizons in Quaternary soils, possibly as early as Pliocene; calcrete palaeosols of Late Pleistocene (Alley 1998).

Southern Australia, Nullarbor Plain: surface relief is solutional, and limited by aridity, the flat surface indicating plain has been arid since exposure; has shallow calcareous soils above calcrete horizon over crystalline limestone (Mabbutt 1988). Aridity in Eucla Basin since Miocene – immaturity of modern karst (Fujioka and Chappell 2010, citing Benbow 1990). Immaturity of karst development on the plain since it emerged 14-16 Ma (Benbow 1990, citing Jennings 1967) indicative of a (relative) aridity as possibly as old as Oligocene, with at least two major Late Neogene returns to mesic climates marked by palaeochannel reactivation (Benbow 1990). See also Webb and James (2006), Doerr *et al.* (2011). Eastern part with palaeosol carbonates likely forming in early Pliocene; calcrete in Quaternary (Hou *et al.* 2008). Uplift/tilting in Middle-Late Pliocene with Bunda Plateau not inundated by sea subsequently; probably incised locally when younger Garford/Narlaby formations deposited i.e. Early Pliocene, possibly latest Miocene (Benbow *et al.* 1995).

Southern Australia, Bridgewater Formation: calcarenites/calcareous sands dated from 1.8 to 0.125 Ma variably cover Eyre Peninsula, South Australian Gulfs and western Murray Basin due to aeolian transport, substantially indurated with calcrete (Belperio 1995a, 1995b).

Southern Australia: calcareous aeolian dust mantled large areas up to 1000 km inland during Pleistocene glacial periods when sea floor exposed the continental shelf; covered Gawler and Curnamona Cratons; pedogenic process created calcrete (Sheard and Lintern 1998). Gawler Craton: calcretes in near continuous blanket developing late in craton history; carbonate introduced as airborne dust in cycles relating to serial glacial maxima (low sea level) in late Quaternary, modified pedogenically (Lintern 2003).

Southeast Australia, western Murray Basin: Bridgewater calcarenites develop about 1.3 Ma (Bowler *et al.* 2006), occurred throughout Pleistocene (Brown and Stephenson 1991). Bungunnia Limestone calcreted over 0.5-0.6 Ma; limestone exposed at least by 0.7 Ma (Bowler *et al.* 2006) Calcreting of Bridgewater Formation probably also at the same time (*authors note*).

Southeast Australia: pedalfer to pedocal pedogenesis about 0.4-0.7 Ma (Fujioka and Chappell 2009, citing Pillans & Bourman 2001).

Eastern Australia, Cobar Region: aeolian accessions of calcareous dust are reflected in two episodes of calcium carbonate precipitation at 33-21 Ka and 16-13 Ka (Spry 1998).

Desert Lake

Northern Australia, Lake Gregory (Mulan): a large non-saline lake at 0.3 Ma; phases of expansion and drying in last 0.3 Ma (Bowler *et al.* 2001).

Northeast Australia, Lake Buchanan: brief episodes of playa conditions over last 0.8 Ma (Fujioka and Chappell 2010).

Central Australia, Lake Amadeus: ceased being perennial lake about 1 Ma (Fujioka & Chappell 2009, citing Chen & Barton *et al.* 1991). Transition from wet to higher aridity is at or before 0.91 Ma (possibly 1.6 Ma – there are two interpretations of how sediment boundaries relate to magnetostratigraphy) which is earlier than Lake Bungunnia estimated at < 0.73 Ma but is probably 0.5 Ma (Fujioka and Chappell 2010; refer An *et al.* 1986). "Aridity" in Central Australia occurred 0.4 to 1.1 Ma earlier; oldest gypseous dunes pre-dated 0.98 Ma, possibly 0.73 Ma (Chen and Barton 1991). Arid playa conditions begin at Lake Amadeus at or before 0.9 Ma (Fujioka and Chappell 2010 summarize Chen and Barton 1991).

Central Australia, Lake Eyre Basin: dense gypcrete horizons in Quaternary soils, possibly earliest in Pliocene. Gypcrete in Tirari Formation of Late Pliocene-Early Pleistocene is intermittent stream flow under semiarid conditions; gypseous sand of lacustrine conditions in Kutjitara Formation of Middle Pleistocene age, also extensive through southwest Queensland; Tirari Formation exposed in Middle and Late Pleistocene; Late Pleistocene formations of fluvio-lacustrine evaporitic deposits, with recessional shorelines (Alley *et al.* 1999). Alternating high lake and playa phases well preserved in last 130 Ka, and presumed during previous glacial oscillations (Fujioka and Chappell 2010, citing others). Tirari Formation had depositional environment of intermittent stream flow under semiarid conditions and of date greater than 0.5 Ma (Callen *et al.* 1995a) [citing Callen and Nanson 1992, possibly Pliocene-Early Pleistocene]. Tirari Formation: fluvial silt/sands of channels /floodplains (Callen and Benbow 1995). Western Lake Eyre Basin & Torrens Basin also with playa/lunette systems, but stratigraphy & dates uncertain (Callen and Benbow 1995).

Central Australia, Lake Lewis: transition from non-saline to saline conditions, occurred within 0.78 Ma, most likely 0.3-0.4 Ma, though dates dependent on assumed sedimentation rates (Fujioka and Chappell 2010, citing English 2001).

Western Australia, west Australian Wheatbelt: development of saltlakes over last 1 Ma (Commander *et al.* 2001).

Western Australia, Lakes LeFroy & Cowan: ***dating is controversial*** refer Clarke and Pillans (2002) and Zheng *et al.* (2002). Arid Playa conditions commenced around 0.5 Ma with development of Roysalt Formation based on magnetostratigraphic analysis (Zheng *et al.* 1998; Fujioka and Chappell 2010). Onset of aridity is latest Miocene or Early Pliocene based Roysalt Formation – evaporitic/deflationary sediments mostly of gypsum, some halite in upper levels, resembling current conditions; palynomorphs include acacia and chenopods; age of Roysalt Formation based on palynomorph assemblage and presumed stratigraphic equivalency with units elsewhere in Western Australia and in eastern Eucla Basin (Clarke 1994a, 1994b citing Parker 1988).

Southern Australia, eastern Eucla Basin: Pliocene fluvio-lacustrine evaporites in palaeovalleys – reduced intermittent flow, significant drying (Fujioka and Chappell 2010 citing Hou *et al*. 2008). Ilkina Formation: Late Pliocene gypseous clay/silt/sand indicative of saline playa lake in palaeochannels (Benbow *et al.*1995).

Southern Australia, Torrens Basin: Neuroodla Formation mudstone deposits showing transition from humid to evaporative environment with playa lakes, but no effective date for transition or age of upper boundary (Alley and Benbow 1995).

Southeast Australia: Lake Bungunnia became alkaline in final phases by 0.7 Ma, but never saline; (larger) eastern lakes never became saline/alkaline; local salinity in regional hollows over 0.5-0.6 Ma, but local gypseous dunes in deeper parts of the lake during drying phase ~ 0.7 Ma; gypseous dunes in mallee areas are Late Pleistocene (Bowler *et al.* 2006). Fluvio-lacustrine to saline arid transition (in the Tyrrell playa) occurred 0.4-0.7 Ma (Fujioka and Chappell 2009, 2010: citing An *et al.* 1986 and Zhisheng *et al.* 1986). Evaporitic gypseous western Murray Basin formations (Yamba, Tyrrell Beds) are Middle Pleistocene at oldest (Brown and Stephenson 1991; Rogers 1995). [Local] Freshwater lakes transition to seasonally dry, with saline groundwater after 25 Ka that continued to 15 Ka (Mabbutt 1988).

Desert Upland

[Desert Upland formed through climatic transformation of pre-existing topography. Exception may be the Flinders Ranges in SA, which possibly rose to current elevations in the Late Pliocene (Alley 1998). Best age estimates therefore based on formation of arid landscapes in the regional neighbourhood.]

Central Australia, MacDonnell Ranges: desiccation of Lake Amadeus about 1 Ma (see Desert Lake notes). Alcoota Tableland: Miocene or Lower Pliocene a trend to drier conditions (Mabbutt 1988).

Southern Central Australia, Davenport Ra: formation of Stony Desert (see Stony Desert notes).

Southeast Australia: Flinders/Olary/Barrier Ranges:

Western Australia, Pilbara:

Shield Plain

[Shield Plain formed through climatic transformation of pre-existing topography. Best age estimates are based on formation of arid landscapes in the regional neighbourhood.]

Western Australia, Yilgarn Plateau:

Southern Australia, Gawler Craton:

Central Australia, Arunta Block: Alcoota Tableland – trend to drier conditions in Miocene or Lower Pliocene (Mabbutt 1988).

Riverine Desert

Central Australia, Lake Eyre Basin: episodic fluvial and lacustrine sedimentation from Late Palaeocene to the present; Namba/Etadunna formations mainly lacustrine deposits of ?Late Oligocene to Pliocene relate to shallow, brackish to freshwater lakes through much of Lake Eyre Basin (Callen *et al.* 1995a) [and which would be floodplain systems]. Gypsum in Tirari Formation of Pliocene-Early Pleistocene age indicates seasonally arid conditions (Callen and Benbow 1995).

Southwest Australia, western Eucla Basin: palaeodrainage of regular flow in Yilgarn Craton valleys ceased in Middle Miocene (van de Graaff *et al.* 1977). Drainage throughflow lasting to end of Miocene prevented accumulation of gypsic evaporites, having dolomitic sediments form in alkaline conditions of lacustrine systems (Clarke 1994a, 1994b; Alley 1998; Alley *et al.* 1999).

Southern Australia, eastern Eucla Basin: palaeodrainage with carbonaceous sediments of Kingoonya Member of Late Miocene-Early Pliocene age indicate mesic valleys; sand & clay with evaporites of Pliocene-Quaternary, indicate valley with evaporative conditions (being semi-arid climates at least); Garford Formation Middle Miocene-Upper Pliocene with sediments of mixed clay and sand, of dolomitic nature in younger parts, indicative of aridity; these fluvio-lacustrine sediments occasionally exposed; supported chenopod shrubland in Early Pliocene; lowlands and floodplains present in Middle Miocene-Early Pliocene (Alley *et al.* 1999; Hou *et al.* 2003; Hou *et al.* 2008). Garford Formation younger phase at Late Miocene-Early Pliocene transition: floodplain, lacustrine lagoonal swamp in locally evaporative environments (Benbow *et al.* 1995).

Southern Australia, St Vincent Basin: Hindmarsh Clay of Quaternary age, possibly including Early Pleistocene, includes alluvial fan and valley flat playa lake deposition (Callen *et al.* 1995b).

Southeast Australia, Murray Basin: no riverine plain in western Murray Basin during the Neogene due to combination of Late Miocene to Pliocene marine incursion/retreat and Lake Bungunnia (Brown and Stephenson 1991; Rogers *et al.* 1995; Stephenson and Brown 1989). Shepparton Formation Pliocene-Quaternary age [not found in western basin] is extensive, alluvial floodplain of eastern Riverine Plain surface including palaeodrainage features and only has arid forms (aeolian sand and dust) associated with current surface features; western Shepparton Formation equivalent is Moorna Formation, being fluvial channel deposits of Late Pliocene to ?Early Pleistocene (Brown and Stephenson 1991). Calivil Formation is Late Miocene-Pliocene fluvial valley-fill and alluvial fan environments of eastern Basin with carbonaceous content [*i.e.* mesic conditions] (Brown and Stephenson 1991). Increasing aridity is reflected by a change from fluviatile to aeolian and saline gypseous sediment at ~500 000 years BP in the Murray Basin (Belperio 1995b). Blanchetown Clay of Late Pliocene-Middle Pleistocene age is gypsiferous in upper sequences, top of which dates to 0.62 Ma (Rogers 1995). The evaporitic units relate to the drying phase of Lake Bungunnia (Brown and Stephenson 1991).

Desert Clay Plain

Northern Australia, Barkly Tableland: Age indeterminate and origin unclear, but region inherently stable for very long time; about 25Ma very shallow valleys had brackish to freshwater lakes in subdued landscape, which present day drainage mimics so topography is little changed (Edgoose 2003) [i.e. when climate became semi-arid is most critical time].

Appendix XI: Correspondence of chenopod assembly to Australian saltmarsh biogeography

Floristic Group (1)	**Floristic Subgroup (1)**	**Chenopod Group**	**Chenopod Subgroup [Provinces]**	**Notable coastal taxa**	**Saintilan cluster (2009a,b)**
Suaeda arbusculoides-Halosarcia indica julacea [**C**]		Northern Tropical	[All in Group]	*Suaeda arbusculoides* (central range) *Atriplex humilis*	Northern: North
Suaeda arbusculoides-Halosarcia indica julacea [**C**]		Eastern Highlands	Northern subtropical [Burdekin & Fitzroy Uplands]	*Suaeda arbusculoides* (eastern range)	Northern: East
Sclerostegia arbuscula-Juncus kraussii [**C**]	*Stipa stipoides-Agrostis billardierei*	Eastern Highlands	Southern temperate [Macquarie, Kosciuskan & Tasmanian Uplands]	*A paludosa ssp. paludosa* *Atriplex billardierei* East coast ranges of *Atriplex cinerea*, *A. australasica*, *Rhagodia candolleana*	Southern: South (Vic, southern NSW,eastern Tas Regions)
Sclerostegia arbuscula-Juncus kraussii [**C**]	*Halosarcia halocnemoides-Limonium bivernosum*	Subcontinental Arid-Mediterranean	Central southern: south coastal cluster [Eyre Peninsula, Gulfs Ranges, Murray Lowlands]	*Atriplex australasica* (western range) *A. paludosa ssp. cordata*,	Southern: South (SA Gulfs Region)
Sclerostegia arbuscula-Juncus kraussii [**C**]	*Halosarcia halocnemoides-Rhagodia baccata*	Subcontinental Arid-Mediterranean	Western: south coast [Yilgarn Plateau, Western Coastlands]	*Atriplex hypoleuca* *Rhagodia baccata*	Southern: West
Sclerostegia tenuis [**I**]		Subcontinental Arid-Mediterranean	Central southern (excludes southern coastal cluster & Central Lowlands East): [10 provinces]		N/A
Halosarcia pergranulata [**C**,**I**]		Subcontinental Arid-Mediterranean	Central southern (eastern Eyre Murray Centre): [Murray Lowlands, Central Lowlands East]	*Atriplex australasica* (western range)	
Halosarcia doleiformis-H. leptoclada [**C**,**I**]		Subcontinental Arid-Mediterranean	Yilgarn Centre [Yilgarn Plateau, Western Coastlands, Pilbara]	*Neobassia astrocarpa* *A. paludosa* ssp. *moquiniana* *A. paludosa ssp. baudinii* *Rhagodia latifolia* *R. preissii* ssp. *obovata* *Suaeda arbusculoides* (western range)	Northern: West

Correspondence of Floristic Groups (Bridgewater and Cresswell 2003) with Chenopod Assembly Groups. (1) Halosarcia, Sclerostegia revised to *Tecticornia* by (Shepherd and Wilson 2007) **C** – Coastal group; **I** Inland group

Appendix XII: Sampling of collection records through Australasian Virtual Herbarium for analysis of habitats and land types

Coast Disposition / Species [Subspecies]	Total Collection Records	Date for Total	Total Records Examined	COAST			INLAND		
				Collection Records Examined	Records with no Information	Duplicates	Collection Records Examined	Records with no Information	Duplicates
COAST OBLIGATE									
Atriplex billardierei	101	27/04/2017	86	86	22	25	n/a	n/a	n/a
Atriplex humilis	5	27/04/2017	5	5	1	2	n/a	n/a	n/a
Atriplex hypoleuca	60	27/04/2017	60	60	13	19	n/a	n/a	n/a
Atriplex isatidea	106	27/04/2017	98	98	23	12	n/a	n/a	n/a
Suaeda arbusculoides	120	27/04/2017	93	93	13	17	n/a	n/a	n/a
Tecticornia australasica	198	27/04/2017	78	78	3	23	n/a	n/a	n/a
+ [Rhagodia baccata subsp. dioica]	34	5/06/2017	34	34	14	8			
COAST FACULTATIVE									
Atriplex australasica	214	2/06/2017	194	134	67	23	60	23	13
Atriplex cinerea	1057	27/04/2017	748	723	214	262	25	6	5
Atriplex paludosa	732	27/04/2017	661	476	139	162	185	36	40
Chenopodium glaucum	568	27/04/2017	376	182	83	31	194	64	43
Maireana oppositifolia	376	2/06/2017	286	141	57	23	145	34	30
Neobassia astrocarpa	175	27/04/2017	160	80	19	19	80	11	32
Rhagodia baccata **+**	277	27/04/2017	253	200	65	29	53	15	6
Rhagodia candolleana	1194	27/04/2017	543	438	141	99	105	16	7
Rhagodia latifolia	112	27/04/2017	107	72	19	12	35	5	3
Suaeda australis	897	11/01/2018	439	335	98	61	104	26	16
Threlkeldia diffusa	633	27/04/2017	381	251	71	50	130	26	10
# [Rhagodia preissii subsp. obovata]	180	5/06/2017	111	111	40	25	45	11	11
INLAND FACULTATIVE									
Rhagodia preissii #	836	5/06/2017	142	142	51	28			

Appendix XIII: Land types of chenopod species

Subfamily Chenopodioideae

Plant Species	Land Type
***Atriplex* Clade 1**	
Atriplex amnicola	RL, CS
Atriplex cephalantha	DL, RL
Atriplex cinerea	CS
Atriplex isatidea	CS
Atriplex incrassata	SP
Atriplex nummularia	RL, KP
Atriplex rhagodioides	RL
Atriplex yeelirrie	DL
***Atriplex* Clade 2**	
Atriplex acutibractea	KP, SH, DL
Atriplex acutiloba	RL, DL
Atriplex angulata	RL, SP
Atriplex billardierei	CS
Atriplex bunburyana	RL, DL
Atriplex codonocarpa	DL
Atriplex cordifolia	DL, RL
Atriplex cornigera	DU, RL
Atriplex crassipes	RL
Atriplex cryptocarpa	KP
Atriplex eardleyae	RL
Atriplex eichleri	RL
Atriplex elachophylla	RL
Atriplex eremitis	SD, CS
Atriplex exilifolia	DL
Atriplex fissivalvis	SP
Atriplex flabelliformis	RL, DL
Atriplex holocarpa	RL, SP, DL
Atriplex humifusa	RL, CP
Atriplex humilis	CS
Atriplex hymenotheca	DL
Atriplex hypoleuca	CS
Atriplex infrequens	RL
Atriplex intermedia	RL
Atriplex kochiana	SP
Atriplex leptocarpa	RL
Atriplex limbata	RL, SD
Atriplex lindleyi	RL, SP, DL
Atriplex lobativalvis	RL
Atriplex macropterocarpa	SP
Atriplex morrisii	RL
Atriplex muelleri	RL, MP
Atriplex nana	DL
Atriplex nessorhina	DL, SD
Atriplex obconica	RL
Atriplex paludosa	CS, DL
Atriplex papillata	DL
Atriplex pseudocampanulata	RL
Atriplex pumilio	DL
Atriplex quadrivalvata	RL, SH, SP
Atriplex quinii	SP, SH
Atriplex semibaccata	MP, DL
Atriplex semilunaris	SH, DU, RL, DL
Atriplex spinibractea	RL
Atriplex spinulosa	DU
Atriplex spongiosa	SP, RL, DL
Atriplex stipitata	MP, KP, SD
Atriplex sturtii	RL
Atriplex suberecta	MP, RL, DL
Atriplex turbinata	RL
Atriplex velutinella	DL, SD
Atriplex vesicaria	KP, SP, RL, DL, CS, DU, SD
***Atriplex australasica* Clade**	
Atriplex australasica	CS, RL
Chenopodieae I Clade	
Chenopodium auricomiforme	RL, MP
Chenopodium auricomum	RL
Chenopodium curvispicatum	KP
Chenopodium desertorum	SD, MP, DU, SH
Chenopodium erosum	MP
Chenopodium gaudichaudianum	SD, KP
Chenopodium glaucum	CS, MP
Chenopodium hubbardii	RL
Chenopodium nitrariaceum	RL
Einadia hastata	MP, CS
Einadia nutans	MP, RL, CS
Einadia polygonoides	MP
Einadia trigonos	MP
Rhagodia acicularis	SH
Rhagodia baccata	CS, MP
Rhagodia candolleana	CS, KP, SD, MP
Rhagodia crassifolia	KP, CS
Rhagodia drummondii	DL
Rhagodia eremaea	DU, SD, SH
Rhagodia latifolia	CS, SD
Rhagodia parabolica	DU, MP, RL
Rhagodia preissii	KP, CS
Rhagodia spinescens	RL, DL, SD
Rhagodia ulicina	KP
***Dysphania* Clade**	
Dysphania carinata	MP, RL
Dysphania cristata	RL
Dysphania glandulosa	RL, SH
Dysphania glomulifera	RL, MP
Dysphania kalpari	SD, RL
Dysphania littoralis	CS, RL
Dysphania melanocarpa	DU, SH, RL
Dysphania plantaginella	RL, CS, DL
Dysphania platycarpa	RL
Dysphania pumilio	CS, MP, RL
Dysphania rhadinostachya	DU, SH, SD

Plant Species	Land Type
Dysphania saxatilis	SH, DU
Dysphania simulans	DL
Dysphania sphaerosperma	DL
Dysphania truncata	RL, SD
Dysphania valida	MP, DU
***Scleroblitum* Clade**	
Scleroblitum atriplicinum	RL

Subfamily Camphorosmoideae

Plant Species	Land Type
MaireanAff Subgroup	
Maireana amoena	DL
Maireana aphylla	RL, SP
Maireana appressa	DL
Maireana astrotricha	SP, DU, RL
Maireana atkinsiana	DL
Maireana brevifolia	MP, SH, RL, CS
Maireana campanulata	SP, DU
Maireana cannonii	DL, RL, CS
Maireana carnosa	DL
Maireana cheelii	RL, TA
Maireana ciliata	SP, KP, RL
Maireana convexa	SD, SH
Maireana coronata	RL, DL, SP, CP
Maireana decalvans	MP, RL
Maireana dichoptera	CP, RL
Maireana diffusa	DL
Maireana enchylaenoides	MP, RL, KP
Maireana eriantha	SP
Maireana erioclada	KP, MP
Maireana eriosphaera	DL
Maireana excavata	MP, RL
Maireana georgei	SD, DU, KP, SH, RL
Maireana glomerifolia	SH, DL
Maireana humillima	MP, RL
Maireana integra	DL, KP, DU
Maireana lanosa	SD, DL, RL
Maireana lobiflora	RL
Maireana luehmannii	DL
Maireana marginata	MP, SH
Maireana melanocarpa	DL
Maireana melanocoma	DU, SH
Maireana microcarpa	RL
Maireana microphylla	MP, RL
Maireana murrayana	DU, SH
Maireana oppositifolia	CS, DL
Maireana ovata	SP, DU
Maireana pentagona	RL, MP
Maireana pentatropis	KP, SD, DL
Maireana planifolia	SH, DU, SD
Maireana platycarpa	DL, KP
Maireana polypterygia	DL
Maireana prosthecochaeta	SH
Maireana pyramidata	RL, SD, DL
Maireana radiata	KP, SD
Maireana rohrlachii	MP, KP
Maireana schistocarpa	SP, DU, SD
Maireana scleroptera	RL
Maireana sedifolia	KP, DU
Maireana spongiocarpa	SP, DU
Maireana stipitata	DL
Maireana suaedifolia	DL
Maireana thesioides	SH
Maireana tomentosa	DL
Maireana trichoptera	KP, DL
Maireana triptera	SP, DL, KP, SH
Maireana turbinata	KP, SP
Maireana villosa	DU, SH, CP
Affiliate species	
Eremophea aggregata	KP
Eremophea spinosa	DU, SD
Neobassia astrocarpa	CS, DL
Roycea divaricata	DL
Roycea pycnophylloides	DL
Roycea spinescens	DL
Enchylaena lanata	MP, SH, DL
Enchylaena tomentosa	CS, MP, DU, KP, RL, SD
Didymanthus roei	DL
Dissocarpus biflorus	CS, RL
Dissocarpus fontinalis	SP, RL
Dissocarpus latifolius	RL, SD, SP
Dissocarpus paradoxus	SD, KP, RL
Eriochiton sclerolaenoides	KP
Malacocera albolanata	RL, DL
Malacocera biflora	SP, RL
Malacocera gracilis	DL
Malacocera tricornis	RL
SclerolaenAff Subgroup	
Sclerolaena alata	DL
Sclerolaena anisacanthoides	RL, SP, CP
Sclerolaena articulata	SP
Sclerolaena beaugleholei	DU, RL
Sclerolaena bicornis	RL, CP, CS
Sclerolaena bicuspis	SP
Sclerolaena birchii	MP, RL, SD
Sclerolaena blackiana	SP
Sclerolaena blakei	SP
Sclerolaena brachyptera	SP, RL
Sclerolaena brevifolia	KP
Sclerolaena burbidgeae	RL
Sclerolaena calcarata	RL, SP, CP
Sclerolaena clelandii	DL
Sclerolaena constricta	SP, RL, DL
Sclerolaena convexula	DU, SD

Plant Species	Land Type
Sclerolaena cornishiana	SD, SH, RL
Sclerolaena costata	DU, SD, RL
Sclerolaena crenata	RL, DL
Sclerolaena cuneata	SP, RL, SH
Sclerolaena decurrens	SP, RL
Sclerolaena densiflora	SH, DU
Sclerolaena deserticola	DL, SH
Sclerolaena diacantha	KP, CS, SD, RL, MP
Sclerolaena divaricata	RL, SP
Sclerolaena drummondii	SH, MP
Sclerolaena eriacantha	DU, SP
Sclerolaena eurotioides	DL
Sclerolaena everistiana	RL, SP
Sclerolaena fimbriolata	DL
Sclerolaena fontinalis	RL, SP
Sclerolaena forrestiana	SD
Sclerolaena fusiformis	SH
Sclerolaena gardneri	RL
Sclerolaena glabra	SP, RL
Sclerolaena holtiana	SD, DL, RL, SP
Sclerolaena hostilis	SH, RL
Sclerolaena intricata	SP, RL
Sclerolaena johnsonii	SD
Sclerolaena lanicuspis	SP, RL, DU, SH, CP
Sclerolaena limbata	SP, RL, DU
Sclerolaena longicuspis	SP
Sclerolaena medicaginoides	SH
Sclerolaena microcarpa	SH
Sclerolaena minuta	DU, SP, SH

Plant Species	Land Type
Sclerolaena muelleri	DL, RL
Sclerolaena muricata	RL, CP
Sclerolaena napiformis	MP
Sclerolaena obliquicuspis	KP
Sclerolaena parallelicuspis	SP
Sclerolaena parviflora	SD, KP
Sclerolaena patenticuspis	KP, DU, RL
Sclerolaena ramulosa	RL, MP
Sclerolaena recurvicuspis	RL
Sclerolaena stelligera	RL
Sclerolaena stylosa	KP
Sclerolaena symoniana	DL
Sclerolaena tatei	SP, DL
Sclerolaena tetracuspis	MP, RL
Sclerolaena tetragona	RL
Sclerolaena tricuspis	RL
Sclerolaena tridens	RL
Sclerolaena tubata	RL
Sclerolaena uniflora	CS, KP
Sclerolaena urceolata	DL
Sclerolaena ventricosa	SP, RL
Sclerolaena walkeri	RL
Affiliate species	
Neobassia proceriflora	SP, RL
Threlkeldia diffusa	CS, DL
Threlkeldia inchoata	RL, SP
Osteocarpum acropterum	RL, DL, SP
Osteocarpum dipterocarpum	RL, DL
Osteocarpum pentapterum	SP, RL
Osteocarpum salsuginosum	DL, RL
Osteocarpum scleropterum	RL

Subfamily Salsoloideae

Plant Species	Land Type
***Salsola* (Kali) Clade**	
Salsola australis	CS, MP, DU, SP, KP, RL, CP, SD, DL

Subfamily Suaedoideae

Plant Species	Land Type
***Suaeda* (Brezia) Clade**	
Suaeda arbusculoides	CS
Suaeda australis	CS, RL

Subfamily Salicornioideae

Plant Species	Land Type
***Tecticornia* Clade**	
Tecticornia annelida	DL
Tecticornia arborea	RL
Tecticornia arbuscula	CS
Tecticornia auriculata	CS, DL
Tecticornia australasica	CS
Tecticornia bibenda	DL
Tecticornia bulbosa	DL
Tecticornia calyptrata	DL, RL
Tecticornia chartacea	RL
Tecticornia cupuliformis	RL
Tecticornia cymbiformis	DL
Tecticornia disarticulata	CS, DL, KP
Tecticornia doleiformis	DL
Tecticornia entrichoma	RL
Tecticornia fimbriata	DL
Tecticornia flabelliformis	CS, DL
Tecticornia fontinalis	DL
Tecticornia globulifera	DL
Tecticornia halocnemoides	DL, CS
Tecticornia indefessa	DL
Tecticornia indica	CS, DL
Tecticornia laevigata	DL
Tecticornia lepidosperma	CS, RL
Tecticornia leptoclada	DL
Tecticornia loriae	DL, RL
Tecticornia lylei	DL, RL
Tecticornia medullosa	DL, SP
Tecticornia medusa	DL
Tecticornia mellaria	DL
Tecticornia moniliformis	DL
Tecticornia nitida	DL
Tecticornia papillata	SP
Tecticornia peltata	DL
Tecticornia pergranulata	DL, CS
Tecticornia pluriflora	DL
Tecticornia pruinosa	DL, CS
Tecticornia pterygosperma	DL, CS
Tecticornia sparagosa	DL
Tecticornia syncarpa	DL, CS
Tecticornia tenuis	DL, RL, SP
Tecticornia triandra	RL
Tecticornia undulata	DL
Tecticornia uniflora	DL
Tecticornia verrucosa	RL, CS
***Sarcocornia* Clade**	
Sarcocornia blackiana	CS, DL, RL
Sarcocornia globosa	DL
Sarcocornia quinqueflora	CS, DL, RL

Key	Land Type Name
CS	Coast
MP	Mesic Plain & Range
RL	Riverine Desert
DL	Desert Lake
SD	Sand Desert
DU	Desert Upland
SP	Stony Desert
CP	Desert Clay Plain
SH	Shield Plain

Issues with classifying habitats

Some species presented difficulty in classifying habitats, with descriptions lacking or inconclusive. Even widespread taxa could have little information over a significant part of its range.

The main issue with coastal habitat type was distinguishing Cliff-Rocky from Karst types. The substrate for various Cliff-Rocky types may not be specified (e.g. cliffs, rocky slope, boulder debris). Karst was only assigned with clear mention of calcareous, indurated substrates in habitat notes (e.g. coral, calcarenite, limestone, raised shell bed). Coast facultative species are probably more prone to this issue than Coast obligates, as they occur in areas with both calcareous and non-calcareous lithologies. Calcareous and igneous substrates dominate western and southern rocky coastlines, both often being present along coastal section. Conversely, coastal dune systems contain various degrees of calcareous material that distinguishing calcareous from siliceous coastal dunes is considered difficult.

Collection records were essential to determining proportion of occupation in specific shoreline habitats and various criteria were applied to assign habitat type. A coastal locality name including a habitat type (e.g. Cottesloe Beach) is insufficient for typing. However, for species with scarce data, inference was drawn from additional notes and a locality name (e.g., ‘on deep sand’ at ‘Middleton Beach’). Recent collections with accurate position likely based on GPS, could confirm coastal location, allowing suitable interpretation from other sources. A precise locality, could plot to the estuary habitat mapping layer on ALA [OzCoasts – http://www.ozcoasts.org.au/search_data/datasets.jsp.] or interpreted with imagery. This recourse assisted distinguishing Inland facultative species from Inland obligate species.

For inland taxa, sampling collection records was only essential for the uncommon taxa. With generally few collections, all records were checked for classifying habitat types.

Typing habitats by compiling collection records can introduce bias. Multiple records from a single site, with duplicates in several herbaria, favour the nature of accessible locations that are visited frequently. Collection density reflects priorities, preferences or interests of both herbaria and collectors. Regular excursion to the many islands of Bass Strait can give coastal chenopods a rocky habitat bias. Consistent recording of habitat is also a recent practice. Older collections that dominate some regional efforts, lack habitat information.

To minimise bias, collection records were sampled in arbitrarily objective fashion to derive proportions of habitat occupation of coastal species and the land type mix of inland species. For each species, the fewer records available, the more were included in sampling. For any species of less than 100 records, all records were checked for habitat type. The entire range of each species, as defined by collection plot points, was sampled. Collection duplicates were recorded singly. In classing land type, any habitat for less than 10% of records was treated as insignificant. Those of more than 10%, were included equally, irrespective of frequency of occurrence in land types. Such rules and awareness of biases emerged as AVH records were examined for compilation of habitats. The number of records without habitat information prompted need to examine as many records as possible.

The observation of Chapman (1976) that shingle beaches are relatively unimportant to terrestrial plants needs some clarification. Though not common, and perhaps subject to strict definition of shingle beach, collection records revealed three notable regional occurrences. Shingle beaches are prominent around Tasmania and surrounding islands. On subtropical east and west coasts and islands, chenopods grow on coral cays, often described as coral shingle. These habitats were classed as Cliff-Rocky, or as Karst, if a calcareous substrate was noted.

Appendix XIV: Detail for *Atriplex* species samples used in molecular analyses

Atriplex **Clade**	**Plant Species**	**ISB Nº**	**Collect Date**	**Collector Reference**	**Seq1**	**Seq2**	**Herbarium/ *Accession Nº***	**Source**
1	Atriplex amnicola	Chen 0540			Nr			ISB
1	Atriplex amnicola [OG]	Chen 3481	26/01/2016	JM 1601/65 A	Nr	G		MJG+
1	Atriplex cephalantha	Chen 3495	20/02/1990	E.M.Goble-Gawatt EGG93	Nr		PERTH 02375222	PERTH
1	Atriplex cinerea	Chen 3290	28/01/2015	JM 1501/71	Nr		MJG 018613	MJG
1	Atriplex cinerea	Chen 3315	1/08/2015	JM 1508/01-1	Nr		MJG 018666	MJG
1	Atriplex incrassata	Chen 3320	25/06/2015	JM 1506/08-2	Nr			MJG+
1	Atriplex incrassata	Chen 3321	27/06/2015	JM 1506/23 B	Nr			MJG+
1	Atriplex incrassata [OG]	Chen 3404	27/06/2015	JM 1506/56 A		G		MJG+
1	Atriplex isatidea	Chen 0538		S. Jacobs 9164	Nr		*HM587519*	ISB/Kad2010
1	Atriplex isatidea	Chen 3479	26/01/2016	JM 1601/61 A	Nr			MJG+
1	Atriplex isatidea	Chen 3486	26/01/2016	JM 1601/61 C	Nr			MJG+
1	Atriplex nummularia	Chen 0415		G. M. Towler 323	Nr		*HM587534*	ISB/Kad2010
1	Atriplex nummularia ssp. spathulata	Chen 3287	22/01/2015	JM 1501/19	Nr		MJG 018619	MJG
1	Atriplex rhagodioides	Chen 3278	19/11/2014	JM 1411/32	Nr		MJG 018624	MJG
1	Atriplex rhagodioides	Chen 3475	9/04/2016	JM 1604/1(-2)	Nr			MJG+
1	Atriplex yeelirie	Chen 2381			Nr			ISB
2	Atriplex acutibractea	Chen 3266	20/05/2014	JM 1405/8	Nr	G	MJG 018647	MJG
2	Atriplex acutibractea	Chen 3286	22/01/2015	JM 1501/16	Nr		MJG 018618	MJG
2	Atriplex acutibractea ssp. acutibractea	Chen 2358			Nr			ISB
2	Atriplex acutibractea ssp. karoniensis	Chen 2359			Nr			ISB
2	Atriplex acutiloba	Chen 3455	7/09/2013	DJ Duval 2717	Nr	G	AD 264150	ADELAIDE
2	Atriplex angulata	Chen 3279	20/11/2014	JM 1411/43	Nr		MJG 018622	MJG+
2	Atriplex angulata	Chen 3314	25/06/2015	JM 1506/13 A	Nr	G	MJG 018655	MJG+
2	Atriplex billardierei	Chen 0564			NrI		*HM587485*	ISB/Kad2010
2	Atriplex billardierei	Chen 3472	1/01/2007	Tyson, P.A. 312	Nr		MEL 2320020	MELBOURNE
2	Atriplex bunburyana	Chen 1810			Nr			ISB
2	Atriplex bunburyana	Chen 2382			Nr			ISB
2	Atriplex bunburyana	Chen 3480	23/01/2016	JM 1601/28		G		MJG+
2	Atriplex codonocarpa	Chen 0539			NrI		*HM587492*	ISB/Kad2010

***Atriplex* Clade**	**Plant Species**	**ISB Nº**	**Collect Date**	**Collector Reference**	**Seq1**	**Seq2**	**Herbarium/ *Accession Nº***	**Source**
2	Atriplex codonocarpa	Chen 3494	4/09/2013	R. Davis s.n.	Nr	G	PERTH 8559546	PERTH
2	Atriplex cordifolia	Chen 1830			Nr			ISB
2	Atriplex cordifolia	Chen 3452	26/04/2002	D & J Symon 16818		G	AD 131479	ADELAIDE
2	Atriplex cornigera	Chen 1833			Nr			ISB
2	Atriplex crassipes	Chen 3453	16/09/2008	M Barnett BS612-211		G	AD 229436	ADELAIDE
2	Atriplex crassipes ssp. crassipes	Chen 0907		S. Jacobs 9348	Nr		MJG 013375	MJG
2	Atriplex cryptocarpa	Chen 3288	23/01/2015	JM 1501/24 A	Nr	G	MJG 018617	MJG
2	Atriplex cryptocarpa	Chen 3289	23/01/2015	JM 1501/26 B	Nr		MJG 018616	MJG
2	Atriplex eardleyae	Chen 3280	21/11/2014	JM 1411/55	Nr		MJG 018623	MJG
2	Atriplex eardleyae	Chen 3292	30/01/2015	JM 1501/121	Nr	G	MJG 018615	MJG
2	Atriplex eichleri	Chen 3293	20/05/2015	JM 1505/5	Nr	G	MJG 018632	MJG
2	Atriplex eichleri	Chen 3316	15/08/2015	JM 1508/72 A	Nr		MJG 018678	MJG
2	Atriplex elachophylla	Chen 0912			NrI		*HM587501*	ISB/Kad2010
2	Atriplex elachophylla	Chen 3456	14/08/1998	PD Canty BS23-28130	Nr		AD 112966	ADELAIDE
2	Atriplex eremitis	Chen 3492	19/10/1999	D. Duero WE-49	Nr		PERTH 08636184	PERTH
2	Atriplex exilifolia	Chen 1823			Nr			ISB
2	Atriplex exilifolia	Chen 2362			Nr			ISB
2	Atriplex fissivalvis	Chen 3317	28/06/2015	JM 1506/59	Nr		MJG 018660	MJG
2	Atriplex fissivalvis	Chen 3318	12/08/2015	JM 1508/14 B	Nr	G	MJG 018670	MJG
2	Atriplex flabelliformis	Chen 2364			Nr			ISB
2	Atriplex holocarpa	Chen 3295	22/05/2015	JM 1505/42	Nr	G	MJG 018636	MJG
2	Atriplex holocarpa	Chen 3319	25/06/2015	JM 1506/04	Nr		MJG 018651	MJG
2	Atriplex humifusa	Chen 2365			Nr			ISB
2	Atriplex humifusa	Chen 3458	3/09/2013	DJ Duval 2686		G	AD 264120	ADELAIDE
2	Atriplex hymenotheca	Chen 0536			NrI		*HM587514*	ISB/Kad2010
2	Atriplex hymenotheca	Chen 3459	13/09/1998	MN & SD Lyons 3424	Nr		AD 221429	ADELAIDE
2	Atriplex hymenotheca	Chen 3493	10/09/2009	M. Hislop 3929	Nr		PERTH 08260605	PERTH
2	Atriplex hypoleuca	Chen 3483	29/01/2016	JM 1601/82	Nr			MJG+
2	Atriplex hypoleuca	Chen 3485	30/01/2016	JM 1601/85 D-1	Nr			MJG+
2	Atriplex infrequens	Chen 1829			Nr			ISB
2	Atriplex infrequens	Chen 3476	20/05/2016	JM 1605/5 A		G		MJG+

Atriplex **Clade**	**Plant Species**	**ISB Nº**	**Collect Date**	**Collector Reference**	**Seq1**	**Seq2**	**Herbarium/** ***Accession Nº***	**Source**
2	Atriplex intermedia	Chen 3272	23/09/2014	JM 1409/14	Nr	G	MJG 018641	MJG
2	Atriplex kochiana	Chen 3322	12/08/2015	JM 1508/13 B	Nr	G	MJG 018668	MJG
2	Atriplex kochiana	Chen 3323	13/08/2015	JM 1508/42 A	Nr		MJG 018675	MJG
2	Atriplex leptocarpa	Chen 3276	19/11/2014	JM 1411/19 A	Nr	G	MJG 018626	MJG
2	Atriplex leptocarpa	Chen 3302	26/05/2015	JM 1505/118 A(-1)	Nr	G	MJG 018642	MJG
2	Atriplex limbata	Chen 0902		S. Jacobs 9341	Nr		MJG 013371	MJG
2	Atriplex limbata	Chen 3299	25/05/2015	JM 1505/89-1	Nr		MJG 018645	MJG
2	Atriplex limbata	Chen 3324	13/08/2015	JM 1508/30	Nr	G	MJG 018674	MJG
2	Atriplex lindleyi	Chen 3275	19/11/2014	JM 1411/15	Nr		MJG 018627	MJG
2	Atriplex lindleyi ssp. conduplicata	Chen 3271	22/09/2014	JM 1409/07	Nr	G	MJG 018640	MJG
2	Atriplex lindleyi ssp. conduplicata	Chen 3301	26/05/2015	JM 1505/104	Nr		MJG 018643	MJG
2	Atriplex lindleyi ssp. inflata	Chen 3325	28/08/2015	JM 1508/88-1	Nr		MJG 018676	MJG
2	Atriplex lindleyi ssp. quadripartita	Chen 3300	26/05/2015	JM 1505/102-1	Nr	G	MJG 018644	MJG
2	Atriplex lobativalvis	Chen 3326	12/08/2015	JM 1508/07 B-1	Nr	G	MJG 018667	MJG
2	Atriplex macropterocarpa	Chen 3303	23/05/2015	JM 1505/57	Nr	G		MJG+
2	Atriplex macropterocarpa	Chen 3327	12/08/2015	JM 1508/15	Nr		MJG 018671	MJG
2	Atriplex morrisii	Chen 3328	13/08/2015	JM 1508/27-2	Nr	G	MJG 018673	MJG
2	Atriplex muelleri	Chen 0670			NrI		*HM587531*	ISB/Kad2010
2	Atriplex muelleri	Chen 3498		LS 377 Mainz	Nr	G		ISB
2	Atriplex nana	Chen 3478	23/01/2016	JM 1601/31		G		MJG+
2	Atriplex nana	Chen 2373			Nr			ISB
2	Atriplex nessorhina	Chen 0913			NrI		*HM587532*	ISB/Kad2010
2	Atriplex nessorhina	Chen 3461	3/11/2009	DJ Duval 1648	Nr	G	AD 232259	ADELAIDE
2	Atriplex obconica	Chen 3329	26/05/2015	JM 1505/116	Nr		MJG 018650	MJG
2	Atriplex obconica	Chen 3330	26/06/2015	JM 1506/25 A	Nr	G	MJG 018656	MJG
2	Atriplex paludosa	Chen 3269	4/07/2014	JM 1407/31 A	Nr		MJG 018631	MJG
2	Atriplex paludosa	Chen 3281	26/11/2014	JM 1411/58	Nr		MJG 018621	MJG
2	Atriplex paludosa	Chen 3284	17/12/2014	JM 1412/13-1	Nr	G	MJG 018639	MJG
2	Atriplex papillata	Chen 3273	18/11/2014	JM 1411/7 B	Nr	G	MJG 018629	MJG
2	Atriplex papillata	Chen 3277	19/11/2014	JM 1411/24 A	Nr		MJG 018625	MJG
2	Atriplex pseudocampanulata	Chen 2357		S. Jacobs 9244	Nr		MJG 013366	MJG

***Atriplex* Clade**	**Plant Species**	**ISB Nº**	**Collect Date**	**Collector Reference**	**Seq1**	**Seq2**	**Herbarium/ *Accession Nº***	**Source**
2	Atriplex pseudocampanulata	Chen 3477	21/05/2016	JM 1605/12 A		G		MJG+
2	Atriplex pumilio	Chen 3496	28/04/2006	G. Byrne 1993		G	PERTH 07803796	PERTH
2	Atriplex quadrivalvata	Chen 3484	30/06/2015	JM 1506/97		G		MJG+
2	Atriplex quadrivalvata var. quadrivalvata	Chen 1824			Nr			ISB
2	Atriplex quadrivalvata var. quadrivalvata	Chen 2368			Nr			ISB
2	Atriplex quadrivalvata var. sessilifolia	Chen 1825			Nr			ISB
2	Atriplex quinii	Chen 3297	24/05/2015	JM 1505/68 A	Nr		MJG 018636	MJG
2	Atriplex quinii	Chen 3331	30/06/2015	JM 1506/96 B	Nr	G	MJG 018663	MJG
2	Atriplex semibaccata	Chen 2355			Nr			ISB
2	Atriplex semibaccata	Chen 3283	10/12/2014	JM 1412/9-1	Nr		MJG 018638	MJG
2	Atriplex semibaccata	Chen 3291	28/01/2015	JM 1501/74	Nr	G	MJG 018614	MJG
2	Atriplex semilunaris	Chen 2354		S. Jacobs 9167	Nr		MJG 013377	MJG
2	Atriplex semilunaris	Chen 3482	26/01/2016	JM 1601/67A		G		MJG+
2	Atriplex spec. (at Edgbaston)	Chen 3468	8/04/2010	Thompson, E.J. MUT403	NrE		BRI AQ 862759	BRISBANE
2	Atriplex spec. (at Mirrica)	Chen 3469	21/07/2010	Silcock, J.L. JLS482	NrE		BRI AQ 851163	BRISBANE
2	Atriplex spec. Davenport Downs	Chen 3466	14/08/2012	Pennay, C. CP575	NrE		BRI AQ 920699	BRISBANE
2	Atriplex spec. Doongmabulla	Chen 3465	1/04/1992	Thompson, E.J. GAL20	NrE		BRI AQ 543059	BRISBANE
2	Atriplex spec. Doongmabulla	Chen 3471	26/10/2014	Fensham, R.J. 6448	NrE		BRI AQ 854167	BRISBANE
2	Atriplex spec. Edgbaston	Chen 3467	4/04/2011	Thompson, E.J. MUT481	NrE		BRI AQ 852082	BRISBANE
2	Atriplex spinibractea	Chen 3473	6/02/4014	Jeanes, J.A. 3074; Lay G.M.	Nr	G	MEL2372916	MELBOURNE
2	Atriplex spinulosa	Chen 0541			Nr			ISB
2	Atriplex spongiosa	Chen 3296	24/05/2015	JM 1505/66 A	Nr			MJG+
2	Atriplex spongiosa	Chen 3332	28/06/2015	JM 1506/66	Nr	G	MJG 018635	MJG
2	Atriplex stipitata	Chen 0437		S. Jacobs 9095		G	MJG 013392	MJG/Kad2010
2	Atriplex stipitata var. Gracile	Chen 3333	30/06/2015	JM 1506/106	Nr	G	MJG 018665	MJG
2	Atriplex stipitata var. Gracile	Chen 3407	28/08/2015	JM 1508/87		G	MJG 018677	MJG
2	Atriplex stipitata var. Robust	Chen 3294	20/05/2015	JM 1505/15	Nr		MJG 018633	MJG
2	Atriplex sturtii	Chen 3474	4/07/2008	Latz, P.K. 23587	Nr	G	MEL 2332598	MELBOURNE
2	Atriplex suberecta	Chen 3274	19/11/2014	JM 1411/14	Nr	G	MJG 018628	MJG
2	Atriplex suberecta	Chen 3285	20/01/2015	JM 1501/2	Nr		MJG 018620	MJG
2	Atriplex turbinata	Chen 3334	25/06/2015	JM 1506/01-1	Nr	G	MJG 018654	MJG

***Atriplex* Clade**	**Plant Species**	**ISB N^{o}**	**Collect Date**	**Collector Reference**	**Seq1**	**Seq2**	**Herbarium/ *Accession N^{o}***	**Source**
2	Atriplex velutinella	Chen 3298	25/05/2015	JM 1505/82-1	Nr		MJG 018646	MJG
2	Atriplex velutinella	Chen 3335	25/06/2015	JM 1506/03-2	Nr	G	MJG 018653	MJG
2	Atriplex vesicaria	Chen 1811			Nr			ISB
2	Atriplex vesicaria	Chen 3267	20/05/2014	JM 1405/13	Nr		MJG 018649	MJG
2	Atriplex vesicaria	Chen 3268	20/05/2014	JM 1405/14	Nr		MJG 018648	MJG
2	Atriplex vesicaria	Chen 3270	4/07/2014	JM 1407/32 A	Nr	G	MJG 018630	MJG
2	Atriplex vesicaria	Chen 3282	10/12/2014	JM 1412/7 B	Nr		MJG 018637	MJG
OG	Atriplex sphaeromorpha [OG]	Chen 3489		Sukhorukov	Nr			ISB

Key

OG: Outgroup species

ISB No: Chenopod sample number Institut fur Spezielle Botanik, Johannes Gutenberg University, Mainz (now Institut fur Molekulare Physiologie)

Collector Reference: Name and Field Id for species collection. “JM” is collection by author.

Seq1/Seq2: Molecular sequences used in analysis
Nr – ITS1/2 & ETS markers
NrI – ITS1/2 markers only
NrE – ETS markers only
G – Genotyping-by-Sequencing

Source: Institution source/location of voucher specimen, sample, information
MJG – Herbarium at Universitat Mainz
ISB – Institut fur Spezielle Botanik at Universitat Mainz; sample used in unpublished earlier analyses
ADELAIDE, BRISBANE, MELBOURNE, PERTH – Australian Herbaria
Kad2010 – Published in Kadereit *et al.* (2010)
MJG+ - Species sample collected by JM held at ISB and to be lodged in Herbarium at Universitat Mainz

Appendix XV: Modified protocols to Genotyping-by-Sequencing sample preparation

[Supplied by Ursula Martine, Laboratory Technician, Johannes Gutenberg University at Mainz]

DNA Extraction

DNA-Extraction of 20mg sample material with DNAeasy Plant Kit Qiagen, following Qiagen protocol with the following modifications:

- Lysis time step 8, extended to 60 minutes, RNase A for the last 10 minutes of lysis time. Mixed all for 10 minutes during incubation by inverting the tube
- Elution for 30 minutes, step 18 with only 50µl to increase the final concentration; at Step 19, 50µl and 30 min, a separate tube was used

DNA Sequencing

For GBS, the established protocol (Elshire *et al.* 2011) was used with some variations:

- DNA is digested with BamH I HF (NEB R3136) at 37°C
- Following Elshire *et al.* (2011), an adapter titration was initially made to establish a good DNA library and a minimum of adapter dimers. For *Atriplex* (200ng DNA), 0.75ng adapter was determined to be sufficient
- Each DNA sample was 200ng in a maximum of 5µl. This volume was not exceeded for digestion (20µl = 25%). For samples with lower concentration, the adapter concentration and the volume was adjusted later in the pooling step before the library PCR. The same DNA input was applied in the PCR as other samples
- One preparation is a batch of 25 samples
- Digestion (20µl): 200ng DNA, 2µl Cut Smart buffer 10x, 0.5µl BamH I HF (10U), adapter 20µl dH2O. 2hrs at 37°C, cool to 4°C
- Ligation (50µl): 20µl digest DNA, 5µl ligase buffer 10x, 1.5µl adapter (0.75ng), 1µl T4 DNA Ligase (NEB M0202), 22.5µl dH2O. 1.5hr 22°C, 30min 65°C, cool to 4°C
- A pool of 25 samples is made; 10µl of each sample (starting with 200ng or adjusted volume for samples of less amount)
- Clean up with Macherey Nagel Nucleospin Gel and PCR clean up Kit (#740609.50). One column used and repeated in the washing step once more, all in all 3 times. Elution: 2 times with 25µl, for 10 minutes each, collected in the same tube
- Library PCR: 6 separate PCRs
- For each PCR: 2µl sample (from step before), 5µl NEB Taq 5x Mastermix (M0285), Primer (10µM) forward and reverse each 0.5µl (final 0.2µM), adapter 25µl dH2O. 5min 72°C, 30 sec 98°C, then 18 cycles of 10 sec 98°C, 30 sec 65°C, 40 sec 72°C, followed by final extension 5 min 72°C, cool at 4°C
- 6 PCRs are pooled and cleaned up with Macherey Nagel NucleoSpin PCR clean up Kit

Appendix XVI: Distribution of chenopod subfamilies

Distribution of subfamilies was compiled through aggregate maps of component genera. For clades within Chenopodioideae and Suaedoideae, this would include exotic species, recently arrived, however their species ranges largely are contained with the ranges of native taxa.

Camphorosmoideae, Chenopodioideae, Salicornioideae and Salsoloideae occupy much of the continental interior, as shown in figure A1. The predominantly coastal Suaedoideae has inland populations of southwest and southeast Australia. Greater intensity of collection effort through the Biological Survey of South Australia, reveals clear boundaries of South Australia in the Salsoloideae.

Broad geography of distribution

Broad-scale geographic observations of subfamily distributions are:

1. Northern limits to denser distributions of the Camphorosmoideae and Chenopodioideae are closely proximate, straddling a line connecting Derby, Halls Creek, Newcastle Waters, Hughenden and Townsville. A similar limit for Salsoloideae is north of this line. In Northern Australia, coastal Salicornioideae, Suaedoideae and Salsoloideae are the main chenopod presence.

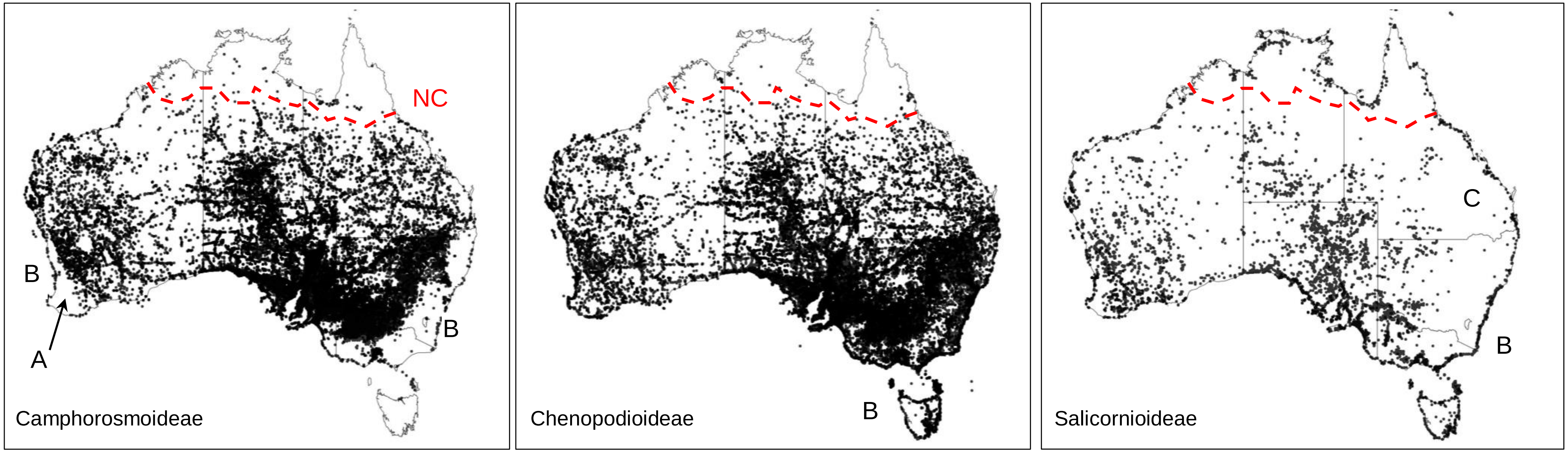
2. Salicornioideae is the least extensive of the widespread subfamilies, being absent or scarce in eastern Australia. Northern limits are south of the Derby-Townsville limits of other subfamilies.

3. Camphorosmoideae and Salsoloideae are very scarce in Tasmania, uplands of New South Wales and Victoria and coastal plains of Western Australia. Both are in subtropical uplands of central-eastern Queensland.

4. Chenopodioideae is the most widespread subfamily, of contiguous range from east coast to west coast, including mesic south-eastern and south-western Australia.

5. All subfamilies are coastally prominent, including where the immediate hinterland lacks chenopods (Salicornioideae, Suaedoideae on north and east coasts; Camphorosmoideae on south-west and south-east coasts; Chenopodioideae around Tasmania; Salsoloideae on the east coast).

6. Chenopodioideae and Salicornioideae are more extensively distributed along coastlines. Salicornioideae is near-continuously spread over all coasts. The mostly coastal Suaedoideae is discontinuously spread along the north, west and south coasts.



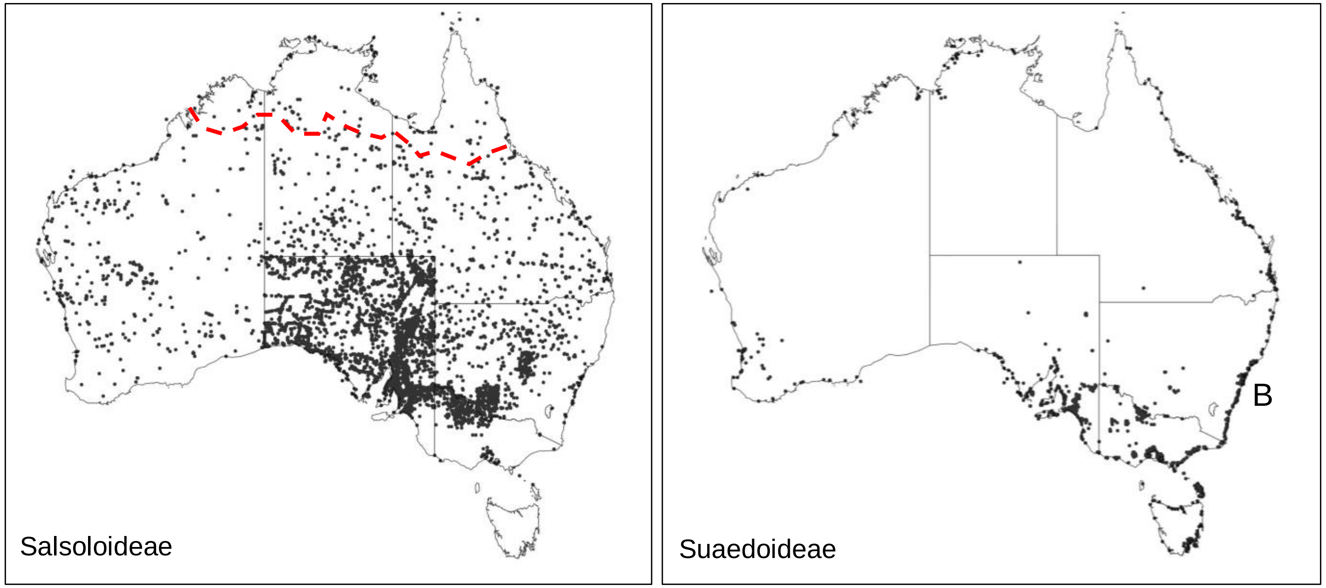


Figure A1: Distribution of chenopod taxa in subfamilies. Patterns include:

A – Absence of Camphorosmoideae on the western coastal plain of Western Australia. Other subfamilies are relatively less dense there.

B – Coastal occurrences without associated hinterland populations as noted in Shmida (1985); less obvious in Salsoloideae.

C – Relative scarcity of Salicornioideae in northern and eastern Queensland and eastern New South Wales, where other rich subfamilies are more abundant and diverse.

NC – Approximate northern limit (in red) to a denser distribution of the Camphorosmoideae. Relative to other subfamilies: Chenopodioideae have a similar limit; Salsoloideae have a more northerly limit; Salicornioideae have a notably more southern limit.

Appendix XVII: Additional work completed during the course of post-graduate study

McDonald J, Biffin E, Lowe AJ (2016) Broad genetic variation in fragmented populations of endangered bluebushes *Xanthopus* **34** (3) p6-9 (Newsletter of the Nature Conservation Society of South Australia)

McDonald J, Breed MF, Gellie N, Blyth C, Lowe AJ (2017) *A life cycle review of Maireana sedifolia, with a focus on seeding triggers* Environment Institute University of Adelaide, South Australia

Baruch Z, Christmas MJ, Breed MF, Guerin GR, Caddy-Retalic S, **McDonald J**, Jardine DI, Leitch E, Gellie N, Hill K, McCallum K, Lowe AJ (2017) Leaf trait associations with environmental variation in the wide-ranging shrub *Dodonaea viscosa* subsp. *angustissima* (Sapindaceae) Austral Ecology **42** p553-561

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