

Vegetation Patterns across the Sydney Basin during the Last Glacial Maximum based on Plant Biogeography, Ecology, Geomorphology and Climate

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Despite the importance of the Last Glacial Maximum (LGM) in the formation of modern Australian vegetation, no comprehensive account exists of the likely vegetation of this period in the Sydney Basin. Likely past LGM vegetation events and patterns for this region are proposed, based on geomorphological, palynological and archaeological studies, combined with current geographical distributions of endemic, restricted and common plant species, inferences from basic ecological characteristics, observed vegetation community interactions, and morphological or genomic variation.

Based on ecological attributes (stress-tolerators, competitors, ruderals), and geographic distributions, individual species are associated with likely past survival during the drier and colder LGM climate (28 000-18 000 years BP), across the different landscapes within the region. These include the old, climatically buffered, infertile (OCBIL) Sydney sandstone plateau systems; the old but more fertile shale (OCFEL) areas (Illawarra, western Sydney, Central Tablelands); the younger fertile alluvial lowlands (YODFELs); and the now-inundated LGM continental shelf/coastal plain.

Potential LGM vegetation scenarios include Blue Mountains moisture-related stress-tolerant heath, mallee, seepage and cliffline vegetation on an LGM subalpine zone (>800 m elev.) with snowmelt and effectively better moisture; dry grassland and mallee shrubland on the Central Tablelands and western Sydney shale areas; and eastward movement of western clay soil species through Hunter Valley/Southern Highland connections and sclerophyll shrubs across mid-elevation dry sandstone. The importance of the coastal plain/continental shelf, including coastal wallum vegetation, is suggested as the origin of many species' distribution disjunctions.

By interweaving circumstantial evidence and speculation, hypotheses and narratives can be developed to provide a spur to plant ecological and biogeographic research and advance research in the field.

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INTRODUCTION

Over the past half-century much effort has gone into mapping and describing the vegetation communities of New South Wales, their patterns in relation to soils and current climate, and their ecological responses to impacting factors particularly fire. Rarely has current vegetation or work on rare species been linked with possible past vegetation histories. There are exceptions mainly relevant to very distant time periods, e.g. highlighting the antiquity of species such as the Wollemi Pine, *Wollemia nobilis*

(from a 200 million-year-old plant family) (Jones et al. 1995), formation of Gondwana rainforests during the Cretaceous period (about 140 million years ago), and evolutionary histories of various phylogenies over similar time periods (e.g. Weston and Jordon 2017; Bryceson et al. 2023).

The Last Glacial Maximum (LGM) (28 000-18 000 years BP) is an inherently interesting period, encompassing the Ice Age era in the Northern Hemisphere, popularised in commercial entertainments, and occurring within the period

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of Aboriginal occupation in eastern Australia (Attenbrow 2002). The Sydney Basin landscape is a major Australian biogeographical area, but despite the influence of the severe climatic disruptions of the LGM on the formation of the modern vegetation (Mooney et al. 2017), there is no comprehensive account of its vegetation history in this period. The relatively dry climate, the stability of the sandstone landscapes and frequency of major fire events have left few surviving sites with evidence of past vegetation histories for geomorphological, palynological and archaeological studies. Peat-forming conditions are limited and most begin more recently than the LGM.

The various historical sources, pollen, fossil testate amoebae, charcoal and the geomorphology only provide a broad, non-specific, picture of LGM structural vegetation structure of the Sydney area during the LGM (e.g. Hesse et al. 2003; Robbie and Martin 2007; Chalson and Martin 2008; Mooney et al. 2021). There was vegetation, except perhaps in higher parts of the upper Blue Mountains. There is no evidence of glaciation, though treeless conditions are inferred by limited occurrences of clifftop sand dunes (Hesse et al. 2003). There was some eucalypt-dominated vegetation in sheltered sites in the lower Blue Mountains (Robbie and Martin 2007), and essentially shrubby vegetation (i.e. with much less tree cover) on the coastal sandstone plateaus. There was contrasting grassy but treeless vegetation on shale soils in western Sydney (Chalson and Martin 2008).

Can the contemporary distributions of extant plant species, at least for those with particular ecological characteristics, expand this structural picture? Biogeography relates occurrences of plant species with landscape and climate at continental and local scales; it has been integral to advances in scientific thinking on major issues including evolutionary history and continental drift (Weston and Jordon 2017). Evolutionary studies use biogeographic information to interpret taxa changes over millennia. Can contemporary plant distributions be interpreted as “fossil” evidence of past distributions? Can current distributions of rare plants, unexpected occurrences of more common ones and geographical distributional limits of others, together with their ecological characteristics (particularly distance dispersal and longevity), tell us something about past vegetation patterns over more recent periods of time, and specifically during the Last Glacial Maximum?

Rare plants may tell us about their past

Some plant species are widespread and common across a landscape, some are widespread but rare,

others are rare but locally common, or sometimes very localised (Rabinowitz et al 1986; Kunin and Gaston 2012). Plant distributions are generally considered in relation to ecology and habitat; concurrent distributions may be generalised into plant communities and interpreted through landscape and vegetation mapping. This classification process depends mainly on the distributions of the widespread and common species. Rare and very localised species do not contribute much to the landscape picture, though conservation management is often focussed on our inherent interest in them.

Plants may be rare because we have destroyed their habitat (e.g. clearing for agriculture or urban development) or changed the conditions under which they prospered (e.g. grazing by livestock or rabbits) (NSW Office of Environment & Heritage 2023). However, some plant species are naturally rare, that is, they have always been of limited occurrence in the current landscape, at least as we understand it. Within the Sydney region many of these rare species are geographically restricted, many are restricted to sandstone habitats; many are Central Coast/Central Tablelands endemics; and some species occur naturally in very limited local clusters. Others may have populations separated by large distances, i.e. disjunct distributions, in relation to the species' apparent dispersal mechanisms, often on related sandstone or similar landscapes, which are themselves widely separated (particularly on the South Coast and Southern Tablelands). Over long periods of time, small differences between isolated populations of a species may develop in response to differing local habitat/climatic conditions or from random drift, a process known as vicariance. Major differences may indicate the evolution of separate species over a long period of time. Slight morphological variation, recognised by botanists as subspecies, varieties or local forms, may be evidence of change over shorter or more recent time periods.

The Sydney area

The Sydney area here includes both the Sydney Basin Bioregion, a major sedimentary geological basin, and the eastern edge of the South Eastern Highlands Bioregion with contrasting metamorphic geology (NSW National Parks and Wildlife Service 2003). The area covers the NSW Central Coast and Central Tablelands Botanical Subregions (Figure 1) (Benson and McDougall 1993), extending from Newcastle to Nowra and inland to Oberon and Bathurst. It includes major areas of National Park (NP) including the one million ha of the Greater Blue Mountains World Heritage Area (GBMWhA).

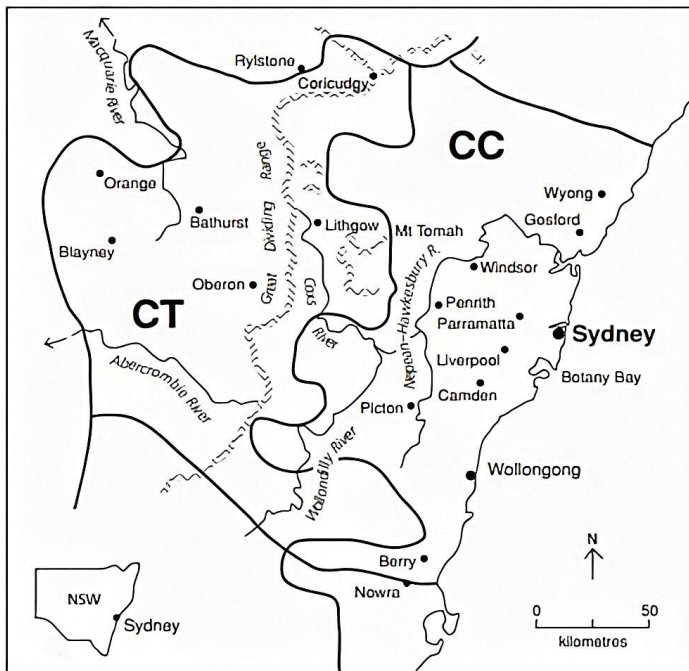


Figure 1. Sydney area showing Central Coast and Central Tablelands Botanical subregions.

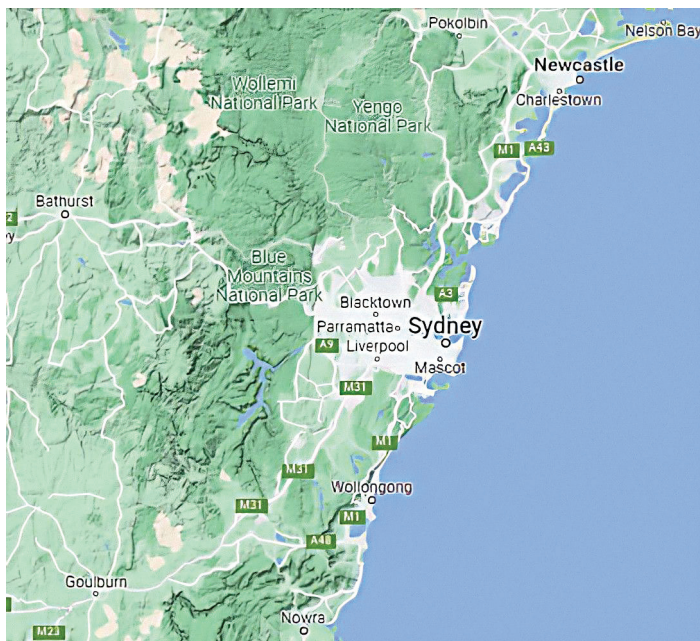


Figure 2. Sydney area landforms, the darker green dissected sandstone landscapes contrasting with the low elevation western Sydney Cumberland Plain.

The distance from the coast west to the upper Blue Mountains is about 100 km with an elevation rise from sea level at Sydney to about 1200 m in the Blue Mountains and Great Dividing Range. Geologically the area is centred on the Triassic Wianamatta Shale and Tertiary alluvial sandy clay deposits of the low-

lying Cumberland Plain, which includes most of western Sydney and extends about 50 km inland, and includes the alluvial flats of the Hawkesbury-Nepean River. The Cumberland Plain is surrounded by an arc of older Triassic Hawkesbury and Narrabeen Group coastal and mid-elevation sandstone plateaus (Figure 2), including Brisbane Water, Ku-ring-gai Chase, Royal, Nattai, Blue Mountains, Yengo and Wollemi National Parks. Annual rainfall is high on the coast (1200 mm pa), dropping to about 600 mm in western Sydney, and then increasing with elevation to about 1200 mm in the upper Blue Mountains. Soil fertility in the Sydney Basin is generally low, especially on the Triassic sandstones, which are characterised by shrubby sclerophyll vegetation structurally dominated by eucalypt woodland and open-forest (Keith 2004). Much of the area is within the Greater Blue Mountains World Heritage Area (GBMWA), which was listed for World Heritage in 2000 for outstanding universal values related to the exceptional richness and unique values of its biodiversity (NSW National Parks and Wildlife Service 1998).

Biodiversity

Sydney area vegetation has been of scientific interest since Joseph Banks and Daniel Solander made the first botanical collections at Botany Bay in 1770 (Benson and Eldershaw 2007). The new plants stunned the scientific community in Europe and further exploration of the flora of the Blue Mountains did not disappoint. The Sydney area includes about 2000 native plant species, more than 100 of which are endemic. The case for listing the Blue Mountains for World Heritage cited the biodiversity richness of the eucalypt forest flora (almost 100 species), the diversity of habitats, and the number of endemic species (NSW National Parks and Wildlife Service 1998). The Sydney Montane Heaths, for example, have some outstanding examples of vicariant biogeography, the phenomenon

whereby closely related species replace one another at different locations (Keith 2004). Many species have localised and/or disjunct distributions, for example, *Darwinia* spp., *Persoonia* spp. and mallee eucalypts (Rutherford et al. 2016).

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The high species diversity associated with low nutrient landscapes worldwide, such as in the southwest Australian Floristic Region, the Greater Cape area in South Africa and Pantepui in South America, has been recognised in the OCBIL theory. This multi-hypothesis formulation was developed to increase understanding of the evolution, ecology and conservation of biological and cultural diversity on old, climatically buffered, infertile landscapes, designated OCBILs (Hopper 2021, Hopper et al. 2021). Hopper has suggested that on OCBIL landscapes such as the Sydney Blue Mountains sandstone area, sclerophyll flora has evolved with a particular range of morphological and ecological characteristics, including stress-tolerance features, accentuated persistence, commonly clonal old individuals, and slow individual growth. Other OCBIL ecological features include: limited dispersal ability; seed simply being shed around the parent resulting in fidelity to certain habitats thereby increasing local endemism; and nutritional and other specialisations such as cluster roots, hemi-parasitism and ant-adapted dispersal (exemplified in many Fabaceae - Berg 1975). Species with these stress-tolerator characteristics, including both dicot shrubs and monocot geophytes make up 40-80% of local Sydney heath floras (Keith 2004), including many rare and endemic species confined to plateaus and ridgetops. Some terrestrial orchids have particular soil, microbial and pollinator requirements restricting their habitats. Stress-tolerator and OCBIL characteristics align closely with characteristics likely to have facilitated species survival *in situ* during the harsh conditions of the LGM.

Associated with the sandstone OCBIL landscapes are more fertile clay soil landscapes exposed on interleaved shales forming old, climatically-buffered relatively fertile landscapes (OCFELs) (Hopper et al. 2021). Of broadly similar age to the OCBILs these support grassy woodlands and rainforest species with some OCBIL characteristics indicative of long periods of stable existence. In contrast, areas of younger fertile alluvial and riparian soils, and Recent dune soils, may be classed as YODFELs, i.e. younger, often disturbed, more fertile lowland landscapes (Hopper 2021), and may have quicker growing and more readily-dispersed species than the OCBIL sclerophylls. The importance here is the age of the landscape rather than just the fertility. Some classic OCBIL landscapes such as the Sydney sandstones have probably been in existence contemporaneously with mesic rainforest on OCFEL landscapes since Gondwanan times. The juxtaposition of OCBIL, OCFEL and YODFEL ecosystems is a major contributor to Sydney area habitat diversity.

Scope of this work

Research on climate change is providing increasing evidence of past Pleistocene and Holocene climates, previously only open to speculation, giving greater confidence for vegetation interpretation. This work develops an historical ecological narrative describing likely past vegetation patterns across the Sydney Basin, using climatic, geomorphological, palynological and archaeological studies, together with current geographical distributions of plant species, and inferences from basic ecological characteristics, vegetation community interactions and morphological or genomic variation (together with a set of assumptions about past vegetation behaviour). The time frame being considered is from the Pleistocene Last Glacial Maximum (LGM) (28 000-18 000 years BP), through the subsequent warming events of the early and mid-Holocene, to the onset of increased climatic variability and the fluctuating climatic patterns associated with increased frequency and/or strength of the El Niño Southern Oscillation (ENSO). This first paper uses plant species distributions and ecology to infer evidence of Last Glacial Maximum vegetation in the Sydney Basin. Vegetation areas dealt with include the coastal sandstone plateaus and LGM continental shelf, upper Blue Mountains and Tablelands, and Western Sydney landscapes. Following work will cover the impacts of the Holocene warming (14 000-6 000 years BP), and the subsequent progression into the contemporary period (the last 6 000 years) associated with increased climatic variability and the development of the El Niño southern oscillation (ENSO).

Late Pleistocene climates in southeastern Australia

During the last 100 000 years of the Pleistocene Period, conditions became increasingly colder and drier in southeast Australia, with a progressive buildup of ice (Mooney et al. 2017), but with enhanced effective precipitation during some intervals, such as cool and humid conditions from 57 000-29 000 years BP. The severe climatic conditions culminated in the Last Glacial Maximum (LGM) extending from about 28 000-18 000 years BP. Average global temperatures were about 7 °C colder than in the 20th century. Sea level dropped to 125 m below that of today. Northern Europe and North America were covered in massive ice sheets. Britain was covered in ice, except for Graminoid and Forb Tundra in the southeast, to become Deciduous Forest in the modern era (Binney et al 2017).

Less severe climatic conditions occurred in Australia, which had only minor periglacial activity (Kosciusko and Tasmania) but was essentially free of ice and mostly remained vegetated, but

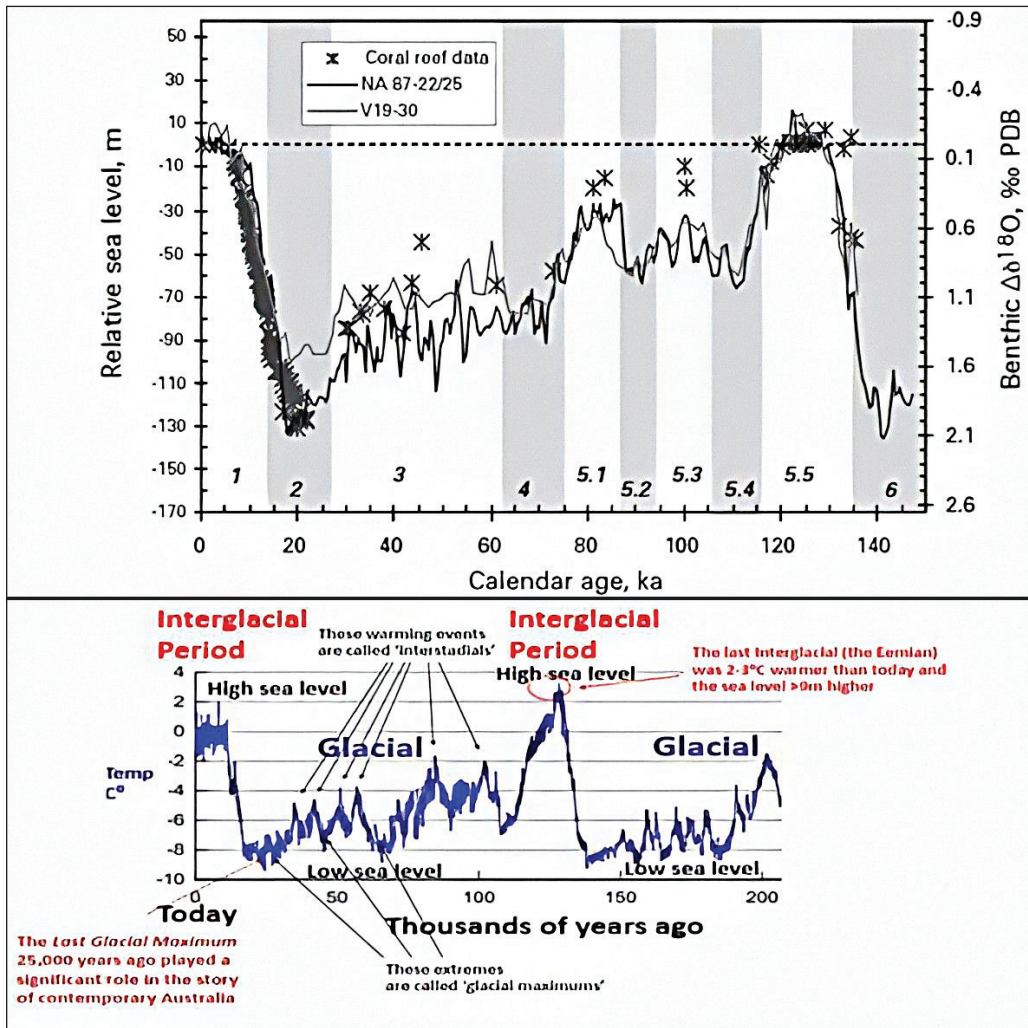


Figure 3. Sea level change over the last 150 000 years from Waelbroeck et al. (2002) (upper graph) with glacial and interglacial periods highlighted (USA) (lower graph).

LGM 28000-18000 yrs BP	General	Coast	Montane	Present day	References
Mean air Temperature	8-10 °C lower		winter up to 8 °C lower	12-20 °C	Williams et al., 2009, Barrows et al. 2022
Rainfall	Up to 50% lower,		snow at high elevations low evaporation	700-1600 mm pa, light snow	Williams et al. 2009, Mooney et al. 2021
Atmospheric CO ₂	185-190 ppm			280 ppm	Mooney et al. 2017
Winds			Strong winds 4 times more frequent		Hesse et al. 2003
Southern Ocean temperatures	-2 to -6° C lower			18-23° C	Williams et al. 2009
Sea level	125 m lower at 21-19,000 yrs BP;	Hawkesbury drowned river valley estuary			Reeves et al 2013 Lewis et al 2013
LGM Coastal plain	8-15 km wide with low sandstone plateaus and podsolised dune sand	?freshwater swamps on Parramatta, Georges, Hacking			Albani et al. 2015

Table 1. Summary of major Last Glacial Maximum (28 000-18 000 yrs BP) climatic and landscape conditions relevant to the Sydney area.

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experienced a period of high aridity, and was much drier and windier, with increased evapotranspiration, and cooler temperatures (Mooney et al. 2017). In mainland southeast Australia LGM temperatures were up to 8 °C lower than today and up to 4 °C cooler in Tasmania. Sea surface temperatures were up to 5 °C cooler (current annual range 18-23 °C off Sydney) with rapid warming after 20 000 years BP to attain present values by 15 000 years BP (Williams et al. 2009). Winter rainfall was much reduced although periodic extreme flood events are evident in the fluvial record (Williams et al. 2009). Atmospheric CO₂ at 180 ppm was 25-30% lower than in the following Holocene (270 ppm) (Mooney et al. 2017) and less than half current levels of 417 ppm. Sea levels during the LGM were about 125 m lower than current pre-industrial levels (Sloss et al. 2007, Lewis et al. 2013, Reeves et al. 2013 (Figure 3) (Table 1).

In the period 28 000-18 000 years BP, areas of southwest Western Australia that support eucalypt forests today appear to have been shrublands (Sniderman et al. 2019). LGM vegetation in western Tasmania was subalpine woodland and shrubland, or alpine grassland, herbland, and heathland, with sclerophyll woodland and rainforest taxa below 100 m on coastal valley floors. Major vegetation changes were primarily climatically driven, responding to variations in temperature in the west and to temperature and precipitation in the east (Colhoun and Shimeld 2012).

In south-eastern Australia late Pleistocene paleochannels of Murray-Darling Basin rivers were larger, with high seasonal discharge and sediment loads indicating increased moisture availability in Tableland catchments from snowpack, enhanced orographic rainfall, or CO₂ feedbacks with vegetation cover (Mueller et al. 2017, Hesse et al. 2018, Barrows et al. 2022). Modelling of precipitation suggests LGM snowfall was a common winter occurrence across southern Australia (Mueller et al. undated). Periglacial conditions with mean winter temperature 8 °C colder than present affecting much of southeastern Australia, down to 680 m on the Southern Tablelands, are likely (Barrows et al. 2022). Northern Tablelands LGM montane vegetation appears wetter than previously thought, with higher moisture conditions and a more positive water balance than occurs today (Ellerton et al. 2017). On either side of the LGM peak (24 000 years BP), Willandra Lakes in western NSW retained water and supported human activity; elsewhere in Australia during the cold and dry times, water was present to sustain human populations (De Deckker et al. 2020).

While Sydney area vegetation changes were primarily climate-driven, as in Tasmania, a substantial

landscape change peaking with the LGM was the development of a coastal Plain (Albani et al. 2015) adding an area of about 250 000-300 000 ha between the Hunter and Shoalhaven Rivers and, in relative terms, pushing the hinterland and mountains 8-15 km further inland and the mountains another 150 m higher.

Increased warming and the end of LGM climatic conditions

By 17 000 BP post-LGM increases in temperature were evident across Australia (Reeves et al. in Mooney 2017). Low sediment rates in Sydney cores confirm LGM low rainfall conditions continuing well into the late Pleistocene (Mooney et al. 2021) with minimum effective precipitation in southern Australia from 14 000 to 12 000 yrs BP (Williams et al 2009), delaying the recovery of tree-dominated communities. There were relatively low levels of biomass burning in the period 24 000 to 18 000 years BP (Mooney et al. 2011). In Western Tasmania Cool temperate rainforest developed again after about 14 000 yr BP, with maximum development of *Nothofagus cunninghamii* rainforest in the early Holocene (Colhoun 2000).

From 14 000 to 9 000 years BP (Pleistocene–Holocene transition) temperature increased considerably (approx. 4 °C). Warmer wetter conditions and low fire activity associated with climatic stability peaked about 6 000 years BP (Black et al. 2008; Moritz et al. 2009; Das et al. 2019). In contrast, from about 6 000 years BP, the El Niño phase of ENSO developed in frequency and/or strength, increasing climate variability, a significant influence on vegetation composition, with impacts felt through drought and fire (Mooney et al. 2017). As temperatures rose from about 18 000 years BP, increasing ocean volumes led into the early Holocene sea level rise of c. 60 m, from about 11 000 – 7000 years BP during deglaciation over most of the Earth (Smith et al. 2011). Sea levels temporarily reached more than a metre above current levels between 7 000 and 2 000 years BP before falling back to current levels (Lewis et al 2013, Sloss et al. 2007). The vegetation responses to these post-LGM changes will be dealt with in later papers.

METHODS

Plant ecology and postulating past vegetation patterns

Sources of botanical evidence to reconstruct past vegetation patterns and species groupings include current flora distribution patterns, ecological strategies and tolerances, and historical pollen and fossil evidence. Using this information, together with a set of assumptions about past vegetation behaviour, species groups have been retrofitted, as it were, into

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a number of past physical landscape scenarios based on currently accepted views of late Pleistocene-Quaternary climatic conditions (Table 1).

In doing this the following ecological assumptions have been made:

1. same landform/topography interactions (with additional LGM coastal plain), e.g. rainfall increases with elevation and declines with distance from coast, with rain-shadow effects as today; mean temperature declines with elevation, i.e. rainfall and temperature are related to geomorphology/elevation;
2. current existing pool of south-eastern Australian species is available, but may have had different geographic distributions;
3. species niche conservatism ecologies constrained by current basic ecological envelopes, i.e. ecological limitations are imposed by soils and geology though climatic envelope may be more flexible;
4. 10-20 000 years is too short for species level evolution, but allowing small genetic and/or morphological differences (e.g. subspecies, forms) to develop as species respond to climate change through migration, isolation and local extinction;
5. species interactions with past climate

influences are consistent with current plant strategy schemes and knowledge, i.e. competitor/stress-tolerator/ruderal strategies, fire response categories, etc.

And the following provisional interpretations applied:

1. That for species with limited dispersal abilities (i.e. stress-tolerator/OCBIL characteristics) disjunct distributions are likely to be evidence of previously more extensive distributions, fragmented by subsequent unfavourable climatic or other conditions, rather than new colonisations.
2. That for species with readily animal- or bird-dispersed propagules, disjunct distributions are more likely to be more recent introductions/colonisations, rather than fragmentations.

Using National Herbarium of New South Wales (PlantNET) and Australasian Virtual Herbarium (AVH) data sources, species occurrence maps were examined to identify species with particular patterns of disjunction, with particular focus on endemics, dominants, edge of range, etc., that could indicate past landscape change, e.g. climatic isolation, loss of LGM coastal plain, distance invasion, and any reported evidence of taxonomic or genetic variation (e.g. Table 2). Geographical areas or topographic sites with high

Habitat	Species	Distribution	Life form CSR/fire response	Pop. distr. type
Ridgetop sandstone	<i>Zieria covenyi</i>	Katoomba	ST/Respr.	single
	<i>Pultenaea genowlan</i>	Newnes Plateau	ST/Respr.	single
	<i>Eucalyptus camfieldii</i>	Ku-ring-gai to North Head	ST/Respr.	disjunct
	<i>Eucalyptus gregsoniana</i>	Newnes Plateau	ST/Respr.	
	<i>Melaleuca deanei</i>		ST/Respr.	disjunct
Low nutrient clay	<i>Acacia meiantha</i>	Clarence, Mullion Range, Turon	ST/Respr.	disjunct
	<i>Micromyrtus minutiflora</i>	Castlereagh area	Rud/fire sens	disjunct
	<i>Dillwynia tenuifolia</i>	Castlereagh area	Rud/fire sens	disjunct
	<i>Pultenaea parviflora</i>	Castlereagh area	ST/Respr.	single
	<i>Allocasuarina glareicola</i>	Castlereagh area	ST/Respr.	single
Wianamatta Shale woodland	<i>Grevillea caleyi</i>	Terrey Hills	Rud/fire sens	single
	<i>Pimelea spicata</i>	western Sydney, Kiama	ST/Respr.	disjunct
Riparian	<i>Marsdenia viridiflora</i>	Mt Annan	ST/Respr.	disjunct
	<i>Asterolasia buxifolia</i>	Hartley	Rud/fire sens	single
	<i>Leptospermum deanei</i>	Lane Cove valley	Rud/fire sens	single
	<i>Boronia deanei</i>	Newnes Pl. Kanangra	ST/Respr.	disjunct
Coastal sand	<i>Hibbertia hermanniifolia</i>	Bents Basin		disjunct
	<i>Banksia aemula</i>	La Perouse, Agnes Banks, Sth limit	ST/Respr.	disjunct
Montane heath	<i>Eucalyptus cunninghamii</i>	BI Mtns, Wanganderry	ST/Respr.	Wide disjunct
	<i>Isopogon prostratus</i>	Newnes Pl.-Vict.	ST/Respr.	Wide disjunct
Ridgetop metasediments	<i>Eucalyptus pulverulenta</i>	Mt Blaxland, Bombala	ST/Respr.	Wide disjunct

Table 2. A selection of rare plant species, local endemics etc, illustrating life forms and types of distributions. ST/Respr.=Stress tolerator/ resprouter.

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numbers of rare or endemic species or with clusters of species with similar disjunction patterns were identified.

Ecological strategies and tolerances of individual species

Various groupings of plant species based on functional traits have been developed to conceptualise ecological responses (Noble and Slatyer 1980; Keith et al. 2007). To consider the likely responses of individual plant species in past climate scenarios, a combination of Grime's (2006) Competitor/Stress-tolerant/Ruderal (CSR) lifeform strategies (Grime 2006; Grime and Pierce 2012) and Australian fire response terminology (Gill 1981; Keith and Tozer 2012) is used (Table 3). Three broad groups are recognised: stress-tolerators/resprouters (many OCBIL species), ruderals/fire-sensitives and competitors. Competitors are not generally recognised in fire ecology (though included in some schemes (Keith et al. 2007) but some species with both resprouter fire responses, and vigorous seeding recruitment capabilities (facultative resprouters), such as many tree eucalypts (Nicolle 2006) are clearly competitive. It should be recognised that characteristics such as the large size and quick growth of competitors make them competitive in today's conditions though in dry, low CO₂ LGM environments these characters are likely to have made them uncompetitive (Woillez et al. 2011).

While collective and institutional efforts have historically been focused on formally describing plant species, much less effort has been focussed on describing their ecologies, the main exceptions

being fire ecology responses and, more recently, seed biology and genetics of rare and endangered species. Much of the ecological data applicable to these lifeforms is taken from the Ecology of Sydney Plants series (Benson and McDougall 1993-2005), major ecological reviews including Fabaceae (Auld 1996), Myrtaceae (Myerscough 1998), Orchidaceae (Weston et al. 2005), Proteaceae (Myerscough et al. 2006) and Rutaceae (Auld 2001) together with many personal observations made by the author over a long career in Sydney plant ecology.

Historical pollen and fossil evidence

Worldwide, pollen analyses are a primary source for historical vegetation interpretation. Records provide an extensive late Quaternary vegetation history for Tasmania (Colhoun and Shimeld 2012), for example, but because of limited suitable deposition sites, there is very little plant macro-fossil or pollen evidence for this period for Sydney. References with pollen core diagrams were studied for additional ecological signals from clearly defined taxa. Helene Martin and her students have produced important studies but pollen identification is generally limited to genus or family, limiting ecological inferences in a floristically rich area. Chalson and Martin (1995) provide a pollen reference set for 20 of the important Myrtaceae species, but the Sydney area has over 100 eucalypts (Hager and Benson 2010) and about 30 *Leptospermum* species. Within a family or genus, individual species may have very different growth-forms and ecologies but similar-looking pollen. Family Casuarinaceae taxa in the Sydney area include a large fire-sensitive

Grime CSR functional classes	Australian fire ecology strategies	Notes
Stress Tolerators Small, long-lived, prevail in habitats with limited resources, low rates of photosynthetic activity and respiration	Primary resprouters Resprout from basal or epicormic shoots post- fire; generally low seedling recruitment success	Long-lived sclerophyll or mesic trees, shrubs and graminoids, generally slow-growing and low recruitment, often vegetative spread, poor competitors
Ruderals Short-lived, have low leaf dry weight, longer flowering period, high rate of photosynthetic capacity and respiration, and high leaf nitrogen content	Fire-sensitive/Obligate seeders Killed by fire; recruitment from seed either soil-stored (with dormancy) or canopy-stored (serotinous) exploiters of temporally available resources	Shortlived but includes early maturing eucalypts such as <i>Eucalyptus oreades</i> with longevities up to 100 years
Competitors High levels of canopy height, leaf dry weight, and maximal lateral spread, rapid resource capture and growth, excluding other species	Competitors not specifically recognised in fire succession, but important in directional rather than cyclic change, where ecological/climate conditions are changing over longer time periods	Competitors with both resprouting survival and high seedling recruitment (invasiveness) are opportunistic as conditions change e.g. tree eucalypts or non-fire colonisers

Table 3. Ecological functional classes for CSR plant strategy schemes of Grime (2006) and equivalent Australian species fire response strategies (Gill 1981, Keith and Tozer 2012).

tree (*Casuarina cunninghamiana*), a smaller root-suckering, saline-tolerant tree (*C. glauca*), large fire-sensitive shrubs (*Allocasuarina distyla*, *A. littoralis*, *A. verticillata*) and low-growing resprouter shrubs (*Allocasuarina nana*, widespread; and *A. diminuta* and *A. glareicola*, very localised).

Sites can represent local pollen catchments or a much wider and different habitat. Plant families with abundant wind-dispersed pollen (Chenopodiaceae, Asteraceae, Casuarinaceae, Poaceae, ferns and mosses) predominate in cores, but could have been carried many kilometres. Aerial dispersal of material over large distances can occur in dust storms and fire storms. The chances of deposition and survival mean that many species with limited pollen production and specialised insect pollination are not recorded. Major groups may be missing; there are very few records of Fabaceae, Rutaceae, Orchidaceae and Xanthorrhoeaceae, for example, preserved in sediments.

RESULTS

LIKELY VEGETATION ON THE CONTINENTAL SHELF COASTAL PLAIN DURING THE LAST GLACIAL MAXIMUM

The continental shelf coastal plain

About 125 000 years BP, as the milder conditions of the Last Interglacial began to cool, sea level began to recede, from a level about 10 m higher than today, to a lowest level, 120 m lower than currently, at about 20 000 years BP (Albani et al. 2015) (Figure 3). For up to 100 000 years the continental shelf off eastern Australia, from Torres Strait to Tasmania, was exposed to some degree, before re-inundation by about 7 000 years ago. From about 50 000 to 12 000 years BP, the bulk of the exposed landscape is likely to have remained a stable geomorphological feature contributing, at its most extensive, a substantial area of essentially terrestrial habitat, an area of about 250 000 - 300 000 ha between the Hunter and Shoalhaven Rivers at about 18 000 years BP.

The current continental shelf visible in the satellite images approximates the LGM coastal plain, which extended about 8-15 km beyond the present Sydney shoreline. The late Quaternary paleogeomorphology from Broken Bay to Botany Bay is described by Albani et al. (2015). The land sloped eastward from the present coastline down to a rocky sandstone coast, up to 20 m above the LGM sea level. Rock platforms and outcrops about 60-80 m in elevation (Hawkesbury and Narrabeen sandstones and shales) extended up to 8 km from the current coastline (the limit of scan surveys - Albani et al. 2015) interspersed with sandsheets and dunes,

leached of nutrients and redistributed by wind, as the sea had gradually retreated over the previous 100 000 years. The current seacoast cliffs would have been substantial topographic features up to 150 m high, albeit 8-15 km inland (Figure 4).

As a result of the size of its catchment and relative discharge, the Hawkesbury River system dominated the shelf morphology and adjacent hinterland north of Sydney. Its paleochannel formed large embayments below the LGM strandline, and it strongly resembled a drowned river valley, relative to the outline of the LGM paleo-shoreline (Albani et al. 2015).

In contrast, from about 50 000 to 12 000 years BP, Sydney Harbour would have been dry land with a small Parramatta River paleo-watercourse forming a narrow symmetrical gorge and sinuous path across the coastal sandstone shelf and draining out into perched freshwater swamps or seepage areas. There



Figure 4. The coastline off Sydney between the Hawkesbury and the Georges Rivers at the height of the LGM based on bedrock geomorphology and showing paleo sea level and drainage features that were active at the time. (from Albani et al. 2015)

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were similar paleo-watercourses for the Botany and Georges systems, and smaller drainages perched on the coastal shelf. Small sandy beaches were associated coastal features here.

Beyond Sydney major catchment paleodrainage systems included the Hunter and Shoalhaven, while smaller catchments now draining into coastal lakes such as Tuggerah and Illawarra are likely to have drained into freshwater swamps. Present-day reefs and islands (e.g., Five Islands, Illawarra), would have added higher sandstone hills to the mostly sand or sandstone landscape though some shale bedrock exposures are likely off the Central Coast and Illawarra.

Estuarine saltmarsh on the LGM coast

At the peak of the LGM the drowned river valley of the Hawkesbury was about 3 km wide and extended for about 15 km eastwards from present-day Broken Bay (Albani et al. 2015) (Figure 4). As a tidal estuary it was probably fringed or perhaps filled with sandy or silty sediments, its large catchment making up for the generally low LGM sedimentation rates (Mooney et al. 2021). Estuarine vegetation at

this time is likely to have included seagrasses and saltmarsh, but not the characteristic mangroves of today. Mangroves are essentially tropical (Rogers et al. 2017) but sea surface temperatures in the Southern Ocean were 3-6 °C colder (Mooney et al. 2017), i.e. about 14-17 °C for LGM Sydney, conditions likely to have been too cold for the current Sydney mangroves, *Avicennia marina* (current southern limit Wilsons Promontory, Victoria, is about 15-19 °C today) and *Aegiceras corniculatum* (southern limit Tuross Head, 17-21 °C). Mangroves are inferred to have colonised the Sydney coastline from the north as sea temperatures warmed later in the Holocene.

Seagrasses are readily dispersed and likely to have had some LGM representation. Current species include temperate species of *Posidonia*, *Ruppia* and *Zostera* (Kuo et al. in Sainty et al. 2012) likely favoured by LGM conditions. Those present at any particular time would have depended on both temperature conditions and local habitats.

East coast saltmarsh flora is ecologically temperate and southern in origin (Adam 1990; Boon et al. 2015). Of 53 saltmarsh dominants in Victoria, only about 25

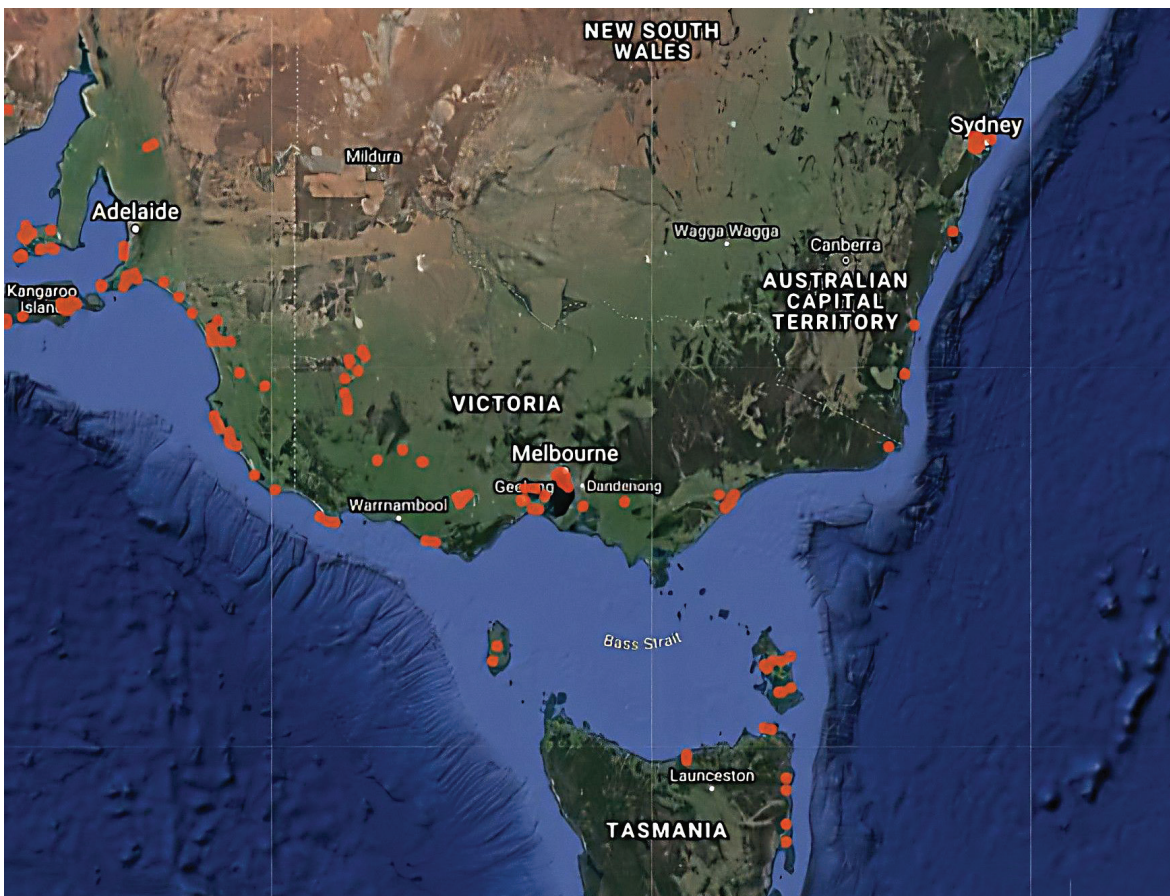


Figure 5. Saltmarsh species *Wilsonia backhousei* is mainly southern with a couple of disjunct limited occurrences as far north as Sydney that could be remnants of a wider LGM distribution. (AVH 2022)

species also occur in NSW (G. Carr in Sainty et al. 2012), and of the seven main Ecological Vegetation Classes in Victorian saltmarshes, only four occur in NSW. Unlike the NSW saltmarsh flora, current Victorian saltmarsh includes shrubby chenopods and many annuals (about 38 species). During the LGM a floristically richer saltmarsh than today is likely for the Hawkesbury estuary probably including many Victorian species; disjunct northern outliers are interpreted as evidence of former extent rather than recent colonisation (Table 4, Figure 5). For the smaller coastal Parramatta, Botany and Georges River paleo-watercourses that debouched above sea level during the LGM, saltmarsh vegetation is only likely to have established in the Holocene when sea level rose high enough to drown their valleys, by which time cold-adapted southern species are likely to have retreated south.

Coastal scrub and swamp forest

As sea level retreated with the LGM, nearby existing vegetation would have colonised local bare

and increasingly dry microhabitats; more stress-tolerant coastal headland forms of coastal species may have developed during this time (e.g. *Actinotus helianthi*, *Acacia suaveolens* - Morrison and Rupp 1995). Though the relatively favourable coastal rainfall and temperature conditions would have moved progressively eastward with newly exposed coastline, the widespread cool dry LGM conditions would have favoured now-common southern shrub species (e.g. *Melaleuca ericifolia* (Figure 6), *Melaleuca armillaris*, *Myoporum insulare*, *Acacia sophorae* subsp. *sophorae*) as well as some now rare species such as *Melaleuca biconvexa* (Figure 7). These are likely to have fringed the LGM saltmarshes and littoral habitats. The large coastal swamp forest species of today, *Melaleuca quinquenervia*, *Melaleuca nodosa*, *Eucalyptus robusta*, *Casuarina glauca*, *Leptospermum laevigatum*, *Leptospermum lanigerum* and *Leucopogon parviflorus* have substantially northern distributions and are likely

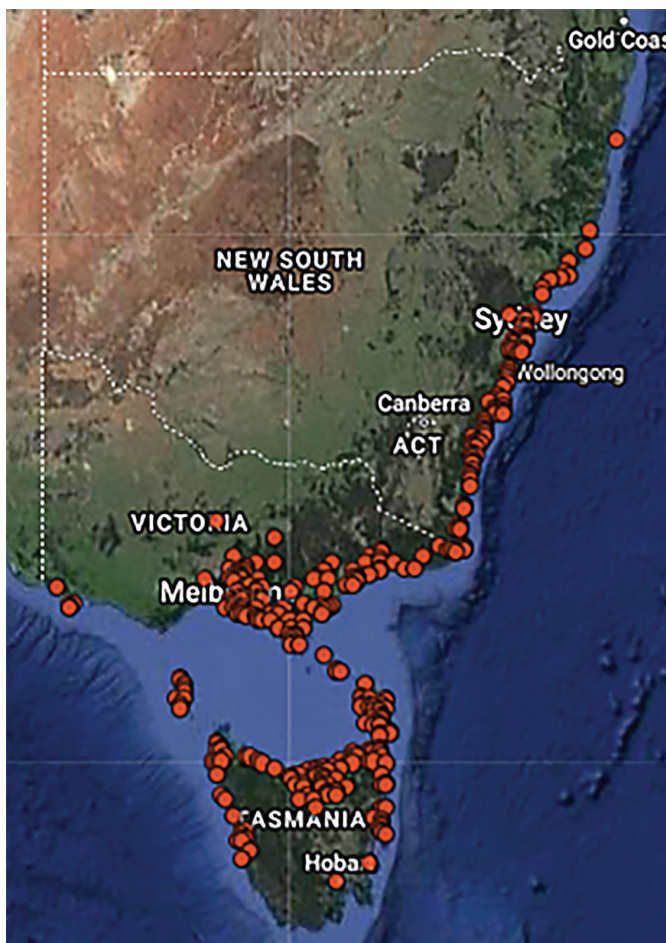


Figure 6. A more northern distribution along the LGM coastal plain is likely for the now southern coastal shrub *Melaleuca ericifolia*. (AVH 2022)

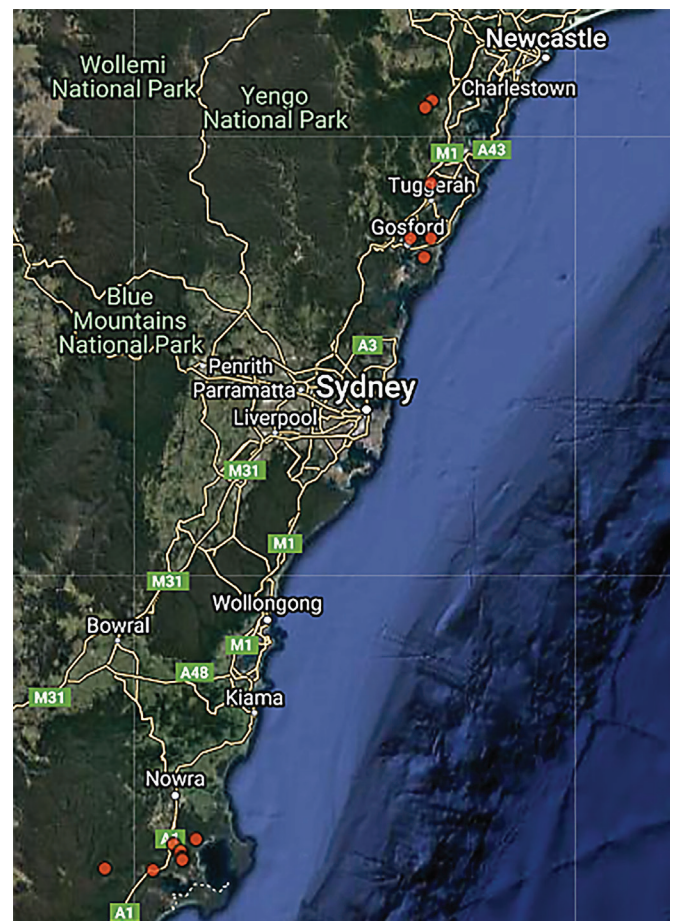


Figure 7. Disjunct occurrences of coastal shrub *Melaleuca biconvexa* (Port Macquarie to Jervis Bay) may be remnants of a more widespread former occurrence on the alluvial flats of the LGM estuarine coastal plain. (AVH 2022)

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Saltmarsh species	Main occurrence	Disjunct northern outliers
<i>Atriplex cinerea</i> , shrub	Southern Australia	Snapper Island (N-limit), Botany Bay, Five Islands Illawarra
<i>Austrostipa stipoides</i> , grass	Vict., SA., Tas., saltmarsh, seacliffs	Shellharbour (N-limit), Jervis Bay
<i>Gahnia filum</i> , graminoid	Vict., SA., common	Georges River, Jervis Bay, Moruya saltmarsh
<i>Selliera radicans</i> , perennial herb	Southern saltmarsh	Gosford (N-limit); inland occurrences e.g. Lake Bathurst, could indicate waterbird dispersal
<i>Tecticornia pergranulata</i> subsp. <i>pergranulata</i> , shrub	Coastal saltmarsh, Vict. (Sainty et al. 2012).	Isolated up-river saltmarsh in Homebush Bay
<i>Wilsonia backhousei</i> , spreading perennial	Victoria, common	Parramatta River, Jervis Bay
<i>Wilsonia rotundifolia</i> , low spreading perennial	Essentially southern Australia	Royal NP, Jervis Bay, coastal disjunct occurrences (also Lake Bathurst and Deniliquin)

Table 4. Disjunct northern outliers of southern saltmarsh interpreted as evidence of former LGM saltmarsh distributions.

to have been restricted to the North Coast and Queensland, together with their associated fauna. Luly et al. (2010) used global climate models to suggest *Pteropus poliocephalus* (Grey headed flying fox), and its rainforest and eucalypt LGM habitat (assuming current habitat trees, *Melaleuca quinquenervia*, *Eucalyptus robusta*, *Eucalyptus tereticornis* and *Eucalyptus siderophloia*), was only a third of its modern extent, with its core distribution focused on the North Coast region of NSW and the bioclimatic envelope shifted eastwards onto the then-existing LGM coastal plain.

Wallum vegetation on the LGM Coastal plain sands

Remnants of the LGM coastal plain survive as southeast Queensland's sand islands. Pollen cores from North Stradbroke Island, now dominated by characteristic wallum sand vegetation, indicate floristic similarity during the LGM, with swamp vegetation suggesting coastal rainfall was relatively high at the time (Tibby et al. 2017). Further south, from a sandy Newcastle swamp Williams (2005) described a sharp increase in Casuarinaceae pollen at the height of the LGM (which could be any of *Casuarina glauca*, *Allocasuarina littoralis*, *A. torulosa*, *A. distyla* or *A. verticillata*), and essentially sclerophyll taxa pollen throughout the LGM period consistent with the presence of wallum (including Cyperaceae, Haloragaceae, *Myriophyllum*, *Triglochin* and Restionaceae pollen relevant to the immediate swamp site, and *Angophora* /*Corymbia*/ *Eucalyptus* (4 types), *Dodonaea triquetra*, *Amperea*, *Monotoca*, *Calytrix*, *Banksia*, *Pomaderris*, *Plantago*, Fabaceae, Myrsinaceae, Rutaceae, Asteraceae, Poaceae and ground ferns, relevant to the surrounding area.

It appears likely that in the 100 000 years as sea level receded following the last Interglacial, wallum species from the north would have gradually moved

south onto the exposed continental shelf, and colonised dune sands as they were gradually leached to extreme infertility. At Myall Lakes on leached low-nutrient Pleistocene sands with podsols up to 125 000 years old, Myerscough and Carolin (1986, 2014) recognised 13 sand communities including North Coast Banksia wallum, Dry heath and Dry Heath Forest. They describe stress-tolerator/resprouter OCBIL ecologies with lignotuber-like mass roots for *Banksia aemula*, and *Melaleuca nodosa*, and very long-lived mallee growth forms of *Corymbia gummifera* and *Eucalyptus acmenoides* (compared with tree forms in other sites). Many other species were short-lived seeders. Dune-swale vegetation relates to drainage and waterlogging conditions supporting Wet Heath, including northern species *Banksia oblongifolia*, *Banksia robur*, and *Baloskion pallens*, and essentially southern species *Gymnoschoenus sphaerocephalus*, *Xanthorrhoea resinosa* and *Sprengelia incarnata* in swamps. Boundaries between vegetation on highly leached and younger sands are very sharp (Myerscough 2020). On the younger Holocene sands (< 6500 year-old) are poorly-developed podsols, with Dry Sclerophyll Forest of *Eucalyptus pilularis*, *Angophora costata* and *Banksia serrata* with Competitor/ facultative-resprouter ecologies allowing quick colonisation and movement onto disturbed sites.

Similar wallum vegetation on leached podsols, fringed by young coastal dunes, is likely to have developed across the LGM coastal plain from Myall Lakes to Botany Bay. At Tomago, near the Hunter River estuary, local endemic *Eucalyptus parramattensis* subsp. *decadens* occurs on near sea level Pleistocene sands with characteristic wallum *Banksia aemula* (Bell 2022), and on similar soils in endangered Kurri Kurri sand-swamp woodland near Cessnock, which suggests a former larger LGM coastal plain population.

South of the Hunter, highly leached Pleistocene sand is now restricted to coastal headland remnants at Redhead, Munmorah, Bouddi National Park (Siddiqi et al. 1973), North Head (80 m elevation), Long Bay and La Perouse (Eastern Suburbs Banksia Scrub). There is an inland southern occurrence at Agnes Banks (25 m elevation) (Benson 1981) supporting key wallum heath *Banksia aemula* (Figure 8) and other wallum species with similar northern distributions and southern limits, e.g. *Baloskion pallens* (Figure 9) (Table 5). This suggests southward movement of vegetation such as that at Myall Lakes along a Sydney LGM sandplain.

Sand masses off Sydney, beyond the sandstone clifflines, were completely lost as Holocene sea -level rose, but prior sand accumulation taking place across the Botany Bay basin (a Rose Bay sand core dates to c. 47,000 years BP - Stephen Gale, University of Sydney, pers. comm.) would have developed a landscape of old leached and relatively younger sands with various wallum vegetation species, as well as exposed sandstone rock platforms and gully habitats with dune, swale, swamp and woodland, with floristics enriched by southward movement. During the LGM *Banksia*

aemula coastal wallum vegetation, now at its southern limits in the Eastern Suburbs (Table 5) (remnants now protected as Eastern Suburbs Banksia Scrub), may have intruded farther inland, along the dry incised Cooks River and lower Georges River to Milperra. A cluster of wallum species (including *Banksia aemula*, *Baloskion pallens*, *Trachymene incisa*, *Hypolaena fastigiata*, *Ricinocarpos pinifolius*, and *Dillwynia glaberrima* (Figure 10)), now found on isolated leached Pliocene–Pleistocene sand dunes at Agnes Banks (elevation 25 m) near Richmond, is consistent with past colonisation from the coast, particularly during periods of strong winds and sand movement. Dune vegetation at Agnes Banks (rainfall 800 mm p.a.) has 47% of species in common with Myall Lakes and 25% with North Stradbroke Island (Benson 1981). Occurrences of various coastal sand species in the Mellong-Howes Valley area may possibly be remnants of more extensive LGM dry sand vegetation.

Coastal swamp vegetation

Evidence of wallum-associated swamp vegetation on North Stradbroke Island throughout the LGM suggests coastal rainfall at the time was relatively high (Tibby et al. 2017), perhaps influenced by East

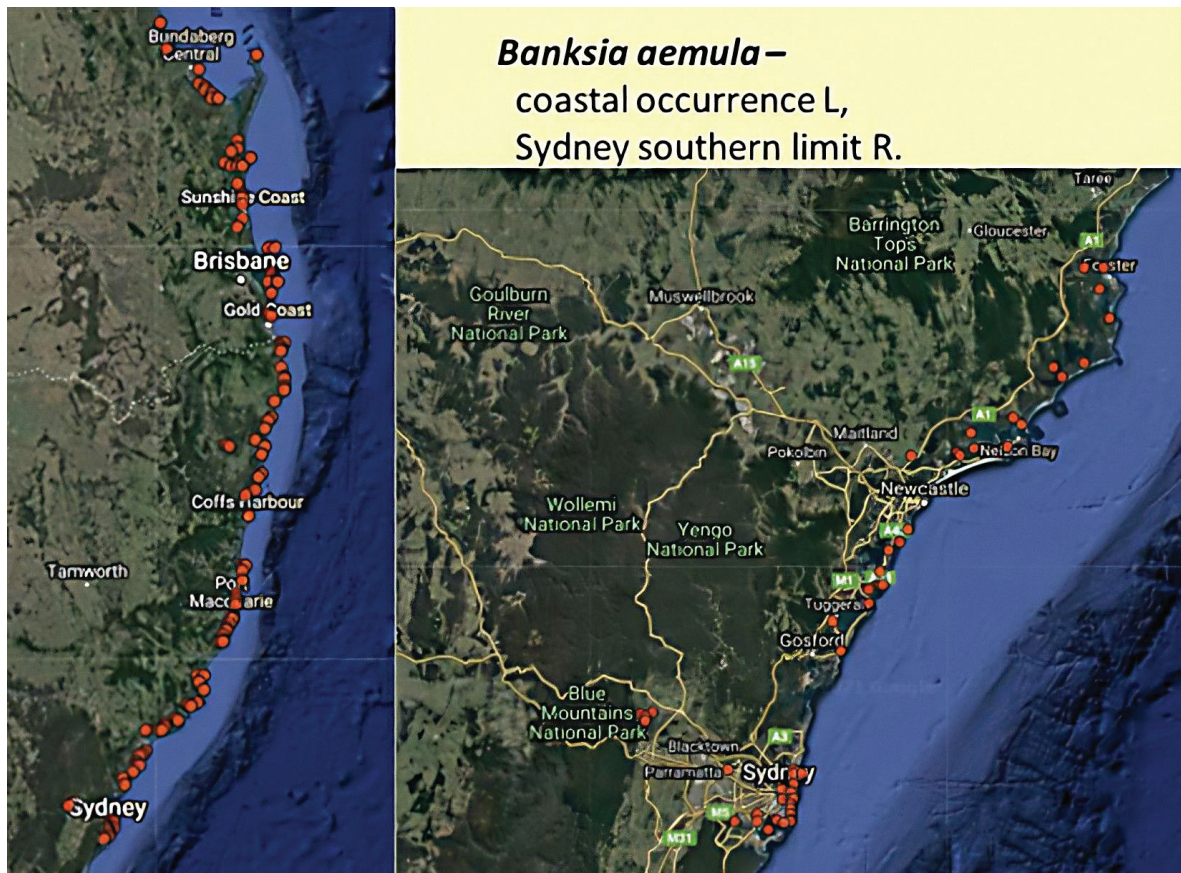


Figure 8. *Banksia aemula*, a characteristic wallum species reaches its southern limit on Pleistocene sand at Botany Bay and is likely to have been important species on the LGM coastal plain. (AVH 2020)

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Coast Lows (Ellerton et al. 2017). Assuming similar rainfall conditions, it is likely that similar LGM sedge and shrub swamp vegetation occurred on the coastal plateaus and adjacent coastal plain farther south. Pollen analyses from *Machaerina/Gymnoschoenus sphaerocephalus* (Figure 11) moorland at 400 m elevation on the Woronora Plateau (at Gallaghers Swamp, Avon River) (Macphail, in Hope 2010)) shows

Gymnoschoenus in almost continuous site occupation for the past 22,000 years, together with *Lepidosperma*, Restionaceae (probably *Empodisma minus*), Asteraceae and *Chionogentias* species (possibly *Gentiana wingecarribiensis*). Similar vegetation on poorly-drained swales of coastal Sydney sand plains (Eastern Suburbs) and headwater depressions on sandstone plateaus (Ku-ring-gai and Royal National

Wallum dune species	Southern limit
<i>Macarthuria neocambrica</i>	Munmorah
<i>Acacia baueri</i> subsp. <i>baueri</i>	La Perouse
<i>Bauera capitata</i>	La Perouse
<i>Sprengelia sprengelioides</i>	La Perouse
<i>Styphelia viridis</i> subsp. <i>viridis</i>	Jibbon
<i>Banksia aemula</i>	La Perouse, Agnes Banks
<i>Baloskion pallens</i>	Agnes Banks
<i>Acacia quadrilateralis</i>	Eastern Sydney with an outlier at Ulladulla

Table 5. Northern Wallum ecosystem species with southern limits in the Sydney area

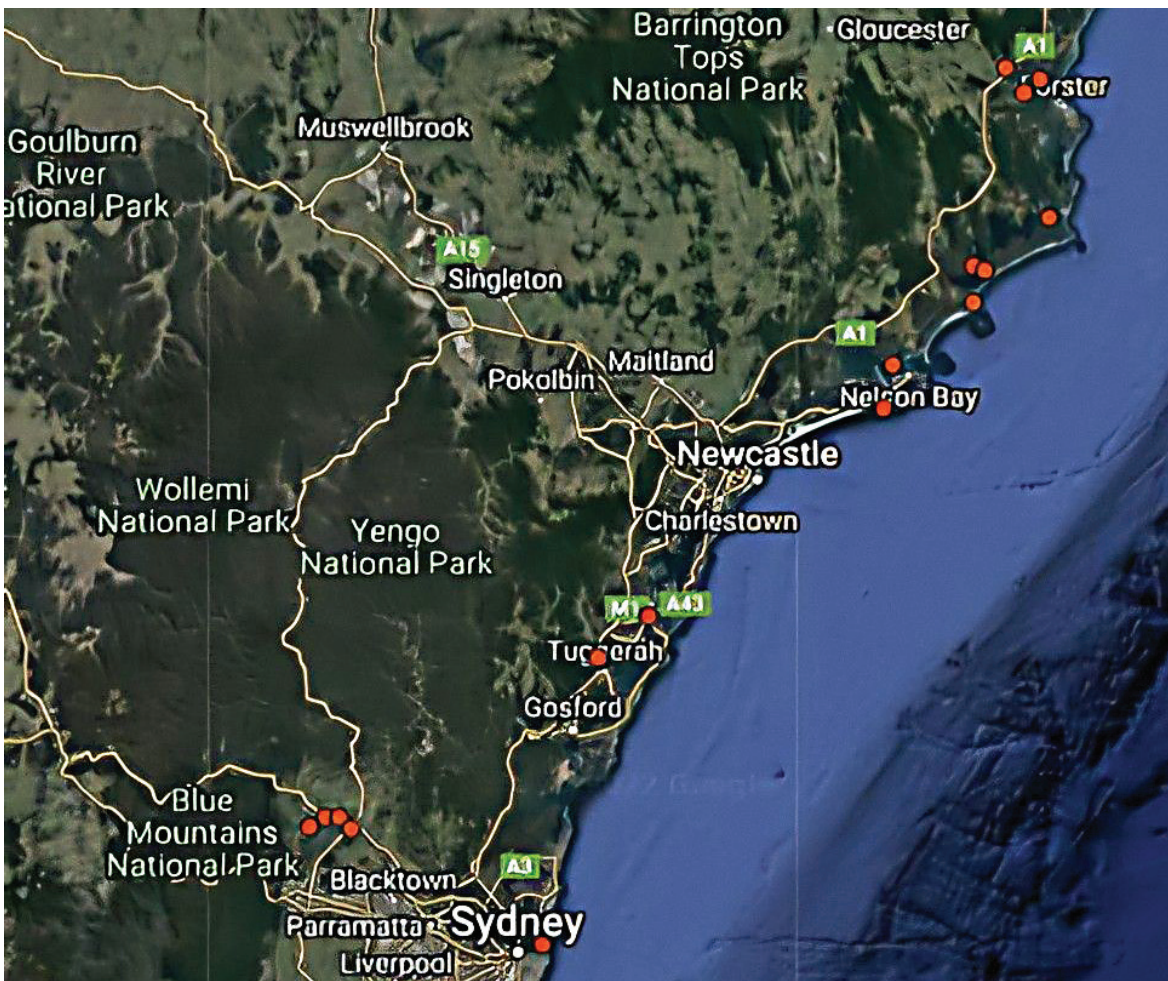


Figure 9. Restiad, *Baloskion pallens* has its southern limit on isolated hinterland Pleistocene sanddunes at Agnes Banks, west of Blacktown, suggesting a previous more extensive occurrence on the LGM coastal plain. (AVH 2022)

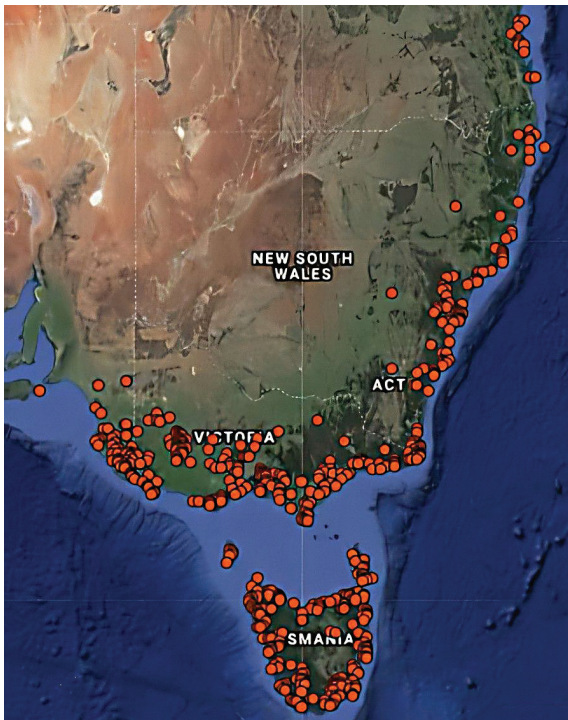


Figure 10. Extensive, essentially southern, coastal distribution of *Dilwynia glaberrima* suggests extensive occupation of sandy deposits on the LGM coastal plain, but little subsequent fragmentation with sea level rise. An occurrence on sand inland at Agnes Banks, disjunct from other current coastal Sydney sites suggests LGM connections. (AVH 2022)

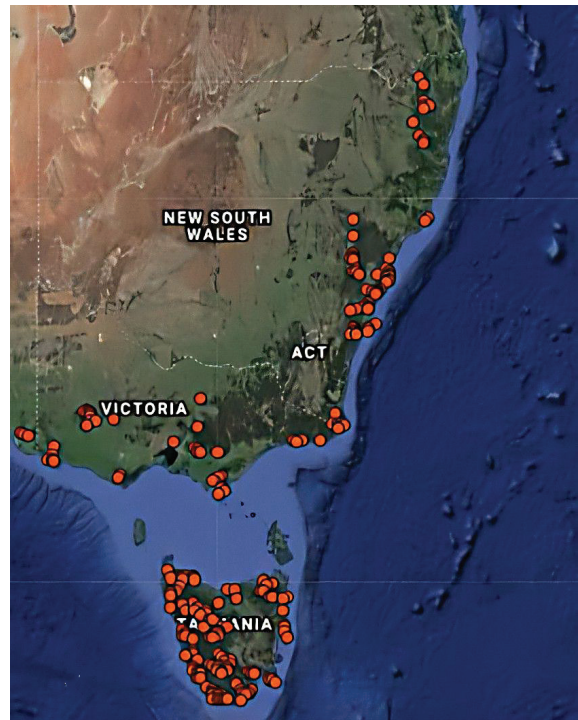


Figure 11. Distribution of Buttongrass, *Gymnoschoenus sphaerocephalus* highlights its essentially southern distribution and, north of Myall Lakes, its restriction to higher (cold) habitats. Past connections along the LGM coastal plain as far as Myall Lakes are likely. (AVH 2023)

Parks) today includes both widespread northern species such as *Banksia oblongifolia* and *Banksia robur* as well as essentially southern species *Gymnoschoenus sphaerocephalus* and *Sprengelia incarnata*.

Coastal sandstone and sand habitats - Woody obligate seeders

Woody short-lived obligate-seeders (c. 5-50 year life spans) are ruderal /fire sensitive shrub species that are important components of current sand and sandstone floras, and make up a substantial component of both species and biomass in sclerophyll heath vegetation (Keith 2004). Many have long-lived dormant soil seedbanks (many species in families Fabaceae, Rutaceae, Ericaceae, Sterculiaceae) while others are serotinous and carry canopy-stored seed banks (Casuarinaceae and many Proteaceae, particularly the big woody shrubs such as *Banksia ericifolia* and *Hakea teretifolia*, which rely on quick growth and abundant mass seedling recruitment for their competitiveness). Both strategies are now associated with episodes of mass recruitment and rapid seedling growth in good conditions (e.g. post-drought or post-fire) and are abundant where rainfall

conditions are adequate for periodic recruitment, though they can survive with infrequent or low fire regimes (assuming fire events < adult plant ages).

Fire events would have been relatively infrequent during the LGM (Mooney et al. 2011) with low temperatures, low atmospheric CO₂, slow growth and little buildup of fuel, except on the wetter coastal fringe where localised Aboriginal burning would have assisted seed recruitment episodes. Coastal conditions may therefore have provided LGM habitats for many ruderal/fire sensitive species which later spread in warmer conditions. For example in South Australia, genetic data suggest refugial populations of the obligate seeder shrub *Goodenia ovata* survived on three southern peninsulas (Fleurieu, Yorke, Eyre) and off-shore Kangaroo Island, which formed a continuous landmass during the LGM, and later spread north (Kireta et al. 2019). *Goodenia ovata* could have survived similarly on Sydney's LGM coastline.

For Sydney endemic obligate-seeder shrub *Acacia linifolia*, species-wide provenance boundaries (Rossetto et al. 2022) suggest recent population spread, probably from limited LGM coastal occurrences.

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Provenance studies of more widespread coastal obligate-seeder shrubs *Acacia longifolia* and *Acacia terminalis* showed large provenance boundaries (i.e. not localised), some level of latitudinal structuring, and a northern boundary at the Hunter River (Rossetto et al. 2022), a pattern consistent with LGM coastal occupation and subsequent successful spread.

In contrast, in the case of *Acacia ulicifolia*, narrower provenance boundaries with some degree of clonality and selfing (Rossetto et al. 2022) is consistent with persistence as a stress-tolerator/resprouter during the LGM and little subsequent expansion. *Acacia suaveolens* also showed narrow provenance boundaries and localised genetic clustering (Rossetto et al. 2022) suggesting LGM persistence rather than recent spread. These findings align with a number of genetically fixed forms described as *Acacia suaveolens* subspecies by Morrison and Rupp (1995): the successful widespread modern coastal form (subsp. *suaveolens*); a Myall Lakes region form with narrower phyllodes restricted to the Holocene sand dunes, and likely to have been more important on the LGM coastal plain; a prostrate windswept coastal headlands form, that perhaps tracked the retreating coastline from headlands on the LGM coastal plain or perhaps evolving in the rapid disturbances as coastal headlands retreated following the post LGM sea level rise; while a montane resprouter form above 300 m with longer and thicker seeds, and a small rootstock form restricted to the Grampians region of Victoria are both possible LGM remnants.

Coastal sandstone as an OCBIL landscape has a higher species richness than coastal sand, as a result of its longer stable history (Table 6). *Darwinia* taxa are a group of now very restricted woody obligate-seeders needing recurring rainfall and fire events to recruit, which may have occurred more widely in LGM sandstone coastal heath and coastal plain vegetation. All 13 NSW taxa occur in the Sydney area or South Coast (8 are endemic), all occur in heath on sandstone or shaly ironstone OCBIL habitat, though some have more specific edaphic requirements (Briggs 1962). Some show evidence of inbreeding

Taxon	Myall Lakes	Royal NP
<i>Darwinia</i>	1	3
<i>Grevillea</i>	0	11
<i>Pultenaea</i>	6	13
<i>Styphelia</i>	1	5
Rutaceae	9	25

Table 6. Occurrence of taxa with many seeder species at Myall Lakes (essentially sand habitats) and Royal NP (essentially sandstone habitats)

(Briggs 1962). Subsequent Holocene warming may have allowed some spread but their current restricted occurrences (many are endangered taxa) are likely to have resulted from loss of favoured habitat by competition from taller shrubs and trees, loss of LGM coastal plain habitat (e.g. *Darwinia leptantha*) and more frequent fire events.

Coastal Clay soil headland species as LGM remnants

Shale bedrock and volcanic dykes (i.e. non-sandstone geology) exposed on the LGM coastal plain would have supported clay soil species, and Grassy coastal headland heath (Keith 2004) is likely to include remnants of previously more extensive LGM clay soil vegetation, particularly where continued coastal exposure has prevented later tree invasion. Stress-tolerator *Themeda triandra* is likely to be a longterm survivor. Rare low-growing ruderal shrub *Pultenaea maritima* appears to have been restricted to isolated coastal occurrences north of Terrigal by post-LGM sea level rise, and is just surviving through a combination of open conditions and fire (Hunter 2016).

In 1905 Linnean Society member R. H. Cambage found isolated coastal occurrences of the small seeder tree *Allocasuarina verticillata*, a species otherwise from drier inland southern Australia (including Bass Strait islands with LGM mainland connections), on Narrabeen shales at Mona Vale and Stanwell Park (Figures 12 and 13). In the first publication to mention vegetation on the LGM coastal shelf, Cambage (1905) concluded *...having in view the isolated occurrence of Casuarina stricta [now Allocasuarina verticillata] along the east coast of NSW, the suggestion that it formed part of the latest flora on the present continental shelf before its final submergence, seems to me less open to destructive criticism than any other put forward.* Drier inland occurrences in the Hunter Valley (Warkworth), and along the Wollondilly (Wanganderry, and Upper Burragorang) suggest coastal occurrences originated from past eastward migration in dry conditions associated with the LGM.

VEGETATION ASSOCIATED WITH THE SANDSTONE PLATEAUS AND UPPER BLUE MOUNTAINS: EVIDENCE OF IN SITU LGM SURVIVAL

Marked differences in regional climate due to orographic and rainshadow effects would have influenced LGM climates. Orographic uplift is likely to have extended the higher coastal rainfall zone inland onto the coastal sandstone plateaus (now Kuring-gai and Royal NPs) which, though 8-15 km inland, with lower LGM sea level were effectively up to 250-300 m high (Figure 14).

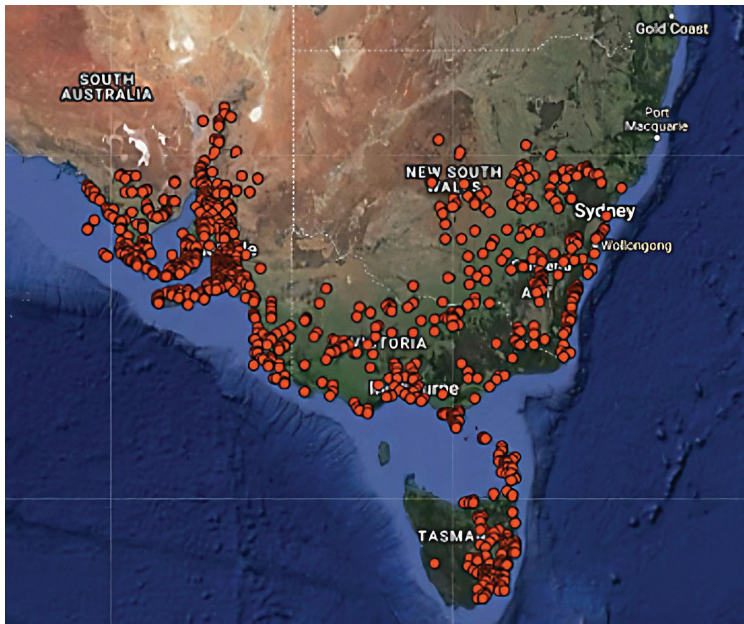


Figure 12. Distribution of *Allocasuarina verticillata* in southern Australia showing coastal and inland occurrences; past LGM inland and coastal plain connections are likely. (AVH 2022)



Figure 13. Richard Cambage recorded the shrub *Allocasuarina verticillata* at Newport in 1905 and suggested it was “part of the latest flora on the present continental shelf before its final submergence.” (Linnean Society of NSW)

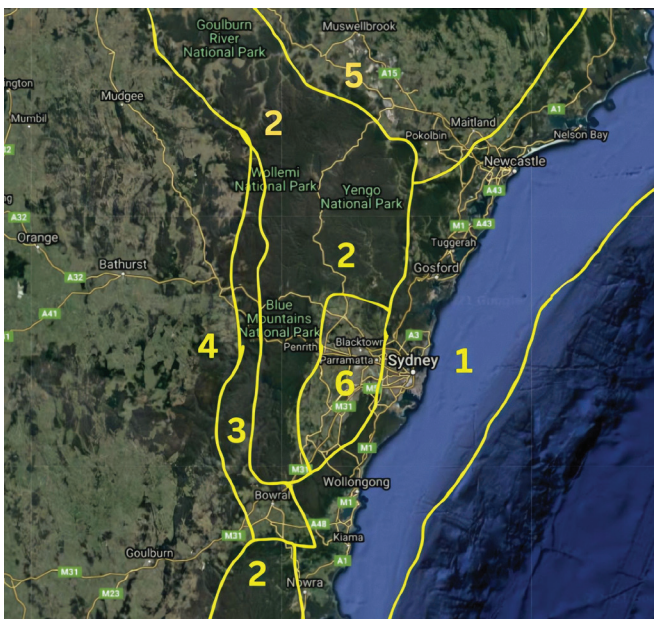


Figure 14. LGM areas Schematic designation of Sydney area LGM landscape regions showing likely extent across the. 1= Coastal sandplain wallum/sandstone heath; 2=Dry mid-elevation hinterland sandstone shrubland; 3=Subalpine sandstone heath/mallee/cliff seepage/gully complex; 4=Tablelands subalpine grassland/mallee; 5= Hunter Valley dry claysoil shrubland corridor; 6=Western Sydney grassland/shrubland.

Further west, rainshadow effects are likely to have resulted in a much drier hinterland. A low rainfall zone on the mid elevation sandstone plateaus from the Nattai north across western Sydney, the

lower Blue Mountains to Yengo and northwest across Wollemi to the Goulburn River is likely. Average LGM temperatures are likely to have been about 11°C (perhaps equivalent to today’s Katoomba/Newnes Plateau conditions) (Table 7), but with more frosts. Summer insolation and seasonality was relatively low, and low rates of sediment accumulation confirm low rainfall conditions (Mooney et al. 2021).

Orographic effects would have increased rainfall in the upper Blue Mountains and Tablelands. Montane areas would have been colder but with less evaporation. Mean winter temperature on the Southern Tablelands was 8 °C lower than present (Barrows et al. 2022). Similar low temperatures are likely on the higher Blue Mountains sandstone plateaus above about 900-1000 m elevation and above 800 m on the Southern Highlands (Katoomba rainfall 1091 mm pa; mean annual temperature 12 °C today could have had an equivalent LGM mean temperature of 5 °C including elevation-related adiabatic cooling). This would be somewhat equivalent to Charlotte Pass (Table 7) and a mean winter temperature of 1-2 °C. South-eastern Australia alpine areas today have mean annual temperatures below 8 °C (Venn et al. 2017).

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COASTAL towns (elevation m)	mean annual temp. °C	LGM estimate (6 °C lower)	LGM temp. equivalent areas today
Port Macquarie (20 m)	18	12	Katoomba/Bombala
Newcastle 33 m	18	12	Katoomba/Bombala
Narrara 20 m	17	11	Newnes Plateau/Oberon
Sydney Obs H 39 m	17	11	Newnes Plateau/Oberon
Parramatta 55 m	18	12	Katoomba/Bombala
Campbelltown 75 m	17	11	Newnes Plateau/Oberon
Richmond 20 m	20	14	Goulburn
Valley Heights 320 m	17	11	Newnes Plateau/Oberon
Wollongong 30 m	17	11	Newnes Plateau/Oberon
Bega 50 m	15	9	Nimmitabel
Phillip Island Victoria	14.5	9	Nimmitabel
MONTANE		1 °C lower to account for LGM elevational adiabatic cooling	
Newnes Plateau (1050 m)	11	4	<Charlottes Pass
Lithgow 950 m	12	5	Charlottes Pass
Katoomba 1017 m	12	5	Charlottes Pass
Bowral 662 m	13	6	Perisher
Bathurst 713 m	13	6	Perisher
Oberon 1088 m	11	4	<Charlottes Pass
Goulburn 670 m	14	7	Perisher
ALPINE			
Bombala 705 m	12	5	Charlottes Pass
Nalbaugh SF 675 m	11	4	<Charlottes Pass
Charlottes Pass 1755 m	5	-2	No current equivalent
Perisher 1735 m	6	-1	No current equivalent
WESTERN PLAINS			
Dubbo (260 m)	17	11	Newnes Plateau/Oberon
Brewarrina	20	14	Goulburn
NORTHERN HEMISPHERE (Britain)			
London (rainfall 621 mm)	11	5	LGM - Graminoid & Forb Tundra
Edinburgh (rainfall 706 mm)	8.5	2.5	LGM Ice sheet

Table 7. An indication of Last Glacial Maximum temperatures. Current mean annual temperatures for some coastal and montane NSW towns and estimated LGM temperatures (6-7 °C lower) and equivalent areas. Comparative areas are not necessarily equivalent in terms of rainfall. Due to lower LGM sea-levels all sites were about 20 km further inland and about 120 m higher.

Recent studies on scree slopes and frost cracking indicate periglacial conditions during the LGM are likely to have affected much of southeastern Australia, down to 680 m on the Southern Tablelands (including Wombeyan Caves) (Barrows et al. 2022). Enhanced effective precipitation from reduced evaporation and snow melt is likely to have increased vegetation survival in montane conditions. Modelling of precipitation into snow and rain indicates that LGM snowfall was a common occurrence in July across the Great Dividing Range (the Macquarie River catchments draining much of the Central Tablelands, developed snowpack depths equivalent to 94% of present-day mean annual runoff depths) (Mueller et al. undated).

Stress-tolerators in sclerophyll heath - Evidence of *in situ* LGM survival

Species with strong persistence traits (Bond & Midgely 2001) are likely to have been favoured in the harsh LGM conditions - low stature, longevity, clonal spread, drought/fire tolerance and strong habitat fidelity (localised propagule dispersal). These characteristics are also associated with species with a long history of *in situ* occupation (long before the LGM) on (OCBILs) in Western Australia (Hopper 2021).

The stable, erosion-resistant plateaus and ridges of the low nutrient Sydney sandstone are similar to OCBILs, and there are many species with OCBIL site characteristics, essentially stress-tolerant resprouters

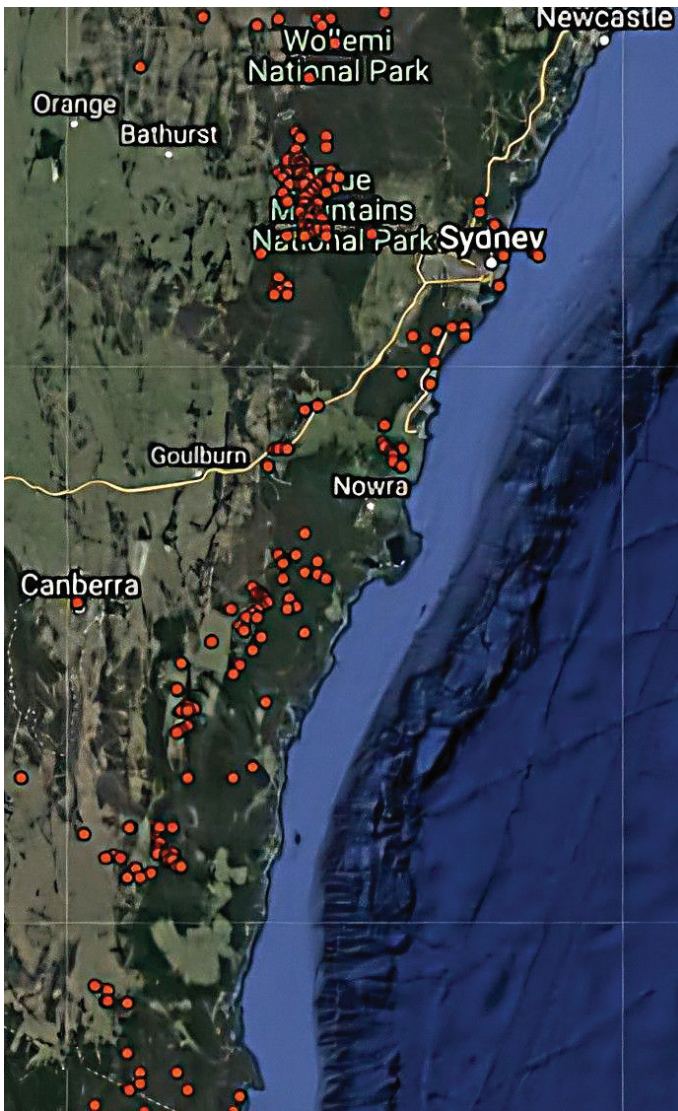


Figure 15. *Allocasuarina nana* distribution (Northern limit Upper Cudgong River) showing extensive montane and more limited coastal distribution, suggesting former wider LGM occurrence, now reduced. (AVH 2019)

in sclerophyll heath and woodland vegetation (Keith et al. 2004, Keith and Tozer 2012). Such species include long-lived resprouter shrubs, mallee eucalypts, prostrate/clonal groundcover species, and rhizomatous geophytes (Keith and Tozer 2012). Many are rare and endemic species confined to heath habitats, and likely to have occupied these sites throughout the LGM. Others are more widespread. For example, *Allocasuarina nana* has massive multi-stemmed rootstocks, sheds its seeds only a few metres from its canopy and is abundant today in montane sandstone heath (Figure 15). It also has limited occurrences on Sydney coastal plateaus (but only as limited patches in high light sites lacking tree

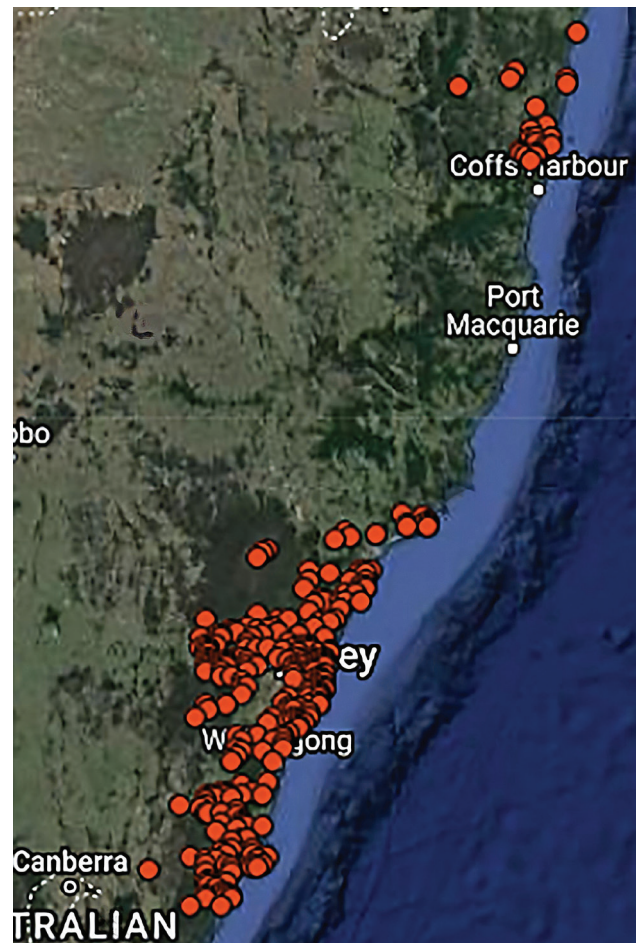


Figure 16. *Lambertia formosa* distribution suggests wider occurrence (North Coast outlier via LGM coastal plain), while Sydney populations south of Wollongong show morphological difference (consistently longer leaves) (PlantNet 2023). (AVH 2022)

cover), which is an overall distribution consistent with being previously more extensive in colder, drier LGM conditions. Examples of other stress-tolerator/OCBIL heath species with fragmented montane and coastal distributions indicative of marked contractions include *Allocasuarina diminuta* subsp. *mimica*, *Acacia baueri* subsp. *aspera*, *Monotoca ledifolia* and *Darwinia fascicularis* subsp. *oligantha* (Table 9).

Other stress-tolerator/OCBIL shrubs are widespread in both heath and woodland today, including *Lambertia formosa*, *Lomatia silaifolia*, *Hakea laevipes*, *Isopogon anemonifolius*, *Isopogon anethifolius*, *Banksia spinulosa*, *Acacia ulicifolia*, *Platysace linearifolia*, *Xanthorrhoea* species and

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Particular LGM conditions	Ecology attributes	Advantaged growth-forms	Likely life forms
Low temperature, Low rainfall, Low atmospheric CO ₂ Short growing season	Cold tolerance	Long-lived slow-growing short or multistemmed trees	STRESS TOLERATORS (resprouters) mallee eucalypts
	Drought-tolerance Wind tolerance Longevity	Small perennial low-growing or prostrate shrubs	STRESS TOLERATORS (resprouters) OCBIL shrubs, geophytes, sedges
High wind	Wind pollination, wind dispersal	Mass seed release	RUDERALS Asteraceae, Poaceae
Periodic wet periods Open conditions	Rainfall pulse recruitment	Shortlived drought dormant/seasonal ephemeral herbs	RUDERALS herbs, monocot
		Disadvantaged growth-forms	
Low temperature, Low rainfall, Low atmospheric CO ₂	Moisture, CO ₂ demanding)	Long-lived trees	Most tree eucalypts COMPETITORS
	Frost, snow, high wind sensitive (through moisture loss	Quick-growing woody shortlived perennials	RUDERALS Fire dependent seeder species, Mesic species
Low atmospheric CO ₂	CO ₂ requiring	C4 grasses	<i>Themeda</i>
Low fire incidence	Obligate fire, smoke dormancy recruitment	Shortlived fire ephemerals	Obligate seeders, Fabaceae

Table 8. Sandstone habitat life forms likely to be either advantaged or disadvantaged during Last Glacial Maximum conditions of lower temperature, rainfall, CO₂, and strong wind particularly at high elevations

Stress Tolerator/ OCBIL heath species with fragmented montane and coastal distributions	
<i>Allocasuarina nana</i>	montane sandstone heath and on the Sydney coast
<i>Allocasuarina diminuta</i> subsp. <i>mimica</i>	(Blue Mountains, Bundanoon, Orchard Hills, Heathcote. Kingsford
<i>Acacia baueri</i> subsp. <i>aspera</i>	Upper Blue Mountains and on the coast near Mt Keira
<i>Monotoca ledifolia</i>	Upper Blue Mountains, Woronora Plateau and Howes Valley
<i>Darwinia fascicularis</i> subsp. <i>oligantha</i>	Upper Blue Mountains, Southern Highlands and Maroota in western Sydney
Stress Tolerator/OCBIL shrubs widespread in both heath and woodland today	
<i>Lambertia formosa</i>	Sydney populations south of Bargo River show morphological difference (consistently longer leaves)
<i>Lomatia silaifolia</i>	Separate southern and northern populations of <i>Lomatia silaifolia</i> differ genomically
<i>Platysace linearifolia</i>	Rhizomatous capacity

Table 9. Remnants of the LGM sandstone heath landscape: Examples of Stress Tolerator/ OCBILs) in current sclerophyll heath and woodland vegetation

many geophytic species in families Liliaceae, Phormiaceae, Iridaceae, and Orchidaceae (Table 9). These have evidently been able to cope with later changes particularly the likely increase in tree cover competition associated with Holocene warming and increased atmospheric CO₂. Evidence of previously wider distributions becoming isolated may show up in local morphological variation. Sydney populations of *Lambertia formosa* south of Bargo River show local morphological difference (consistently longer leaves - PlantNET 2023), while the North Coast outlier suggests wider past connections via the former LGM coastal plain distribution (Figure 16). Separate southern and northern populations of *Lomatia silaifolia* differ genomically (Milner et al. 2012).

Mallee eucalypts – longevity, growth form and distributions

About 15% of the almost 100 eucalypt species in the Greater Blue Mountains World Heritage Area (GBMWA) are mallees (Hager and Benson 2010). All are characteristic Stress-tolerator/ OCBIL species, low-growing, multi-stemmed plants, with fire-resistant survival and habitat fidelity, and restricted seed dispersal and recruitment, compared to most tree-form species (Booth 2017).

Mallees are very long-lived; more so than trees in the same habitat, which are physically limited by an ever-growing, but increasingly scarred trunk, vulnerable to wind, fungal decay, termites, etc. One individual of the Western Australian mallee

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Genus/subgenus	Section/series	Mallee species	Occurrence	Habitat
Eucalyptus/ Symphyomyrtus	sect. Latoangulatae ser. Annulares (red mahoganies)	<i>E. cryptica</i> (cattai)	Coast, dry ridges, Restricted, Dural	Dry, low rainfall
Eucalyptus/ Symphyomyrtus	Sect. Pumilio (Grey gums)	<i>E. pumila</i>	Hunter Valley, one site, Pokolbin, sandstone shrubland	Dry, low rainfall
Eucalyptus/ Symphyomyrtus	sect. Exsertaria ser. Exsertae (eastern red gums)	<i>E. dealbata</i> subsp. <i>aperticola</i>	Hunter Valley, Dry ridges, scrubby heath, restricted near Denman	Dry, low rainfall
Eucalyptus/ Symphyomyrtus	sect. Maidenaria ser. Recurvae	<i>E. recurva</i>	Southern Tablelands restricted Braidwood	Dry, low rainfall
Eucalyptus/ Symphyomyrtus	sect. Maidenaria ser. Viminales (white gums)	<i>E. pulverulenta</i>	Central Tablelands, restricted ridges Lithgow,	Dry, low rainfall
Eucalyptus/ Eucalyptus	ser. Pachyphloiae (stringybarks)	<i>E. camfieldii</i> <i>E. bensonii</i> <i>E. ligustrina</i>	Coast, mountains heath, <i>E. camfieldii</i> and <i>E. bensonii</i> restricted dry ridges	Dry, high rainfall
Eucalyptus/ Eucalyptus	ser. Psathyroxyla subser. Considerianae	<i>E. multicaulis</i>	Blue Mtns heath, widespread	Dry, high rainfall
Corymbia	sect. Corymbia Red Bloodwoods	<i>Corymbia</i> <i>gummifera</i> mallee	Coast, dry heath restricted Royal NP	Dry, high rainfall
Eucalyptus/ Symphyomyrtus	sect. Maidenaria ser. Foveolatae (swamp gums)	<i>E. camphora</i> subsp. <i>camphora</i> <i>E. aquatica</i>	Cudgegong and Megalong Valley, (Penrose endemic), peatswamp margins, restricted	Wet, high rainfall
Eucalyptus/ Symphyomyrtus	sect. Maidenaria ser. Viminales	<i>E. baeuerlenii</i>	Wentworth Falls, restricted, clifflines	Wet, high rainfall
Eucalyptus/ Eucalyptus	ser. Strictae (mallee ashes)	<i>E. stricta</i> (sens lat.) <i>E. obstans</i> / <i>burgessiana</i> <i>E. dendromorpha</i> <i>E. cunninghamii</i>	Coast, upper BM, Sth Highlands heath, periodically wet sites, mostly widespread	Wet, high rainfall
Eucalyptus/ Eucalyptus	ser. Pauciflorae (snow gums)	<i>E. gregsoniana</i>	Newnes Plateau, restricted, heath periodically wet sites	Wet/high rainfall
Eucalyptus/ Eucalyptus	ser. Fraxinales	<i>E. luehmanniana</i>	Coast, restricted, moist sites	Wet, high rainfall
Eucalyptus/ Eucalyptus	ser. Longitudinales (sallees)	<i>E. stellulata</i> <i>E. moorei</i>	Tablelands, upper BM swamp periodically wet sites, frost hollows	Wet, high rainfall

Table 10. Mallee eucalypts in the Sydney area, occurrence and habitat from dry to wet. Classification follows Nicolle (2021)

Eucalyptus argutifolia is estimated to be almost 2000 years old (11 m across, estimated lignotuber growth of 1.5–3.4 mm outwards per year based on its clonal extent - Kennington and James 1997; Hopper 2021)). Using similar measures, mallee-form individuals of *Corymbia gummifera* in coastal heath in Royal National Park with lignotubers up to 10.5 m across (Mullette 1978) could be 1500-3000 years old, and southern NSW Mongarlowe mallee, *Eucalyptus recurva* (with only 6 remaining individuals at 3 sites) with lignotubers up to 12 m across (Commonwealth Dept of Environment 2015) could possibly be 1700-4000 years old. Clonality has been reported in the rare mallee *Eucalyptus cryptica* (previously called ‘sp. Cattai’ -Wilson et al. 2023), clonal samples in some cases being located as much as 30 m apart (Rutherford et al. 2022), suggesting extensive rhizomatous

growth and indefinite long-term survival providing habitat conditions remain stable. Mallee longevity (c. 3000-5000 years) could have allowed survival of individuals through the severest peak of the LGM though the trade-offs (clonality, genomic bottlenecks) may have reduced recovery ability (Table 10).

Coastal sandstone mallees

With low temperatures and low CO₂, but better local rainfall, LGM coastal vegetation is likely to have included both obligate seeder and stress-tolerator/resprouter shrubs including mallees. Many Sydney mallees are regional endemics with strong habitat fidelity; most are conspicuously associated with wet habitats and/or high rainfall (>1200 mm pa), including the Green ash mallees (Strictae, the biggest mallee group), snow gums and sallies, and Tableland swamp gums, and often associated with wet heaths

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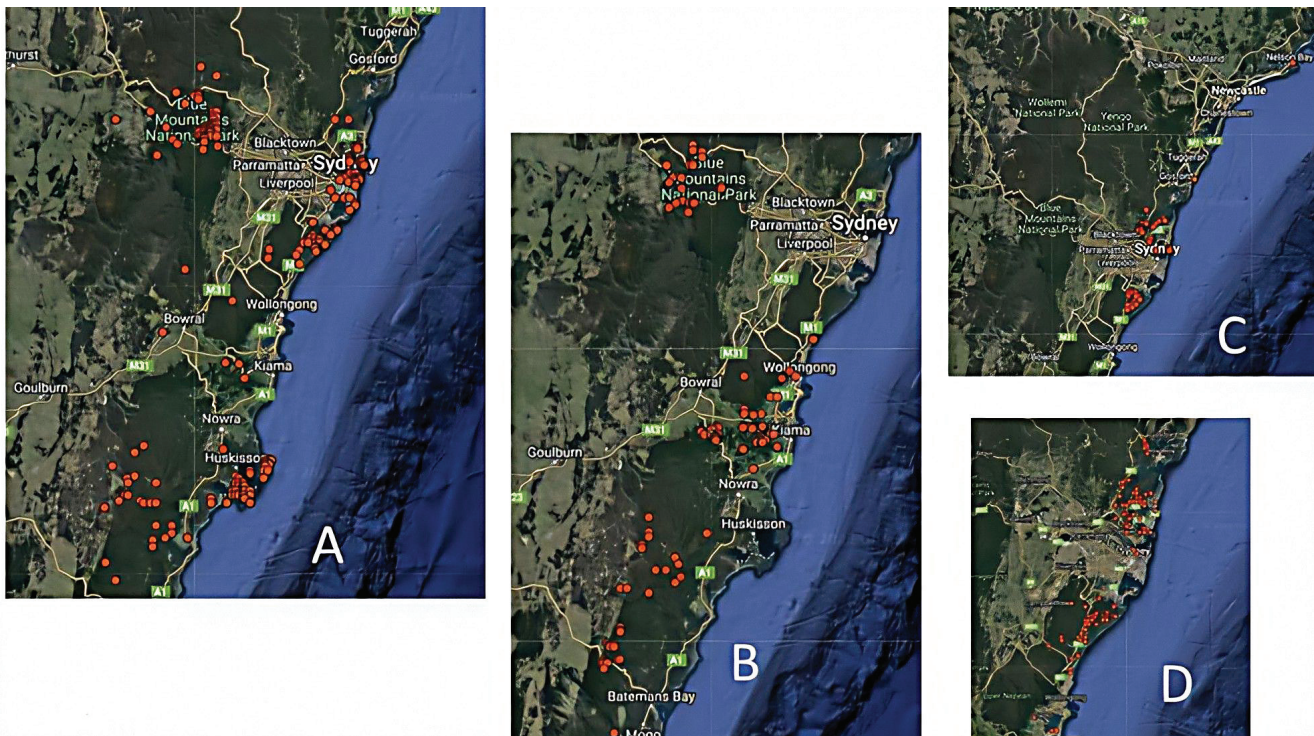


Figure 17. Mallee species A. *Eucalyptus burgessiana*, B. *Eucalyptus dendromorpha*, C. *Eucalyptus camfieldii* and D. *Eucalyptus luehmanniana* all show disjunct occurrences indicative of former wider distributions including likely LGM coastal connections. (AVH 2022)

(Table 10). Their current scattered distributions suggest previously more extensive occurrences, now contracted and fragmented (Figure 17).

Relatively recent fragmentation events may be implied by small genomic differences not associated with clear morphological variation. For example, for the green ash mallee *Eucalyptus burgessiana* (including *E. obstans*), Rutherford et al. (2018) found that though local genomic connectivity is maintained in populations with up to 40 km distance separations (Beacon Hill to Royal NP), population-level differentiation is evident between Sydney and Jervis Bay populations, about 100 km apart. This is consistent with post-LGM sea level rise loss of intervening LGM coastal plain populations. Populations of *Eucalyptus camfieldii* and *Eucalyptus luehmanniana* in Ku-ring-gai and Royal NPs could have also been similarly linked through the coastal plain. However, the endemic coastal sandstone shrub *Angophora hispida*, occupying similar habitat to these mallees (localised low elevation patches of sandstone heath between Yengo and Royal NPs shows an absence of such population genetic structure, indicating there were no major biogeographical barriers restricting gene flow (Rutherford et al. 2020). Whether it ever extended beyond its current distribution (i.e. farther

south) is unknown, but like northern populations of *Eucalyptus burgessiana*, it is still maintaining genetic connectivity despite fragmentation of habitat, presumably via a range of bird and insect pollinators.

Extensive LGM moisture-dependent mallee vegetation on the upper Blue Mountains

On the basis of Northern Tablelands pollen records Ellerton et al. (2017) suggested LGM montane conditions with a more positive water balance were effectively wetter than previously thought. Little Llangothlin Lagoon (1360 m) held permanent water during the late LGM), and with temperatures 9-11°C below present, supported subalpine herbfield and eucalypt mallee woodland (presumably the current frost-tolerant mallees *Eucalyptus pauciflora* and *Eucalyptus stellulata*). Llangothlin Catchment is on soils derived from basalts and granites.

Applying recent climate findings (Ellerton et al. 2017; Barrows et al. 2022; Mueller et al. undated) to the Blue Mountains sandstone landscapes, an LGM subalpine zone (>800-900 m) with a moisture-related subalpine vegetation can be defined extending along the eastern edge of the Central Tablelands from the upper Cudgegong/Coricudgy in the north, south through the upper Blue Mountains to Kanangra,

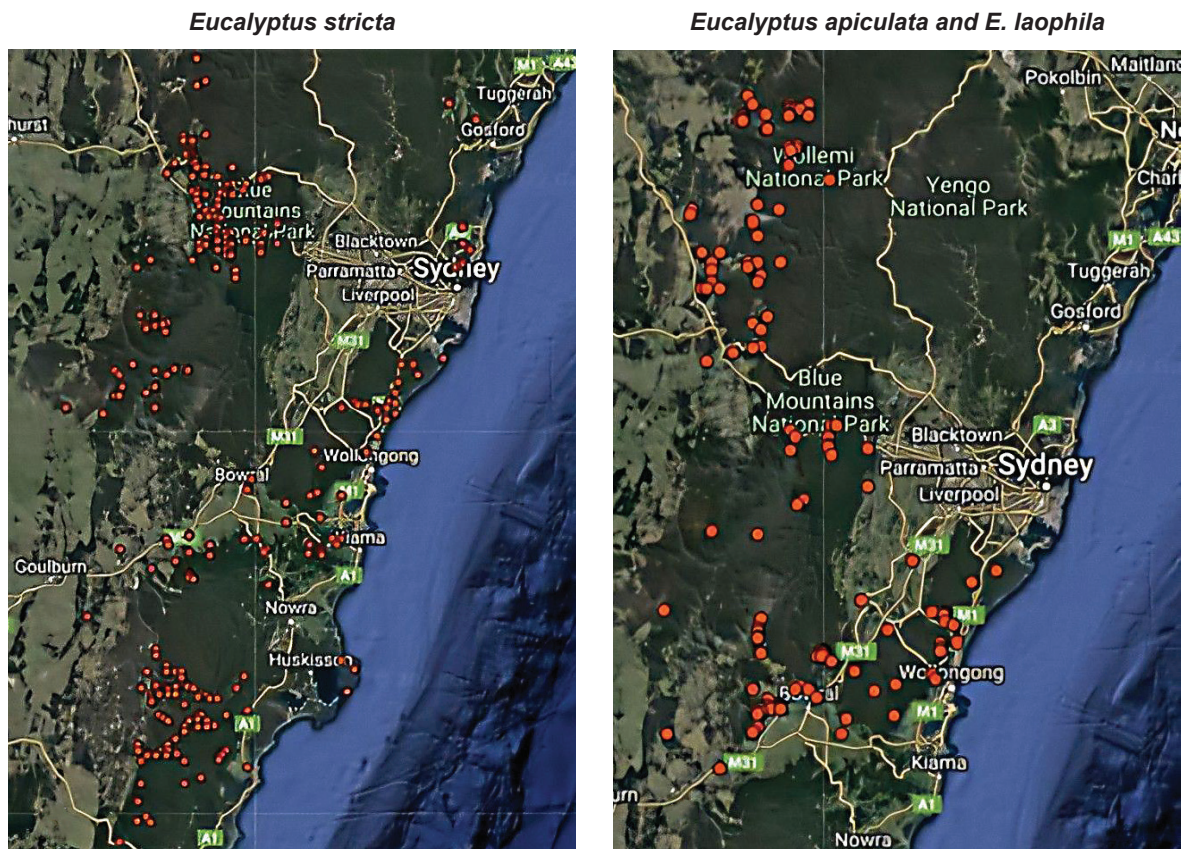


Figure 18. LEFT: *Eucalyptus stricta* has a widespread distribution associated with heath and rocky sandstone OCBIL landscapes and like *Allocasuarina nana*, with a relatively narrow coastal band, consistent with previous more extensive occurrences in LGM conditions. RIGHT: The narrower leaves (phenotypic plasticity) and drier sites for *Eucalyptus laophila* (Newnes Plateau, Wollemi National Park), and *Eucalyptus apiculata* (west of Wollongong) (both in *E. stricta* genomic envelope) at current elevational limits may indicate some post-LGM montane elevation expansion. (AVH 2022)

and east along the Southern Highlands to Robertson (Figure 14 - Area 3). This area is surprisingly consistent with the distributions of the moisture-dependent sandstone mallees, stringybark mallees on better-drained soils (Table 10), and most of the stress-tolerator/resprouter shrub species such as *Allocasuarina nana* and *Lambertia formosa*, as well as smaller prostrate montane heath species, many of which appear to be indicative of previously more extensive occurrences across this area.

Eucalyptus stricta, for example, the most widespread of the Sydney mallees, is associated with rocky sandstone heath and wet sites near peat swamps and, like *Allocasuarina nana*, with relatively few coastal occurrences and more extensive population concentrations on the upper Blue Mountains, Southern Highlands and Budawang area (Figure 18), consistent with widespread past landscape predominance. Mallees with similar sandstone habitats but more limited distributions are *Eucalyptus gregsoniana* and *Eucalyptus moorei* (Table 10). Today montane

mallees are subject to only brief snowfalls but the mallee habit with small crowns on tall very flexible stems would appear resilient to heavier winter snowpack

Subalpine vegetation on the Upper Blue Mountains sandstone plateaus and cliffs

At higher elevations, a surprisingly diverse LGM landscape is likely as a result of local climatic conditions and geomorphology. Bare ground or open vegetation on dry exposed sandstone at high elevations with high wind velocities is suggested from remnant sand-dunes on the Newnes Plateau active during the LGM (Hesse et al. 2003); perhaps drier conditions in the northwest of the region at this time isolated the higher areas of Coricudgy and the upper Cudgegong.

The high daisy pollen abundance recorded from LGM Tablelands pollen cores is not reflected in any Asteraceae richness in current sandstone heath. Most montane shrubs today are in stable sites with reliable periodic moisture, with features of benefit in LGM

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Alpine species	Lifeform	Habitat	Substrate	Fertility	Locality
<i>Asplenium flabellifolium</i>	fern	moist	ss	low	BM, CSS
<i>Empodisma minus</i>	graminoid	wet	ss	low	BM, NP, CSS
<i>Gonocarpus micranthus</i>	herb	wet	ss	low	BM, NP, CSS
<i>Asperula gunnii</i>	herb	wet	ss	low	BM, NP
<i>Celmisia longifolia</i>	herb	wet	ss	low	NP
<i>Celmisia tomentella</i>	herb	wet	ss	low	BM, KAN
<i>Baeckea utilis</i>	shrub	wet	ss	low	KAN, NP
<i>Epacris paludosa</i>	shrub	wet	ss	low	KAN, NP
<i>Epilobium gunnianum</i>	herb	wet	ss	low	KAN, NP
<i>Blechnum pennamarina</i>	fern	wet	ss	low	KAN
<i>Myriophyllum pedunculatum</i> subsp. <i>pedunculatum</i>	herb	wet	ss	low	NP
<i>Epacris microphylla</i>	shrub	wet-dry	ss	low	BM, NP, CSS
<i>Stylidium graminifolium</i>	herb	wet-dry	ss	low	BM, NP, CSS
<i>Oxylobium ellipticum</i>	shrub	dry	ss	low	BM
<i>Carex gaudichaudiana</i>	graminoid	wet	shale	med	BM, NP
<i>Neopaxia australasica</i>	herb	wet	shale basalt	med	KAN
<i>Rhodanthe anthemoides</i>	herb	dry	shale ss	med	BM, CP, CSS
<i>Viola betonicifolia</i>	herb	dry	shale	med	BM, CP
<i>Crassula sieberiana</i>	herb	dry	shale ss	med	BM, CP, CSS
<i>Microseris lanceolata</i>	herb	dry	shale basalt	med	KAN
<i>Pimelea ligustrina</i>	shrub	dry	shale basalt	med	BM, KAN
<i>Geranium potentilloides</i>	herb	dry	shale basalt	med	BM,
<i>Lagenifera stipitata</i>	herb	dry	shale basalt	med-high	BM, NP, CP
<i>Carex breviculmis</i>	graminoid	dry	shale basalt	med-high	BM, CP
<i>Melicytus dentatus</i> [<i>Hymenanthera</i>]	shrub	dry	shale basalt	med high	BM, KAN
<i>Oreomyrrhis eriopoda</i>	herb	dry	shale basalt	med high	BM, NP,
<i>Polystichum proliferum</i>	fern	dry	shale basalt	high	BM

Table 11. Distribution of Buttongrass, *Gymnoschoenus sphaerocephalus* highlights its essentially southern distribution and, north of Myall Lakes, its restriction to higher (cold) habitats. Past connections along the LGM coastal plain as far as Myall Lakes are likely. (AVH 2023)

conditions such as low spreading or prostrate growth forms, slow growth and longevity features such as root-suckering, frost and snow tolerance, temperature-induced flowering and short growing-season responses. Now restricted species such as *Phyllota squarrosa*, *Mirbelia platyloboides*, *Persoonia hindii*, *Isopogon prostratus* and *Kunzea cambagei* are likely to have been more abundant on the treeless LGM uplands. Many have patchy or fragmented populations in the upper Blue Mountains and/or Southern Highlands, and farther south. For example the prostrate sclerophyll shrub

Isopogon prostratus has a series of localised small disjunct populations on sandstone landscapes from Newnes Plateau along the Southern ranges to Nadgee, and a final southern occurrence in Victoria (Benson and von Richter 2010) (Figure 19). Its seed, dispersed from serotinous fruits in the leaf litter, is limited to within a metre or so of its cones, maintaining long-term habitat fidelity but with very little colonising potential. In open windy LGM conditions, they may have moved larger distances (African Proteaceae seeds can move up to 500 m (Bond 1988).



Figure 19. The prostrate resprouter shrub *Isopogon prostratus* is likely to have been important in the open LGM heath. Its groundlevel flowers and serotinous fruits keep its populations very localised, but its sporadic occurrences from Newnes Plateau to Victoria suggest a former more continuous LGM distribution. (Photo Ian Baird)

Links with the Kosciuszko alpine flora are few. Of about 200 current Kosciuszko alpine (i.e. above the treeline) taxa (Costin et al. 1979), only about 14% (27 species) also occur in the Sydney area (Table 11). About half of these occur on relatively dry fertile habitats on the Great Divide consistent with the LGM shrub or grassland steppe vegetation of the pollen studies (discussed below). The other half, about 14 species, occur in wet bog or swamp habitats in the Blue Mountains, many on Newnes Plateau (Table 11). Many of these are separated by long distances from their main Kosciuszko occurrences (e.g. *Celmisia longifolia* and *Celmisia tomentella*). Other taxa have similar but less fragmentary disjunctions, some reaching as far as the Northern Tablelands.

In the LGM subalpine landscape, water inception rather than surface run-off is likely to have been important (Mueller et al. undated). Moisture run-off into aquifers of alternating sandstone and shale strata (predominating features of the sandstone geology) would have emerged as cliff-line seepages and springs, providing habitat for small alpine shrubs, herbs and ferns.

The lack of Kosciuszko connections and the survival of its own wet cliff-face and groundwater-dependant assemblages is consistent with a separate long vegetation history for the Blue Mountains. A classic example is the palaeoendemic dioecious conifer *Pherosphaera fitzgeraldii*, now restricted to a few waterfall-spray habitats near Katoomba (Smith 1981), with plants showing a very limited genetic variation across its range (Wyn Jones pers. comm.). It may have been more widespread during the LGM, and contracted subsequently, like its only surviving

relative, the similarly poorly-dispersing, partly clonal *Pherosphaera hookeriana*, a major LGM vegetation component in Tasmanian. The latter now persists in small populations directly descended from nearby glacial populations (Macphail, et al. 2014; Worth et al. 2021).

Now-restricted Blue Mountain angiosperm species associated with moist sandstone cliff-line habitats include stress-tolerator OCBIL shrubs *Eucalyptus baeuerlenii*, *Isopogon fletcheri*, *Epacris hamiltonii* and *Epacris apiculata*; geophytes *Alania cunninghamii*, *Blandfordia cunninghamii* (Coleby 2006), and rhizomatous herb *Euphrasia bowdeniae*. Species in periodically waterlogged habitats include *Boronia deanei*, *Dillwynia stipulifera* and *Olearia quercifolia*, the clonal *Haloragodendron gibsonii* (Sydes and Peakall 1998), ruderal/fire-sensitive *Sprengelia monticola*, *Leionema lachneoides*, and *Acacia ptychoclada* as well as more common species including ferns (*Gleichenia rupestris*) and monocots. These all have requirements for permanent moisture but could have survived in local mesic LGM microhabitats.

Though current groundwater-dependant montane peat swamps only date from about 12 000-10 000 years BP, with similar dates on the Woronora Plateau (Young 2017), the big water-dependent but stress-tolerator tussock sedges occurring on the LGM coast, *Gymnoschoenus sphaerocephalus*, *Xyris ustulata* and *Lepidosperma limicola* may have also survived the drier LGM subalpine conditions confined to locally moist seepages with snow melt and enhanced effective precipitation from reduced evaporation (Barrows et al. 2022). There is no evidence that more extensive *Gymnoschoenus* Buttongrass moorland (as in Tasmania) was part of the LGM subalpine Blue Mountains vegetation, nor whether any particular species were predominant.

Were species at high elevations limited by lack of pollinators?

Evidence here is very limited. It is likely that most plant species' survival in high elevation LGM conditions was primarily limited by the harsh growing conditions. Windy conditions would have assisted wind-pollinated plants such as members of the Casuarinaceae, Asteraceae and Poaceae.

The limited literature on LGM climate and bird distributions relate to continental scales or rainfall (e.g. Magpie-(Toon et al. 2007); Shrikethrush (Lamb et al. 2019); butcherbirds (Kearns et al. 2014)), rather than regional elevation responses that may impact pollination. Honeyeaters are important pollinators for many species of Proteaceae, Fabaceae and Myrtaceae; current autumn migration routes take them along

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the coast and into the upper Blue Mountains up to at least 1000 m elevation. Such routes are likely to depend on flower source availability (Munro et al. 1993). Assuming LGM flowering was in the warmest seasons, plants could have been sought out and pollinated during bird migration. Shrub-pollinating mammals including bush rats and possums are likely to have survived in LGM heath. Mountain Pygmy Possum, *Burramys parvus*, now confined to alpine habitats at Mt Hotham and Kosciuszko as well as the Blue Mountains is likely to have been separated earlier than the LGM, and has a need for rocky boulder habitat with low temperatures. This would have rendered most of the intervening region unsuitable, even in times of glacial maxima (Hoser 2020). Insects, particularly native bees (Halictidae, Colletidae), are important for Ericaceae and Fabaceae (Johnson and McQuillan 2011; Bernhardt et al. 2019). While there were probably enough pollinators for generalist plant species to survive, species dependent on particular insect interactions (e.g. some terrestrial orchids) may have been restricted to lower elevations, due to limitations of temperature and wind on specific insect survival. Some now rare remnant LGM stress-tolerator shrubs are self-fertile (e.g. *Haloragodendron gibsonii* - Sydes and Peakall 1998) and able to maintain seed production in absence of outcrossing opportunities or pollinators.

Dry sandstone country: species invade from the west

On the mid-elevation essentially dry rainshadow sandstone areas between the coast and the higher Tablelands (Figure 14 - Area 2), without the elevational benefit of snowpack and reduced lower evaporation, the cold dry windy LGM conditions and lower atmospheric CO₂, could probably only support dry scrub or shrubland. In this area, mallees are rare (Table 10) though small trees of *Angophora bakeri* and *Corymbia eximia* are LGM possibilities. Of the few mallee species occurring there now, *Eucalyptus pumila* and *Eucalyptus dealbata* subsp. *aperticola* are restricted to scrubby heath at a few sites on the southern rim of the Hunter Valley (Bell and Nicolle 2020). There is no suggestion of previously wider occurrences such as the Green Ashes, though in the case of *Eucalyptus cryptica*, now restricted to sandstone ridges at Dural-Annangrove, Rutherford et al. (2022) found varied genetic diversity across populations and unexpectedly high clonality via its underground lignotuber. This is consistent with a past more extensive local population, reduced, perhaps in the early Holocene, by more vigorous invading red mahogany trees, and then persisting through clonal longevity on isolated low nutrient ridges. It is now

being impacted by hybrid swamping (Rutherford et al. 2022).

Eucalyptus dealbata subsp. *aperticola* is possibly a remnant of an LGM dry country invasion by *Eucalyptus dealbata* sens. lat. (subsp. *aperticola* occurs within 40 km of subsp. *dealbata*). The dry LGM conditions would have enabled drier western species to invade Sydney sandstone. Dry country shrubs *Calytrix tetragona*, *Gaudium parvifolium*, *Acacia triptera*, *Leucopogon muticus*, *Boronia anethifolia*, *Isopogon dawsonii*, *Harmogia densifolia*, *Cryptandra spinescens*, *Gompholobium aspalathoides* and *Allocasuarina gymnanthera* were recorded with *Eucalyptus dealbata* subsp. *aperticola* (Bell and Nicolle 2020). All are low-nutrient shrub species (many are obligate seeders) with essentially north-western NSW occurrences, e.g. Narrabri and Pilliga. Some species, such as *Allocasuarina luehmannii*, appear to have spread eastward as far as the lower elevation sandstone of the Goulburn River and Wollemi/Yengo National Parks, some to the coastal Sydney sandstone plateaus (e.g. *Leucopogon muticus*) and presumably along the LGM coastal plain south to Nowra (e.g. *Eucalyptus beyeriana* (Figure 20), *Gaudium parvifolium*, *Cassinia cunninghamii*). Phylogenomic studies of *Calytrix tetragona* identified almost 20 infraspecific groups across southern Australia, suggesting vicariance and long-term site fidelity (Nge et al. 2021). Research on some other common, widespread, and often variable species may disclose similar patterns of variation.

Obligate seeders are not likely to have been advantaged in LGM conditions, particularly away from the coast where warmer wetter conditions and some degree of Aboriginal burning is likely. However, in drier hinterland areas with little fuel build-up and rare fires, long stable periods could have helped some larger woody obligate seeders with a combination of ruderal and drought stress-tolerator traits. Common Western Slopes and Tablelands conifer *Callitris endlicheri* has extensive western Blue Mountains occurrences and a few isolated eastern populations (Coxs River, Burragarang Valley and Darkes Forest - a coastal sandstone heath Endangered population (NSW Scientific Committee 2004)). *Callitris rhomboidea* and *Callitris muelleri* have widely separated upper Blue Mountains and coastal (Mosman, Chatswood-Terrey Hills) distributions, as well as disjunct occurrences in the Southern Highlands (*Callitris muelleri*) and at Nowra (*Callitris rhomboidea*). These occurrences are consistent with more extensive distributions in LGM and post-LGM warming conditions but, as fire-sensitive seeders, it is likely ENSO-related increased

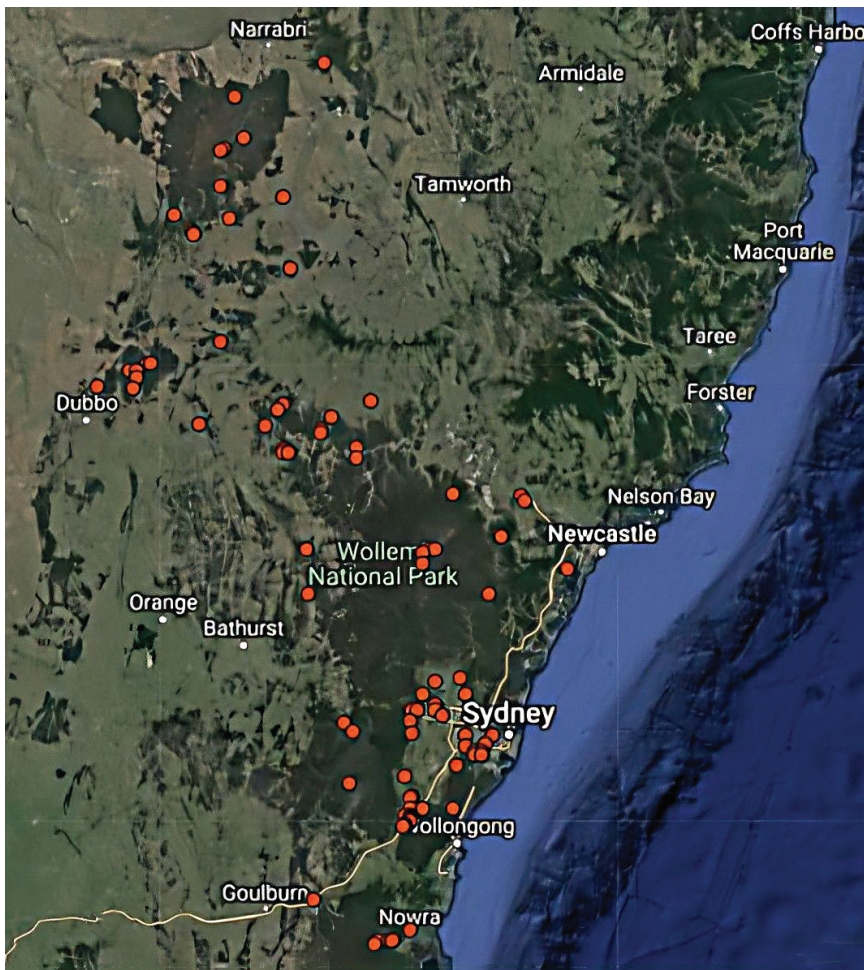


Figure 20. Distribution of *Eucalyptus beyeriana* suggests eastward spread via the lower elevation sandstone Goulburn River and Wollemi/Yengo NPs and coastal sandstone plateaus, with the LGM coastal plain enabling spread south to Nowra. (AVH 2022)

fire/drought conditions over the last 6000 years have confined occurrences to the current localised rocky ridges, harbour headlands or riparian sites that act as fire refugia. Martin (1994) reports *Callitris* pollen at Kurnell from 8000-5000 years BP, but reduced levels thereafter.

Mallee/tree species and Sheltered Eucalypt Woodland concentrations

Harsh conditions or frequent fire today may reduce some essentially tree-form eucalypts to stunted trees, though they rarely form true multi-stemmed mallees. Most are in *Eucalyptus* subgenus *Eucalyptus* with essentially southern temperate distributions (i.e. northern limits coinciding with Sydney sandstone limits) –including *Eucalyptus sieberi*, *E. piperita*, *E. considiana*, *E. racemosa* and *E. scias*. Some have very strong drought resilience (Zolfaghar et al. 2015) for example *Eucalyptus sieberi*, *E. piperita*,

E. racemosa and *E. globoidea*. Unlike the montane mallees they all currently occupy well-drained sites, are quick growing with rapid seedling recruitment and are unlikely to have benefitted in low LGM CO₂, winter snowpack and waterlogged soils. All could have possibly survived harsh LGM conditions, at least in sheltered sites; nearby prior site occupation and rapid expansion with post-LGM warming may account for their predominance as trees at higher elevations today.

Eucalypt pollen identified by Robbie and Martin (2007) from about 19 000 years BP at Mountain Lagoon (500 m elevation) in the lower Blue Mountains includes sandstone habitat *Eucalyptus piperita* and *E. racemosa*, shale country *E. crebra*, or perhaps sandstone habitat *E. beyeriana* though specific identification of eucalypts even with living material may be difficult. Tree/mallee *Angophora* and *Corymbia* species, *Angophora costata*, *A. bakeri* (except Rutherford's Kings Tableland *A. bakeri* mallee) and *Corymbia gummifera* have northern distributions, and appear more temperature-sensitive based on their generally low-elevation restricted ranges (<900m). They

are thus more likely to have been confined to the LGM coast. The likely spread of dryland species with clay soil affinities, e.g. *Eucalyptus sideroxylon*, *E. fibrosa*, *E. moluccana* and *E. crebra*, into western Sydney at the same time along nearby river systems is discussed below.

Persistence of rainforest and mesic vegetation

Rainforest species richness is highest at tropical and subtropical latitudes. Subtropical and northern Warm Temperate assemblages have predominantly Queensland and northern NSW distributions (e.g. Gondwana Rainforests World Heritage Area) but extend with decreasing floristic richness as far south as the Shoalhaven River (Metcalf and Green 2017). Cool Temperate assemblages occur in southern NSW, Victoria, and Tasmania. Rainforest habitat is generally restricted to higher nutrient soils than soils derived only from sandstone: on basalt caps

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in the Blue Mountains, some shale outcrops in the Permian sandstones or exposed in gullies in the Blue Mountains and along the coast, volcanics in the Illawarra, and some locally enriched coastal alluvial soils (Keith 2004).

During the LGM suitable east coast habitat for many rainforest species including *Doryphora sassafras* (Figure 21), *Elaeocarpus reticulatus*, *Callicoma serratifolia*, *Tristaniopsis collina*, *Tristaniopsis laurina* and *Pittosporum multiflorum* was less in extent, on average 65%, than occupied at present (Das et al. 2019). In the Sydney area, sheltered Blue Mountains gullies or coastal sites on fertile soils would have provided LGM refugia for these mesic species as well as cool adapted Temperate rainforest species including *Ceratopetalum apetalum* (Heslewood et al. 2014). Multiple stems from swollen stem bases in woody species such as *Atherosperma moschatum*, *Eucryphia moorei* and *Doryphora sassafras* (Johnstone and Lacey 1983) would have provided persistence and extended longevity in LGM conditions. Other Temperate tree species can occur as multi-stemmed shrubs (e.g. *Ceratopetalum apetalum*) suggesting that LGM mesic refugial pocket vegetation may have been as scrub rather than as rainforest.

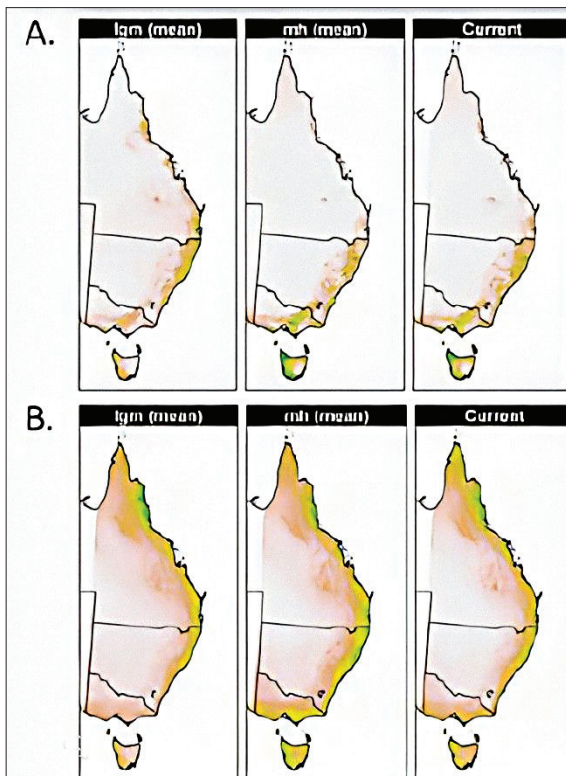


Figure 21. Habitat suitability models for LGM, Mid Holocene and current periods for cool adapted *Doryphora sassafras* (A) contrast with a recent Indo-Malesian migrant, *Toona australis* (B) (adapted from Rossetto et al. 2018).

Refugial limitations may have restricted subsequent expansion for some species. Genetic evidence indicates that during the LGM and earlier glacial periods, *Atherosperma moschatum* in south-eastern Australia was reduced to four separate regions, including the northern Barrington Tops/ Upper Blue Mountains, and Monga on the South Coast; followed by local dispersal in the Holocene (Worth et al. 2011). Cool Temperate *Nothofagus cunninghamii* occurred in the northern Kosciuszko region 35 000 years ago as indicated by old wood (Caine and Jennings 1968). The species is now restricted to Victoria and Tasmania where current populations are derived from short-range dispersal (about 100 km) from nearby LGM glacial refugia (Worth et al. 2009).

Conditions on the LGM coast would have been milder than in the mountains. *Eucryphia moorei* (Figure 22) is likely to have survived the LGM in coastal sites such as the Illawara and extended into Warm Temperate rainforest later. The recent discovery of the local endemic and long-lived clonal tree species *Daphnandra johnsonii* (and an endemic gall midge apparently dependent on its seed) on volcanics in the Kiama area (Lemmon 2019; Kolesik et al. 2019) suggests long-term site persistence before, and presumably throughout, the LGM on higher nutrient, old, climatically-buffered relatively fertile OCFEL landscapes (Hopper et al. 2021). This is a parallel situation to sclerophyll OCBILs). Disjunct occurrences of some dry rainforest climbers (stress-tolerator resprouters with extensive root spreads, and possibly clonal), on clay soils in coastal Wollongong and inland western Sydney (Razorback, Cobbitty) and Hunter Valley sites (such as *Cynanchum elegans* at Mt Dangar, Razorback, Shellharbour and *Marsdenia viridiflora* at Razorback) may be remnants of LGM dry scrub vegetation. These are more genetically diverse in southern areas than Indo-Malesian lineages (such as the recent Indo-Malesian migrant *Toona ciliata*) with a recent history of north to south migration (Rossetto et al. 2018) (Figure 21).

Tough, vegetatively spreading but moisture-sensitive ferns such as *Calochlaena dubia*, some *Blechnum*, *Microsorium* and *Asplenium* species. are likely to have survived the LGM with reduced distributions. In Europe, *Asplenium* polyploid complexes can indicate glacial refugia (Vogel et al. 1999). LGM refugia have been shown to be important for South Island New Zealand ferns (Marske and Boyer 2024). The larger long-lived trunked ferns *Dicksonia antarctica*, *Cyathea australis* (considered hardy in cultivations to -6 °C) and *Todea barbara*

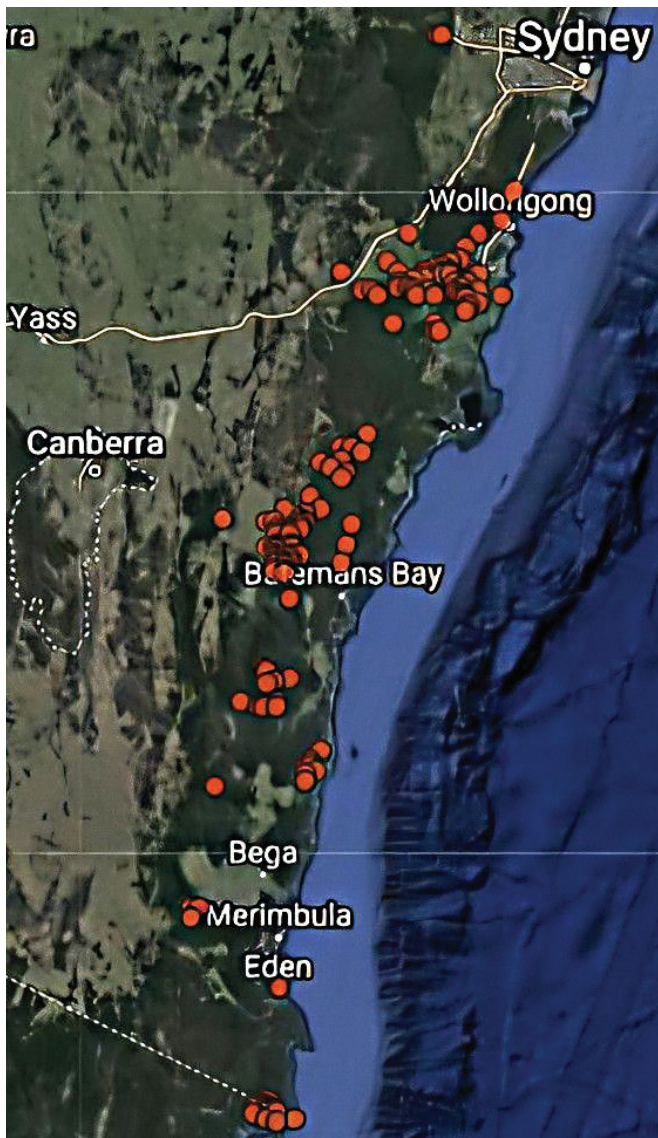


Figure 22. Southern cool temperate tree *Eucryphia moorei* is likely to have survived the LGM in coastal sites such as the Illawarra and extended into warm temperate rainforest subsequently. Is its disjunct record at Springwood west of Sydney a remnant or a chance migrant? (AVH 2022)

have wide distributions in creeks and moist forest in the Blue Mountains and along the Tablelands and coast from Queensland to Tasmania but isolated remnant inland populations including Mt Kaputar (near Narrabri) for *Dicksonia*, Rockley (south of Bathurst) for *Cyathea*, and Mingham Springs (west of Orange) for *Todea* suggest the drier LGM conditions reduced previous wider distributions. Increased Holocene rainfall may have expanded Blue Mountains populations. The Illawarra-Southern Highlands is a particular refugial area with 51% of NSW fern species occurring in the Minnamurra

Rainforest (Mills 2023), with similarities to the North Coast Nightcap-Border Ranges and Dorrigo areas identified as paleo-refugial areas of high genetic diversity (Rossetto et al. 2018), and presumably OCFELs, based on studies on rainforest species in Royal National Park and Barrington Tops, were identified as mostly recolonised areas by Rossetto et al. (2018).

THE CENTRAL TABLELANDS AND GREAT DIVIDING RANGE

Treeless alpine daisy-rich grassland and mallee woodland

On the Tablelands mean winter temperature during the LGM was 8 °C colder than present with subalpine conditions down to 680 m (Barrows et al. 2022). The Great Dividing Range area (Oberon, Bathurst, Bowral, Goulburn, at 650-1100 m elevation) is likely to have experienced, cold (4-7 °C subalpine/alpine conditions (Table 7). South-eastern Australian alpine areas today have mean annual temperatures below 8 °C (Venn et al. 2017).

In contrast to the sandstone Blue Mountains, much of the Tablelands is metamorphic in geology with higher nutrient clay soils than the sedimentary Sydney Basin. Pollen analyses for similar clay landscapes in south-eastern Australia (Lake George and southern Victoria) indicate LGM vegetation of Asteraceae, Chenopodiaceae, Myrtaceae and Poaceae, and has been interpreted variously as xerophytic shrub, heath and woodland, or semi-arid grassland steppe (Pickett et al. 2004; Mooney et al. 2017). Chenopodiaceae is indicative of drier inland winter rainfall areas often on calcareous soils or perhaps local saline areas, and with low occurrence on the Tablelands today may

represent largely wind or dust-storm transported pollen. However, during the LGM, grassy/low shrub vegetation with many current Tablelands perennial grasses and herbs is likely to have occurred across the drier Tablelands, with much of the Bathurst Plains essentially treeless in the 19th century (Semple 1997). This applies also to the grassy clay soil woodlands of western Sydney, where Poaceae and Asteraceae are still well-represented. Fossil Asteraceae pollen appears related to *Cassinia* (Chalson and Martin 2008), relatively short-lived coloniser shrubs in the area today. Of about 200 current Kosciuszko alpine

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(i.e. above the treeline) taxa (Costin et al. 1979) only about 14% (27) also occur in the Sydney area and about half of these occur on relatively dry fertile habitats on the Great Divide (Table 11), consistent with LGM grassy/shrub vegetation observed in pollen studies.

The enhanced effective precipitation resulting from low temperatures, reduced evaporation and snow melt suggested for the LGM at montane elevations on the Northern (Ellerton et al. 2017) and Southern Tablelands (Barrows et al. 2022) is also applicable to the Central Tablelands where similar LGM moisture-dependent swamp and subalpine woodland is likely. The current distribution of small tree/mallee *Eucalyptus stellulata* (Figure 23) (frost hardy to $-14\text{ }^{\circ}\text{C}$) across the Tablelands, together with isolated occurrences on Barrington

Tops, Coolah Tops and New England farther north, coincides with areas of likely LGM subalpine to alpine conditions. The present *Eucalyptus stellulata* ecology and moist frost-hollow habitat suggest its occurrence as part of an extensive LGM Central Tablelands moisture-dependent subalpine mallee woodland. Occurrences of other now restricted, mostly poorly-drained habitat mallee/small trees provide support for this view (*Eucalyptus camphora* subsp. *camphora* (Cudgong and Megalong Valley); *Eucalyptus aggregata* (Bathurst-Wallerawang, Southern Highlands); *Eucalyptus aquatica* (Southern Highlands swamp endemic); and *Eucalyptus macarthurii* (Boyd Plateau, Southern Highlands)). Other LGM mallee woodland species probably included *Eucalyptus dives* current distribution of which probably aligns well with the

extent of LGM alpine woodland on non-sandstone landscapes across south-east Australia) and *Eucalyptus pauciflora* (widespread, cold-tolerant to $-23\text{ }^{\circ}\text{C}$, but low drought tolerance). Highland populations of *Eucalyptus pauciflora* in Tasmania appear to have originated from lowland refugia rather than from *in situ* high-altitude refugia (Gauli et al. 2014).

Some of the Kosciuszko alpine species in the Sydney area are bog or swamp habitat species, consistent with the LGM swampy, gravel floodplain habitat, surrounded by alpine daisy-rich grassland, reported for Southern Tablelands Micalong Swamp at 980 m elevation (Kemp and Hope 2014). Other species likely to be remnants of an LGM mosaic of moist subalpine mallee woodland and montane daisy-rich grassland include cold-tolerant shrubs such as *Grevillea acanthifolia* and *Grevillea juniperina*, with adult growth tolerating temperatures of $-12\text{ }^{\circ}\text{C}$ reported in northwest USA horticulture). Both of these species have a series of allopatric essentially montane subspecies, suggesting a widely distributed taxon in LGM conditions that has subsequently fragmented (Table 12). A further case is seen in the localised endemics *Callistemon megalongensis* and *Callistemon purpurascens* in similar wet habitat in Megalong Valley. None of these species gives the impression of benefitting in the current climate.

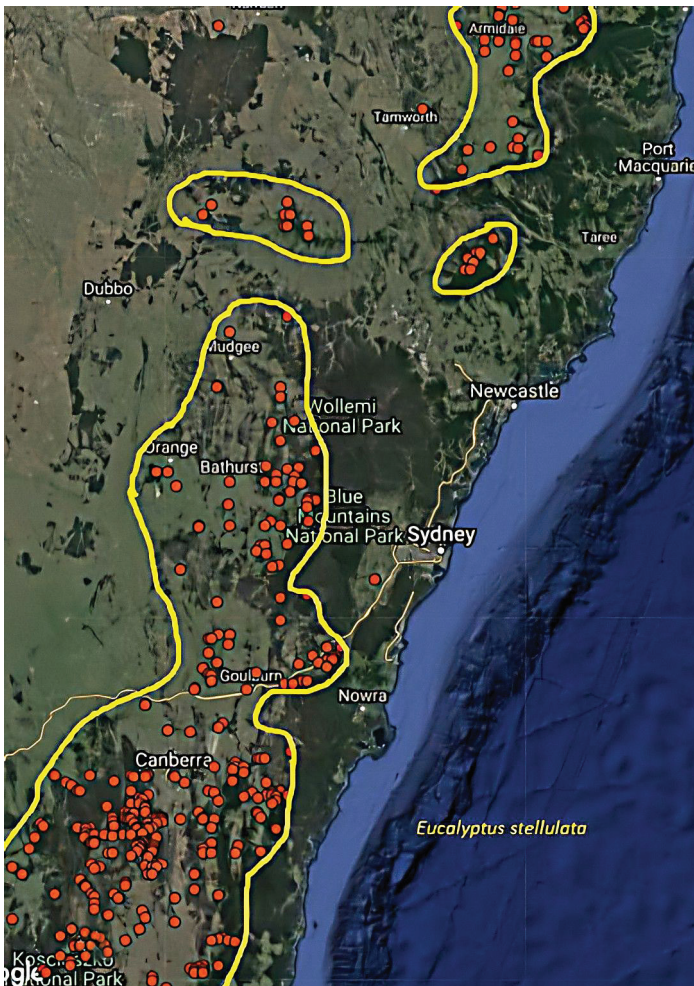


Figure 23. Distributional extent of the small tree/mallee *Eucalyptus stellulata* approximates the area of LGM alpine grassland shrubland along the Great Divide inferred from soil/geomorphology. Now confined to wet sites and frost hollows it is a suggested remnant of such landscape conditions during the LGM. (AVH 2022)

<i>Grevillea</i> taxa	Distribution	Growthform	Habitat
<i>Grevillea acanthifolia</i> subsp. <i>stenomera</i>	NT Tenterfield - Werrikimbe	Low spreading shrub	Heath near streams
subsp. <i>acanthifolia</i>	CT Blue Mtns	shrub	Peatswamps
subsp. <i>paludosa</i>	ST Nalbaugh	Shrub	Sphagnum bogs
<i>Grevillea juniperina</i> subsp. <i>allojohnsonii</i>	NT-NWS	Prostrate shrub	
subsp. <i>juniperina</i>	CC Western Sydney	Shrub	Woodland
subsp. <i>sulphurea</i>	CT western Blue Mtns Coxs R-Tallong	Weakly erect shrub	Streamside or riparian
subsp. <i>trinervis</i>	CT Hampton-Bindo Ck	Spreading low shrub	?Woodland
subsp. <i>villosa</i>	ST Braidwood	Erect shrub	Riparian
subsp. <i>amphitricha</i>	ST Braidwood- Nerriga	Prostrate shrub	Woodland, grassland
subsp. <i>fortis</i>	ACT Molonglo R	Robust shrub	Above permanent watercourses

Table 12. The allopatric subspecies of *Grevillea acanthifolia* and *Grevillea juniperina* are mostly shrubby or prostrate and associated with moist cold sites mainly on the Tablelands, and suggest a widely distributed taxon in LGM conditions, subsequently fragmented. USA horticulture suggests survival in temperatures as low as -12 °C for both species.

WESTERN SYDNEY LANDSCAPES AND THE LGM The fertile landscapes of the Cumberland Plain: LGM Treeless shrubland/grassland vegetation

During the LGM Western Sydney's mean temperature was probably about 11°C, equivalent to today's Upper Blue Mountains (Table 7), and in the rainshadow of the adjacent mountains and farther from the coast, much drier with rainfall of perhaps 300-400 mm p.a. compared with today's 600-800 mm (Figure 14 - Area 6). Such conditions would have been too dry for today's dominant Cumberland Plain trees and shrubs. Based on a 38,000 year Castlereagh pollen core (Chalson and Martin 2008) considered this to have been a treeless LGM shrubland/grassland, similar to the semi-arid grassland steppe reported for the Tablelands and southeastern Australia more broadly (Kershaw et al. 1991). Most pollen identifications are limited to families, such as Poaceae and Cyperaceae. Chalson and Martin (2008) attributed the abundant daisy pollen *Tubuliflorites pleistocenicus* to *Cassinia arcuata* or *Calomeria amaranthoides* but this needs further elucidation. Schmidt-Lebuhn and Constable (2013) include both these species in a narrowly-circumscribed clade with a range of Sydney *Cassinia* species including *Cassinia arcuata*, *C. aculeata*, *C. aureonitens*, *C. cunninghamii*, *C. compacta*, *C. denticulata*, *C. laevis*, *C. longifolia*, *C. quinquefaria* and *C. trinervia*. Many of these species now occur sporadically, and are often rare, across Sydney from coast to montane habitats mainly on medium to higher nutrient soils (basalt shales or shale-enriched sandstone) on disturbed/post-fire sites. Their likely success as colonizing species with some wind dispersal under past conditions of continuous habitat may have been overlooked. The limited 19th century records suggest a greater abundance in the now urban

and western Sydney area, particularly in shale forests, than is evident in the present remnant vegetation.

Pollen core Poaceae could include C₃ perennial grasses (*Dichelachne*, *Elymus*, *Microlaena*, *Poa*) and C₄ perennial grasses (*Aristida*, *Bothriochloa*, *Sorghum*, *Sporobolus*, *Themeda*), all of which occur today in Cumberland Plain Woodland and in Tableland habitats. The herb and geophyte groundcovers in Cumberland Plain Woodland today include many non-woody stress-tolerator/resprouters with persistent rootstocks allowing survival through drought and fire. *Brunoniella australis*, *Eremophila debilis*, *Plantago gaudichaudii*, *Asperula conferta* exhibit ecologies that would have also coped with dry and windy conditions, frosts, ice and slow growth in lower atmospheric CO₂, and they probably benefitted from the absence of tree canopy competition.

Connections with drier Western NSW for clay soil species

Drier periods would have allowed western species to move eastward. Isolated populations of Western tussock grass *Triodia scariosa* in the Capertee Valley (Mt Gundangaroo) suggest eastwards spread in dry LGM conditions, and fragmentation in the following wetter Holocene. The Hunter Valley immediately north, though a barrier to north-south movement for rainforest and sclerophyll flora, provided a low elevation low rainfall corridor between the Western Slopes clay soils and the Newcastle- Cessnock hinterland, allowing medium-nutrient-requiring western species to penetrate eastward. Bell and Driscoll (2016) list 30 western mid layer shrubs and understorey species in the upper Hunter Valley, many of which extend eastwards to the Muswellbrook and Singleton districts including

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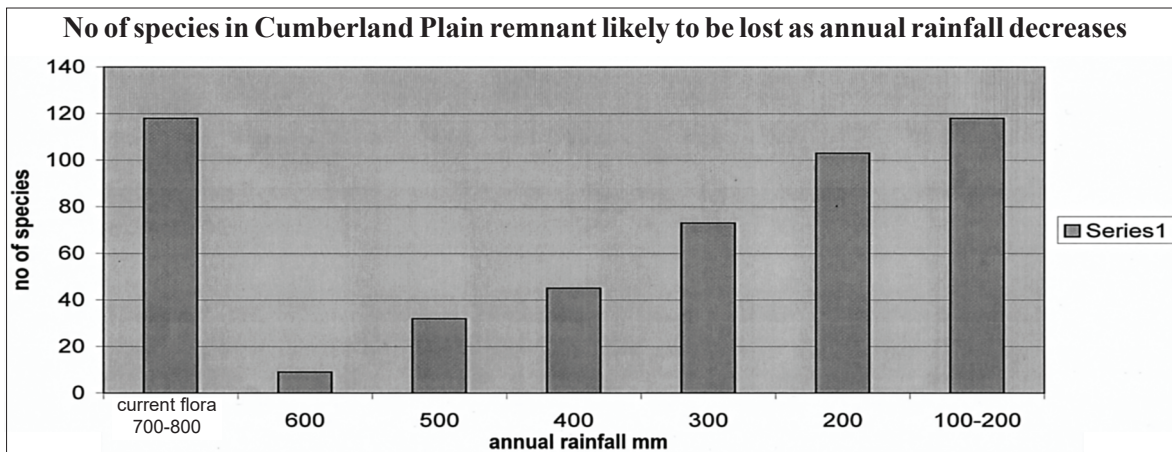


Figure 24. About 40 % (50 species) of the native flora in a Mt Annan Cumberland Plain Woodland site also occur in western areas with rainfall as low as 300 mm pa.

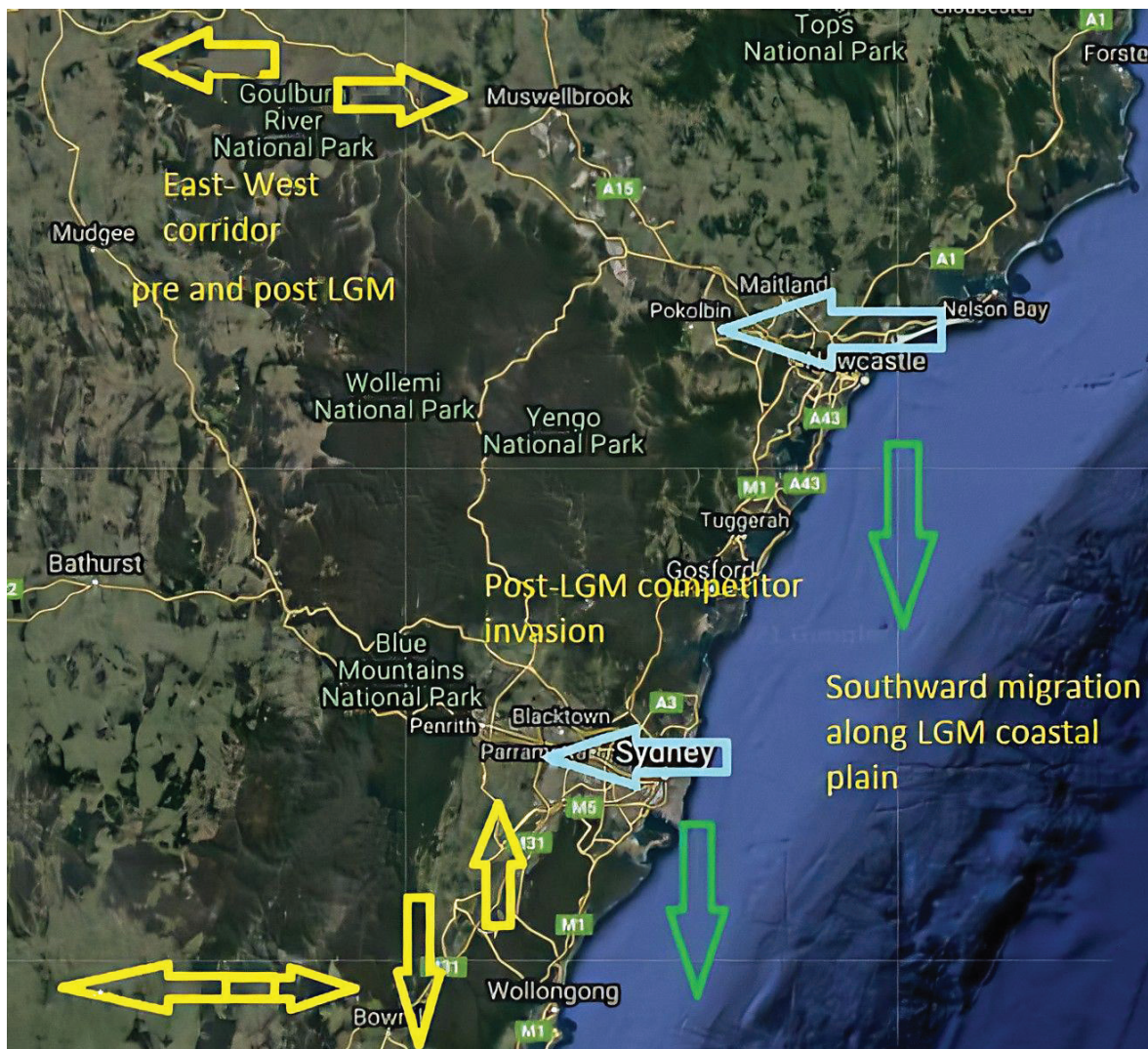


Figure 25. Movement of species on fertile shale basalt corridors (now mostly cleared) in western Sydney and the Hunter; pre and post LGM inland connections (yellow arrows); southward LGM movement along LGM coastal plain (green); and post-LGM coastal invasion of competitor trees and shrubs into Cumberland Plain and Hunter Valley (blue).

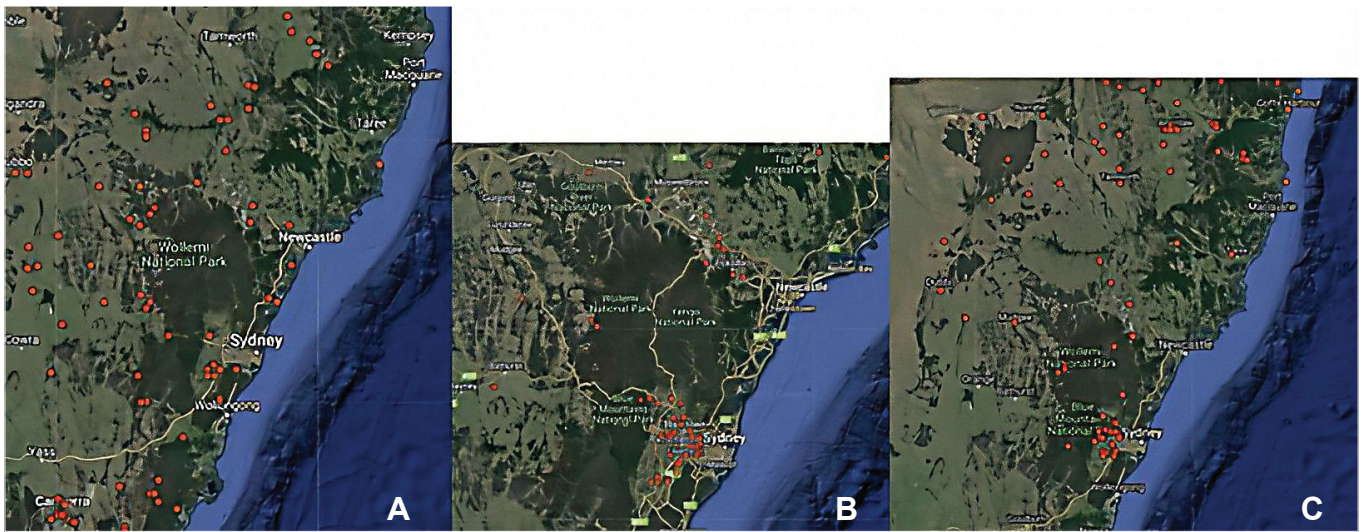


Figure 26. Distributions of Cumberland Plain Woodland groundlayer species A. *Pimelea glauca*; B. *Eremophila debilis*; and C. *Phyllanthus virgatus*, indicate western clay-soil connections through the Southern Highlands (Mittagong, Wombeyan Caves) and Southern and Central Tablelands (Hunter Valley), probably in more extensive grassland during the LGM or previous interglacial; indeed, the severe LGM conditions at the high elevations may have triggered the fragmentation. (AVH 2023)

Eucalyptus camaldulensis, *Allocasuarina luehmannii*, *Allocasuarina verticillata*. The colonising abilities, as well as prolific pollen production of many Casuarinaceae, may explain their abundance in pollen records. Likewise the arid-zone and western *Acacia* species, including *A. aneura*, *A. harpophylla*, *A. melvillei*, *A. homalophylla*, *A. salicina*, and *A. spectabilis*. Remnant populations of some may indicate eastern incursions isolated and outcompeted during subsequent wetter climatic periods.

Many Cumberland Plain groundcover species also occur in the Temperate Montane Grasslands (Keith 2004) and drier Tablelands and Western Slopes (Benson and Howell 2002). A Cumberland Plain Woodland remnant at Mt Annan has about 50 such species (40 %) that also occur in western areas with rainfall as low as 300 mm p.a. (Figure 24). Many Cumberland Plain herbs, grasses and woody shrubs have wind- or animal-dispersed seeds, allowing movement along habitat ‘corridors’ and between ‘islands’ of medium or high nutrient shale, basalt and alluvial soil habitats. Though isolated edaphically by the infertile Blue Mountains sandstone plateaus, western Sydney would have been, and still is, connected through shale soil habitats through the Southern Highlands (Mittagong-Robertson) and Wollondilly-Wombeyan Caves-Taralga areas with the Southern Tablelands and Burratorang-Coxs Valley to the Bathurst plains, areas of grassland habitat during the LGM (Figure 25).

Disjunct distributions of western Sydney ground

layer species suggest previous, mostly now broken, western connections. For example, *Sida corrugata*, *Calotis lappulacea* and *Glossocardia bidens* have widespread western occurrences while *Phyllanthus virgatus* has occurrences connecting with the northwest. *Brunoniella australis*, *Cymbonotus lawsonianus*, *Arthropodium minus* and *Lotus australis* have connections with Coxs River, extending to Kanimbla Valley. The now rare pea *Swainsona monticola* and small Cumberland Plain Woodland shrub *Pimelea glauca* occur at Bathurst. *Zornia dyctiocarpa* has disjunct populations in both the Illawarra and Southern Tablelands and an extensive subtropical - tropical distribution (Figure 26). None of these species occurs on the surrounding sandstone OCBIL landscapes.

The general lack of endemism in the Cumberland shale groundcover flora (particularly in comparison with the Castlereagh Tertiary alluvium flora) suggests relatively recent invasion, and though many species have faunal-assisted seed dispersal, others do not. There are some local endemics including *Grevillea juniperina* subsp. *juniperina*, with its six related subspecies on the Tablelands (Table 12) it has a similar distribution pattern to the groundcover species. In contrast *Pimelea spicata*, a small local endemic herbaceous resprouter, has its main distribution across the Cumberland Plain and a separate isolated population at Shellharbour on the Illawarra coast (Figure 27). Yapp et al. (2019) found little between-population genetic connectivity in *P. spicata* with individuals within

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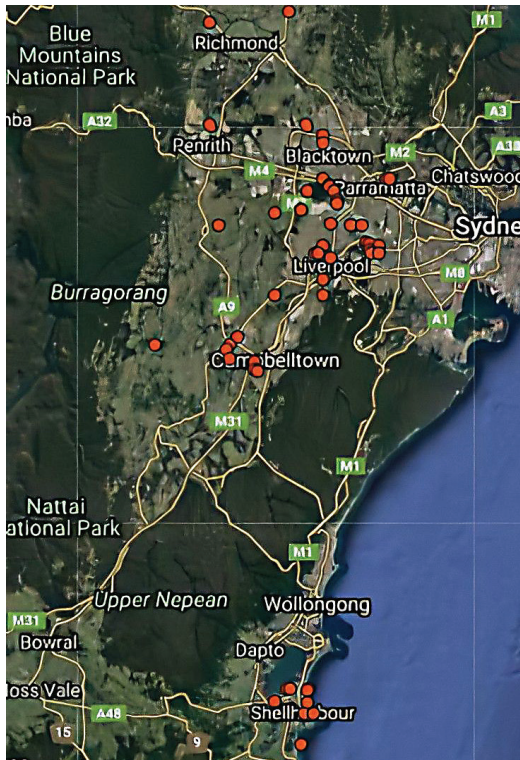


Figure 27. Local endemic *Pimelea spicata* occurs on shale soil across the Cumberland Plain, but surprisingly the most northern occurrences are genetically most similar to the disjunct southern coastal Shellharbour occurrences. Given the coastal position at Shellharbour, a possibility is that during the LGM *Pimelea spicata* also extended eastward from the Hawkesbury across the more mesic shale areas of northern Sydney and onto the coastal plain, with southern extension to the Illawarra. (AVH 2023)

populations similar to each other but differing from those at other sites, findings consistent with relatively long *in situ* presence across Western Sydney. However, surprisingly, they found the most northern occurrences (Freemans Reach and Wilberforce) were genetically most similar to the disjunct southern Shellharbour occurrences, and clearly differentiated from the intervening central Cumberland Plain populations. Given the coastal position at Shellharbour, a possibility suggested by the genetics is that during the LGM *Pimelea spicata* also extended eastward from the Hawkesbury across the more mesic shale areas of northern Sydney and onto the coastal plain on outcropping Narrabeen Group & Permian strata with southern extension to the Illawarra. With increased Holocene warming it may have been outcompeted by increasing Turpentine-Ironbark Forest shading, and isolated at Shellharbour by rising sea level.

The low nutrient sandy clays on the ancient Tertiary alluvials

Tertiary sediments in the Windsor-Castlereagh-Penrith and Milperra-Liverpool-Holsworthy areas, as well as South Maroota, have characteristic vegetation with some localised species. Soils are low-nutrient sandy dispersible clays, sometimes with ironstone gravels. Broadly described as Sydney Sand Flats Dry Sclerophyll Forest and considered unique to the Sydney-Newcastle area (Keith 2004), the vegetation is quite different from the adjacent Wianamatta Shale Cumberland Plain Woodland; there are relatively sharp boundaries and few species in common (Benson 1992). The western area today is the driest part of Sydney,

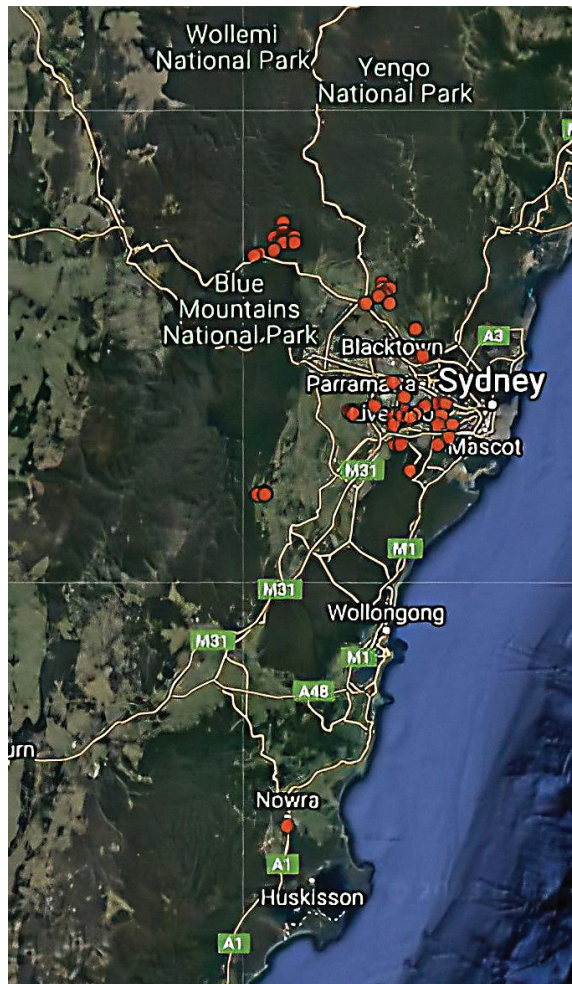


Figure 28. *Acacia pubescens* occurs as scattered root-suckering clusters on low nutrient clays from the lower Blue Mountains to the Georges and Cooks Rivers in the south, and Oakdale northwest of Wollongong, suggesting survivors of previously more extensive populations. A coastal outlier at South Nowra may indicate previous LGM coastal plain connections. (AVH 2022)

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Species	Distrib.	Habitat	Grime/ fire ecology	Likely LGM habitat
<i>Acacia pubescens</i>	west Syd. disj.	Low nutrient clay	ST/Res	LGM open heath or open shrubland
<i>Allocasuarina glareicola</i>	Castlereagh	Low nutrient clay	ST/Res	LGM open heath or open shrubland
<i>Eucalyptus sideroxylon</i>	west Syd. disj.	Low nutrient clay	ST/Res	LGM western invading tree
<i>Micromyrtus minutiflora</i>	Castlereagh area	Low nutrient clay	Rud/ ?Kss	LGM desert ephemeral
<i>Dillwynia tenuifolia</i>	Castlereagh, Maroota, Howes Valley	Low nutrient clay	Rud/ Kss	LGM desert ephemeral
<i>Pultenaea parviflora</i>	Castlereagh area	Low nutrient clay	Rud /Kss	LGM desert ephemeral
<i>Prostanthera scutellarioides</i>	Castlereagh area	Low nutrient clay	Rud /Kss	LGM desert ephemeral
<i>Grevillea juniperina</i> subsp. <i>juniperina</i>	west Syd broad pop	Low nutrient clay	Rud- Comp/ Kss	LGM shrubland
<i>Dodonaea falcata</i>	Castlereagh, Bondi, Howes V. disj.	Low nutrient clay	Rud/ ?K	LGM desert ephemeral
<i>Darwinia biflora</i>	Maroota -Turramurra	shale /ss ironstone	Rud/ Kss	LGM ephemeral

Table 13. Rare or regionally restricted species on Low Nutrient Clay habitats in western Sydney, showing possible LGM occurrence/ecology. All are likely to have declined with warmer wetter conditions and increased competition. Grime categories ST=Stress Tolerant, R=Ruderal; Fire resp. Res= resprouts, Kss=killed, seeder; Regional pop. disj=disjunct pops.

in the rain-shadow of the Blue Mountains and coastal plateaus, with the dryness probably accentuated during the LGM by lower rainfall and increased distance from the coast. The essentially sclerophyll flora includes endemics: a mixture of stress-tolerator/resprouter shrubs and geophytes, consistent with an OCBIL landscape (its elevation of 15-40 m was above the 10 m sea level height at the beginning of the last Interglacial). It also has ruderal/fire-sensitive shrubs, and trees and shrubs with wider western connections.

The stress-tolerant resprouter shrubs include restricted local Castlereagh endemic shrubs *Allocasuarina glareicola* and *Acacia pubescens* (Figure 28) and more regionally widespread *Acacia bynoeana*, *Macrozamia spiralis* and *Xanthorrhoea minor*. All are likely to have coped with the dry LGM conditions and can be interpreted as survivors of previously more extensive LGM open heath or open shrubland (Table 13). Most now occur sporadically in small populations but have strong soil habitat-fidelity for low-nutrient sandy to sandy dispersible clay soils, or somewhat shaly ironstone cappings; these populations are likely to have benefitted from LGM conditions.

The ruderal/fire sensitive obligate-seeder

species include local endemics *Dillwynia tenuifolia*, *Pultenaea parviflora*, *Micromyrtus minutiflora*, *Persoonia nutans* and *Prostanthera scutellarioides*, mostly species with limited seed distance-dispersal (consistent with long term OCBIL site occupation). Some have disturbance-related ecologies involving rainfall events for successful recruitment such as *Micromyrtus minutiflora*, and are able to establish from soil seedbanks without fire (though heat and smoke significantly increase germination) but need open conditions to do so (Bangel et al. 2023). Survival in LGM conditions, especially for obligate-seeder Fabaceae species, could have involved very long seed dormancy periods, alternating with shorter periods as adults, effectively a desert-ephemeral ecology with reduced need for regular rainfall. For *Dillwynia tenuifolia* at least, fruiting success from both cross- and self-pollination events (Rymer et al. 2002) would allow build-up of soil seedbanks, allowing rapid exploitation of disturbed areas. In the drier LGM conditions, with low CO₂ and reduced biomass, a very low fire frequency, perhaps a once per century event might have been enough to reset populations. On the basis of its population genetics Rymer et al. (2002) suggested

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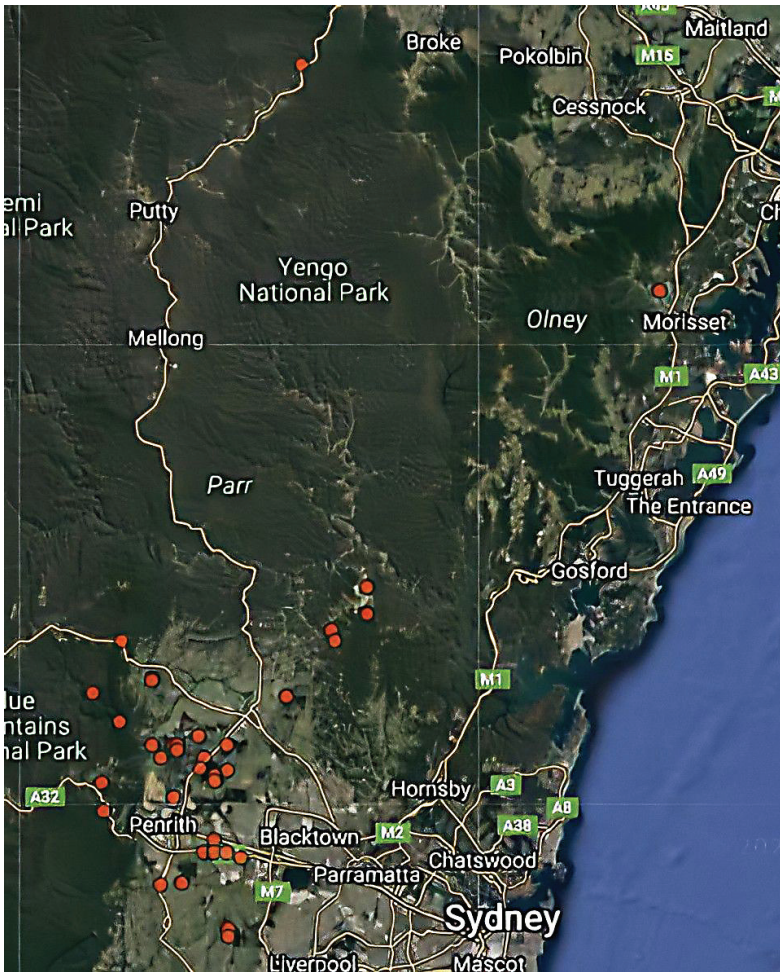


Figure 29. *Dillwynia tenuifolia* is now restricted to particular low nutrient clay habitats but population genetics suggests the species was previously more continuously distributed across its range. (AVH 2023)

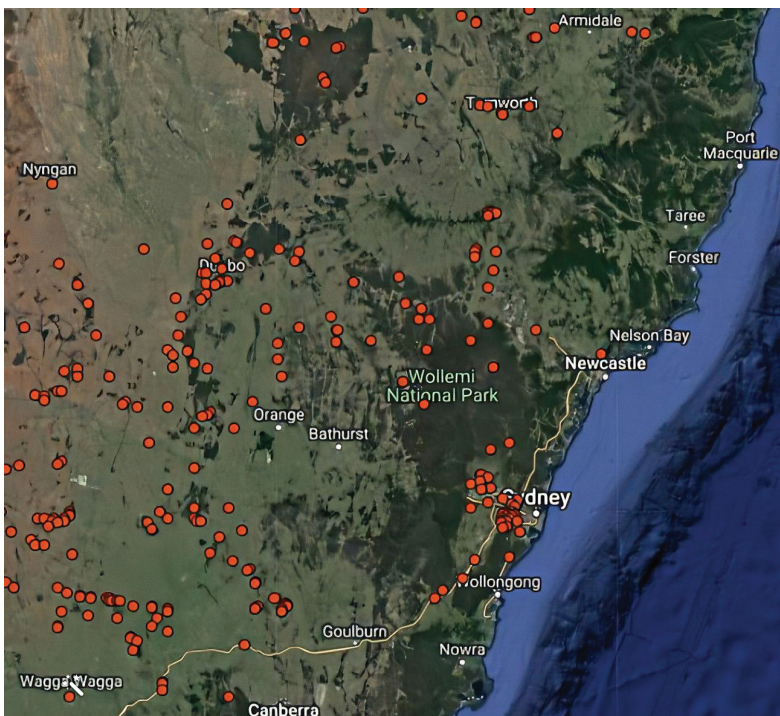


Figure 30. *Eucalyptus sideroxyylon* occurs in drier Western Slopes woodland, in particular Gilgandra (near Dubbo) and Pilliga Scrub (north of Dubbo) (areas with substrate similarities to Castlereagh) and may have moved east into western Sydney in drier LGM or early Holocene conditions. (AVH 2022)

that *Dillwynia tenuifolia* may have formerly been more continuously distributed over its current range (western Sydney, South Maroota, Howes Valley), and subsequently retreated to its current distribution of separate populations (Figure 29). If so, an overall population linking disparate sites (including Kemps Creek, Castlereagh, Marsden Park, South Maroota, and Howes Valley) across the intervening sandstone country, is likely during the LGM or early Holocene climatic conditions. Subsequent retreat on all but low nutrient clay sites, outcompeted by tree canopy and tall shrub growth in warmer wetter conditions is a possibility.

Different histories are likely for the Castlereagh tree species. Eastward invasion in drier LGM or early Holocene conditions may have allowed *Eucalyptus sideroxylon*, *E. fibrosa* and *E. crebra*, which now mainly occur in drier Western Slopes woodlands such as Gilgandra and the Pilliga Scrub (areas with substrate similarities to Castlereagh), to invade western Sydney (Figure 30). *Eucalyptus crebra/beyeriana* pollen is reported from Mountain Lagoon from about 19 000 years BP (Robbie and Martin 2007). These trees and small, also western shrubs (e.g. *Melaleuca diosmatifolia* and *M. thymifolia*) at Castlereagh and in the Coxs-Burraborang-Wollondilly Valleys, Capertee Valley, or associated with the Hunter Valley, indicate availability of more or less continuous clay soil/alluvial habitat passages through the sandstone landscapes. *Eucalyptus fibrosa*, *E. crebra*, *Melaleuca diosmatifolia* and *Angophora bakeri*, for example, occur together on Shoalhaven Group shales in the Kedumba Valley (Keith and Benson 1988).

Eucalyptus parramattensis subsp. *parramattensis* occurs on low elevation Central Western Slopes to the coast (Figure 31) on poorly-drained periodically wet sites with very low nutrient sandy or sandy clay substrates. It occurs in the Goulburn and Capertee River valleys with *Eucalyptus sideroxylon*, *E. crebra* and *E. racemosa*, as it does at Castlereagh, and suggests a previously more widespread distribution, with

perhaps eastward invasion associated with the LGM, when its current drought-sensitivity (Payne et al. 2012) may have been countered by lower LGM precipitation/evaporation conditions.

In contrast to the other Castlereagh woodland trees, *Angophora bakeri* is also common on low rainfall Dharug-Yengo, lower Blue Mountains and western Woronora sandstone as well as the sandy clay sites. Occurrence during the LGM included montane areas - a genomically distinct *Angophora bakeri* mallee population survives in upper Blue Mountains heath (Rutherford et al. 2021).

In summary it is possible that a pre-LGM low open sclerophyll shrub vegetation at Castlereagh included stress-tolerant species with OCBIL origins, as well as obligate-seeder ruderals with more widespread distributions on ironstone cappings and sandy residuals, as at Kemps Creek, Liverpool-Milperra-Birrong areas, Maroota and Mellong – Howes Valley. Invasion by drier western tree and shrub species associated with dry LGM conditions is likely. All are likely to have declined subsequently with warmer wetter conditions and increased competition from coastal species.

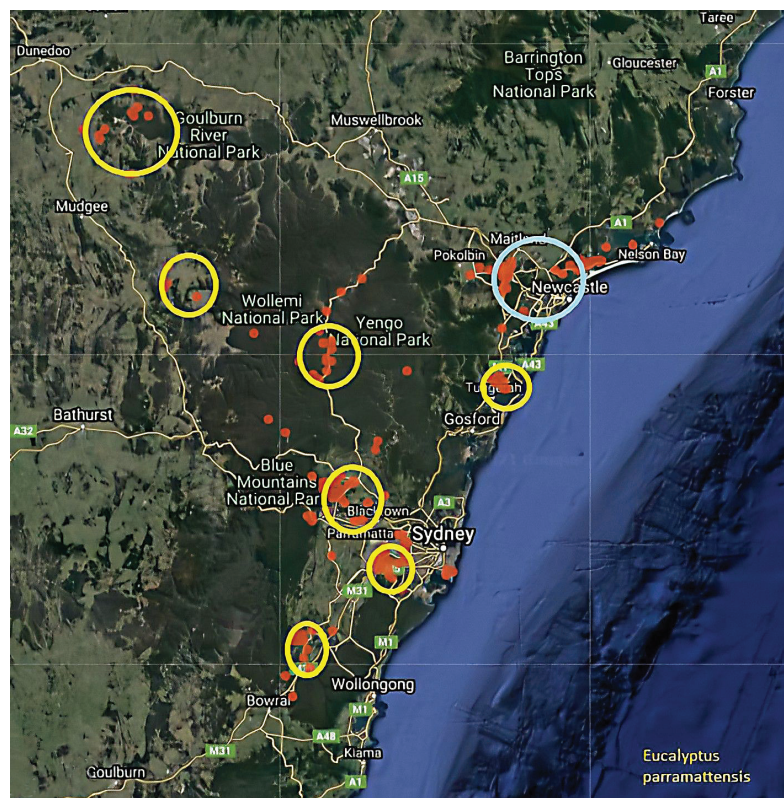


Figure 31. Distribution of disjunct occurrences of *Eucalyptus parramattensis* subsp. *parramattensis*, and subspecies *decadens*, near Newcastle. Now very restricted subspecies *decadens* is likely to have been more extensive on the now-lost LGM coastal plain. (AVH 2022)

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DISCUSSION

This work began as a personal quest for understanding the distribution of rare species and whether an ecological history open to hypothesis testing could be developed. Of necessity this work had been an exercise in conjecture supported by circumstantial evidence and I am surprised at how much has been able to be fitted together to provide a reasonably satisfying account.

Assuming the LGM as the major event

The extreme climatic conditions of 20 000 years ago were not new to the landscape. There had been a series of alternating eight glacial periods in the last 800 000 years (Jouzel et al. 2007) with components of the vegetation presumably responding to each shift by moving up or down climatic gradients. The LGM would have exacerbated the vegetation impacts of the preceding ones and has left the most impressionable impact. Cycles of population expansion, fragmentation and isolation would have already happened for many species as a result of the local extinctions and bottlenecks of earlier glacial cycles. Throughout the work questions of timing, age and rate of species change, arise. Morphological differences are the basis of traditional taxonomic interpretation (species, subspecies, forms etc.) but they do not necessarily pick up more subtle variation developed over periods of 10 000 years.

Though not immediately observable, such patterns may be seen with genetic studies, which will probably lead to a reassessment of some traditional species. Events leaving their imprints on geomorphological features, such as the emergence and submersion of the LGM coastal plain, are pivotal for timing events but have been rarely invoked in relation to species patterns.

A Sydney perspective that can be expanded

This work has been approached from a Sydney region perspective. That similar historical vegetation changes occurred concurrently north and south of Sydney is evident in similar distribution patterns for analogous species on similar geological substrates. For example, botanists have long observed that on the Southern Tablelands, and on the chain of montane islands extending from Sydney to Gippsland (Victoria) (Table 14) including Newnes Plateau/Blue Mountains; Hilltop-Mittagong-Penrose; Nerriga-Budawang; Deua-Wadbilliga; and Bombala-Nalbaugh many relatively rare shrub taxa turn up on sites with similar low-nutrient (OCBIL) (mostly sandstone) landscapes. These sites are generally isolated from each other by hundreds of kilometres (Figure 32). The distance-dispersal characteristics and habitat similarity for many of these species suggest similar histories in response to contemporary climatic cycles as suggested for the Sydney area.

Southern Tableland connections		NP	uBM	Mitt	Nerr	Deua	Bom	SM	Vic
STRESS TOLERATORS									
<i>Eucalyptus stricta</i>	Mallee	x	x	x	x				
<i>Eucalyptus bauerlenii</i>	Mallee		x		x	x			
<i>Boronia deanei</i> - 2 subsp.	Shrub	x		x	x		x		
<i>Genoplesium superbum</i>	geophyte	x			x				
<i>Acacia kybeanensis</i>	shrub	x						x	x
<i>Dillwynia stipulifera</i>	shrub	x			x				
<i>Isopogon prostratus</i>	Prostrate	x		x	x	x	x		x
<i>Mirbelia platyloboides</i>	Prostrate	x		x					
<i>Kunzea cabbagei</i>	Prostrate	x		x					
<i>Phyllota squarrosa</i>	Prostrate	x	x						
<i>Phyllota humifusum</i>	Prostrate			x					
RUDERALS									
<i>Sprengelia incarnata</i>	shrub	x	x	x	x		x		x
<i>Grevillea renwickiana</i>	Prostrate				x				

Table 14. Examples of disjunct species with montane connections between Sydney and Victorian border. NP=Newnes Plateau, Clarence, uBM=Upper BI Mtms, Mitt=Hilltop, Mittagong, Penrose, Nerr=Nerriga, Mongarlow, Budawang, Deua=Deua National Park, Bom=Bombala/ Nalbaugh 1000 m SM=Snowy Mtms, Vic=Victoria

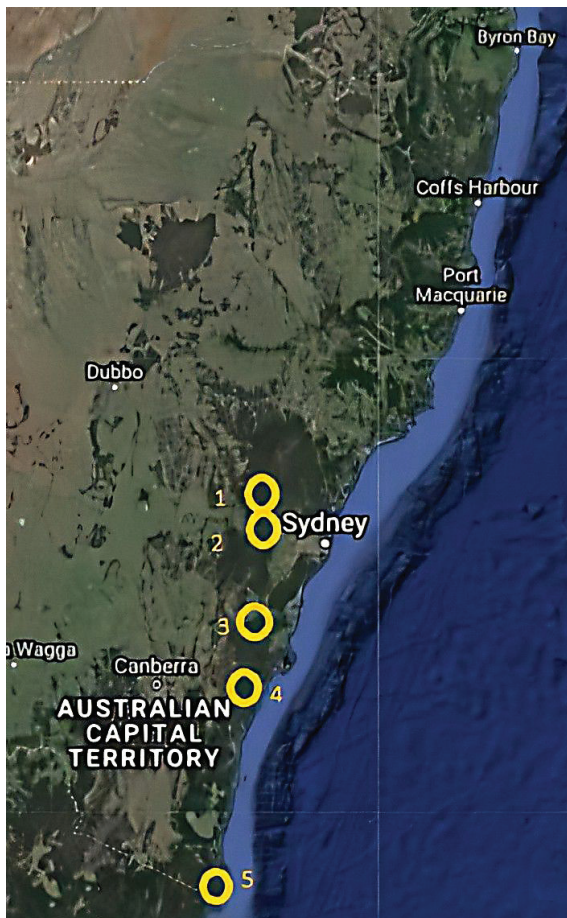


Figure 32. Major disjunct montane sandstone areas in southern NSW. 1 Newnes Plateau; 2 Blue Mountains; 3 Southern Highlands; 4 Nowra-Nerriga; 5 Nadgee.

McDougall et al. (2023) report the isolated Devonian quartzite/sedimentary rock summit of Mt Imlay (886m elevation) near Eden is home to the endemic mallee *Eucalyptus imlayensis*. Two close relatives occur nearby, *Eucalyptus elaeophloia*, only on high-elevation Nunniong Plateau in East Gippsland, and *Eucalyptus baeuerlenii* on the sandstone island chain Deua-Wadbilliga, Nerriga-Budawang and upper Blue Mountains. The restricted distributions of these *Eucalyptus* section Maidenaria series *Viminalis* mallees (Nicolle 2021) parallel the Sydney area section *Eucalyptus* series *Strictae* Green mallees and support the regional significance of mallee eucalypts as glacial era survivors.

To the north of Sydney, substrate limitations (the northern end of Sydney sandstone, the shale/alluvial soils of the Hunter River Valley and Barrington volcanics) are barriers to movement of the sclerophyll shrub flora but coastal connections associated with the LGM coastal plain have allowed southward movement for (animal-dispersed)

mesic species. The coastal sandplain would have also provided a more continuous corridor (now broken) for northward and southward movement of oligotrophic (OCBIL) taxa, allowing connections between the Sydney Basin with the Moreton Basin sandstones around Grafton (the North Coast Dry Sclerophyll Forests of Keith 2004), which have a remarkable number of taxa sister to Sydney sandstone endemics. Connections from there to Gibraltar Range and other leucogranite outcrops (Northern Escarpment Dry Sclerophyll Forests and Northern Montane Heaths of Keith 2004) where sclerophyll endemic taxa with similar OCBIL characteristics to the Sydney sandstones have developed (e.g., Gibraltar Range National Park - Clarke and Myerscough 2006) suggest similar parallel histories with the Sydney area. For example, interesting parallels are evident with related mallees. Gibraltar Range swamp-endemic *Eucalyptus dissita* (section *Eucalyptus* series *Longitudinale* - Nicolle 2021), is a habitat counterpart to the closely related Blue Mountains wet heath *Eucalyptus moorei* subsp. *moorei* (Sheringham et al. 2021). The related *Eucalyptus stellulata* also occurs there but is more widespread. Swamp gum *Eucalyptus camphora* subsp. *relicta* (*Eucalyptus* subgenus *Symphyomyrtus* section *Maidenaria*; counterpart of southern *Eucalyptus camphora* subsp. *camphora*) is associated with closed wet heaths and *Sphagnum* Bogs in Warra National Park.

Phylogenetic analyses of northern species of series *Strictae* mallee ashes (Rutherford et al. 2015) placed three northern NSW species *Eucalyptus approximans*, *E. codonocarpa* and *E. microcodon*, Sydney region *Eucalyptus cunninghamii*, and southern NSW-Victoria border species *Eucalyptus kybeanensis* and *E. paliformis* in a single clade, though the northern, Sydney and southern species are in isolated patches at least 300-400 km apart geographically. Rutherford (2020) suggested vicariance (speciation following population isolation) as an explanation. These distributions indicate past vegetation histories for Southern and Northern Tablelands low-nutrient montane landscapes paralleling the Sydney area; a bigger picture incorporating both needs to be developed.

Remnant LGM sites and in situ conservation

Interesting sites with concentrations of likely LGM refugial species are recognisable (Table 15). Some are already recognised for their endemic flora, though their conservation significance as evidence of vegetation history has not been previously identified.

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Landscapes with LGM remnants	Examples	Example species	Vulnerability issues
Moist sandstone Clifflines OCBIL	Upper Blue Mtns Fire refugia	<i>Ptherosphaera fitzgeraldii</i>	increased warming and fire, weeds
Sandstone mesas, ridgetops, mallee heath OCBIL	Newnes Plateau; Genowlan Point heath (Capertee Valley) (NSW Scientific committee)	<i>Pultenaea praecipua</i> <i>Isopogon prostratus</i>	Competition from canopy shading
Ridgetops with clay residuals and/or remnant ironstone cappings OCBIL	Mangrove Mtn, Warrah trig, Duffys Forest, Maroota, Menai, Heathcote, Waterfall	<i>Grevillea caleyi</i>	Small, fragmented areas
Widespread sandstone plateau woodland OCBIL	Long lived resprouter shrubs often widespread	<i>Allocasuarina nana</i> , <i>Lambertia formosa</i>	Recruitment limitations with frequent fire
Pleistocene leached sand sites Remnants of the LGM Coastal plain flora	Redhead, Munmorah Bouddi North Head la Perouse, Agnes Banks, Kurri Kurri sand swamp WL	<i>Banksia aemula</i>	Small, fragmented areas
Coastal Themeda grassy headland, OCFEL	Low nutrient clays	<i>Themeda triandra</i> , <i>Allocasuarina verticillata</i>	Small, fragmented areas
Low nutrient sandy clay vegetation, Tertiary alluvium, OCBIL	Castlereagh, Windsor Penrith, Milperra; Kurri sand swamp woodland	<i>Micromyrtus minutiflora</i> , <i>Allocasuarina glareicola</i>	Small, fragmented areas
Western Sydney Cumberland Plain Woodland Medium nutrient shale OCFEL	groundcover species, often with vegetative spread	<i>Pimelea spicata</i> , <i>Brunoniella australis</i> geophytes	Lack of recognition, small size
Mallee swamp woodland, OCFEL	Western BI Mtns, Penrose	<i>Eucalyptus camphora</i> , <i>E. stellulata</i> , <i>E. aquatica</i>	Small size
Western BI Mtns Medium nutrient clays, OCFEL	Box woodland Basalt caps and diatremes	<i>Triodia scariosa</i> , groundcover species	Small, fragmented areas
Dry country shale and volcanics with Dry rainforest and vine thicket, corridor remnants, OCFEL	Native Vineyard Cobbitty Hunter valley remnants	Long-lived vines, <i>Cynanchum elegans</i>	Small, fragmented areas Weed infested

Table 15. Landscapes with likely concentrations of remnant or persistent species suggesting Last Glacial Maximum *in situ* occurrence. All occur as small fragmented areas.

Most are OCBILs, sandstone or low-nutrient clay sites, but others are parts of more fertile shale OCFEL landscapes (Wianamatta and Permian Shales) with assemblages including long-resident faithful species (as well as including trees and shrub invaders). Though these sites do not show the extent of local endemism evident on the sandstone OCBILs, probably because the main families (Asteraceae, Poaceae) have much better propagule dispersal, the groundcover flora includes many species with extensive root suckering or rhizomes (such as *Brunoniella australis*) consistent with very long association with sites.

The continued occurrence of rare species in their natural wild sites has significant scientific and heritage value for understanding historical landscape changes. Ex-situ conservation (seedbanks, etc.) is being increasingly developed for many localised or restricted species, but it is important to recognise *in-situ* conservation measures are necessary to retain the biogeographical significance

of species/site associations. The recognition and continuing association of other species with particular sites is important as associated taxa such as invertebrates and fungi may be similarly restricted and relict (Moir et al. 2011).

Conservation responses for out of climate phase species

The recognition that vegetation communities may include clusters of species with different histories has implications for conservation assessment and management. Low-nutrient OCBIL landscapes that have remained stable and vegetated for very long periods may include faithful species that have evolved in association with the site though past periods of major climatic change. Actual species behaviour under different past climates is unknown, especially where there are no analogous climatic sites today. Such species may not necessarily have characteristics associated with current ecological health indicators, such as large seedsets,

vigorous seedling recruitment or high genetic diversity. They may, however, retain abilities for coping with cold or drought beyond necessary requirements today. Species that have coped with LGM conditions may retain considerable resilience, not necessarily evident from their narrow remnant sites. In relatively stable but limited habitats, such as ridges and mountain tops, survival may be through attributes such as continued underground vegetative expansion (essentially continuous lignotuber expansion, or localised spread via root-suckering, e.g. *Banksia paludosa* (Baird and Benson 2022)). These may allow species to persist during periods when seedset or recruitment conditions are unfavourable, and presumably evolve new forms and ecologies if reproduction recommences. Many of these species such as mallees may be very long-lived, perhaps thousands of years.

Successful seed production is often an important conservation management measure for Endangered Species Recovery plans, but seed production may be difficult to achieve in many naturally restricted species that may be clonal or partly clonal. Pressure to intrude genetically by translocation of individuals from other sites may introduce pathogens and do little genetically for populations of long-lived plants that have survived past changes despite restricted propagule production, provided these natural populations remain undisturbed.

As well as the restricted (mostly listed as rare or endangered) slow-growing woody shrub resprouters species, postulated as likely relics, there are others with widespread occurrence and longevity which appear to be almost indestructible (e.g. *Allocasuarina nana* - Pannell and Myerscough 1993), though the recent fire seasons particularly the 2019/2020 drought/fire season have shown their vulnerability in terms of both death and failed recruitment (demonstrated with *Banksia spinulosa* (Whelan and Ayre 2022), *Xanthorrhoea resinosa* (Tozer and Keith 2012) and *Gymnoschoenus sphaerocephalus* (pers. obs.). Ecological factors may also be endangering in non-drought years, such as competitive overshadowing of heath and swamp vegetation, or grazing and browsing of small woody shrubs by feral animals, including new threats from goats and deer. Protection of any occasional seedling recruitment cohorts may be of primary importance.

Plant species distributions and ecological implications can provide testable hypotheses for exploring past vegetation patterns with genetic and growth studies. Ecological studies on temperature responses, competition for light and water, and relationships with seasonality, growth and aging may provide further insights. Further work, particularly

genomic studies interpreted in historical contexts, and long-term field studies, is needed. In practice, different species are likely to have had more complex, and much longer histories than the relatively simple story postulated here.

Finally, this project raises a host of questions relating to other elements of the LGM biodiversity, especially the biota intimately connected with plants, for example specialized insect-pollinator relations as with orchids, and with mycorrhizal and other fungi. Are these all subsequent blow-ins or survivalists? Where were vertebrates and invertebrates (particularly those sensitive to temperature) during the LGM?

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REFERENCES

- Adam, P. (1990) Saltmarsh Ecology. Cambridge University Press, Cambridge.
- Albani A. D., Rickwood P. C., Quilty P. G. and Tayton J. W. (2015) The morphology and late Quaternary paleogeomorphology of the continental shelf off Sydney, NSW. *Australian Journal of Earth Sciences* 62:6, 681-694, DOI: 10.1080/08120099.2015.1095242
- Attenbrow, V. (2002) *Sydney's Aboriginal past: investigating the archaeological and historical records*. University of NSW Press.
- Auld, T.D. (1996) Ecology of the Fabaceae in the Sydney region: fire, ants and the soil seedbank. *Cunninghamia* 4, 531-551.
- Auld, T.D. (2001) The ecology of the Rutaceae in the Sydney region of south-eastern Australia: Poorly-known ecology of a neglected family. *Cunninghamia* 7(2), 213-239.
- AVH Australasian Virtual Herbarium <https://avh.chah.org.au>
- Baird, I.R.C. and Benson, D. (2022). Root-suckering and clonality in a Blue Mountains *Banksia* taxon (Proteaceae). *Proceedings of the Linnean Society of New South Wales* 144, 109-127.

LAST GLACIAL MAXIMUM VEGETATION SYDNEY BASIN

- Bangel, T., Hewitt, A., Morris, E.C. and Haigh, A.M. (2023) Factors influencing the germination, establishment and distribution of *Micromyrtus minutiflora* (Myrtaceae), in western Sydney, New South Wales. *Australian Journal of Botany* **71**, 12–27. doi:10.1071/BT22058
- Barrows, T.T., Mills, S.C., Fitzsimmons, K., Wasson, R. and Galloway, R. (2022). Low-altitude periglacial activity in southeastern Australia during the late Pleistocene. *Quaternary Research* **107**, 125-146.
- Bell, S.A.J. (2022) Differing habitat defines two metapopulations of a threatened Hunter Valley eucalypt: *Eucalyptus parramattensis* subsp. *decadens*. *Cunninghamia* **22**, 11-25.
- Bell, S. and Driscoll, C. (2016) Hunter Valley Weeping Myall Woodland – is it really definable and defendable with and without Weeping Myall (*Acacia pendula*)? *Cunninghamia* **16**, 15-30.
- Bell, S. A. J. and Nicolle, D. (2020) Glen Gallic Mallee (*Eucalyptus dealbata* subsp. *aperticola*, Myrtaceae), a new taxon from the sandstone escarpment of the Hunter Valley, New South Wales. *Telopea* **23**, 141-150.
- Benson, D. (1981) Vegetation of the Agnes Banks sand deposit, Richmond, New South Wales. *Cunninghamia* **1**(1), 35-54.
- Benson, D. (1992) The natural vegetation of the Penrith 1: 100 000 map sheet. *Cunninghamia* **2**, 541–596.
- Benson, D. and Eldershaw, G. (2007) Background to encounter: the 1770 landscape of Botany Bay, the plants collected by Banks and Solander and rehabilitation of natural vegetation at Kurnell. *Cunninghamia* **10**, 113-137.
- Benson, D. and Howell, J. (2002). Cumberland Plain Woodland ecology then and now: interpretations and implications from the work of Robert Brown and others. *Cunninghamia* **7**, 631-650.
- Benson, D.H. and McDougall, L. (1993) Ecology of Sydney plant species part 1: Ferns, fern-allies, cycads, conifers and dicotyledon families Acanthaceae to Asclepiadaceae. *Cunninghamia* **3**, 257– 422.
- Benson, D.H. and McDougall, L. (1994) Ecology of Sydney plant species part 2, dicotyledon families Asteraceae to Buddlejaceae. *Cunninghamia* **3**, 789–1004.
- Benson, D.H. and McDougall, L. (1995) Ecology of Sydney plant species part 3, dicotyledon families Cabombaceae to Eupomatiaceae. *Cunninghamia* **4**, 217–431.
- Benson, D.H. and McDougall, L. (1996) Ecology of Sydney plant species part 4, dicotyledon family Fabaceae. *Cunninghamia* **4**, 553–752.
- Benson, D.H. and McDougall, L. (1997) Ecology of Sydney plant species part 5, dicotyledon families Flacourtiaceae to Myrsinaceae. *Cunninghamia* **5**, 330–544.
- Benson, D.H. and McDougall, L. (1998) Ecology of Sydney plant species part 6: dicotyledon family Myrtaceae. *Cunninghamia* **5**, 808–987.
- Benson, D.H. and McDougall, L. (1999) Ecology of Sydney plant species part 7a: dicotyledon families Nyctaginaceae to Primulaceae. *Cunninghamia* **6**, 402–509.
- Benson, D.H. and McDougall, L. (2000) Ecology of Sydney plant species part 7b: dicotyledon families Proteaceae to Rubiaceae. *Cunninghamia* **6**, 1017–1202.
- Benson, D.H. and McDougall, L. (2001) Ecology of Sydney plant species part 8: dicotyledon families Rutaceae to Zygophyllaceae. *Cunninghamia* **7**, 241–462.
- Benson, D.H. and McDougall, L. (2002) Ecology of Sydney plant species part 9: monocotyledon families Agavaceae to Juncaginaceae. *Cunninghamia* **7**, 695–930.
- Benson, D.H. and McDougall, L. (2005) Ecology of Sydney plant species part 10 Monocotyledon families Lemnaceae to Zosteraceae *Cunninghamia* **9**, 16–212.
- Benson, D. and von Richter, L. (2010) Recent ecological observations on growth rates and seed production in *Isopogon prostratus* (Proteaceae), a little-known prostrate shrub from south-eastern NSW and Victoria. *Cunninghamia* **11**, 283-286.
- Benson, J. and Allen, C. (2007) Vegetation associated with *Wollemia nobilis* (Araucariaceae). *Cunninghamia* **10**, 255-262.
- Berg, R.Y. (1975) Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* **23**, 475–508.
- Bernhardt, P., Camilo, G.R. and Weston, P.H., (2019) Shaken vs scraped: floral presentation contributes to pollinator guild segregation in co-blooming *Symphionema montanum* and *Isopogon anemonifolius* (Proteaceae). *The Garden's Bulletin Singapore* **71**, 377-396.
- Binney, H, Edwards, M, Macias-Fauria, M, Lozhkin, A, Anderson, P Kaplan, JO, Andreev, A, Bezrukova, E, Blyakharchuk, T, Jankovska, V, Khazina, I, Krivonogov, S, Kremenetski, K, Nield, Ja, Novenko, E, Ryabogina, N, Solovieva, N., Willis, K. and Zernitskaya, V. (2017) Vegetation of Eurasia from the last glacial maximum to present: Key biogeographic patterns. *Quaternary Science Reviews* **157**, 80-97.
- Black M.P., Mooney, S. and Attenbrow, V. (2008) Implications of a 14 200 year contiguous fire record for understanding human—climate relationships at Goochs Swamp, New South Wales, Australia. *The Holocene* **18**, 437-447.
- Bond, W.J. (1988) Proteas as ‘tumbleseeds’: wind dispersal through the air and over soil. *South African Journal of Botany* **54**, 455-460.
- Boon, P.I. et al. (2015) Coastal wetlands of Victoria, south-eastern Australia: providing the inventory and condition information needed for their effective management and conservation. *Aquatic Conservation: Freshwater and Marine Ecosystems* **25**, 454-479.
- Booth, T.H. (2017) Going nowhere fast: a review of seed dispersal in eucalypts *Australian Journal of Botany* **65**, 401-410. <https://doi.org/10.1071/BT17019>

- Briggs, B.G. (1964) The control of interspecific hybridisation in *Darwinia*. *Evolution* **18**, 292-308.
- Bryceson, S.R., Hemming, K.T., Duncan, R.P. and Morgan, J.W. (2023). The contemporary distribution of grasses in Australia: A process of immigration, dispersal and shifting dominance. *Journal of Biogeography* **50**, 1639–1652.
- Cabbage, R.H. (1905) Notes on the native flora of New South Wales. Part IV. The occurrence of *Casuarina stricta* Ait., on the Narrabeen shales. *Proceedings of the Linnean Society of NSW* **30**, 376-391.
- Caine, N. and Jennings, J.N. (1968) Some blockstreams of the Toolong Range Kosciusko State Park, New South Wales. *Journal and Proceedings of the Royal Society of NSW* **101**, 93-103.
- Chalson, J.M. and Martin, H.A. (1995) The pollen morphology of some co-occurring species of the family Myrtaceae from the Sydney Region. *Proceedings of the Linnean Society of NSW* **115**, 163-191.
- Chalson, J.M. and Martin, H.A. (2008) A 38,000 year history of the vegetation at Penrith Lakes, New South Wales. *Proceedings of the Linnean Society of NSW* **129**, 97-111.
- Clarke, P. J. & Myerscough, P. J. (2006) Introduction to the biology and ecology of Gibraltar Range National Park and adjacent areas: patterns, processes and prospects. *Proceedings of the Linnean Society of NSW* **127**, 1-3.
- Coleby, D. (2006) The natural distribution and ecology of *Blandfordia cunninghamii* (Blandfordiaceae). *Cunninghamia* **9**, 537-544.
- Coleby, D. and Druitt, R. (2020). Observations on average trunk diameters of *Eucalyptus cunninghamii* (Myrtaceae) in relation to elemental concentrations of their substrates. *Proceedings of the Linnean Society of New South Wales* **142**, 45-48.
- Coleby, D. and Druitt, R. (2021) Distribution, ecology, and morphology of the rare mallee *Eucalyptus cunninghamii* (Myrtaceae), Blue Mountains, New South Wales. *Cunninghamia* **21**, 1– 10.
- Colhoun, E. (2000) Vegetation and climate change during the Last Interglacial-Glacial cycle in western Tasmania, Australia. *Palaeogeography Palaeoclimatology Palaeoecology* **155**(1), 195-209.
- Colhoun, E.A. and Shimeld, P.W. (2012). Late-Quaternary vegetation history of Tasmania from pollen records. In: Haberle, S.G., David, B. (Eds.), *Peopled Landscapes: Archaeological and Biogeographic Approaches to Landscapes*. *Terra Australis* **34**. The Australian National University, Canberra, pp. 297-328.
- Costin, A.B., Gray, M., Totterdell, C.J. and Wimbush, D.J. (1979) *Kosciusko Alpine Flora*. CSIRO/ Collins: Australia.
- Commonwealth Department of the Environment (2015) *Conservation Advice, Eucalyptus recurva* Mongarlowe mallee. Canberra. <http://www.environment.gov.au/biodiversity/threatened/species/pubs/11004-conservation-advice.pdf>.
- Das, S.K., Baumgartner, J.B. and Beaumont, L.J. (2019) Identifying climate refugia for 30 Australian rainforest plant species, from the last glacial maximum to 2070. *Landscape Ecology* 2019 DOI:10.1007/s10980-019-00924-6
- De Deckker, P., Moros, M., Perner, K., Blanz, T., Wacker, L., Schneider, R., Barrows, T.T., O’Loingsigh, T. and Jansen, E. (2020). Climatic evolution in the Australian region over the last 94 cal ka BP - spanning human occupancy -- and unveiling the Last Glacial Maximum. *Quaternary Science Reviews* **249**, 106593. <https://doi.org/10.1016/j.quascirev.2020.106593>.
- Ellerton, D., Shulmeister, J., Woodward, C. and Moss, P. (2017) Last Glacial Maximum and Last Glacial–Interglacial Transition pollen record from northern NSW, Australia: evidence for a humid late Last Glacial Maximum and dry deglaciation in parts of eastern Australia. *Special Issue Article*, School of Geography, Planning and Environmental Management, University of Queensland. doi:10.1002/jqs.2960
- Gauli, A., Steane, D.A., Vaillancourt, R.E. and Potts, B.M. (2014). Molecular genetic diversity and population structure in *Eucalyptus pauciflora* subsp. *pauciflora* (Myrtaceae) on the island of Tasmania. *Australian Journal of Botany* **62**, 175-188.
- Gill, A.M. (1981) Adaptive responses of Australian vascular plant species to fires. In *Fire and the Australian Biota*. Ed. A.M. Gill, R.H. Groves and I.R. Noble. Australian Academy of Science: Canberra, pp. 243-271.
- Grime, J.P. (2006) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd Edition. (Wiley).
- Grime, J.P. and Pierce S. (2012) *The Evolutionary Strategies that Shape Ecosystems*. Wiley-Blackwell, Chichester.
- Hager, T. and Benson, D. (2010) The eucalypts of Greater Blue Mountains World Heritage Area: distribution, classification and habitats of the species of *Eucalyptus*, *Angophora* and *Corymbia* (family Myrtaceae) recorded in its eight conservation reserves. *Cunninghamia* **11**, 425-444.
- Hesse, P. P., Humphreys, G. S., Selkirk, P. M., Adamson, D. A., Gore, D. B., Nobes, D. C., Price, D. M., Schwenninger, J. L., Smith, B., Tulau, M. and Hemmings, F. (2003) Late Quaternary aeolian dunes on the presently humid Blue Mountains, Eastern Australia. *Quaternary International* **108**, 13-32.
- Hesse, P. P., Williams, R., Ralph, T. J., Fryirs, K. A., Larkin, Z. T., Westaway, K. E., and Farebrother, W. (2018). Palaeohydrology of lowland rivers in the Murray-Darling basin, Australia. *Quaternary Science Reviews* **200**, 85–105. <https://doi.org/10.1016/j.quascirev.2018.09.035>
- Hope, G. (2010) Fire histories from charcoal and palaeoecology in sedge and shrub bogs. *Proceedings of the 2007 Buttongrass Moorland Management Workshop* pp. 36-41. Nature Conservation Report 2010/4. Department of Primary Industries, Parks, Water and Environment, Hobart, Tasmania.

LAST GLACIAL MAXIMUM VEGETATION SYDNEY BASIN

- Hopper, S.D. (2021) Out of the OCBILs: new hypotheses for the evolution, ecology and conservation of the eucalypts. *Biological Journal of the Linnean Society* **20**, 1–31.
- Hopper S.D., Lambers H, Fiedler P.L. & Silviera FAO. (2021). OCBILtheory examined: reassessing evolution, ecology, and conservation in the world's ancient, climatically-buffered and infertile landscapes. *Biological Journal of the Linnean Society* **133**, 266-296.
- Hoser, R.T. (2020) From a putative new taxon to a mutt! Formal descriptions of three new genetically divergent Mountain Pygmy Possums from Victoria and New South Wales closely associated with *Burrumys parvus* Broom, 1896. *Australasian Journal of Herpetology* **42**, 3-10.
- Hunter, J.T. (2016) Monitoring of *Pultenaea maritima* Technical Report for Saving Our Species DOI: 10.13140/RG.2.2.35144.11520
- James, E. A. and McDougall, K.L. (2014) Spatial genetic structure reflects extensive clonality, low genotypic diversity and habitat fragmentation in *Grevillea renwickiana* (Proteaceae), a rare, sterile shrub from south-eastern Australia. *Annals of Botany* **114**, 413-23. doi: 10.1093/aob/mcu049
- Johnson, K.A. and McQuillan, P.B. (2011). Comparative floral presentation and bee-pollination in two *Sprengelia* species (Ericaceae). *Cunninghamia* **12**, 45-51.
- Johnstone, R.D., and Lacey, C.J. (1983) Multi-stemmed trees in rainforest. *Australian Journal of Botany* **31**, 189-195.
- Jones, W.G., Hill, K.D. and Allen, J.M. (1995) *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. *Telopea* **6**, 173–176
- Jouzel, J., Masson-Delmotte, V., Cattani, O., Dreyfus, G. and 28 others (2007). Orbital and Millennial Antarctic Climate Variability over the past 800,000 Years. *Science* **317**, 793-796.
- Kearns, A.M., Joseph, L., Toon, A. and Cook, L.G. (2014) Australia's arid-adapted butcherbirds experienced range expansions during Pleistocene glacial Maxima. *Nature Communications* DOI: 10.1038/ncomms4994
- Keith, D. (2004) *Ocean Shores to Desert Dunes: the native vegetation of NSW and the ACT*. NSW Dept of Environment and Conservation, Hurstville NSW.
- Keith, D. (2011) Relationships between geodiversity and vegetation in south-eastern Australia. *Proceedings of the Linnean Society of NSW* **132**, 5-26.
- Keith, D.A. and Benson, D.H. (1988) The natural vegetation of the Katoomba 1:100 000 map sheet. *Cunninghamia* **2**, 107-143.
- Keith, D.A., Holman, L., Rodoreda, S., Lemmon, J. and Bedward, M. (2007) Plant functional types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology* **95**, 1324-1337.
- Kemp, J. and Hope, G. (2014) Vegetation and environments since the Last Glacial Maximum in the Southern Tablelands, New South Wales *Journal of Quaternary Science* **29**, 778–788.
- Keith, D.A. and Tozer, M.G. (2012) Vegetation dynamics in coastal heathlands of the Sydney basin. *Proceedings of the Linnean Society of New South Wales* **134**, 181-197).
- Kennington, W.J. and James, S.H. (1997) Contrasting patterns of clonality in two closely related mallee species from Western Australia, *Eucalyptus argutifolia* and *E. obtusiflora* (Myrtaceae) *Australian Journal of Botany* **45**, 679–689.
- Kershaw, A.P., D'Costa, D.M., Mason, J.M. and Wagstaff, B.E. (1991). Palynological evidence for Quaternary vegetation and environments of mainland southeastern Australia. *Quaternary Science Reviews* **10**, 391-404.
- Kireta, D., Christmas, M.J., Lowe, A.J. and Breed, M.F. (2019) Disentangling the evolutionary history of three related shrub species using genome wide molecular markers. *Conservation Genetics* doi.org/10.1007/s10592-019-01197-x
- Kolesik, P., Butterworth N., Lemmon, J., Gibson, T. and Wallman, J.F. (2019) First gall midge (Diptera: Cecidomyiidae) known to feed on plant family Atherospermataceae: a new species of *Asphondylia* damaging the endangered Australian tree *Daphnandra johnsonii*. *Austral Entomology* **58**, 317–323.
- Kunin, W.E. and Gaston, K.J. eds., (2012). *The biology of rarity: causes and consequences of rare—common differences* (Vol. 17). Springer Science & Business Media.
- Lamb, A. M., da Silva, A.G., Joseph, L., Sunnucks, P. and Pavlova, A. (2019) Pleistocene-dated biogeographic barriers drove divergence within the Australo-Papuan region in a sex-specific manner: an example in a widespread Australian songbird. *Heredity* **123**, 608–621 <https://doi.org/10.1038/s41437-019-0206-2>
- Lemmon, J. (2019) New discoveries for the endangered Illawarra Socketwood (*Daphnandra johnsonii*, Atherospermataceae). *Australasian Plant Conservation* **28** (2).
- Lewis, S. E., Sloss, C. R., Murray-Wallace, C. V., Woodroffe, C. D. and Smithers, S. G. (2013). Post-glacial sea-level changes around the Australian margin: a review. *Quaternary Science Reviews* **74**, 115-138.
- Luly, J.G., Blair, D., Parsons, J.G., Fox, S. and VanDerWal, J. (2010) Last Glacial Maximum habitat change and its effects on the grey-headed flying fox (*Pteropus poliocephalus* Temminck 1825). Chapter 6 ANU e press doi: 10.22459/TA32.11.2010.06
- McDougall, K.L., Wright, G.T., Bredell, P.M., James, E.A. and Simmons, L. (2023) Mount Imlay – an island of floristic significance on the brink. *Cunninghamia* **23**, 1– 9.
- Macphail, M. (1973) Pollen analysis of a buried organic deposit on the backshore at Fingal Bay Port Stephens new South Wales. *Proceedings of the Linnean Society of NSW* **98**, 222-233.
- Macphail, M., Sharples, C., Bowman, D., Wood, S. and Haberle, S. (2014) Coastal erosion reveals

- a potentially unique Oligocene and possible periglacial sequence at present-day sea level in Port Davey, remote south-west Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **148**, 43-59.
- Martin, A.R.H. (1994) Kurnell Fen: an eastern Australian coastal wetland, its Holocene vegetation, relevant to sea-level change and aboriginal land use. *Review of Palaeobotany and Palynology* **80**, 311-332.
- McDougall, K.L., Wright, G.T., Bredell, P.M., James, E.A. and Simmons, L. (2023) Mount Imlay – an island of floristic significance on the brink. *Cunninghamia* **23**, 1–9.
- Marske, K.A. and Boyer, S.L. (2024) Phylogeography reveals the complex impact of the Last Glacial Maximum on New Zealand’s terrestrial biota. *Journal of the Royal Society of New Zealand*, **54**, 8-29.
- Metcalfe, D. J. and Green, P.T. (2017) Rainforests and vine thickets. In D.A. Keith, ed., *Australian Vegetation*, 3rd edn. Cambridge University Press, pp. 257-280.
- Mills, K. (2023) *South Coast Ferns. A complete guide to the ferns and fern allies of the NSW South Coast*. 193 pp. Paperback. ISBN: 978-0-85881-0.
- Milner, M.L., Rossetto, M., Crisp, M.D. & Weston, P.H. (2012) The impact of multiple biogeographic barriers and hybridization on species-level differentiation. *American Journal of Botany* **99**, 2045-2057.
- Moir, M.L., Vesk, P.A., Brennan, K.E.C., Keith, D.A., McCarthy, M.A. and Hughes, L. (2011) Identifying and managing threatened invertebrates by assessing coextinction risk. *Conservation Biology* **25**, 787–796.
- Mooney, S.D., Harrison, S.P., Bartlein, P.J., Daniiau, A.L., Stevenson, J., Brownlie, K.C., Buckman, S., Cupper, M., Luly, J., Black, M. and Colhoun, E. (2011) Late Quaternary fire regimes of Australasia. *Quaternary Science Reviews* **30**, 28-46.
- Mooney, S.D., Sniderman, K., Kershaw, A.P., Haberle, S. and Roe, J. (2017) Quaternary vegetation in Australia. In D.A. Keith, ed., *Australian Vegetation*, 3rd edn. Cambridge University Press, pp. 63-88.
- Mooney, S.D., Martin, L., Goff, J. and Young, A.R.M. (2021) Sedimentation and organic content in the mires and other sites of sediment accumulation in the Sydney region, eastern Australia, in the period after the last glacial maximum. *Quaternary Science Reviews* 272: 107216 <https://doi.org/10.1016/j.quascirev.2021.107216>
- Morrison, D.A. and Rupp, A.J. (1995) Patterns of morphological variation within *Acacia suaveolens* (Mimosaceae). *Australian Systematic Botany* **8**, 1013 – 1027.
- Mueller, D., Jacobs, Z., Cohen, T.J., Price, D.M., Reinfelds, I.V. and Shulmeister, J. (2018) Revisiting an arid LGM using fluvial archives: a luminescence chronology for palaeochannels of the Murrumbidgee River, south-eastern Australia. *Journal of Quaternary Science* **33**, 777-793.
- Mueller, D., Reinfelds, I., Cohen, T., Larsen, J., Barrows, T., Shulmeister, J. and Williams, M. (undated) Does snowpack accumulation, ablation and altitudinal tree line depression explain palaeo runoff yields in Southern Australia over past glacial cycles? UOW/ UOQ Poster.
- Mullette, K.J. (1978) Studies of the lignotubers of *Eucalyptus gummifera* (Gaertn. & Hochr.). I The nature of the lignotuber. *Australian Journal of Botany* **26**, 9 – 13.
- Munro, U., Wiltshcko, W. and Ford, H.A., (1993). Changes in the migratory direction of Yellow-faced Honeyeaters *Lichenostomus chrysops* (Meliphagidae) during autumn migration. *Emu-Austral Ornithology* **93**, 59-62.
- Myerscough, P.J. (1998) Ecology of Myrtaceae with special reference to the Sydney region. *Cunninghamia* **5**, 787-807.
- Myerscough, P.J. (2020) Myall Lakes National Park, the Boolambayte Sand Ridge: its extent, vegetation, geomorphology and marks of European settlement. *Proceedings of the Linnean Society of New South Wales* **142**, 77-90.
- Myerscough, P.J. and Carolin, R.C. (1986) The vegetation of the Eurunderie sand mass, headlands and previous islands in the Myall Lakes area, New South Wales. *Cunninghamia* **1(4)**, 399-466.
- Myerscough, P.J. and Carolin, R.C. (2014). Vegetation of beach sand ridges and geomorphological processes in the valley of the Upper Myall River, NSW. *Cunninghamia* **14**, 17–53.
- Myerscough, P.J., Whelan, R.J. and Bradstock (2006) Ecology of Proteaceae with special reference to the Sydney region. *Cunninghamia* **6**, 951-1015.
- Nge, F. J., Biffin, E., Waycott, M. and Thiele, K. R. (2021) Phylogenomics and continental biogeographic disjunctions:insight from the Australian starflowers (*Calytrix*). *American Journal of Botany Research Article* DOI: 10.1002/ajb2.1790
- NSW National Parks and Wildlife Service (1998) *Nomination of the Greater Blue Mountains Area for inscription on the World Heritage List by the Government of Australia*. Prepared by the NSW National Parks and Wildlife Service and Environment Australia.
- NSW National Parks and Wildlife Service (2003) Sydney Basin Bioregion. Chapter 15 in *The Bioregions of New South Wales: their biodiversity, conservation and history*.
- NSW Office of Environment & Heritage (ongoing) Threatened Species Profile Search webpage. Electronic Resource, On-Line, some interactivity: <http://www.environment.nsw.gov.au/threatenedSpeciesApp/>
- NSW Scientific Committee (2004) Woronora Plateau population of *Callitris endlicheri* (a tree) - Endangered population determination - final.
- Nicolle, D. (2006) A classification and census of regenerative strategies in the eucalypts (*Angophora*, *Corymbia* and *Eucalyptus*—Myrtaceae), with special reference to the obligate seeders. *Australian Journal of Botany* **54**, 391–407.

LAST GLACIAL MAXIMUM VEGETATION SYDNEY BASIN

- Nicolle, D. (2021) Classification of the Eucalypts (*Angophora*, *Corymbia* and *Eucalyptus*). <http://www.dn.com.au/Classification-Of-The-Eucalypts.html>
- Noble, I.R. and Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5–21.
- Ooi, M.K.J. et al. (2017) Climatic influence over vegetation pattern and process. In D.A. Keith, ed., *Australian Vegetation*, 3rd edn. Cambridge University Press, pp. 102–206.
- Pannell, J.R. and Myerscough, P.J. (1993) Canopy-stored seed banks of *Allocasuarina distyla* and *A. nana* in relation to time since fire. *Australian Journal of Botany* **41**, 1 – 9.
- Payne, R., Chalmers, A. and Laxton, J. (2012) Understanding the characteristics of a groundwater-dependent ecosystem: *Eucalyptus parramattensis* woodland at Porters Creek Wetland, NSW. *Cunninghamia* **12**, 121–211.
- Pickett, E.J., Harrison, S.P., Hope, G., Harle, K., Dodson, J.R., Peter Kershaw, A., Colin Prentice, I., Backhouse, J., Colhoun, E.A., D’Costa, D. and Flenley, J. (2004). Pollen-based reconstructions of biome distributions for Australia, Southeast Asia and the Pacific (SEAPAC region) at 0, 6000 and 18,000 14C yr BP. *Journal of Biogeography* **31**, 1381–1444.
- PlantNET (ongoing) The Plant Information Network System of The Royal Botanic Gardens and Domain Trust, Sydney. ELECTRONIC RESOURCE, ONLINE: <http://plantnet.rbgsyd.nsw.gov.au/>.
- Rabinowitz, D., Cairns, S., Dillon, T. (1986) Seven forms of rarity and their frequency in the flora of the British Isles. In: Soule’ ME (ed) *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Massachusetts.
- Reeves, J., et al. (2013). Climate variability over the last 35,000 years recorded in marine and terrestrial archives in the Australian region: an OZ-INTIMATE. *Quaternary Science Reviews* **74**, 21–34.
- Robbie, A. and Martin, H.A. (2007) A history of the vegetation from the last glacial maximum at at Mountain Lagoon, Blue Mountains, New South Wales. *Proceedings of the Linnean Society of NSW* **128**, 57–80.
- Rogers, K., Boon, P., Lovelock, C. and Saintilan, N. (2017) Coastal Halophytic Vegetation. In D.A Keith, ed. *Australian Vegetation* 3rd edn. Cambridge: Cambridge University Press pp. 544–569.
- Rossetto, M., Beaumont, L., Das, S., and Yap, S. (2018) *Bioclimatic discordance: Combining molecular and environmental data to identify floristic refugia and corridors*. Report prepared for NSW Office of Environment and Heritage by Royal Botanic Gardens and Domain Trust/ Macquarie University.
- Rossetto, M. Wilson, P.D., Bragg, J. Cohen, J., Fahey, M., Yap, J-Y. S. and van der Merwe, M. (2022) Perceptions of similarity can mislead provenancing strategies—An example from five co-distributed *Acacia* species. *Diversity* **2020**, 12, 306; doi:10.3390/d12080306
- Rutherford, S (2020) Insights into speciation and species delimitation of closely related eucalypts using an interdisciplinary approach. *Australian Systematic Botany* **33**, 110–127. DOI: 10.1071/SB18042
- Rutherford, S., Wilson, P. G., Rossetto, M. and Bonser, S.P. (2016) Phylogenomics of the green ash eucalypts (Myrtaceae): a tale of reticulate evolution and misidentification. *Australian Systematic Botany* **28**, 326–354.
- Rutherford, S., Bonser, S.P., Wilson, P.G. and Rossetto, M. (2017) Seedling response to environmental variability: the relationship between phenotypic plasticity and evolutionary history in closely related *Eucalyptus* species. *American Journal of Botany* **104**, 1–18.
- Rutherford, S., Rossetto, M., Bragg, J. G., McPherson, H., Benson, D., Bonser, S. P. and Wilson, P.G. (2018) Speciation in the presence of gene flow: population genomics of closely related and diverging *Eucalyptus* species. *Heredity* **121**, 126–141.
- Rutherford, S., Wan, J.S.H., Cohen, J.M., Benson, D. and Rossetto, M. (2021) Looks can be deceiving: speciation dynamics of co-distributed *Angophora* (Myrtaceae) species in a varying landscape. Article in *Evolution* · February 2021 DOI: 10.1111/evo.14140
- Rutherford, S. (2022) Evolutionary processes in an undescribed eucalypt: implications for the translocation of a critically endangered species. *Annals of Botany* DOI: 10.1093/aob/mcac091
- Rymer, P.D., Morris, E.C. and Richardson, B.J. (2002) Breeding system and population genetics of the vulnerable plant *Dillwynia tenuifolia* (Fabaceae). *Austral Ecology* **27**, 241–248.
- Sainty, G., Hosking, J., Carr, G. and Adam, P. (2012) *Estuary plants and what’s happening to them in south-east Australia*. Sainty and Assoc., Sydney.
- Semple, W.S. (1997). Native and naturalised shrubs of the Bathurst granites: past and present. *Cunninghamia* **5**, 4–9.
- Sheringham, P., Copeland, L.M., Gray, R. and Dijkstra, K. (2021) Survey of rare mallee *Eucalyptus dissita* in Gibraltar Range National Park, NSW Northern Tablelands. *Cunninghamia* **21**, 17–26.
- Siddiqi, M.Y., Carolin, R.C. and Anderson, D.J. (1973) Studies in the ecology of coastal heath in New South Wales I Vegetation structure. *Proceedings of the Linnean Society of NSW* **97**, 211–224.
- Sloss, C.R., Murray-Wallace, C.V., and Jones, B.G. (2007). Holocene sea-level change on the southeast coast of Australia: a review. *The Holocene* **17**, 999–1014.
- Smith, D.E., Harrison, S., Firth, C.R. and Jordan, J.T. (2011) The early Holocene sea level rise. *Quaternary Science Reviews* **30**, 1846–1860.
- Smith, J. (1981) The distribution and conservation status of a rare conifer, *Microstrobus fitzgeraldii* (Podocarpaceae). *Cunninghamia* **1**, 125–128.
- Sniderman, J. M. K., Hellstrom, J., Woodhead, J. D., Drysdale, R. N., Bajo, P., Archer, M., and Hatcher, L. (2019). Vegetation and climate change in southwestern Australia during the Last Glacial Maximum. *Geophysical Research Letters* **46**, 1709–1720. <https://doi.org/10.1029/2018GL080832>

D. BENSON

- Sydes, M.A. and Peakall, R.O.D. (1998) Extensive clonality in the endangered shrub *Haloragodendron lucasii* (Haloragaceae) revealed by allozymes and RAPDs. *Molecular Ecology* **7**, 87-93.
- Tibby, J., Barr, C., Marshall, J.C., McGregor, G.B., Moss, P. T., Arnold, L. J., Page, T. J., Questiaux, D., Olley, J., Kemp, J., Spooner, N., Petherick, L., Penny, D., Mooney, S. and Moss, E. (2017) Persistence of wetlands on North Stradbroke Island (south-east Queensland, Australia) during the last glacial cycle: implications for Quaternary science and biogeography. *Journal of Quaternary Science* **32**, 770-781.
- Toon, A., Mather, P.B., Baker, A.M., Durrant, K.L. and Hughes, J.M. (2007) Pleistocene refugia in an arid landscape: analysis of a widely distributed Australian passerine. *Molecular Ecology* **16**, 2525-2541. doi: 10.1111/j.1365-294X.2007.03289.x
- Tozer, M. G. and Keith, D.A. (2012) Population dynamics of *Xanthorrhoea resinosa* Pers. over two decades: Implications for fire management. *Proceedings of the Linnean Society of NSW* **134**, 249-266.
- U3A (2016) Ice age Australia Powerpoint presentation U3A Bermagui, NSW
- Venn, S. et al. (2017) Alpine, Sub-alpine and Sub-Antarctic vegetation of Australia. In D.A. Keith, ed., *Australian Vegetation*, 3rd edn. Cambridge University Press, pp. 461-489.
- Vogel, J.C., Rumsey, F.J. Schneller, J.J., Barrett, J.A. and Gibby, M. (1999) Where are the glacial refugia in Europe? Evidence from pteridophytes. *Biological Journal of the Linnean Society* **66**, 23-37.
- Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.C., McManus, J.F., Lambeck, K., Balbon, E. and Labracherie, M. (2002) Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records. *Quaternary Science Reviews* **21**, 295-305.
- Warman, D. and Beckers, D. (2011) Status of the Vulnerable shrub *Astrotricha crassifolia* (Araliaceae) in Brisbane Water National Park, NSW: an update. *Cunninghamia* **12**, 129-136.
- Weston, P.H., Perkins, A.J. and Entwisle, T.J., (2005). More than symbioses: orchid ecology, with examples from the Sydney Region. *Cunninghamia* **9**, 1-15.
- Weston, P.H. and Jordan, G.J. (2017) Evolutionary biogeography of the Australian flora in the Cenozoic era. In D.A. Keith, ed., *Australian Vegetation*, 3rd edn. Cambridge University Press, pp. 40-62.
- Whelan, R.J. and Ayre, D.J. (2022) High adult mortality and failure of recruitment in a population of *Banksia spinulosa* following high-intensity fire. *Austral Ecology* **47**, 1162-1167.
- Williams, M., Cook, E., van der Kaars, S., Barrows, T., Shulmeister J. and Kershaw P. (2009) Glacial and deglacial climatic patterns in Australia and surrounding regions from 35 000 to 10 000 years ago reconstructed from terrestrial and near-shore proxy data. *Quaternary Science Reviews* **28**, 2398-2419.
- Williams, N. J. (2005) The environmental reconstruction of the last glacial cycle at Redhead Lagoon in coastal, eastern Australia. PhD thesis, University of Sydney.
- Wilson, T.C., Rutherford, S., Yap, J.Y.S., Douglas, S.M., Lee, E. and Rossetto, M. (2023) *Eucalyptus cryptica* (Myrtaceae): a critically endangered new species. *Australian Systematic Botany* **36**, 386-400.
- Willez, M.N., Kageyama, M., Krinner G, de Noblet-Ducoudre, N., Viovy, N, and Mancip, M. (2011). Impact of CO₂ and climate on the Last Glacial Maximum vegetation: results from the ORCHIDEE/IPSL models. *Climate of the Past* **7**, 557-577.
- Worth, J.R.P., Jordan, G.J., McKinnon, G.E. and Vaillancourt, R.E. (2009) The major Australian cool temperate rainforest tree *Nothofagus cunninghamii* withstood Pleistocene glacial aridity within multiple regions: evidence from the chloroplast. *New Phytologist* doi: 10.1111/j.1469-8137.2008.02761.x
- Worth, J.R.P., Marthick, J.R., Harrison, P.A., Sakaguchi, S. and Jordan, G.J. (2021) The palaeoendemic conifer *Pherosphaera hookeriana* (Podocarpaceae) exhibits high genetic diversity despite Quaternary range contraction and post glacial bottlenecking. *Conservation Genetics* **22**, 307-321.
- Yap, J-YS., Wilson, T.C. and Rossetto, M. (2019) Conservation genomics of *Pimelea spicata* (Spiked Rice-flower) in support of management and translocation activities. Research Centre for Ecosystem Resilience, Royal Botanic Garden Sydney.
- Young, A. (2017) *Upland swamps in the Sydney region*. Ann Young, Thirroul NSW.
- Zolfaghar, S., Villalobos-Vega, R., Cleverly, J. and Eamus, D. (2015) Co-ordination among leaf water relations and xylem vulnerability to embolism of *Eucalyptus* trees growing along a depth-to-groundwater gradient. *Tree Physiology* **35**, 732-743. <https://doi.org/10.1093/treephys/tpv039>

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