

Palaeoecology of southeast Australian ecosystems, with a
focus on the Bass Strait area: Implications for ecosystem
management

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Declaration

I declare that this thesis contains my original work towards my PhD, and due acknowledgement has been made in the text where other materials have been used.

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Abstract

Global change poses a major threat to ecosystems and biodiversity. This is particularly evident in southeast Australia, where never-before-seen wildfires are associated with ecosystem destruction, as well as the loss of wildlife, human lives and significant infrastructures. In order to tackle these challenges, there is a need for better understanding of long-term ecosystem changes in the region. This understanding will help in building robust knowledge baselines for management and restoration goals.

The Bass Strait islands provide a rare opportunity to investigate the long-term roles of climate and human land use in driving ecosystem and fire regime changes, due to their unique history of human occupation, which contrasts with surrounding southeast Australian regions. The Bass Strait islands saw declining populations at the same time as population intensification occurred in southeast Australia in the mid–late Holocene. The Bass Strait islands can thus be regarded as rare natural laboratories where climatic and anthropogenic drivers of long-term ecological dynamics can be disentangled. The knowledge of the different roles of climate and anthropogenic land use on ecosystems and fire regimes gained from these natural laboratories can be applied to areas of southeast Australia to inform management strategies in an era of significant ecological changes. Therefore, this thesis provides a deeper understanding of past links between ecosystem change, changes in climate, fire regimes, and human land use in southeast Australia, using the Bass Strait area as a case study. Specific questions addressed include, (1) What drove vegetation and wetland changes in southeast Australia during the last glacial and Holocene? (2) What was the role of humans in vegetation and fire-regime changes in southeast Australia during the Holocene? (3) How can this deep-time knowledge contribute to better managing the ecosystems and fire regimes of the Bass Strait islands and southeast Australia at large? In order to answer these questions, multiple wetland sediment cores were analysed to reconstruct vegetation, fire, and wetland histories of one of the least researched Bass Strait islands (i.e. truwana/Cape Barren Island) and compared to existing palaeoecological records from neighbouring regions of southeast Australian mainland and Tasmania. The thesis places these findings into a broader regional context, by analysing changes in vegetation and fire regimes and associated drivers of change across southeast Australia, applying a quantitative approach for the first time.

The results suggest that climate primarily drove ecosystem change across southeast Australian region in the last ~35,000 years. Specifically, temperature change and shifts in Southern Westerly Winds (SWW) were key drivers of vegetation and wetland changes during the last glacial period, while sea-level change, and precipitation changes related to El Niño Southern Oscillation (ENSO) and SWW were more important during the Holocene. Indigenous people used fire to maintain open and diverse woodlands during the Holocene, and a combination of climate and anthropogenic land use controlled Holocene fire regimes across southeast Australia. On a finer spatial scale, insights from the Bass Strait islands suggest Indigenous frequent burning reduced the area burnt by climate-driven fires during the Holocene. Indigenous fire management minimized contiguous woody fuel accumulation over the landscape, which in turn reduced fire spread. The suppression of Indigenous cultural fire management by European colonisation, combined with climate change, created novel fire regimes in southeast Australia in the last 200 years.

The reinstatement of an Indigenous cultural burning approach is recommended to help reduce the occurrence of destructive fires in southeast Australian forests and to preserve rare ecosystems, such as heathlands. This will help in restoring ecosystem health and biocultural heritage in southeast Australia. Monitoring of wetland hydrology and salinity is also recommended to preserve wetlands of significant ecological values in Bass Strait and the wider region.

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Chapter 1 INTRODUCTION

The global environment is currently undergoing major changes due to anthropogenic impacts and changing climate (Malhi et al., 2020; Bergstrom et al., 2021). Growing human population, consumption and land use collectively mount pressure on the natural environment, causing ecosystem biodiversity loss and altering natural climatic patterns (Camill, 2010). For instance, 178 million hectares of forest have been lost globally to human activities since 1990 (FAO, 2020). A significant increase in atmospheric CO₂ over the last century due to growing economic industrialization has enhanced the Earth's greenhouse effect and resulted in climatic warming, which is causing an increase in the frequency and severity of extreme events, such as floods, droughts, high temperatures and destructive fires (IPCC, 2014). Some of the most recent examples of extraordinary climate-driven events are the catastrophic 2020 wildfires in California and southeast Australia, which burned about 2 million and 19 million hectares of land area, respectively (Filkov et al., 2020; CAL FIRE, 2020). Flooding events were also recorded in many parts of the world in 2021, claiming many lives and displaced thousands from their homes (Cornwall, 2021; NSW Government, 2021).

Extreme climate-driven events are projected to continue over the next century, with major changes in ecosystems and biodiversity (Collins et al., 2013; Keeley and Syphard, 2016; Rogers et al., 2020; Carry et al., 2012; Bradstock et al., 2012; Bradstock, 2010). However, effective management strategies can help minimize the impact of extreme climatic events, increasing or maintain long-term ecosystem resilience. The degree of future changes in ecosystems will thus depend on land managers' strategies and the timing of management interventions. Timely and appropriate management is urgently required in southeast Australia, which is home to some of the most flammable plant communities on earth, with wildfires in the region not only destroying vegetation, wildlife, infrastructures, and livelihoods, but also claiming hundreds of human lives (Filkov et al., 2020; Bergstrom et al., 2021).

Ecologists have been working for several decades to develop management strategies in order to ameliorate environmental changes globally (e.g., Albini, 1976; Rodman et al., 2002; McKenzie et al., 2004; Fearnside and Ferraz, 1995; Lyke, 2000). Contemporary ecological assessments provide information on ecosystem changes/process on a short-term basis, capturing spatial and temporal variations occurring over weeks, months or, in rare cases, a

few years. However, it has been shown that basing ecosystem management strategies on such short-term knowledge/studies may not be reliable due to the longer period required for ecosystems to fully respond to external forces, particularly 'slow' ecosystem drivers such as climatic shifts (Dirk and Gillson, 2020; Davies and Bunting 2010; Carpenter et al., 2001). Combining historical (palaeoecological) data on ecosystem changes and processes with present knowledge provided through contemporary ecological research has been found to produce a robust and more reliable baseline understanding that can be used more confidently to inform management plans and actions (Davies and Bunting 2010; Wingard et al., 2017; Słowiński et al., 2019; Saunders and Taffs, 2009; Roos et al. 2021). This thesis applies that combined approach to informing the conservation and management of key Australian ecosystems.

1.1. Palaeoecological records as a tool in ecosystem management

Time is an important factor in ecosystem processes and patterns as it is required for ecosystems to adapt, adjust, or respond to disturbance (Botkin, 2012). Depending on the nature of disturbance, an ecosystem's response can take from decades (e.g., anthropogenic burning, pervasive agriculture) up to centuries or millennia to fully manifest (e.g., changes in temperature, precipitation and CO₂). Therefore, data derived from only modern or short-term ecological data can misdirect ecosystem interventions, leading to damaging consequences, as such data do not entirely reflect real-time ecosystem processes and patterns (Dirk and Gillson, 2020; Davies and Bunting 2010; Botkin, 2012). An example of erroneous judgments made as a result of not looking back far enough or considering historical knowledge, was when models based on modern salt-water crocodile populations in northern Australia were used as a benchmark for crocodile population restoration in the 1970s after a period of massive commercial hunting in northern Australia (Webb et al., 1984; Messel et al., 1981). The restoration was short-lived and Indigenous historical accounts later revealed that the benchmark used for restoration had only captured less than 50% of true crocodile populations in the area (Webb et al., 1984). Another example was when eradication of wolves was erroneously recommended by biologists in the 1900s in Yellowstone National Park, United States, due to the lack of historical baseline knowledge, which led to the overpopulation of grazing animals (especially elks) and overgrazing of deciduous, woody species, resulting in long-term ecosystem

deterioration (Berger et al., 2008; William, 2008). Wolves have since been reintroduced to Yellowstone to restore their key ecosystem functions and bolster ecological resilience.

Knowledge of past (long-term) changes in ecosystems is becoming increasingly valuable in ecosystem management and conservation (Wingard et al., 2017; Słowiński et al., 2019).

The understanding of past ecosystem changes under different climatic, fire and anthropogenic regimes is now considered critical to building reliable baseline knowledge to tackling future environmental/ecosystem challenges in many parts of the world (Wingard et al., 2017; Słowiński et al., 2019; Spencer et al., 2017; Saunders and Haffs, 2009; Smol, 2009). For instance, studies of past changes in vegetation and floristic diversity have been used in developing frameworks to better understand future ecosystem changes in Europe and North America (Pellat et al., 2015; Birks et al., 2016; Jackson and Overpeck, 2000; Willard and Cronin, 2007; Williams and Jackson, 2007; Jackson and Hobbs, 2009; Watson et al., 2011). In particular, studies of past human land use and fire usage are now being championed in some parts of North America, South America, southern Europe, and Australia to better preserve ecosystems and manage recurrent catastrophic wildfires (Crawford et al., 2015; Bush and Colinvaux, 1994; Cole et al., 2015; Karpińska-Kończak et al., 2014; Fletcher et al., 2021; Mistry et al., 2019; Eloy et al., 2019; White et al., 2011; Keane et al., 2002; Fernandes et al., 2013).

Long-term historical information of past ecosystem changes is derived from palaeoecological records. Palaeoecology is the study of past ecosystems and related changes in the context of climate change, human land use, fire regimes, sea-level change and other external factors, such as volcanic eruption and herbivory (Elias, 2007). Some of the major lines of evidence used in palaeoecology are indicators ('proxies') preserved in sediments and include pollen, charcoal, non-pollen palynomorphs, phytoliths, isotopes and ancient DNA (Smol et al., 2001a, Rawlence et al., 2021). Of these, sedimentary pollen, charcoal, and non-pollen palynomorph records are the most commonly used and are mainly retrieved from lakes and peatlands (bogs, fens, swamps, marshes). Pollen records may also be retrieved from other sedimentary archives, such as ice cores, sediment outcrops, and marine sediments (Faegri and Iversen, 1975; Bradley, 1999; Seppä, 2013; Smol et al., 2001a).

Pollen grains are produced in abundance, can be easily matched with source plants, sometimes at the species level, but more often at genus or family level. Pollen can survive

thousands to millions of years in sedimentary archives compared to other fragile plant remains (e.g., leaves, seeds) that generally suffer from poor preservation and infrequent occurrence in sedimentary records (Faegri and Iversen, 1975). This makes sedimentary pollen studies the most readily available means to obtain snapshots of past vegetation, which is critical to understanding present and future environments since vegetation is the base of terrestrial food chains (Faegri and Iversen, 1975; Bradley, 1999; Seppä, 2013; Green, 1983). Sedimentary pollen records can be used not only to reconstruct past vegetation changes, but to quantitatively estimate past changes in land cover and vegetation diversity (Birks et al., 2016a, Connor et al., 2019; Giesecke et al., 2017, 2019; Seddon et al., 2015; Mariani et al., 2017; Brussel and Brewer, 2021). Also, since vegetation/plant distributions are mainly or partly a reflection of prevailing climates in a region, pollen records can provide information of the region's past climate (e.g., Fletcher and Thomas, 2010a; Hebert and Fitchett, 2020; Cheddadi et al., 2021; Campbell et al., 2017).

Partially combusted plant material (charcoal) remains the most readily available and direct evidence of past fire activities in landscapes (Whitlock and Larsen, 2001; Rehn et al., 2019; Hennebelle et al., 2020). Information gained through the analyses of charcoal particles in sedimentary sequences can provide information on past fire frequency and the amount of vegetation burned in an area (Whitlock and Larsen, 2001; Ali et al., 2012; Power et al., 2008; Mooney et al., 2011; Higuera et al., 2010). Sedimentary charcoal analyses can also aid in understanding human influence on terrestrial ecosystems in the past (Neumann, 2014).

Non-pollen palynomorphs (NPPs) represent diverse organisms including higher plant remains, algae, fungi and zoological remains (van Geel, 2001). NPPs mostly originate from or close to sedimentary deposits (lakes, wetlands) and are sensitive to changes in local environmental conditions, such as hydrology, temperature, salinity, and turbidity (van Geel, 2001). Therefore, NPP analysis is used in gaining insights into past ecological changes in lakes/wetlands, and to also augment vegetation and fire history reconstructions (van Geel, 2001; Smol et al., 2001a, 2001b). NPPs such as fungal and algal remains and testate amoebae are used in supporting pollen-based vegetation reconstructions (e.g., van Geel et al., 1981, 1989; Huntley et al., 2013; Dodson, 1974a; Cook, 2009; Singh et al., 1981; Haberle et al., 2006) to gain deeper insights into local factors associated with past vegetation and fire regime changes. Fungal remains, when combined with charcoal

records, can be useful in inferring past human land use, interactions between humans and other mammals (e.g. megafauna), and to identify potential anthropogenic fires (Rule et al., 2012; Cugny et al., 2010; Raper and Bush, 2009; van Geel et al., 2003, 1981, 1989; Feeser and O'Connell, 2010).

The aforementioned palaeoecological proxies have been widely used in different parts of the world to develop long-term historical data sets to inform management actions in terrestrial and aquatic systems (Wingard et al., 2017; Słowiński et al., 2019; Ross et al., 2021; Mistry et al., 2019). There has been some work on using long-term palaeo data to inform management of lakes and wetlands in Australia, but the same has not extended to the surrounding terrestrial environments (Bergstrom et al., 2021; Barr et al., 2013; Gell, 2019; Saunders and Taffs, 2009). This lack of palaeoecology-informed management in Australia may be partly related to a combination of scarce high-resolution palaeoecological records and the lack of clearly articulated and actionable management implications in the existing palaeoecological literature. As already demonstrated in some other parts of the world (Bergstrom et al., 2021; Willis et al., 2010; Dietl and Flessa, 2011; Mistry et al., 2019; Eloy et al., 2019; White et al., 2011; Keane et al., 2002; Fernandes et al., 2013), the long-term historical knowledge provided by palaeoecology can provide significant insights into effective ecosystem management in Australia, especially in managing recurrent catastrophic fires and preserving biocultural heritage in southeast Australia. This is because palaeoecology can provide replicable data on past wildfire frequency and the extent and dynamics of past cultural landscapes, reinforcing Australian Indigenous narratives about place and time.

1.2. Palaeoecology of Australia and current region of knowledge gap (Bass Strait)

Many parts of the world, especially mid—high latitudes, were characterized by cool, dry non-arboreal vegetation in past glacial periods and variably warm, wet arboreal vegetation during interglacials (Lowe and Walker, 2014). Low latitude areas exhibited much greater spatial and temporal variability in prevailing environments and climates, particularly during the last glacial period (Novello et al., 2017; Montoya et al., 2018; Moss et al., 2013; Kershaw et al., 1986). Australia, occupying latitudinal zones from cool temperate to tropical, is included in this palaeoenvironmental pattern.

Existing palaeoecological records in Australia suggest interglacial-era environments were generally warm and wet, characterized by forests and woodlands; while dry, cool glacial-era environments were characterized by open vegetation communities, especially in temperate areas (Hope et al., 2004; De Deckker et al., 2019a, 2019b). Grassland and Casuarinaceae woodland prevailed in the northern part of Australia during the Last Glacial Maximum (LGM: between 28,000 and 18,000 years ago), with humid forests in high-rainfall areas (Kershaw, 1994; Ellerton et al., 2017; Rowe et al., 2021), while southern Australia is thought to be characterized by herbaceous and shrubby vegetation, with *Eucalyptus* woodlands and *Nothofagus* rainforest refugia in higher rainfall areas (e.g., Sniderman et al., 2019; De Deckker et al., 2019a, Dodson, 1975; Harle et al., 2002, 2004; Colhoun et al., 1999; Worth et al., 2009). Fire activity was minimal during the LGM due to the reduced woody biomass in many areas (Mooney et al., 2011). Woodland and forests started to expand during the lateglacial (18,000–11,700 years ago), as climate became increasingly warmer and wetter, with a maximum expansion during the Holocene (the last 11,700 years) (Hopf et al., 2000; Mackenzie and Moss, 2017; Jones et al., 2017; Stahle et al., 2016, 2017; McWethy et al., 2017; Ellerton et al., 2017; Sniderman et al., 2019; Kershaw et al., 1991). Fire activity increased in many areas during the Holocene as a result of widespread woody vegetation, increased climate variability and human land-use intensification (Mooney et al., 2011; Black et al., 2008; Lourandos, 1983).

Despite the large number of available paleoecological records that have documented past ecosystem/environmental changes in Australia, especially in the south-eastern region, studies are still exceedingly scarce from the Bass Strait islands, which are situated between the southeast Australian mainland and Tasmania. Only one high-resolution study is available for the region (McWethy et al., 2017), with three other low-resolution studies (Ladd et al., 1979, 2020; D'Costa et al., 1993). Additional high-resolution records are required to fully understand spatio-temporal homogeneity/heterogeneity of past vegetation, fire regimes and human land use in this region, which formed a land bridge between the Australian mainland and Tasmania when sea levels dropped during the glacials.

Islands were among the last land masses on earth to be colonised by humans due to their isolated nature and limited space, making them suitable natural laboratories to investigate the role of humans in driving natural vegetation changes (Nogu   et al., 2021).

Palaeoecological research on these remote islands shows that human activities have been the primary driver of Holocene ecological change, revealing the pervasive impacts that

humans have on terrestrial systems more broadly (Nogu   et al., 2021). Palaeoecological studies of islands in Australia have also shown the suitability of islands in researching past sea-level changes, nature of human land use and plant phylogeography (Tibby et al., 2017; Lambrides et al., 2020). However, the unique history of the Bass Strait islands' formation and dynamics of its human occupation make the area interesting and suitable for exploring key palaeoecological questions that can help understand some of the present environmental changes in southeast Australia and more broadly. Bass Strait served as a connecting landbridge for human movement between Tasmania and the Australian mainland during the LGM, and the present islands, including Truwan  /Cape Barren Island, emerged as a result of postglacial sea-level rise between ~14,000 and 6000 years ago (Sloss et al., 2007; Lambeck and Chappell, 2001; Williams et al., 2018). Archaeological records suggest a reduction in the islands' occupation intensity since the separation of islands from the surrounding land masses by the mid-Holocene, following the sea-level high stand between 8000 and 6000 years ago (Sim, 1998; Sloss et al., 2007). Given the islands' anthropogenic land-use history contrasts with the pattern of increasing land-use intensification evident on the southeast Australian mainland at the same time (Lourandos, 1983), the Bass Strait islands provide a rare natural experiment to explore the different roles of climate and anthropogenic land use in driving past ecosystem and fire regime changes.

1.3. Thesis aim and approach

In order to fill the aforementioned knowledge gaps in Australia, this thesis aims to provide a deeper understanding of past links between ecosystem change, changes in fire regimes, climate, sea levels and human land use in southeast Australia, using the Bass Strait islands as a case study (Fig. 1). The thesis will generate insights into the differential roles of climatic and anthropogenic drivers of ecosystem change by comparing Bass Strait's past environmental trajectories to that of neighbouring landmasses with different land-use histories. This will then be used to suggest approaches for ecosystem management informed by long-term observations in Bass Strait and southeast Australia in general (Fig. 1). Specific questions addressed in this thesis include: (1) What drove vegetation and wetland changes in southeast Australia during the last glacial and Holocene? (2) What was the role of humans in vegetation and fire-regime changes in southeast Australia during the Holocene? (3) How can this deep-time knowledge contribute to better managing the

ecosystems and fire regimes of the Bass Strait islands and southeast Australia at large? In order to answer these questions, the research took the following steps: (1) vegetation, fire, and wetland histories of one of the larger Bass Strait islands (truwana/Cape Barren Island) were reconstructed for the last 35,000 years and compared to palaeoecological records from surrounding regions of southeast Australian mainland and Tasmania. (2) Changes in vegetation and fire regimes and associated drivers of change across southeast Australian regions, including Bass Strait, were assessed using a robust quantitative approach for the first time in Australia.

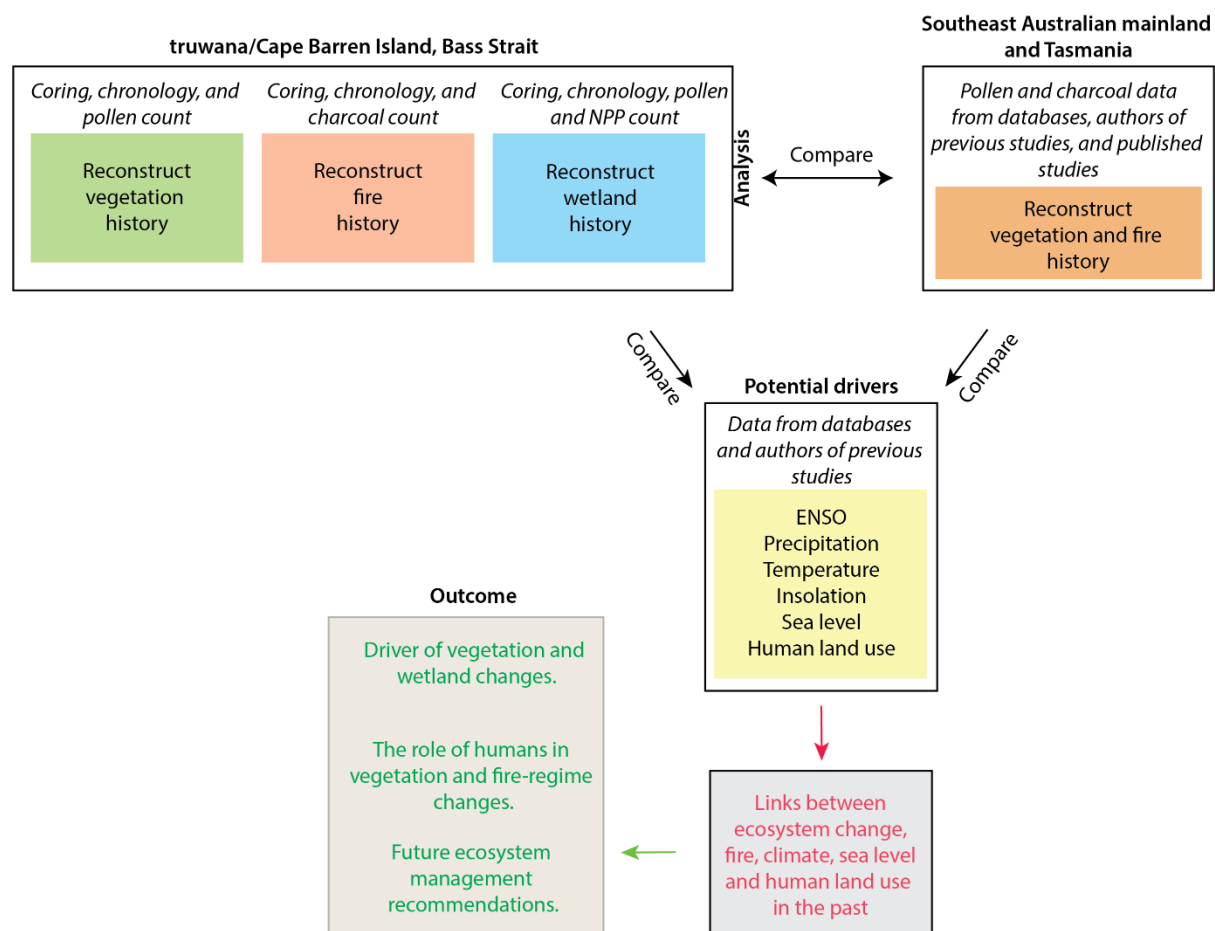


Figure 1: Project workflow for achieving thesis aims.

1.4. Thesis structure

The current chapter (Chapter 1) of this thesis provides a background to the thesis' focus and highlights its aims and objectives. The chapter also provides an overview of the Australian environment, with a focus on southeast Australia, especially the Bass Strait area. Finally, the main approach used in this thesis is outlined in this first chapter. Chapters 2–8

present series of published studies, which address each of the thesis aims and objectives as described in the following section (1.4.1). Chapter 9 summarizes the thesis' major findings, and demonstrates how the aims and objectives were met. Supplementary materials of all published studies presented in chapters 2–8, as well as other materials related to this thesis, are presented in the Appendix.

1.4.1. Published and submitted studies in chapters 2–8.

Chapter 2: Environmental change during the last glacial on an ancient land bridge of southeast Australia— This chapter describes the timing and nature of vegetation, fire regimes and lake level changes in Bass Strait from ~35,000 to 11,000 years ago, when the strait was mostly a land bridge. The chapter includes original data from truwana. Results are interpreted in the context of regional and hemispherical vegetation and climatic changes to better understand the driver(s) of environmental change during the last glacial, as well as the timing of the LGM. The biogeographic roles of the land bridge in biotic dispersal between southeast Australian mainland and Tasmania are also discussed to gain insights into the dynamics of human land-bridge usage and species dispersal in southeast Australia during the last glacial.

Chapter 3: Holocene heathland development in temperate oceanic Southern Hemisphere— key drivers in a global context— Building on chapter 2, this chapter documents the lateglacial and Holocene (the last ~14,000 years) vegetation and fire regime changes in Bass Strait, as well as the drivers of change, based on original data from four sites on truwana. Focus is also placed on understanding the drivers of heathland (a key and vulnerable type of shrubland) development in the past and management recommendations are highlighted to help maintain ecological health in Bass Strait heathlands.

Chapter 4: Myrtaceae pollen morphology study from Bass Strait islands, Australia, is effective in separating region-specific fossil Myrtaceae pollen types— As the Myrtaceae is the dominant plant family in Australia, this chapter presents a systematic study of the pollen of Myrtaceae plants in Bass Strait, one of the few pollen morphological studies in Australia. This is to better understand the composition and dynamics of Myrtaceous plants in the lateglacial and Holocene vegetation of Bass Strait presented in Chapter 3.

Chapter 5: Assessing past ecological changes in wetlands of Bass Strait, southeast Australia—implications for Ramsar management and conservation—This chapter describes how the vegetation, fire regimes and climate discussed in previous chapters have influenced past wetland development in Bass Strait. The study includes a detailed examination of non-pollen palynomorphs as indicators of wetland dynamics. Insights gained into long-term wetland development are then used to suggest management strategies to better conserve Bass Strait wetlands, which are home to some of Australia's rare and endangered fauna and flora species.

Chapter 6: Long-term drivers of vegetation turnover in Southern Hemisphere temperate ecosystems— Compared to previous Bass Strait-focused chapters, this chapter and the next two chapters provide a more regional context of past ecosystem changes across southeast Australia. Using a robust quantitative approach, Chapter 6 compares the vegetation changes in Bass Strait described in previous chapters to other records in the southeast Australian region in order to understand the broader region's long-term pattern of vegetation change. The chapter contributes to a growing international literature on applying rate-of-change analysis to palaeoecological records to reconstruct ecological turnover.

Chapter 7: Indigenous fire-managed landscapes in southeast Australia during the Holocene— new insights from the Furneaux Group islands, Bass Strait—This chapter reveals how ancient cultural landscapes can serve as natural laboratories to investigate present critical environmental questions through the lens of the past. In the case of Australia, one of the key challenging environmental questions is the different roles climate and humans played in past fire regimes. Being able to answer this question will assist in current and future fire management strategies on this fire-prone continent. The roles of fire and Indigenous people are teased apart in this chapter by decomposing fire regimes into biomass burned and fire frequency across southeast Australia (including new records from Bass Strait) and comparing these facets of fire regimes to independent records of climate and human land use in order to identify the primary drivers of fire regimes. Implications of the results for future fire management are also highlighted.

Chapter 8: European colonization and the emergence of novel fire regimes in southeast Australia—This chapter is a sequel to the previous chapter. While Chapter 7 focuses on the last 12,000 years (millennial scale), Chapter 8 focuses on understanding the drivers of southeast Australian fires during the last 700 years (centennial scale), providing a deeper

understanding of what fire regimes looked like prior to and during European colonisation. Identifying the main driver(s) of fire-regime changes during these periods will not only inform current fire management efforts, but also in achieving long-term ecosystem health and preserving biocultural heritage.

The research carried out for this thesis has facilitated co-authorship and collaborations on other separate projects, such as the pre- and post-European quantitative land cover reconstruction of southeast Australia (Mariani et al., in press), archaeology of Sahul (Rowe et al., in press), a palaeofire survey of some Tasmanian sites (Cape Pillar, Three Hummock Island and King Island—ongoing), and educational training material (booklet; see Appendix 10.9) for the Indigenous community of truwana/Cape Barren Island (ongoing).

1.5. Study region/area

Australian landscapes have been shaped by climate and fire for millions of years and the sclerophyllous vegetation that dominates the continent today, especially southeast Australia, emerged as a result of long-term interactions between biota, landscapes and fire (Keith, 2017; Crisp et al., 2011). Indigenous people have been in Australia for at least 65,000 years and during that time they have influenced Australian landscapes and been influenced by them for millennia before European (British) colonization in the 18th century—1788 AD (Keith, 2017).

1.5.1. Vegetation

Vegetation types across the Australian landscape generally follow rainfall, temperature, and humidity gradients (Keith, 2017). The wet, warm (monsoon climate) northern region has vegetation dominated by wet sclerophyll forest and woodland, and savanna, while the dry, arid central region is dominated by grassland and sclerophyll shrubland (Fig. 2). The temperate southern vegetation is dominated by dry sclerophyllous forests, woodlands and shrublands, which are concentrated in the south-eastern region, a region known as one of the most flammable places on earth (Crisp et al., 2011). However, further south in Tasmania, the western part of the island's vegetation is characterized by rainforest and the eastern area is characterized by dry forest and woodlands (Keith, 2017; Fig. 2). Fire activity varies across the continent: fire is generally frequent but with low intensity in the wet

northern monsoon areas of Australia, and reverse is the case in the southern temperate areas such as Tasmania (Miller and Murphy, 2017; Bradstock, 2010; Bradstock et al., 2002).

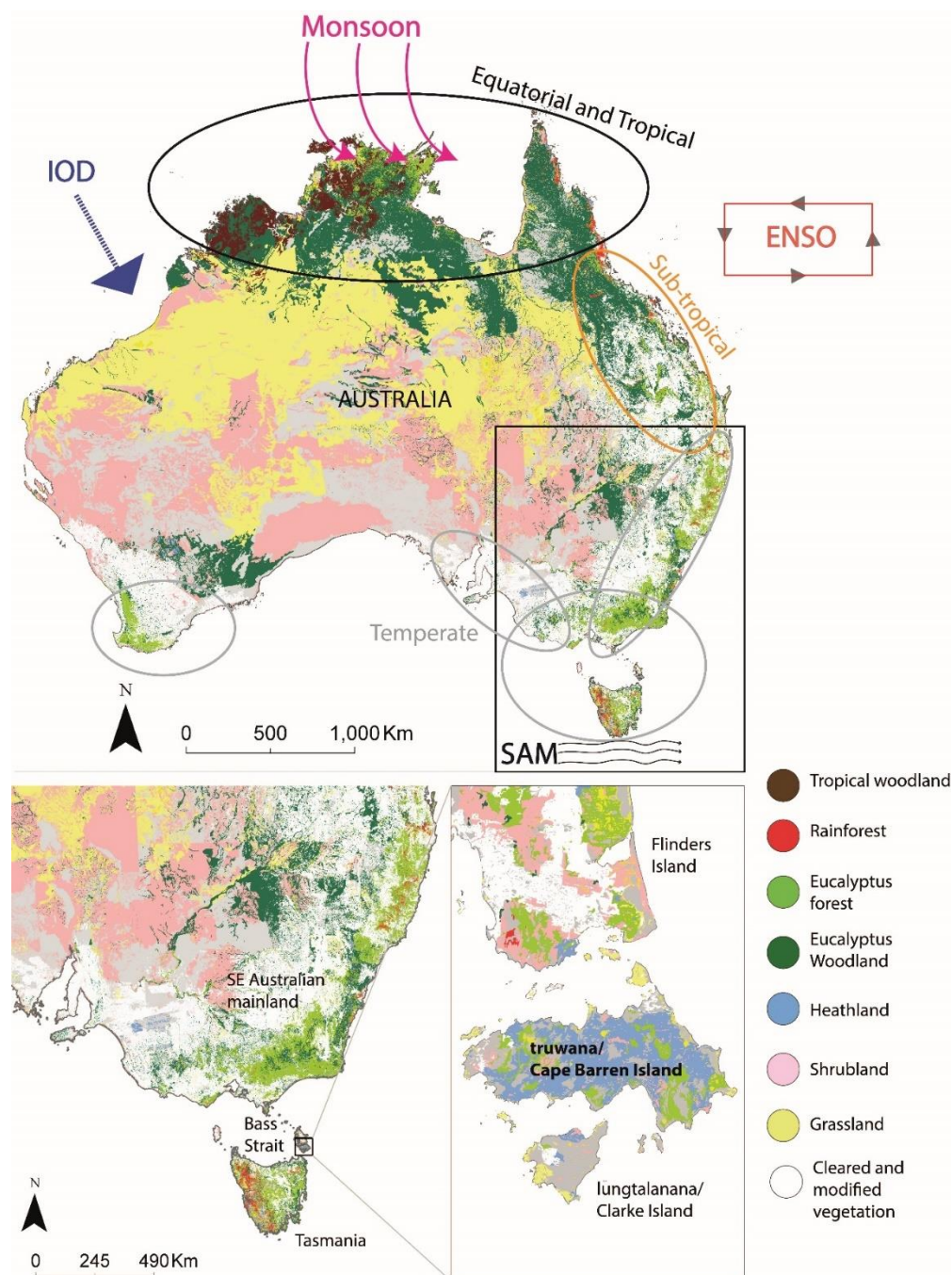


Figure 2: Major vegetation distribution and climate classification (circles), as well as dominant long-term climatic modes in Australia (adapted from the Department of Agriculture, Land and Environment, 2018a—National Vegetation Information System version 5.1 and the Australian Bureau of Meteorology). Areas not covered by the circles are characterized by desert and grassland bioclimates. Inset: the study region of south-eastern Australia, including the fieldwork area of eastern Bass Strait (truwana/Cape Barren Island).

On a much finer scale, in addition to widespread dry sclerophyllous forests, woodlands and shrublands, the temperate southeast Australian vegetation is also composed of wet sclerophyll forest (along the eastern strip of the mainland), alpine herbfield and shrublands at high elevations, and patches of grasslands and heathlands, particularly in coastal and semi-arid zones (Keith, 2017). The Bass Strait area, which is the main study area of this thesis, is also dominated by dry sclerophyllous woodlands, shrublands and heathlands (Harris et al., 2001; Harris and Kitchener, 2005). Various rainforest communities, sedgeland and moorlands dominate western Tasmania's vegetation as this area receives the highest amount of rainfall in southeast Australia (Harris and Kitchener, 2005; Reid et al., 1999).

1.5.2. Climate

The climate of southeast Australia (including Bass Strait) is mainly governed by three climatic modes (Fig. 2), which include ENSO (El Niño Southern Oscillation), Southern Annular Mode (SAM) and Indian Ocean Dipole (IOD) (Australian Bureau of Meteorology, 2010; CSIRO, 2012). ENSO is a three-to-eight-year oscillation between the El Niño phase and the opposite phase, La Niña. El Niño is the product of significant warming of the central and eastern tropical Pacific Ocean sea-surface temperatures, which leads to changes in atmospheric circulation, with the weakening or reversal of prevailing trade winds (Australian Bureau of Meteorology, 2010). The SAM is the non-seasonal north-south movement of westerly winds in the mid- to high-latitudes of the Southern Hemisphere, which occurs in a cycle of weeks–months–decades (Australian Bureau of Meteorology, 2010; Mariani and Fletcher, 2016). The IOD is an annual difference in sea surface temperature between the western and eastern Indian Ocean, and it affects not only Australian climate, but also other countries around the Indian Ocean basin (Australian Bureau of Meteorology, 2010).

Positive ENSO (La Niña years) and IOD phases are associated with high rainfall, reduced fire weather and fire events. Conversely, negative ENSO (El Niño years) and IOD phases are associated with droughts, high temperatures, extreme fire weather and fire events (Mariani et al., 2016a; Risbey et al., 2007). The influence of SAM is strongest in Tasmania and follows an east-west anti-phased pattern. A positive SAM phase features increased summer rainfall (but dry winter) in eastern Tasmania, while a negative SAM phase features

increased summer rainfall in western Tasmania and increased winter rainfall in both eastern and western Tasmania (Australian Bureau of Meteorology).

An ENSO-like climatic oscillation known as Pacific Decadal Oscillation (PDO) or Interdecadal Pacific Oscillation (IPO) also influences the southeast Australian climate (Palmer et al., 2015). While ENSO can persist for months to few years, the PDO/IPO can persist for decades (20–30 years), driving long-term variability in droughts (Mantua and Hare, 2002, Palmer et al., 2015). Asymmetric interactions between the two climatic modes also contribute to variability in precipitation regimes in southeast Australia (Verdon et al., 2004).

1.5.3. Bass Strait geography and history

Bass Strait is located at latitude 38–41°S and longitude 144–148°E, between the southeast Australian mainland and Tasmania, a waterway that connects the Tasman Sea and the Southern Ocean. The strait consists of over 100 islands, with the largest being Flinders Island, King Island (on the western side), *truwana*/Cape Barren Island and *lungtalanana*/Clarke Island (Harris et al., 2001; Fig. 2). *truwana*/Cape Barren Island, the main study site of this thesis, is located in the eastern part of Bass Strait (Furneaux Group), about 35 km northeast of Tasmania between Flinders Island and *lungtalanana*/Clarke Island. *truwana* is the Indigenous given name of Cape Barren Island and most of the island's residents are descendants of European sealers and Aboriginal peoples who, in the early 1800s, settled on smaller nearby islands, but relocated to *truwana* in the late 1870s. Today, *truwana* is under the management of Flinders Council.

1.6. Thesis main methods

This thesis involves the analysis of nine sediment cores in total, which were collected from lagoons and swamps on *truwana*/Cape Barren Island, with the permission of the Tasmanian Aboriginal Corporation and *truwana* Rangers (Plate I). None of these sites have been studied using palaeoecological methods previously. Major proxies analysed in the sediment cores include pollen, non-pollen palynomorphs (NPPs) and charcoal particles. Laboratory processing of these proxies follows the standard palynological procedure in Faegri and Iversen (1975) and the charcoal processing method in Whitlock and Larsen (2001) (Fig. 3).

All samples/specimens were processed and analysed at the Archaeology and Natural History Laboratory, Australian National University. All stratigraphic diagrams were produced using Tilia 2.6.1 (<https://www.tiliait.com/>) and statistical analyses were done using 'R' (R Core Team, 2020) and 'CharAnalysis' programs (Higuera, 2009). Some of the recorded pollen, which will be frequently mentioned throughout this thesis, are presented in Plate IIa and b, especially the Myrtaceae (*Eucalyptus*, *Melaleuca*, *Leptospermum*), Casuarinaceae (*Allocasuarina*/*Casuarina*), Ericaceae (*Monotoca*, *Sprengelia*, *Epacris*), Cyperaceae, Poaceae and Restionaceae.

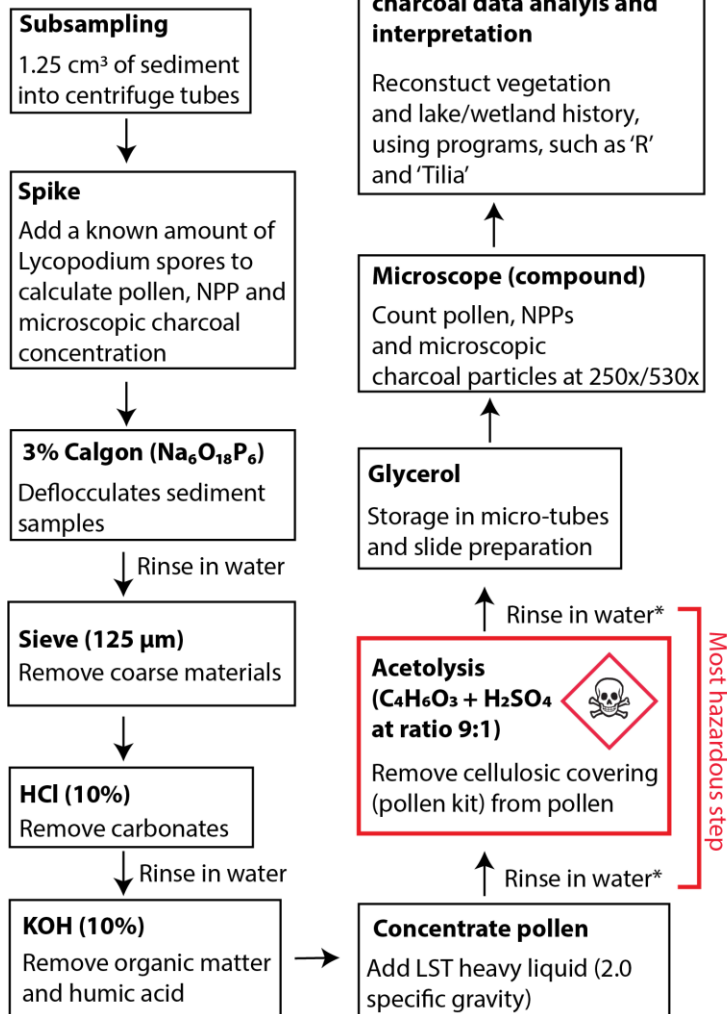


Plate I: Sedimentary core collection on truwana/Cape Barren Island, Bass Strait, with assistance of the truwana Rangers and Tasmanian Aboriginal Corporation (pakana) Rangers. The left image is the author (Matthew Adeleye) holding a freshly collected sediment core with assistance of the truwana ranger behind me (Terry Maynard). The right image is the author (centre) recording sediment core details with Prof. Simon Haberle (right) and Dr. Feli Hopf (left), as well as other truwana rangers in the background.

Indigenous engagement

Prior to our visit to truwana to conduct field work (Plate I), we liaised with the Indigenous community to gain permission to work on Country. We also consulted with the truwana community leadership through the truwana rangers and the Aboriginal Land Council of Tasmania (ALCT) to approve the submission of research outcomes for publication. Each manuscript was submitted to the truwana rangers and the ALCT as a draft for consideration and final approval before being submitted for publication. Once current travel restrictions are eased, we will visit truwana again to present the findings in this thesis to the community and provide them with copies of the thesis and educational booklet containing thesis results in plain language (see Appendix 10.9, page 326).

POLLEN, NPP AND MICROSCOPIC CHARCOAL



*Rinse in glacial acetic acid (CH₃COOH) before rinsing in water to avoid a violent reaction between acetolysis mixture and water

MACROSCOPIC CHARCOAL

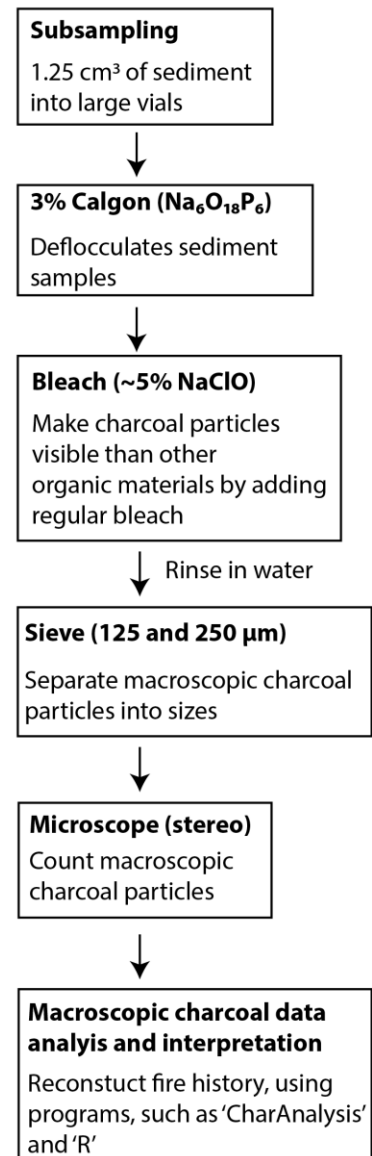


Figure 3: Processing flowchart of major proxies used in this thesis, including pollen, non-pollen palynomorphs (NPPs), and charcoal.

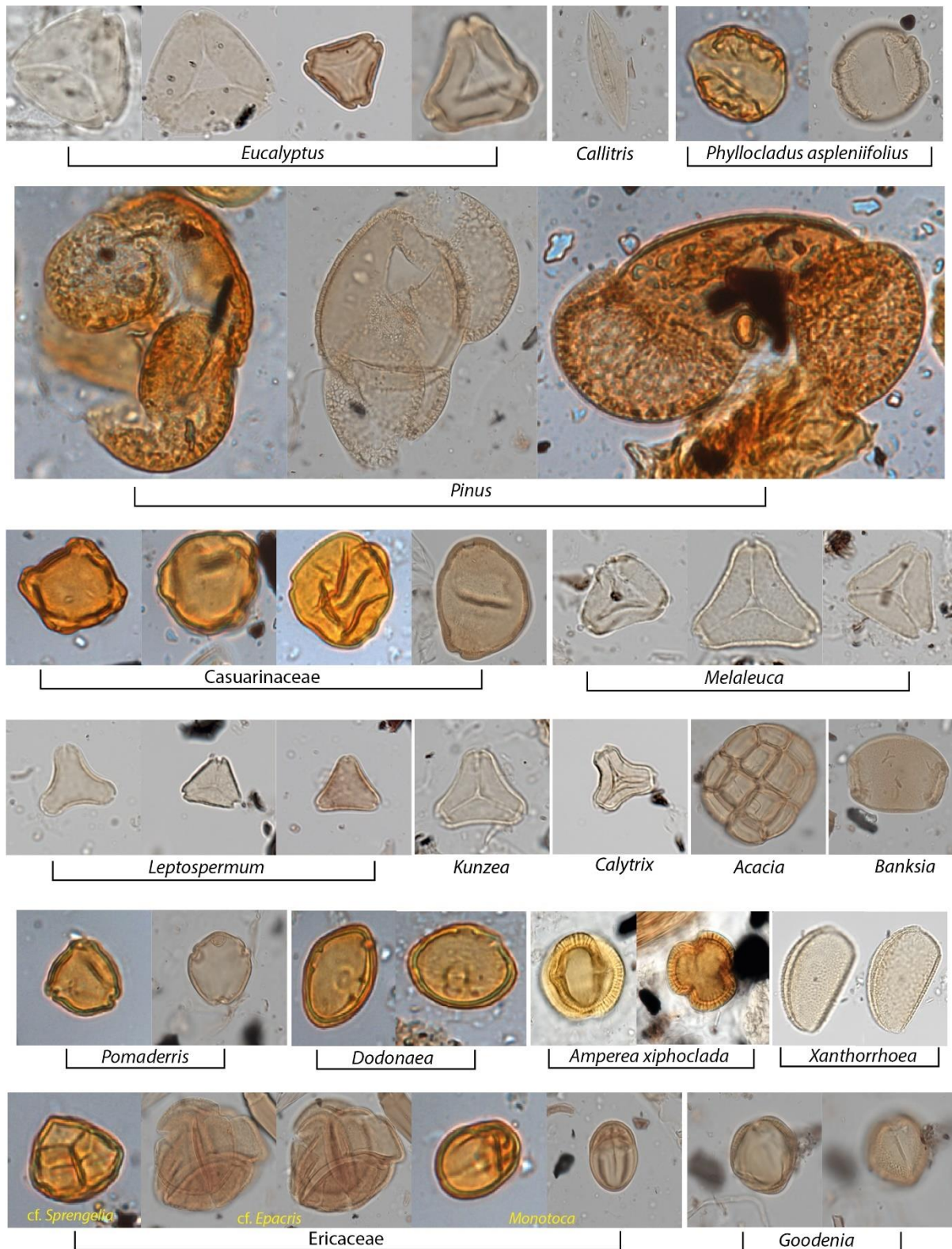


Plate IIa: Some of the pollen types recorded in the truwana/Cape Barren Island records – these types are frequently mentioned throughout this thesis. Arrangement of pollen types follows terrestrial trees, shrubs and herbs to wetland and aquatic herbs, and ends with ferns and fern allies. Taxa represent native plants with the exception of introduced *Pinus*.

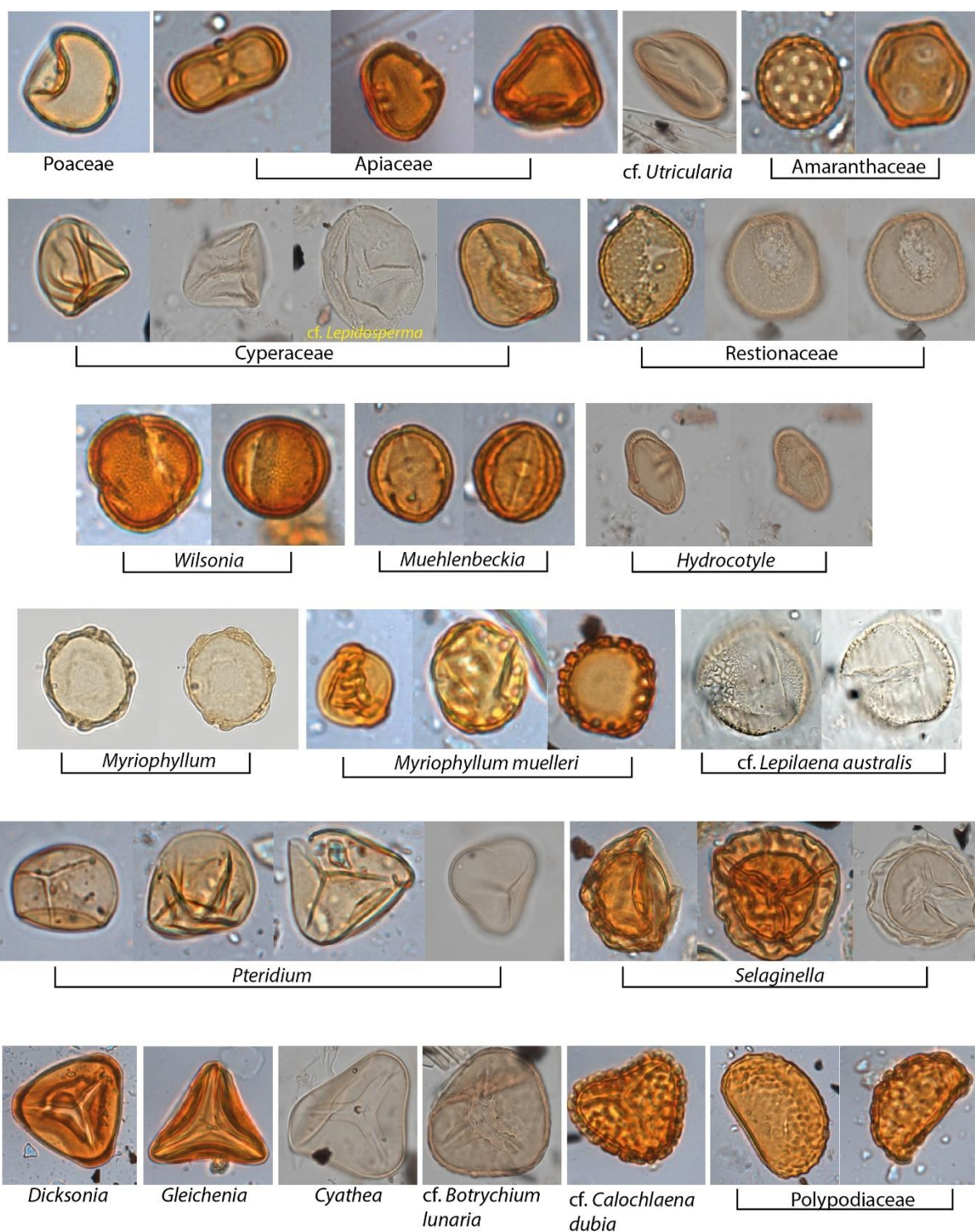


Plate IIb: Plate IIa continued.

Chapter 2 ENVIRONMENTAL CHANGE DURING THE LAST GLACIAL ON AN ANCIENT LAND BRIDGE OF SOUTHEAST AUSTRALIA

The last glacial period environmental changes in Bass Strait and southeast Australia at large are presented in this chapter. In particular, vegetation, lake levels and fire regime changes on the Bassian Land Bridge, which once connected the southeast Australian mainland to Tasmania, are explored and the role of the landbridge in biotic dispersals is highlighted. Finally, the synchronous earlier timing of the Last Glacial Maximum is discussed on a hemispheric scale.

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with
https://policies.anu.edu.au/ppl/document/ANUP_003405

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

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Endorsed

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Date

2.0. Environmental change during the last glacial on an ancient land bridge of southeast Australia

Abstract

The Last Glacial Maximum (LGM) remains an enigmatic period in southeast Australia due to the limited spatial and temporal resolution of its palaeoclimatic records. A major feature of the LGM landscape was the existence of the Bassian Land Bridge, joining Tasmania with the mainland of Australia during periods of low sea level, and potentially facilitating increased biotic movement between these regions. To better understand biogeographical changes on the land bridge and in southeast Australia generally during the LGM, we present a 35 ka-year palaeoecological record from one of the larger islands of Bass Strait. Pollen, charcoal, and non-pollen palynomorphs were analysed in a 1.75-m sediment core from truwana/Cape Barren Island, Bass Strait, to reconstruct changes in vegetation, fire regimes and lake levels on the Bassian Land Bridge. Results were then compared to existing palaeoenvironmental studies in the region to develop a broader context of the prevailing land bridge environment and the potential influence on biotic dispersals in Australia during the last glacial period. Results suggest a major vegetation shift on the Bassian Land Bridge in response to the establishment of the LGM climate, with grassland expansion at the expense of woodland from ~29–11 ka. Floristic richness, biomass burned and lake levels also markedly decreased through this period, with the driest interval being ~25–18 ka. Dryland herbaceous taxa dispersed between the mainland and Tasmania when the landbridge was fully exposed. In agreement with previous studies, our results show that the dry grassland that dominated southeast Australia (and Southern Hemisphere mid-latitude areas) during the LGM also extended across the Bassian Land Bridge. The prevailing environment on the land bridge is likely to have exerted a selective influence on biotic dispersals in Australia during glacial periods.

2.1. Introduction

Ancient land bridges (which today are maritime straits) formed during glacial periods and are known to have served as biogeographic corridors for terrestrial species assembly, distribution, and diversification (Lee et al., 2020; Molina-Venegas et al., 2015; Graham, 2018; DeChaine, 2008; Elias et al., 1996). Human migration was facilitated between

adjacent lands during periods of low sea level (Elias et al., 1996). Land bridges can also serve as ecological filters, capable of driving species divergence/disjunction between land masses on timescales of thousands to millions of years (Qi et al., 2014; Graham, 2018). The emergence and submergence of these land bridges were controlled by sea-level rise and fall during interglacial and glacial periods, respectively. A well-documented example is the Bering Strait/Land Bridge between western Alaska and eastern Siberia, which was the conduit for human migration and other biotic exchange between the Americas and Eurasia during the last glacial period until about 14–10 ka when postglacial sea-level rise submerged the terrestrial pathway (Hopkins, 1967; Mandryk et al., 2001; Wooller et al., 2018; Jakobsson et al., 2017). The history of this land bridge and biotic exchange between the two regions dates back to at least the Cretaceous and has played a major role in North American vegetation assembly (Graham, 2018). Other examples of ancient land bridges that served as biotic corridors in the past include Doggerland, which previously connected Great Britain and Ireland to continental Europe (Vincent et al., 2007), the Gibraltar Strait/Land Bridge between southern Iberian Peninsula and northwest Africa (Monila-Venegas et al., 2015), the Torres Strait/Land Bridge between Australia and Papua New Guinea (Reeves et al., 2008), and the Bass Strait/Land Bridge (the focus of this study) between the southeast Australian mainland and Tasmania (Lambeck and Chappell, 2001).

Bass Strait was a land bridge (Bassian Land Bridge) for several millennia during the peak of the last glaciation about 25–18 ka (Last Glacial Maximum; Lambeck and Chappell, 2001; Orchiston, 1979) and during earlier glacial periods about 40–25 ka (Lambeck and Chappell, 2001). The Bassian Land Bridge allowed people to move between the southeast Australian mainland and Tasmania as early as 40,000 years ago (Cosgrove, 1995; Williams et al., 2018), representing one of the earliest movements of people into high southern latitudes on the globe. In addition to natural species dispersals (e.g., Noetling, 1911; Worth et al., 2017), the movement of people across the Bassian Land Bridge may have also promoted increased biotic (e.g., herbaceous plant) exchange through human-introduction, as well as biotic depletion due to human impacts (Márquez-Corro et al., 2017). The nature of environmental changes on the Bassian Land Bridge during these periods of lower sea level and particularly during the Last Glacial Maximum (LGM) remains poorly understood due to a lack of detailed and well dated palaeoecological records. Two LGM pollen records from Hunter Island and King Island are available, and show the prevalence of herbaceous vegetation on the western margins of the Bassian Land Bridge (Hope, 1978; D'Costa et al.,

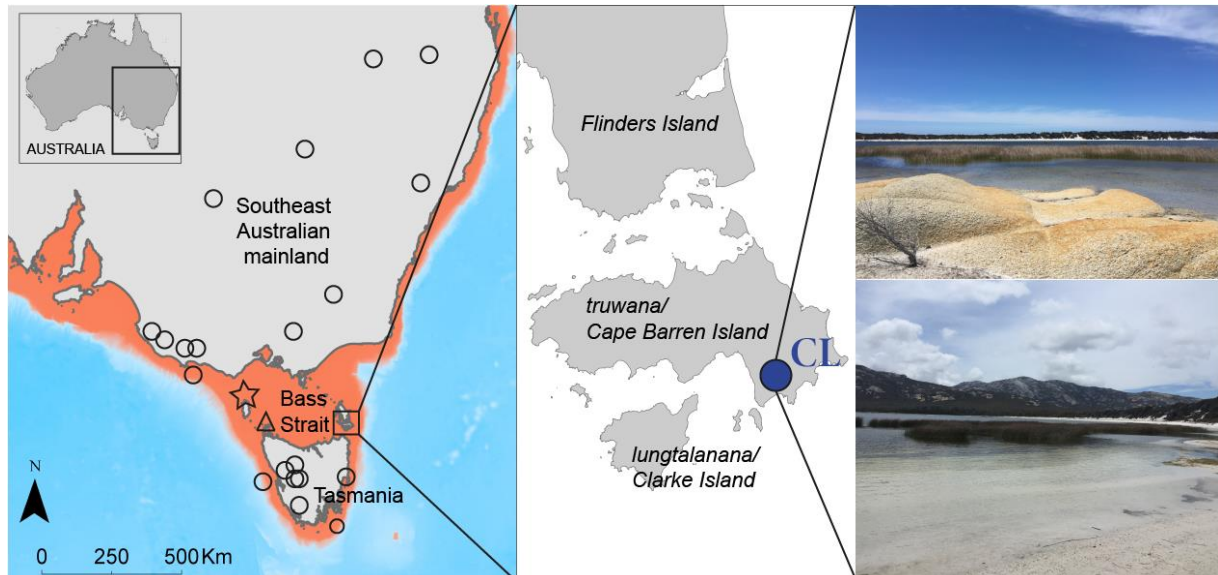
1993; Fig. 1). Similar vegetation prevailed at many southeast Australian sites on the mainland (Dodson and Wright, 1989; Edney et al., 1990; Colhoun et al., 1999; Field et al., 2002; Chalson and Martin, 2007; Mooney et al., 2017; De Deckker et al., 2019). However, the Bass Strait records lack robust chronologies and have low sample resolutions, providing little confidence in our knowledge of the Bassian Land Bridge and southeast Australia's palaeoenvironment/palaeoclimate in general. Analysis of additional, well-dated sediment cores from Bass Strait will increase our confidence and therefore capacity in southeast Australian site comparisons, as well as help to better understand how the land-bridge environment acted as a biogeographic filter that has influenced present-day species distribution.

In this study, we aim to reconstruct the nature of changes in vegetation, fire regimes and the environment of the Bassian Land Bridge during the last glacial period and compare these changes to adjacent southeast Australian mainland and Tasmanian sites. In order to achieve these aims, we analysed fossil pollen, charcoal remains and non-pollen palynomorphs (NPPs) in a 1.75-m sediment core collected from one of the larger islands of Bass Strait (truwana/Cape Barren Island 'CBI'). We then compared our results to existing palaeoenvironmental studies in the region to develop a broader context of the prevailing land bridge environment and the potential influence on biotic dispersals in Australia during the last glacial period.

2.2. Study area (Bass Strait and truwana/Cape Barren Island)

Bass Strait is a ~200-km stretch of water that separates the Australian mainland from Tasmania. Over 100 islands are today found in Bass Strait, and all of these became isolated from the mainland and Tasmania during early-mid Holocene sea-level rise (Lambeck and Chappell, 2001; Sloss et al., 2007; Williams et al., 2018; Fig. 1). During the LGM, low sea-levels exposed the ca. 200 km long by 400 km wide Bassian Land Bridge that connected southeast Australian mainland and Tasmania between 43 ka and 14 ka (Lambeck and Chappell, 2001). Archaeological data from this time indicate the Bassian Land Bridge was used by people to move between the Australian mainland and Tasmania (Cosgrove, 1995; Lambeck and Chappell, 2001; Harris et al., 2001). Granitic mountains and hills stretched between Wilson's Promontory and northeast Tasmania, which later formed the present eastern Bass Strait islands, of which truwana/CBI (our study site) is one of the larger and

more mountainous examples (Harris et al., 2001). 'truwana' (in lowercase) is the Indigenous given name of Cape Barren Island.



Map projection: Australia GDA 1994 MGA Zone 55

Figure 1: Crystal Lagoon coring site on truwana/Cape Barren Island (blue solid circle), Bass Strait, southeast Australia. Also shown are locations of previous palaeoecological records mentioned in this study (black hollow circles), including Cave Bay Cave on Hunter Island (hollow triangle) and Egg Lagoon on King Island (hollow star) in western Bass Strait. Red-shaded areas on southeast Australian map represent the coastline position during the Last Glacial Maximum. Photos show north and south views of Crystal Lagoon, with surrounding dune system.

Truwana/CBI is located on the eastern side of Bass Strait and lies northeast of the main island of Tasmania and south of Flinders Island. Its vegetation is characterized by heathlands, scrub and sclerophyllous forests (Harris and Kitchener, 2005; Fig. 1). The island's area is approximately 480 km² and Devonian Mathinna Beds form the island's oldest geological deposits. The Cenozoic geology is composed of calcareous sandstone, limestone, and basalts (Cocker, 1980) and the Quaternary deposits are composed of aeolian, marine, and alluvial sediments (McClenaghan et al., 2011).

The island's climate is characterized by warm, dry summers with a mean maximum temperature of ~23°C and cool, wet winters, with a mean temperature of ~14°C (Australian Bureau of Meteorology, 2021). The climate is largely modulated by the Southern Annular

Mode (SAM), Blocking Highs and Frontal Systems (Australian Bureau of Meteorology, 2010). SAM is defined by the difference in the zonal mean sea level pressure at 40°S and 65°S and describes the northward and southward movement of the Southern Westerly Winds (SWW) (Lee et al., 2019). During summer, rainfall probability is low when SW winds move northward, while rainfall probability is higher when SWW move poleward. During winter, the reverse is the case. Blocking Highs are strong high-pressure systems formed in higher latitudes at any time of the year and they generally interrupt the flow of low pressure systems across southern Australia. The effect of Blocking Highs ranges from extremely dry to wet and hot to cold conditions depending on their strength and location. The Frontal Systems move from west to east, bringing rainfall and cold fronts, the impact of which is greatest in winter months (Australian Bureau of Meteorology, 2010).

Fire is a major driver of disturbance of the vegetation on truwana/CBI and has shaped the landscape into a mosaic of vegetation with fire boundaries (Perrin, 1998; Sharples et al., 2017). For millennia, a combination of fire and sea-level change was the major driver of vegetation change on the island and surrounding islands (Ladd et al., 1992; McWethy et al., 2017; Adeleye et al., 2021a). Alongside fire, sea-level change (e.g., influence from salt and wind damage from coastline proximity) influenced the development of heathland and scrub in the mid-Holocene and this vegetation dominates the island today (Adeleye et al., 2021a).

2.3. Methods

2.3.1. Coring site (Crystal Lagoon) description

Crystal Lagoon (-40.477381°, 148.350799°, ~8 m asl) is an open-water shallow lake (>1 m depth) on the south-eastern corner of Cape Barren Island. The lagoon is approximately 890 m in diameter and is constrained by 4–5 m high sand dunes (Fig. 1). Today the lagoon is surrounded by a mosaic of heathland, sedgeland, dense scrub, open forest and woodland. The woodlands are dominated by *Eucalyptus nitida*, while heathland and scrub are characterized by *Acacia*, *Banksia*, *Allocasuarina*, *Kunzea*, *Leptospermum* and *Hakea* species. The lagoon margins are patchily occupied by a suite of shrubs including *Allocasuarina monilifera*, *Banksia marginata*, *Kunzea ambigua*, *Leptospermum scoparium*, *Leptospermum laevigatum*, *Hakea* sp., *Acacia mucronata*, *Pultenea juniperina*, *Pomaderris*, and *Myoporum insulare*, and wetland plants (*Scirpus* and *Carex* spp).

2.3.2. Sediment core collection and chronology

A sediment core 1.75 m long was collected from the southwestern margin of Crystal Lagoon, in a water depth of ~1m using a Russian corer. Core lithology was recorded on site before wrapping cores for storage and ex-situ analysis. Bulk sediment subsamples (1cm-thick each) were taken along the sediment core and radiocarbon dates derived by Accelerator Mass Spectrometry (AMS) from DirectAMS, Washington. The derived radiocarbon dates were then calibrated with the SHCal20 curve to create an age-depth model, using the 'rbacon' package in R (Hogg et al., 2020; Blaauw and Christen, 2011; R Development Core Team, 2019). The date (2019) of core collection was assigned to the top sample (0 cm) as -69 calendar years before present (cal yr BP). No limestone is observed around Crystal Lagoon, and this reduces the potential for marine reservoir effects on radiocarbon dates.

2.3.3. Pollen, non-pollen palynomorph (NPP) and charcoal analyses

In order to reconstruct vegetation history, the sediment core was subsampled every 2–4 cm and analysed for pollen following standard pollen preparation techniques including HCl, KOH and acetolysis (Faegri and Iversen, 1975). Pollen and spores were identified with the aid of the online Australasian Pollen and Spore Atlas (<http://apsa.anu.edu.au/>) and at least 300 terrestrial pollen were identified in each sample (except two samples, 60 and 64 cm, in which at least 100 terrestrial pollen were identified due to extremely low pollen concentrations). The sum of terrestrial trees, shrubs and herbs comprises the base pollen sum, and aquatic and spore sums were calculated relative to the base pollen sum. Pollen diagrams were generated using Tilia 2.6.1 (<https://www.tiliait.com/>) and pollen zones determined using CONISS cluster analysis, following square root transformation of pollen percentages. Rarefaction analysis was conducted on pollen data to estimate palynological richness, a proxy for floristic richness that has been empirically proven (Birks et al., 2016), and applied in pollen records of southeast Australian vegetation (see Adeleye et al., 2021b).

In order to estimate the rate of vegetation change through time, a Detrended Correspondence Analysis (DCA) was conducted on pollen data after square-root transformation. The first DCA axis scores were extracted, and sample-to-sample differences were computed to quantify the amount of palynological (vegetation) change. A

Bayesian change point analysis was further conducted to identify major trends in the amount of vegetation change following Wang et al. (2018). All analyses were conducted using the 'vegan' and 'bcpr' packages in R (Oksanen et al., 2020; Wang et al. 2018).

The sediment core was subsampled contiguously for macroscopic charcoal analysis following the method of Whitlock and Larsen (2001) to reconstruct catchment-scale fire activity. The method involves bleaching and washing of sediment samples through 125 and 250 μm sieves. Macroscopic charcoal particles $>125\ \mu\text{m}$ and $>250\ \mu\text{m}$ were counted and expressed as accumulation rates (particles/ cm^2/yr). Microscopic charcoal particles $<125\ \mu\text{m}$ were counted on pollen slides and accumulation rates calculated (particles/ cm^2/yr), using concentration values calculated through the addition of a *Lycopodium* spike (Lund University, *Lycopodium* tablet batch 3862), to infer fire activity at a more regional scale (Whitlock and Larsen, 2001).

Non-pollen palynomorphs (NPPs), as well as aquatic/wetland plants, are sensitive to local changes in hydrology, salinity, temperature and nutrients (van Geel, 2001). We used these proxies to infer past local ecological changes (influenced by lake levels) at Crystal Lagoon. Non-pollen palynomorphs (NPPs) were counted in pollen slides and identified using a key (Sonneman et al., 1999) and Kiel University's online database (https://www.wikis.uni-kiel.de/non_pollen_palynomorphs/doku.php/home). Percentages were calculated relative to the base terrestrial pollen sum.

2.4. Results

2.4.1. Core lithology and chronology

The Crystal Lagoon sediment core was composed of dark (organic) silty clay from 175–100 cm, grey silty clay from 100–56 cm and coarse sand, with minor organic detritus from 56–24 cm, while the top 24 cm is composed of dark silty clay with fibrous plant material. The core age-depth model produced an estimated basal age of ~34.5 ka (Fig. 2, Table 1).

Table 1: AMS radiocarbon dates for Crystal Lagoon, Bass Strait measured at Direct AMS, Washington.

Depth (cm)	Lab ID	¹⁴ C yr BP	Error (1σ)	Calendar age range
17	D-AMS 036715	1063	25	903–958
57	D-AMS 036716	9820	35	11,151–11,256
67	D-AMS 039099	14,706	60	17,797–18,193
73	D-AMS 039100	18,057	65	21,732–22,164
81	D-AMS 036717	19,997	78	23,811–24,195
90	D-AMS 039101	24,334	100	28,159–28,779
110	D-AMS 039102	31,600*	160	35,501–36,248
121	D-AMS 036718	27,113	136	31,007–31,336
140	D-AMS 039103	25,271*	138	29,192–29,892
141	D-AMS 036719	30,935*	215	34,679–35,738
169	D-AMS 036720	29,305	151	33,388–34,250

*Excluded AMS dates due to potential sediment mixing/contamination.

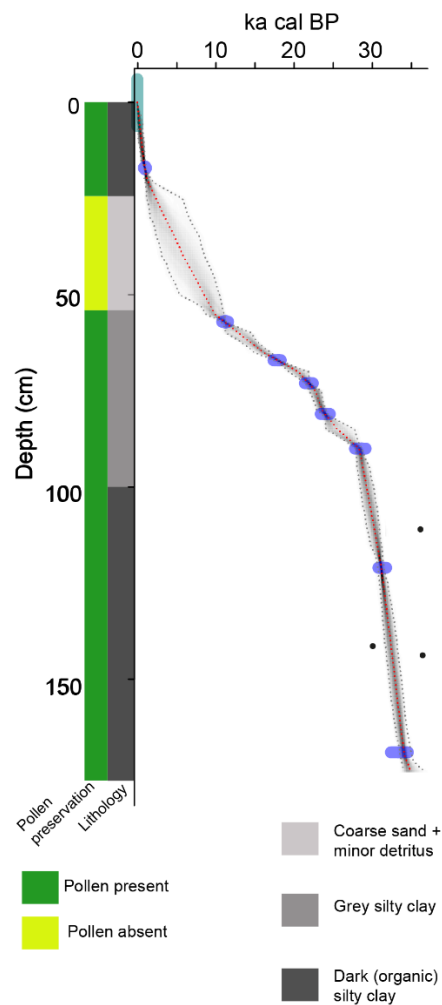


Figure 2: Core lithology and age-depth model for Crystal Lagoon, Bass Strait, showing calibrated ¹⁴C dates (purple), age-depth model (dark grey), 95% confidence intervals of calibrated range (light grey), single model based on the weighted mean age for each depth (red curve), and excluded dates (black

dots). 'ka cal BP' is thousand calendar years before present. Green and yellow-shaded areas indicate pollen preservation in the sediment core, with no preservation in the coarse sand section (yellow; 56cm–25 cm: ~10.6–2.5 ka).

2.4.2. Vegetation and fire history inferred from terrestrial pollen and charcoal

Our results focus on samples from ~35–10.7 ka, which cover the early glacial–LGM transition, LGM and late glacial, as well as the period when truwana/CBI was part of the Bassian Land Bridge (Fig. 2). The sand-dominated Holocene samples (56cm–25 cm: ~10.7–2.5 ka) were found to be devoid of palynomorphs and are provided in Appendix S1 (Fig. S1). The results of the analysis of macroscopic charcoal particles >125 µm and >250 µm exhibited similar trends and are therefore summed (>125+>250 µm). Accumulation rates are presented and reported (Fig. 3).

CONISS cluster analysis identified three major zones (CL-1, CL-2, and CL-3) in the Crystal Lagoon record between ~35 ka and 10.7 ka (see Appendix S1 for detailed pollen zone descriptions). Zone CL-1 (~35–29 ka) at the base of the core features abundant *Eucalyptus*, Restionaceae and *Monotoca*, as well as high charcoal accumulation rates and floristic richness (Fig. 3). Casuarinaceae and Poaceae increase in zone CL-2 (~29–25.2 ka), accompanied by decreasing charcoal accumulation rates and floristic richness. Zone CL-3 (~25.2–10.7 ka) begins with a rapid decline in Casuarinaceae and with a further expansion of herbaceous taxa, especially Poaceae, reaching up to 80% as well as an increase in aquatic/wetland taxa (Fig. 3). There is also a minor increase in *Eucalyptus* in the first part of the zone (CL-3a: ~25.2–18.6 ka) and Casuarinaceae later in the second part of the zone (CL-3b: ~18.6–10.7 ka). Floristic richness is low in zone CL-3, with a slight increase at the end of subzone CL-3b.

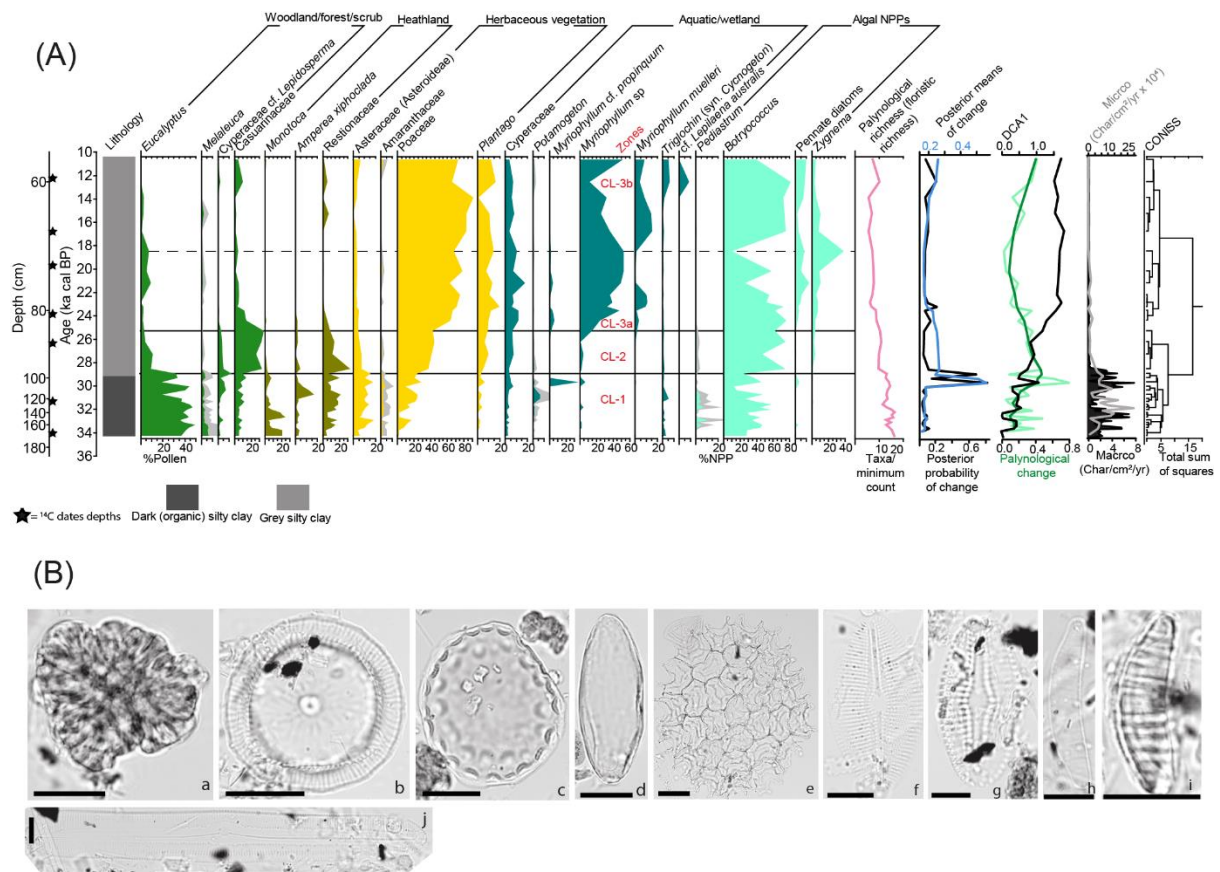


Figure 3: (A) Crystal Lagoon percentage diagram of major (>5%) pollen and NPPs with CONISS-derived zones, lithology, palynological richness, and charcoal records. Also shown is the DCA scores for the first axis and the computed amount of palynological (vegetation) change with loess smoothing (span=0.25), as well as posterior means and probabilities of vegetation change. See Fig. S2 in Appendix S1 for percent diagram of minor pollen and NPPs (<5%). (B) Non-pollen palynomorphs recorded in the Crystal Lagoon core: (a) *Botryococcus* (HdV-766); (b) *Debarya* (HdV-214); (c) *Zygnema* (HdV-141); (d) *Spirogyra* (HdV-130); (e) *Pediastrum angulosum* (HdV-760); (f–g) *Diploneis* cf. *elliptica*; (h–i) *Epithemia* cf. *zebra*; (j) *Pinnularia*. See Table S1 in Appendix S1 for ecological details of NPPs. Scale bar = 20 µm.

2.4.3. Amount of vegetation change through time

Detrended Correspondence Analysis (DCA) shows period of greatest palynological (vegetation) change is from ~30 to 28 ka, while the amount of vegetation change was low in the remaining parts of the record. Results from Bayesian change point analysis also indicate that the period with the highest likelihood of vegetation change was between ~30 ka and 28 ka (Fig. 3).

2.4.4. Changes in Crystal Lagoon inferred from NPPs, aquatic/wetland pollen, core lithology and accumulation rates (see Appendix S1 for NPP ecological details)

Core lithology indicates a transition from organic to inorganic clay in Crystal Lagoon from ~35–29 ka when sedimentation rates were highest (zone CL-1; Fig. 2). *Botryococcus* and *Pediastrum* (Fig. 3) were prevalent during this time and the aquatic macrophyte *Potamogeton* was present. *Zygnema* and pennate diatoms (cf. *Diponeis*, *Pinnularia* and *Epithemia*) gradually increased from ~29 ka (zone CL-2 and CL-3) at the expense of *Pediastrum*, an interval characterized by inorganic clay and low sedimentation rates. Cyperaceae increased from this time as well. *Botryococcus* continued to be present after ~29 ka but decreased between ~25 ka and 18 ka (subzone CL-3a) in favour of *Zygnema* and pennate diatoms. The aquatic macrophyte *Myriophyllum* sp increased extensively in subzone CL-3a. Other NPPs recorded in low abundance in this interval include *Spirogyra* and *Debarya*. *Botryococcus* increased again after ~18 ka (subzone CL-3b), while *Zygnema* decreased, and pennate diatoms (mostly *Epithemia*) continued to be present. *Myriophyllum* sp decreased slightly in favour of *Myriophyllum muelleri* until ~12 ka (Fig. 3).

2.5. Discussion

2.5.1. The Bassian Land Bridge landscape during the last glacial period

This study presents the first detailed record of palaeoenvironmental change in the Bass Strait region of southeast Australia during the last glacial period from ~35 to 10 ka. Our palaeoecological data reveal a major environmental change in the region around 29 ka, which featured a shift from a wet wooded landscape during MIS 3 to a dry grassy landscape during MIS 2 and into early MIS 1 (Fig. 4). The nature of the environmental shift and timing is consistent with vegetation change recorded for other mid–high latitude areas in both hemispheres (including Northern Hemisphere land bridges), as well as global climatic and sea-level shifts during the last glacial period (e.g., Newnham, 2007; Cadd et al., 2021; Langgut et al., 2011; Ager and Phillips, 2018; Lambeck et al., 2014; Fig. 4).

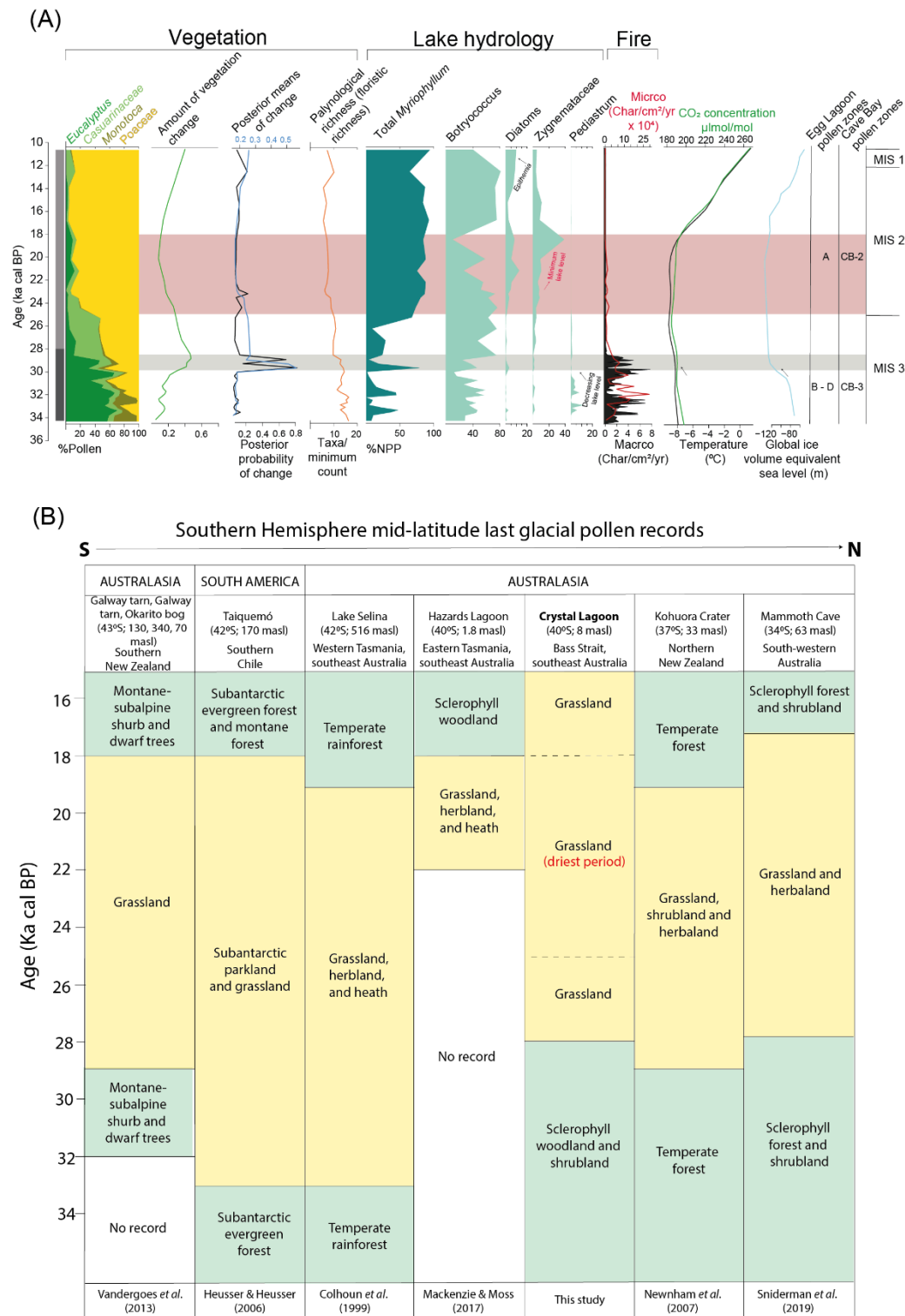


Figure 4: (A) Summary palaeoecological diagram from Crystal Lagoon, showing changes in vegetation, lake hydrology and fire activity in the Bass Strait region in relation to global ice-volume equivalent sea-level change (Lambeck *et al.*, 2014), temperature change (Parrenin *et al.*, 2013) and CO₂ change (Köhler *et al.*, 2017) during the last glacial period (see Fig. 3 for lithology legend). Total Zygnemataceae include *Zygnema*, *Spirogyra* and *Debarya*. Grey-shaded zone indicates the timing of major vegetation shift around 29 ka, which marks the beginning of the full glacial climate, while red-shaded zone indicates the

period of maximum aridity on the Bassian Land Bridge. Also shown are pollen zones of previous records from western Bass Strait, which are comparable to Crystal Lagoon pollen zones. They include Egg Lagoon record on King Island (D'Costa et al., 1993) and Cave Bay Cave record on Hunter Island (Hope, 1978). (B) High-temporal resolution Southern Hemisphere mid-latitude ($<30^{\circ}\text{S}$) last glacial pollen zones, including Crystal Lagoon record in this study (bold), showing dominant vegetation types. Vegetation shift under the full glacial climate is evident in most records at least around 29–28 ka, with grassland expansion (yellow-shaded section).

Early glacial environmental changes on the Bassian Land Bridge

The pollen composition and percentage abundance in Crystal Lagoon during the interval ~35–29 ka are comparable to pollen assemblages in the basal zone of records from Hunter Island and King Island (Hope, 1978; D'Costa et al., 1993; Fig. 4), as well as a recently published record of a single early-glacial sample from Flinders Island (Ladd and Clarke, 2020). This suggests that open *Eucalyptus* woodland with a shrub and herbaceous understorey prevailed on the Bassian Land Bridge from ~35–29 ka, during a time with high levels of biomass burning (Fig. 4). Higher sea levels prior to ~30 ka in conjunction with fire may have favoured salt-tolerant and fire-adapted *Monotoca* heath and heathland along the coastal margins of the Bassian Land Bridge (Howells, 2012; Adeleye et al., 2021a), as well as a heathy understorey within eucalypt woodland (Harris et al., 2001). This vegetation structure and composition, as well as fire regime, are consistent with those recorded for southeast South Australia (Dodson, 1975, 1977) and southeast Australian mainland in general during the end of MIS 3 (Mooney et al., 2011).

Climate during the end of MIS 3 (~35–29 ka) is thought to have been wet and humid in temperate Australia (Bowler et al., 2012; Reeves et al., 2013; Kemp et al., 2019), and high moisture may have allowed the prevalence of a relatively stable, floristically rich woody vegetation with sufficient woody fuel accumulation for major biomass burning (Mooney et al., 2011) on the Bassian Land Bridge. High fuel connectivity due to a dense understorey shrub layer, especially taller shrubs such as *Melaleuca* (ladder fuel), would have also facilitated fire spread.

A wetter climate during the end of MIS 3 is also reflected in algal and aquatic pollen assemblages in the Crystal Lagoon record (Fig. 3). Crystal Lagoon was likely a permanent open freshwater lake system, at least before ~30 ka, as reflected by the abundance of

Pediastrum (mostly *P. angulosum*) and *Botryococcus*, and the scarcity of aquatic macrophytes, especially *Myriophyllum*. *Myriophyllum* species presently occur in shallow waters (<1 m deep) on truwana/CBI (Harris and Kitchener, 2005) and would have possibly occupied the shallower parts of Crystal Lagoon before ~30 ka. *Pediastrum* algae occur in a range of freshwater bodies, but fossil records from temperate zones suggest *Pediastrum* has been mostly associated with open, clear waters (Komarek and Jankovska, 2001). *P. angulosum* abundance during this period may also reflect higher rates of organic sediment deposition and dissolved organic carbon in Crystal Lagoon, suggesting increased runoff into the lagoon due to a relatively high rainfall at this time (Rasmussen and Olsen, 2009; Weckström et al., 2010). The inferred high lake level in Crystal Lagoon prior to ~30 ka aligns with lake-level reconstructions from lakes in central–southern New South Wales around the same time (e.g., Kemp and Spooner, 2007; Kemp and Rhodes, 2010; Bowler et al., 2012; Coventry, 1976).

Full glacial environmental changes on the Bassian Land Bridge

Our DCA analysis and Bayesian change-point analysis suggest the change from a woody to grassy vegetation at Crystal Lagoon around 29 ka was significant. Rarefaction analysis also shows a decline in floristic richness as woodland, scrub, and heathland taxa receded at this time, though this result may partly reflect the potential effect of evenness due to grass pollen dominating the record (see Birks et al., 2016). These prominent changes likely mark the onset of the full glacial climate on the Bassian Land Bridge.

The timing of the LGM in southeast Australia and Australia in general is thought to have occurred from ~20 to 17 ka (Barrows et al., 2002) and featured widespread aridity with grass-dominated herbaceous vegetation, low lake levels and reduced biomass burning in southeast Australia (Kemp and Rhodes, 2010; Bowler et al., 2012; Chalson and Martin, 2008; Colhoun and Shimeld, 2012; Dodson and Wright, 1989; Mooney et al., 2011, 2017; Falster et al., 2018; Colhoun et al., 1999; Harle, 1997; Harle et al., 1999; Harle et al., 2002; Harle et al., 2004; De Deckker et al., 2019). The nature of vegetation shift in southeast Australia during the LGM also extends to other Southern Hemisphere mid-latitude areas, including south-western Australia (Sniderman et al., 2019), New Zealand (Vandergoes et al., 2013; Newnham et al., 2007) and southern Chile (Heusser and Heusser, 2006). However, the aforementioned mid-latitude pollen records indicate an earlier shift in

vegetation and extended LGM period from ~30–28 to 18–17 ka, which is consistent with our pollen record for the Bass Strait area (Fig. 4). While the timing of the LGM remains debatable (Hughes et al., 2013), our result lend support to existing views on an extended LGM timing in the Southern Hemisphere, including in lower latitudes (Petherick et al., 2017; Cadd et al., 2021).

The increase in Poaceae (grass) pollen after ~29 ka, which is also observed in the Hunter Island and King Island records, suggests the replacement of open woodland with extensive grass-dominated vegetation (grassland) on the Bassian Land Bridge under full glacial conditions (Fig. 4). This interpretation is based on the low pollen productivity of temperate grass and its underrepresentation in fossil records (Mariani et al., 2016b). The competitive advantage of grass under a low CO₂ regime may have maintained or enhanced grass biomass and pollen production compared to other C₃ plants under the full glacial climate (Cowling and Sykes, 1999; Gerhart and Ward, 2010). Reduced woody biomass (C₃ plants) likely explains low biomass burnt at Crystal Lagoon and southeast Australia in general during the LGM (29–18 ka; Bradstock, 2010; Mooney et al., 2011). Even so, scattered trees were likely present on the grassy land bridge, as indicated by the presence of Casuarinaceae and *Eucalyptus* after ~29 ka. Though a percentage abundance value of 20% or lesser is generally considered low for Casuarinaceae, given its high pollen productivity and overrepresentation in pollen assemblages (Dodson, 1983). The intense climate-induced physiological stress C₃ plants experienced during the LGM, especially due to extremely low CO₂ levels, may have generally caused low pollen productions in the woody plants (Gerhart and Ward, 2010). It is also possible that high physiological stress may have reduced the recovery of woody taxa when fire did occur.

Arid conditions on the Bassian Land Bridge from ~29 ka are also reflected in shallow water levels in Crystal Lagoon, as indicated by the expansion of *Myriophyllum* and alga types such as *Botryococcus* and Zygnemataceae at the expense of *Pediastrum* (Cook et al., 2011; Fig. 4). Cyperaceae increase at the same time suggest sedgeland/sedge mat expanded into Crystal Lagoon as water levels dropped under arid conditions. Crystal Lagoon likely transitioned from a lake (open water) to wetland system (swamp/pond) at this time.

The major expansion of grass at the expense of woody and heathland taxa on the Bassian Land Bridge after ~29 ka is consistent with vegetation change on the Bering Land Bridge upon its full exposure (Colinvaux, 1967). The decline in heathland taxa on both land bridges

as sea level significantly receded during the LGM likely reflects the dominant role of sea-level and climate change in shaping heathland vegetation distribution, especially on land bridges and small islands. This suggests that the effect of sea-level change on heathland development is not limited to the postglacial period, as we previously recorded for truwana/CBI (Adeleye et al., 2021a), but was likely a common feature of the Quaternary environment, at least in temperate latitudes (Thomas and Kirkpatrick, 1996; Mackenzie and Moss, 2017).

Period of maximum dryness on the Bassian Land Bridge under the full glacial climate

The Bassian Land Bridge pollen record may reflect a hemisphere-wide and global earlier onset (~29 ka) of the full glacial climate (Fig. 4). However, maximum aridity (minimum lake level) is most likely to have occurred on the land bridge between ~25 and 18 ka, as reflected by the expansion of aquatic/wetland plants (*Myriophyllum* and Cyperaceae) and shallow water algae (*Zygnema*) in Crystal Lagoon during this interval (Fig. 4; Cook et al., 2011). Extremely shallow water depth would have allowed *Myriophyllum*-dominated herbland and Cyperaceae sedgeland to cover the entire or most of the lagoon's surface and would have also promoted optimum conditions (e.g., temperatures) for the proliferation of *Zygnema*, potentially causing lagoon eutrophication (Whitford and Schumacher 1963). Sustained extreme dry conditions from ~25 to 18 ka may have contributed to the minimal changes in grassy vegetation composition on the Bassian Land Bridge at this time (Fig. 4).

Lateglacial environmental changes on the Bassian Land Bridge

Terrestrial vegetation compositional change started to increase at Crystal Lagoon after ~18 ka, with the initial return of heathland and taller woody plants from ~16 and 13 ka, respectively, possibly marking the closing stages of the LGM. This likely reflects a regional signal, as *Eucalyptus* woodland development was already evident in areas further inland on truwana/CBI (Big Reedy Lagoon—Adeleye et al. 2021a) and nearby lungtalanana/Clarke Island (Rexy Boy Lagoon—Hopf, F. et al., in prep.) by 14 ka. Woodlands and forests also started to expand in many other parts of the Australian landscape under an increasingly warm climate, as well as increasing CO₂ and sea levels around this period (Colhoun and Shimeld, 2012; Reeves et al., 2013; Mackenzie and Moss, 2017; Ellerton et al., 2017;

Sniderman et al., 2019; Fig. 4). Although Crystal Lagoon's sample resolution between ~18 and 11 ka is low, the continued grassland dominance at Crystal Lagoon until ~11 ka may reflect vegetation response to local controls and/or more variable late glacial climatic changes. This vegetation response may have partly been a function of heterogeneous soil conditions, such as variations in soil organic content, rates of weathering, and soil depth (Harris et al., 2001). A similar extended grassland interval has also been recorded in a podzolic sandy lake (Lake Leake) in South Australia from ~35 to 10 ka (Dodson, 1975).

The increase in *Botryococcus* and decline in *Zygnema* after ~18 ka may reflect a slight/gradual increase in water input in Crystal Lagoon, as climate improved after the LGM. However, the lagoon would have been brackish, as reflected by the increase in *Myriophyllum muelleri* (Kattel et al., 2015) and estuarine benthic diatom *Epithemia* (McCarthy, 2013) after ~18 ka (Fig. 4). A negative moisture balance due to less rainfall and increased evaporation under an increasingly warmer climate may have promoted brackish conditions in Crystal Lagoon and other eastern Tasmanian sites (Mackenzie and Moss, 2017; Jones et al., 2017) during this period.

2.5.2. The role of the Bassian Land Bridge in biotic exchange between Tasmania and the southeast mainland

Land bridges are known to have served as ecological corridors and filters for terrestrial species in the deep past, playing a major role in Earth's biological diversification through time and space (Qi et al., 2014; Graham, 2018). Land bridges have also played a major role in human dispersal around the globe by creating windows of opportunity for migration into new environments/landscapes (Elias et al., 1996; DeChaine, 2008; Graham, 2018; Bird et al., 2005). The Bassian Land Bridge is no exception. People used the Bassian Land Bridge to enter Tasmania from the mainland between ~40 and 36 ka (Lambeck and Chappell, 2001; Cosgrove, 1995; Orchiston, 1979). Plant molecular studies have also shown that the Bassian Land Bridge allowed plant dispersal (e.g., some species of Ericaceae, Fabaceae, Euphorbiaceae) between the mainland and Tasmania during the LGM (Worth et al., 2017; Bridgewater, 1976). While these studies provide an understanding of potential biotic throughflow on the Bassian Land Bridge during the last glacial period, palaeoecological data provide important context on the environmental and climatic conditions associated with biotic exchange.

Vegetation dispersal

Flora dispersal between the Australian mainland and Tasmania when the Bassian Land Bridge was exposed was demonstrated in Bridgewater's (1976) southeast Australian phytogeographic study. Two main dispersal routes on the Bassian Land Bridge were mapped in the study, including the eastern and western land bridges. The eastern land bridge stretched between Wilson's Promontory and northeast Tasmania through Flinders, truwana/Cape Barren and Clarke islands. The western land bridge stretched between Cape Otway and northwest Tasmania through King and Hunter islands (Bridgewater, 1976; Fig. 5).

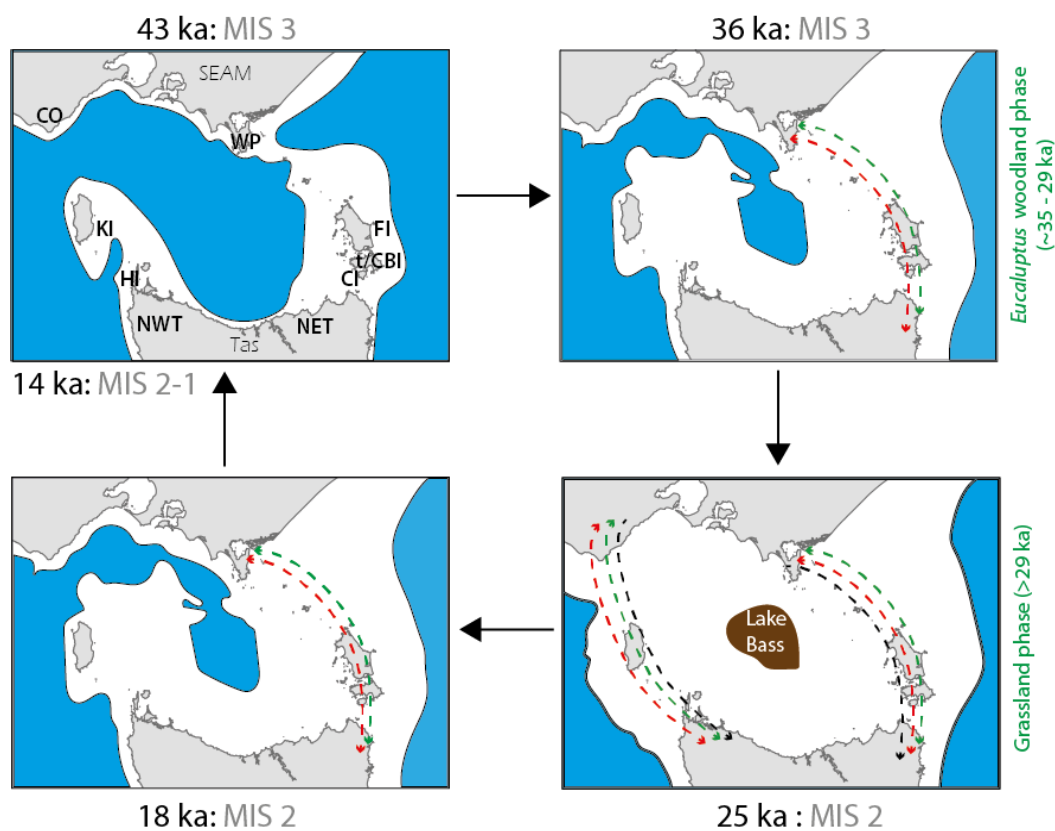


Figure 5: Schematic representation of sea-level/coastline changes on the Bassian Land Bridge during the last glacial period, following Lambeck and Chappell (2001) and Orchiston (1979). The Bassian Land Bridge vegetation phases recorded in this study are also indicated (green text). Note: coastlines around 43 ka and 14 ka are similar (Lambeck and Chappell, 2001). Green-dashed lines indicate major vegetation dispersal routes between the southeast Australian mainland (SEAM) and Tasmania (Tas), which include the eastern and western land bridges, as proposed by Bridgewater (1976). The eastern land bridge stretched between Wilson's Promontory (WP) and northeast Tasmania (NET) through Flinders (FI), truwana/Cape Barren (t/CBI) and Clarke Island (CI). The western land bridge stretched between Cape Otway (CO) and northwest Tasmania (NWT) through King (KI) and Hunter Island (HI). Considering the

duration of the land bridge's exposure, more dispersals would have occurred via the eastern land bridge. Black-dashed lines indicate the direction of grassland expansion during the LGM, as proposed by Hope (1978), which is expansion from the southern SEAM to the Bassian Land bridge and potentially to Tas. Red-dashed lines indicate probable human dispersal routes between SEAM and Tas (Lambeck and Chappel, 2001; Orchiston, 1979).

Worth et al. (2017) expanded on Bridgewater's (1976) study by conducting a DNA sequence study on selected plants species (e.g., species of Myrtaceae, Ericaceae, Casuarinaceae, Fabaceae, Proteaceae, Nothofagaceae) across southeast Australia to investigate the functional traits that mainly controlled the dispersal of plant species through the Bassian Land Bridge during the last glacial period. The study found habitat type to be a major controlling factor of plant dispersals cross the land bridge, and that dry and open vegetation species were more effectively dispersed than wet forest species.

Increased aridity and landscape openness recorded for the Bassian Land Bridge during the last glacial period would have increased the competitive advantage of grass and other herbaceous taxa (e.g., *Plantago*, Asteraceae) over the much-stressed woody *Eucalyptus* and Casuarinaceae, allowing the effective dispersal of herbaceous species between the land bridge's adjacent land masses (Fig. 5). A grassland continuum extending from the mainland to Tasmania likely existed during this period (Hope et al., 1978). *Eucalyptus* and Casuarinaceae would have also been scattered across the grassy land bridge, at least between the adjacent edges of Victoria and northeast Tasmania (Fig. 5; Hope, 1978; Mackenzie and Moss, 2017; Dodson, 1975; Harle, 1997; Harle et al., 2004). Although *Eucalyptus* would have dispersed effectively earlier between these adjacent land masses when conditions were wetter on the land bridge before ~29 ka.

Human and fauna dispersal

It is thought that Indigenous people first arrived in Tasmania using the eastern Bassian Land Bridge from about ~40 ka (Cosgrove, 1995; Lambeck and Chappell, 2001; Orchiston, 1979; Fig. 5). High levels of biomass burning recorded for Crystal Lagoon before ~29 ka may partly reflect Indigenous (managed) burning practices on the wooded land bridge during the initial migration phase. We suggest Indigenous burning may have stabilized woodland vegetation and maintain floristic richness before ~29 ka, a pattern recorded for

the Bass Strait islands and Tasmania during the Holocene (Adeleye et al., 2021b; Romano & Fletcher, 2018; Fig. 4). Sim (1998) in her archaeological study of the eastern Bass Strait, suggested that the large granitic rocks around Crystal Lagoon are suitable for making stone tools (surface stone tool scatters have been recorded around Crystal Lagoon), combined with woodland and freshwater availability, may have been favourable for human occupation in the past. While the ages of the surface scatters of stone tools are unknown, the presence of woodland and open freshwater in Crystal Lagoon may have also provided a suitable occupation site for people before ~29 ka when humans initially entered Tasmania and throughout the late last glacial and into the Holocene (Cosgrove, 1995).

Reduced woody biomass and expanding grassland biomass may have been the primary cause of the decline in charcoal abundance and fire activity around Crystal Lagoon after ~29 ka (Mooney et al., 2011). The decline in fire activity may also partly reflect a major change in Indigenous management strategies (i.e., infrequent, low intensity burning), reflecting a necessary adaptation to a dynamic glacial grassland environment. Williams et al., (2013) in their continental geospatial archaeological study, suggest a major reorganisation in the pattern of Indigenous settlement and subsistence (especially hunting strategies) in Tasmania and other parts of Australia under the LGM climate. Abundant charcoal remains associated with high fire activity in Egg Lagoon during the LGM (D'Costa et al., 1993) may reflect human burning and a more frequent usage of the western land bridge at this time, though the chronology and resolution of this record remains problematic. This may also potentially reflect a spatial heterogeneity in burning strategies associated with the dynamics of Indigenous settlement and subsistence on the Bassian Land Bridge during the LGM, as has been demonstrated on the Tasmanian mainland during the Holocene (Romano and Fletcher, 2018).

The exposure of the Bassian Land Bridge would have not only created a dispersal window for flora and humans, but also for fauna, including megafauna. The timing (~43–37 ka) and cause of megafauna extinction in Tasmania remain contentious and the possibility of coexistence with humans is not agreed upon (Cosgrove et al., 2010; Turney et al., 2008; Roberts and Jacobs, 2008; Gillespie et al., 2012). Our palaeoecological data suggest the environment in which megafauna could have existed/dispersed on the eastern Bassian Land Bridge would have been a largely wooded landscape, with freshwater availability, though with increasingly open and grassy vegetation and shallow lake levels as the glacial climate developed.

Ancient land-bridge environments are generally understudied globally, with only a few detailed studies despite their roles in present-day species distributions. This is the first detailed land-bridge palaeoenvironmental study in the high latitudes of the Southern Hemisphere, and not only has it provided an understanding of the land-bridge environment that supported one of the earliest Southern human migrations, but also offers insights into the sensitivity of land-bridge environments to climate and sea-level changes. Also, our data further support the idea of floral dispersal across the Bassian Land Bridge during the LGM, as in other global land bridges (e.g., Qi et al., 2014; Graham, 2018; Elias et al., 1996; DeChaine, 2008) and also corroborate the idea that it was dry/open vegetation species which preferentially dispersed across the land bridge (Worth et al., 2017).

CONCLUSION

This paper presents the first well-dated last glacial palaeoecological data from the Bass Strait region which served as a major land bridge between Tasmania and the southeast Australian mainland during the LGM. This study set out to understand the nature of changes in vegetation, fire regimes and the local environment on the Bassian Land Bridge during the last glacial period, and how these changes compare to surrounding regions.

Our palaeoecological data reveal a major environmental shift on the Bassian Land Bridge at ~29 ka as conditions became cooler and drier under the full glacial climate. This shift featured grassland expansion at the expense of woodland, with a decline in floristic richness, biomass burned and lake levels. Climate amelioration (primarily increasing moisture availability) eventually supported the return of woody taxa after ~13 ka. In agreement with previous studies, our data indicate an earlier onset of the full glacial climate, with widespread grassland expansion in temperate Australia and Southern Hemisphere mid-latitude areas in general. This study also reinforces the potential role of the Bassian Land Bridge in biotic dispersals between Tasmania and the southeast Australian mainland during the last glacial period.

Chapter 3 HOLOCENE HEATHLAND DEVELOPMENT IN TEMPERATE OCEANIC SOUTHERN HEMISPHERE—KEY DRIVERS IN A GLOBAL CONTEXT

Building on the long-term context provided by the previous chapter, this chapter provides a detailed, multi-site examination of the late glacial and Holocene vegetation development and associated drivers of development in Bass Strait. The drivers of heathland (a rare and endangered dwarf shrubland in Australia) development are particularly identified and discussed in a global context, and implications for management are highlighted.

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with
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I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

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Candidate – Print Name

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Endorsed

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Delegated Authority – Print Name

Signature

Date

3.0. Holocene heathland development in temperate oceanic Southern Hemisphere—key drivers in a global context

Abstract

Understanding long-term heathland development is key in mitigating their current attrition globally. However, such knowledge is limited in Australia and the wider Southern Hemisphere. This study aims to identify potential climatic and environmental drivers of Holocene heathland development in temperate-oceanic Australia (Bass Strait), and also assess the applicability of Iversen's conceptual model of interglacial vegetation development to the area. Multiple sedimentary pollen and charcoal records from truwana/Cape Barren Island (CBI) in Bass Strait were used to reconstruct vegetation and fire history. Rarefaction analysis was used on pollen records to estimate floristic richness for all sites, and magnetic susceptibility and organic content were derived for two of the four sites as proxies for local sedimentary changes. Reconstructed vegetation and fire histories were then compared to independent records of climate and sea-level change in temperate Australia, using a Detrended Correspondence Analysis ordination, to identify major drivers of heathland development. Results show major heathland expansion occurred on truwana/CBI between the early and mid-Holocene in response to sea-level rise, high effective precipitation, reduced seasonality and increased Indigenous burning. Increasing seasonality, low effective precipitation, El Niño-Southern Oscillation intensification, stable sea level, and decreased fire activity drove the expansion of scrub and woodland at the expense of heathland in the late Holocene. The overall vegetation development on truwana/CBI fits poorly with the classic Iversen conceptual model of interglacial vegetation development in the Northern Hemisphere, due to the significant role of interglacial sea-level rise on truwana/CBI. Therefore, a modified model, which takes into account the role of sea-level change is proposed for Southern Hemisphere-temperate-oceanic settings. Overall, heathland developments in both hemispheres reflect some level of homogeneity, considering the roles of increased Indigenous burning and reduced seasonality in both hemispheres. Frequent, controlled burning strategies are recommended to maintain heathland on truwana/CBI.

3.1 Introduction

Heathlands rank among the most diverse ecosystems globally and are widely distributed across tropical and temperate latitudes (Specht, 1979), but mostly distributed in oceanic, continental, and Mediterranean climates in temperate zones of both hemispheres (Keith et al., 2014; Keith, 2017; Fagúndez, 2013). Stress-tolerance is a functional trait of many heathland plants, enabling their adaptation to unfavourable conditions/disturbance, especially nutrient-poor soils and droughts (Lamont and Keith, 2017; Specht, 1979). Heathland species are also generally adapted to fire disturbance and are capable of regenerating rapidly from seedbanks after fires (Kirkpatrick and Harris, 1999).

Northern Hemisphere pollen records have shown that long-term heathland development was driven by Indigenous/traditional land use (burning and deforestation) during the Holocene (Fagúndez, 2013; Motzkin and Foster, 2002), especially in many parts of Europe (e.g., Prøsch-Danielsen and Simønsen, 2000; Webb, 1998; Hjelle et al., 2010). However, decline in soil nutrients as a result of prolonged soil waterlogging associated with less seasonal precipitation variability (low summer insolation) is also thought to have favoured heathland development in the Mediterranean during the mid-Holocene (Fletcher and Sánchez Goñi, 2008). In the Southern Hemisphere, South African Fynbos Mediterranean heathland development has been shown to be driven by climate, Indigenous land use and sea-level change during the Holocene, though European impact also drove heathland development in some areas in the last ~200 years (e.g., Dirk and Gillson, 2020; Meadows et al., 2009). While knowledge of the long-term drivers of heathland development is scarce in Australia, existing pollen records similarly suggest fire associated with Indigenous landscape management practices and factors associated with sea-level rise (e.g., soil podsolization) in coastal areas may have driven heathland developments in temperate Australia's Mediterranean and oceanic settings during the Holocene (Thomas and Kirkpatrick, 1996; Thomas et al., 2001).

The cause of rapid disappearance of heathland in the Northern Hemisphere has been narrowed down to land-use change since the 18th century, explained through management-focused long-term studies (Fagúndez, 2013; Motzkin and Foster, 2002). Similarly, land-use change, such as European land clearing and novel fire regimes, have removed heathlands in many areas of the Southern Hemisphere in modern times. South African Fynbos and Australian heathlands are currently threatened by land clearing and invasive species (Keith,

2014; Kirkpatrick and Harris, 1999). Australian heathlands are also threatened by pathogens (*Phytophthora*) and a lack of fire, which has driven biodiversity loss and replacement of heathlands by scrub and woodland (Kirkpatrick and Harris, 1999; Bargmann and Kirkpatrick, 2014). In order to better manage heathland ecosystems, there is a need to understand their long-term development (Dirk and Gillson, 2020); however, such long-term studies are uncommon in Australia. There are few existing short-term experimental studies of heathland development (Keith et al., 2014), the use of short-term studies as a basis for management and conservation can be misleading, considering the amount of time required for some drivers such as climate change and CO₂ variability to influence vegetation (Dirk and Gillson, 2020). Knowledge of long-term heathland development in Europe has informed management recommendations such as increased Indigenous burning and grazing (Vogels, 2017). In order to achieve informed management and mitigate the disappearance of Australian heathlands under changing fire regimes, climate and anthropogenic land use, there is a need for a better understanding of the drivers responsible for long-term heathland developments.

The glacial-interglacial model for Northern European vegetation development proposed by Iversen (1958) features heathland as an important successional stage in past climate-vegetation dynamics. Based on temperature change and vegetation type, Iversen's model recognizes four phases, which include: (1) the Cryocratic (glacial) phase, defined by a cool climate and treeless landscape; (2) the Protocratic (lateglacial), defined by increasing temperatures, shrub and tree cover; (3) the Mesocratic (~early–mid interglacial) phase, defined by maximum forest cover under a warmer climate; and (4) the Telocratic (~mid–late interglacial), defined by gradual opening of the landscape and decreasing temperatures, which leads back to the Cryocratic.

On millennial timescales, heathlands in temperate settings are generally an intermediate stage (Telocratic) between the warm climate woodland/forest ecosystems (Protocratic and Mesocratic) and cold grassland ecosystems (Cryocratic) (Iversen, 1958; Colhoun, 1996; Daniau et al., 2010). However, studies from both hemispheres have pointed out that temperature change is insufficient to explain vegetation changes in the Telocratic and that other factors, especially soil degradation and anthropogenic land use, have been identified to be important (Colhoun, 1996; Birks et al., 2016a; Tzedakis and Bennett, 1995). This observation led to the introduction of the 'Oligocratic' phase, which is inclusive of all potential regional and local drivers of vegetation change, some of which include seasonal

precipitation, soil nutrients, fire and anthropogenic land use (Colhoun, 1996; Birks et al., 2016a; Andersen, 1994; Birks and Birks, 2004; Combourieu-Nebout et al., 2013; Fyfe et al., 2013). While the modified Iversen's cycle (Andersen, 1994) may be applicable to interpret vegetation development on a continental island, such as temperate Tasmania (Colhoun, 1996), this study seeks to examine if this is applicable to smaller neighbouring islands of Bass Strait.

In this study, long-term vegetation development in a temperate Australian oceanic setting (Bass Strait islands) was reconstructed using palaeoecological techniques and compared it to independent records of climate and sea-level changes. The aim is to identify and understand the potential drivers of the development and maintenance of heathland during the Holocene, as well as assess whether Iversen's conceptual model for interglacial vegetation development is applicable to Southern Hemisphere temperate oceanic settings.

3.2. Methods

3.2.1. Study area (Cape Barren Island, Bass Strait)

Apart from the Bass Strait region being rich in heathlands, it was selected for this study due to its unique history of the islands' formation and dynamics of its human occupation. Bass Strait (glacial-era Bassian Plain) served as a connecting landbridge for human movement between Tasmania and the Australian mainland during the Last Glacial Maximum, and the present islands, including Cape Barren Island where our sampling sites are located, emerged as a result of postglacial sea-level rise between ~14,000 and 6000 years ago (Sloss et al., 2007; Lambeck and Chappell, 2001; Williams et al., 2018; Cosgrove, 1995; Fig. 1). Archaeological and palaeoecological records also suggest human occupation was intense in the region during the early Holocene but was reduced by ~5000 years ago due to encroaching sea level and a decline in resource availability (McWethy et al., 2017; Sim, 1998).

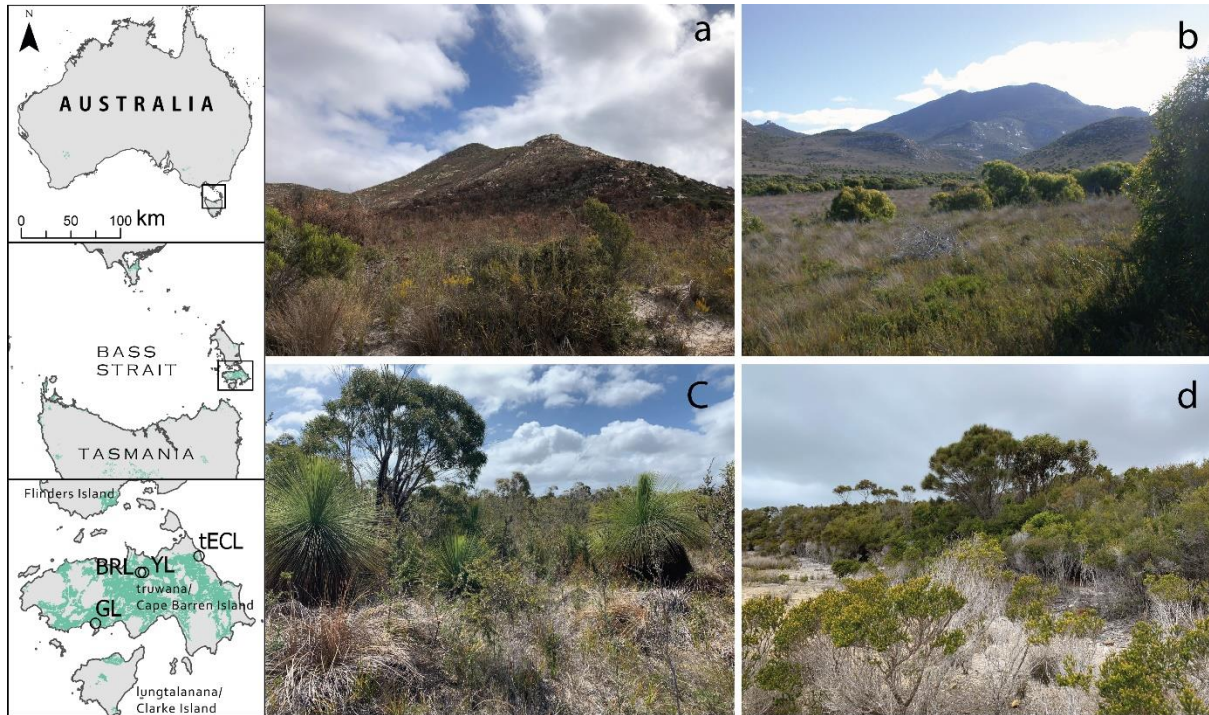


Figure 1: Location map showing the study area and locations of core collection (black circles) on truwana/Cape Barren Island, Bass Strait, southeast Australia. Core sites include, Big Reedy Lagoon (BRL), Yakka Lagoon (YL), truwana East Coast Lagoon (tECL), and Green Lagoon (GL). Green-shaded areas represent present distribution of heathland in Australia (National Vegetation Information System version 5.1, downloaded 22/04/2020). It was noted that Keith et al. (2014), portrayed more extensive heathland areas in southern Australia. Also shown are image examples of heathland and scrub from truwana/Cape Barren Island, which include, (a-b) Ericaceae heathland, (c) *Xanthorrhoea* heathland, and (d) *Melaleuca* scrub.

Cape Barren Island (CBI) is located between mainland Australia and Tasmania. The Indigenous name for CBI is truwana (Fig. 1). Most of the island's residents today are descended from European sealers and Aboriginal peoples who, in the early 1800s, settled on smaller nearby islands, but relocated to truwana/CBI in the late 1870s. Today the truwana Rangers undertake land and sea management work through landscape burning practices and weed control in order to maintain island biodiversity (TAC Members, 2015). The island has an area of ~480 km² and its oldest rock deposit (Mathinna Beds) is Devonian, while calcareous sandstone, limestone, and basalt make up the pre-Quaternary Cenozoic deposit (Cocker, 1980). Quaternary deposits are made up of aeolian, marine, and alluvial sediments (McClenaghan et al., 2011). The island's vegetation is dominated by heathland, scrub and sclerophyllous forests (Fig. 1; Harris and Kitchener, 2005). The

heathlands are mostly on acid sands and siliceous gravels, intermixed with sedgeland, where drainage is poorer and where floristic composition has been affected due to infestation by *Phytophthora cinnamomi*. Families commonly represented include Ericaceae, Myrtaceae, Fabaceae, Orchidaceae, Proteaceae, Dilleniaceae and Asteraceae. Common structural dominants include *Allocasuarina monilifera*, *Banksia marginata*, and *Xanthorrhoea australis* (Harris and Kitchener, 2005; Kirkpatrick and Harris, 1999).

A temperate oceanic climate with mild–cool, wet winters and warm, dry summers prevails on the island, with average monthly temperature ranging from ~13°C in July to 23°C in February, and average annual rainfall ranging between 600 and 1000 mm. The island is under the influence of Southern Westerly Winds (SWW), which modulate zonally symmetric rainfall variability between western and eastern Tasmanian, including eastern Bass Strait (Hendon et al., 2007). Strong SWW flow brings high rainfall to eastern southeast Australia, including truwana/CBI in eastern Bass Strait during spring and summer, and weaker SWW flow brings less rainfall in western southeast Australia, including western Bass Strait during these seasons. Conversely, SWW flow is stronger in western southeast Australia in winter, with high rainfall, but reverse is the case in eastern southeast Australia (Hendon et al., 2007). El Niño Southern-Oscillation (ENSO) also drives interannual variability in precipitation and fires, as El Niño years and weakened SWW are associated with drought, extreme fire weather and severe fire events (Mariani et al., 2016a; Mariani and Fletcher, 2016; Risbey et al., 2009; Kim et al., 2017).

3.2.2. Coring sites (Big Reedy, Yakka, truwana East Coast, and Green Lagoon)

Big Reedy Lagoon (BRL) is a peat swamp and the largest catchment on truwana/CBI, up to 914 m in diameter, and bordered by an arcuate dune ridge on the eastern to southern sides, within which smaller wetlands, such as Yakka Lagoon (YL) have formed. truwana East Coast Lagoon (tECL) is an infilled basin on the NE coast and ~680 m maximum diameter, while on the south coast is Green Lagoon (GL), an open water body with a maximum diameter of 440 m (Fig. 1). Heathlands are part of the surrounding vegetation at all selected sites (see Appendix S1 for full site vegetation descriptions). *Phytophthora cinnamomi* infestation was also observed at many sites across the island, including BRL and has impacted species diversity, especially in *Xanthorrhoea* heathlands (Kirkpatrick and

Harris, 1999). All sediment cores were collected with the permission of the Aboriginal Land Council of Tasmania and support from the truwana and pakana Rangers.

3.2.3. Sediment core collection, Itrax scan, and chronology

Four sediment cores, 2 m, 0.45 m, 0.73 m and 1.35 m in length, were collected from BRL (40.3589°S, 148.2381°E, 26 m asl), YL (40.3589°S, 148.2447°E, 30 m asl), tECL (40.3311°S, 148.2381°E, 1m asl) and GL (40.442967°S, 148.143840°E, 10 m asl), respectively. Recent fires have affected the uppermost sediments at BRL, which is why another core was collected from neighbouring unburnt YL to serve as the surrogate core top of BRL.

Big Reedy and tECL cores were scanned for trace metals and magnetic susceptibility using ITRAX at the Australian Nuclear Science and Technology Organisation. The ratio for molybdenum incoherence/coherence (Mo inc/Mo coh) was used as a proxy for organic content (Woodward and Gadd, 2019). Sediment cores were then subsampled and radiometrically dated by Accelerator Mass Spectrometry (AMS) ^{14}C and resulting ^{14}C dates were used to create an age-depth model (SHCal20) using the 'rbacon' package (Blaauw et al., 2020) in 'R' (R Core Team, 2020; Hogg et al., 2020). For YL and tECL age-depth models, *Pinus* pollen is used as an age marker for approximately 150 yr BP (Romanin et al., 2016).

3.2.4. Pollen and charcoal analyses

In order to reconstruct vegetation history, 1.25 cm³ samples were taken from sediment cores at 1–4-cm intervals for pollen analysis and samples were processed following standard pollen preparation procedures, which included HCl, KOH and acetolysis treatments (Faegri and Iversen, 1975). At least 300 terrestrial pollen grains were identified on slides except for a few depths with extremely low pollen concentrations in which 100 to 150 pollen grains were counted. Pollen and spores were identified using the Australasian Pollen and Spore Atlas (<http://apsa.anu.edu.au/>) and PalaeoWorks reference collections at the Australian National University's Archaeology and Natural History Laboratory. Percent abundance of terrestrial pollen and spores are based on the total sum of terrestrial pollen for each sample. *Lycopodium* spike (Batch no. 3862, 9666 spores) was added to calculate

pollen concentrations (pollen grains/cm³) and pollen accumulation rates (pollen grains/cm²/yr) for each sample. Pollen diagrams were produced using Tilia 2.1.1 and CONISS was used to identify pollen zones (<https://www.tiliait.com/>).

For individual sites fire history reconstruction, contiguous sediment samples (1.25 cm³) were taken from cores and analysed, following the method of Whitlock and Larsen (2001), and macroscopic charcoal particles (>125 µm) counted in each contiguous sediment sample. Macroscopic charcoal records are expressed as accumulation rates (particles/cm²/cal yr). An island-wide fire history is inferred for truwana/CBI by compositing contiguous macroscopic charcoal records with Box-Cox and z-score transformations (Power et al., 2008), using the 'paleofire' package (Blarquez et al., 2014) in 'R' (R Core Team, 2020). Microscopic charcoal particles (<125 µm) were also counted on pollen slides and accumulation rates calculated using *Lycopodium* spike-based concentrations.

3.2.5. Heathland identification in pollen records

Australian heathlands are typically evergreen, dominated by sclerophyllous shrubs (< 2 m tall), often complex and differ from other global heathlands due to the overlap in species composition between heathland, scrub, and woodland (Keith, 2017; Lamont and Keith, 2017). Nonetheless, separation of Australian heathland from scrub/woodland in pollen records is achievable to some extent, based on certain species assemblages and abundance and their current distribution in the study area (Kirkpatrick and Harris, 1999). Previous studies from Australia (e.g., Thomas and Kirkpatrick, 1996; Thomas et al., 2001; Ladd, 1979) have made efforts to infer heathlands from pollen records, using pollen types such as *Allocasuarina*, *Calytrix* and Ericaceae. Although pollen grains of *Calytrix* and Ericaceae are distinctive, one difficulty is separating dwarf *Allocasuarina*, a major component of a heathland, from taller *Allocasuarina* on the basis of pollen. *Xanthorrhoea* and myrtaceous shrubs such as *Leptospermum* and *Melaleuca* are also potential heathland indicators but, the latter are also widely distributed in scrub and forest, including our area of study in the eastern Bass Strait. Due to this overlap, Ericaceae and *Xanthorrhoea* pollen were used as major heathland indicators in this study and other pollen types (e.g., Restionaceae) of plants that are presently mostly found in heathlands in our study area (Harris et al., 2001; Howells, 2012).

3.2.6. Floristic richness estimation

Pollen data (excluding exotic pollen such as *Pinus*) were rarefied in 'R' (R Core Team, 2020) using the 'rarefy' function in 'vegan' package (Oksanen et al., 2018), to estimate past diversity (palynological richness, a proxy for floristic richness in SE Australia, see Adeleye et al., 2021b; Felde et al., 2016). Although differential pollen production may bias pollen-based estimates of floristic richness (Birks et al., 2016b), taxonomic richness of pollen records has been shown to significantly reflect floristic richness of an area (Birks, Felde, and Seddon, 2016), especially when a single climatic or floristic region is considered, as in this study (Meltsov et al., 2013; Adeleye et al., 2021b; Connor et al., 2020).

3.2.7. Ordination and environmental proxies

Relationships between pollen assemblages and potential environmental drivers were determined by conducting a Detrended Correspondence Analysis (DCA) fitted with environmental variables and significance assessed by a permutation test. All analyses were done using the 'vegan' package (Oksanen et al., 2018) in 'R' (R Core Team, 2020). The environmental drivers assessed include reconstructions of sea-level changes, summer and winter insolation, ENSO, fire, precipitation:evaporation ratios, and temperature.

Macroscopic charcoal accumulation rates (CHAR) were used as a proxy for fire activity. High CHAR is generally interpreted as high fire activity and vice versa. An insolation record for 40°S is used to infer seasonal variability (sums of summer: DJF, winter: JJA; Berger and Loutre, 1991), the Laguna Pallcacocha lake sedimentation record as a proxy for ENSO events (Moy et al., 2002), the EPICA Dome C Antarctic deuterium record as a proxy for temperature (Stenni et al., 2001), a reconstructed precipitation:evaporation trend from southwestern Victoria as a proxy for southern Australia SWW-driven effective precipitation (Wilkins et al., 2014), and a biological indicator-based reconstructed sea level curve for SE Australia as a proxy for sea-level change (Sloss et al., 2007).

3.3 Results

3.3.1. Lithology, chronology, and geochemistry

BRL core is mostly composed of fibrous and decomposed peat and the core age-depth model created from AMS ^{14}C dates shows an estimated calibrated basal age of $\sim 13,712$ cal yr BP (calendar years before present) with an average sediment accumulation rate of 0.26 mm/yr (see Table S1 in Appendix S2 for AMS radiocarbon dates for all sites). ITRAX scans show increasing organic content between 200 and 140 cm, reaching ~ 7.4 Molybdenum ratio, and gradually decreased to < 7.4 Molybdenum ratio through the rest of the record. Conversely, magnetic susceptibility is generally low (mostly $< -1.6 \text{ cm}^3/\text{g}$) between 200 and 100 cm and high (mostly $\geq -1.6 \text{ cm}^3/\text{g}$) for the rest of the record (Fig. 2). The YL core is also made up of decomposed and fibrous peat and the age-depth model produced a basal age of ~ 645 cal yr BP with an average accumulation rate of ~ 0.7 mm/yr.

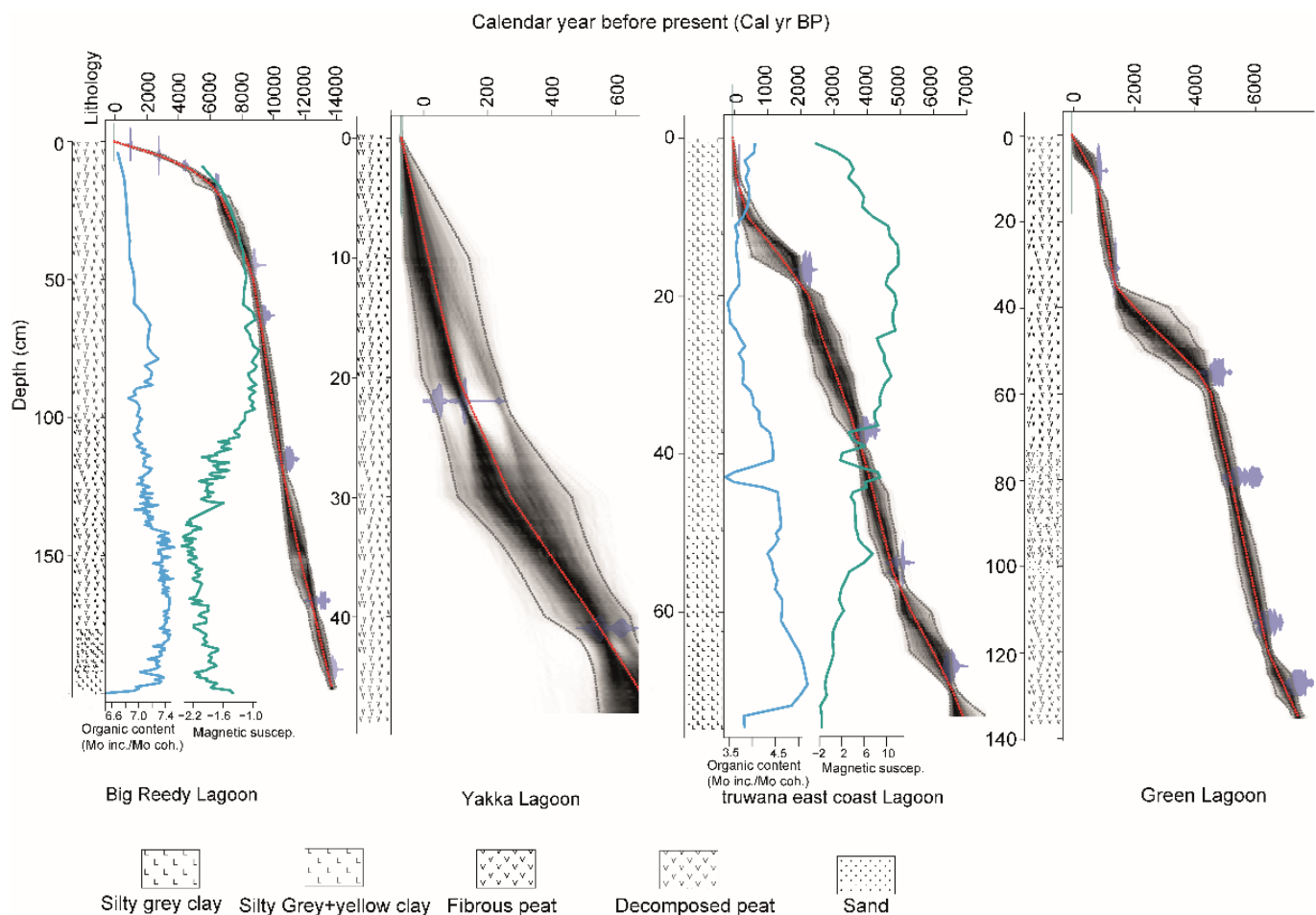


Figure 2: Lithology and age-depth models for each site from truwana/Cape Barren Island, Bass Strait, showing calibrated ^{14}C dates (purple), age-depth model (dark shaded grey), 95% confidence intervals of calibrated range (light-shaded grey), and single model based on the weighted mean age for each depth

(red curve). Blue and green curves represent BRL and tECL organic content (molybdenum incoherence/coherence ratios) and magnetic susceptibility (cm^3/g), respectively. See Appendix S2 for AMS radiocarbon dates for all sites.

The tECL core is composed of silty grey and yellowish clay and the core age-depth model produced a basal age of ~6884 cal yr BP with an average accumulation rate of 0.1 mm/yr. ITRAX scans show a decreasing organic content trend in the record, from >4.5 Molybdenum ratio to <4.5 Molybdenum ratio. Magnetic susceptibility is low (<4 cm^3/g) between 73 and 40 cm and generally high (mostly >4 cm^3/g) for the rest of the record (Fig. 2). The GL core is generally composed of fibrous and decomposed peat and the core age-depth model produced an estimated basal age of ~7410 cal yr BP with an average accumulation rate of 0.26 mm/yr (Fig. 2).

3.3.2. Reconstructed vegetation and fire history (see Appendix S2 for full pollen record results)

Big Reedy and Yakka Lagoon

Zone BR-1 (~14,000–12,800 cal yr BP: 200–177 cm) at the base of BRL core is dominated by *Eucalyptus*, *Melaleuca*, and Poaceae at ~20% each, although *Melaleuca* pollen influx was low during this period (see Fig. S1c in Appendix S2 for influx diagram). *Eucalyptus* expanded further (~30%) in zone BR-2 (~12,800–9100 cal yr BP: 177–63 cm), with a substantial increase in *Allocasuarina* *Casuarina* (*Allocasuarina*) to >30% at the expense of Poaceae. Macroscopic charcoal accumulation rates (CHAR) also increased in this zone to >20 particles/ $\text{cm}^2/\text{cal yr}$, with a brief increase in diversity (floristic richness) to ~15 taxa/minimum count. *Eucalyptus* dropped to <5% in zone BR-3 (~9100–7200 cal yr BP: 63–27 cm) with an initial increase in *Leptospermum* (~40%), which was quickly replaced by *Sprengelia* (~20%), *Epacris* (~30%), Restionaceae (~60%) and *Selaginella* (~10%). CHAR also decreased (<5 particles/ cm^2/yr) in this zone and *Melaleuca* pollen influx (see Fig. S1c in Appendix S2) increased steadily. *Leptospermum* increased again to ~20–40% in the first half of zone BR-4 (~7200–1000 cal yr BP: 27–1 cm) at the expense of *Allocasuarina*, Restionaceae, *Sprengelia*, *Epacris* and *Selaginella*, but dropped to ~10% by ~4000 cal yr BP. *Melaleuca* was consistently present around 20%, with increasing floristic richness,

reaching ~25 taxa/minimum count and small increase in *Monotoca*. There is also an increase in *Allocasuarina* (~20%) and a minor increase in *Eucalyptus* and *Callitris* at ~5–10% towards the end of this zone between ~4000 and 1000 cal yr BP (Fig 3a).

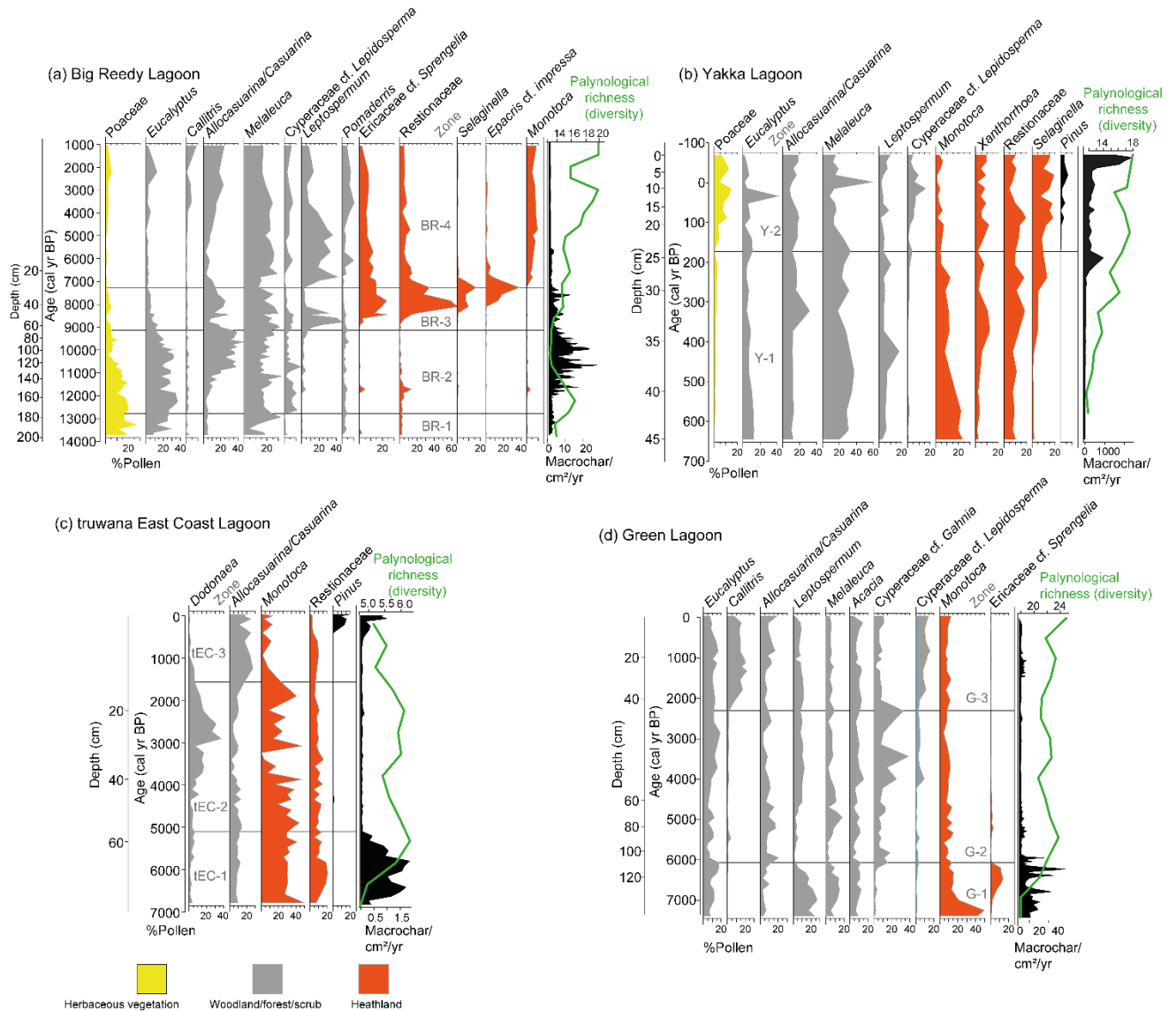


Figure 3: Summary pollen diagram (including CONISS zones), charcoal accumulation and palynological richness for each site on truwana/Cape Barren Island, Bass Strait. Taxa groupings are based on their major distributions on truwana/CBI (See Fig. S1a–S5c and Table S1 in Appendix S2 for full pollen diagrams and full list of indicator plant taxa, respectively). Heathland development is mostly evident in the Big Reedy Lagoon record (a), with an expansion around 8500–7000 cal yr BP. However, pollen records from truwana East Coast Lagoon (tECL) and Green Lagoon (GL) also suggests widespread heathland around this period, as reflected by the abundance of *Monotoca* and *Restionaceae* in tECL, and the abundance of *Monotoca* and *Sprengelia* in GL, especially from ~7000 to 6000 cal yr BP.

In YL, zone Y-1 (~630–173 cal yr BP: 45–24 cm) at the base of the record is mainly dominated by *Melaleuca* (~20%), *Monotoca* (~10–20%) and *Allocasuarina* (~10%). Zone Y-2 (~173 cal yr BP–present: 24–0 cm) is dominated by *Melaleuca*, *Allocasuarina*, Poaceae, *Selaginella* and Cyperaceae at ~10% each, with a major increase in CHAR, ranging between ~300 and 1000 particles/cm²/yr, and consistent increase in floristic richness, reaching ~18 taxa/minimum count. There is also a small increase in exotic *Pinus* (~5%) towards the end of the zone. (Fig. 3b).

truwana East Coast Lagoon

Monotoca and Restionaceae dominate the basal zone tEC-1 at ~20–40% (~7000–5100 cal yr BP: 73–58 cm), with increasing floristic richness (>6 taxa/minimum count) and MAR (~1.5 particles/cm²/yr), while the second zone tEC-2 (~5100–1700 cal yr BP: 58–17 cm) is characterized by the expansion of *Dodonaea*, reaching >20%, and decrease in MAR to <0.2 particles/cm²/yr. *Dodonaea* almost disappeared in zone tEC-3 (~1700 cal yr BP–present: 17–1 cm), *Monotoca* dropped to ~10%, with a minor decrease in floristic richness to ~5 taxa/minimum count, while *Allocasuarina* increased to ~20%. Introduced *Pinus* is also present at ~15% in the last ~200 years, with increased CHAR to ~0.4 particles/cm²/yr (Fig. 3c).

Green Lagoon

Zone G-1 (~7300–6000 cal yr BP: 134–107 cm) at the base of the record is dominated by *Monotoca* (~20–40%) and *Leptospermum* (~20%), with increasing floristic richness (~24 taxa/minimum count) and CHAR (~10–20 particles/cm²/yr). Other taxa, such as *Acacia*, *Melaleuca*, *Sprengelia* and *Eucalyptus*, are also represented at ~10% each in this zone. In zone G-2 (~6000–2300 cal yr BP: 107–42 cm), *Leptospermum*, *Eucalyptus*, *Acacia*, *Melaleuca* and *Allocasuarina* are most represented at ~10% each, with a major decline in CHAR to <10 particles/cm²/yr. There is also major increase in *Gahnia* through the zone, reaching >20%. The topmost zone G-3 (~2300 cal yr BP–present: 42–0 cm) sees an increase in *Callitris* and *Lepidosperma* to ~10%, while *Gahnia* decreased to <10% (Fig. 3d). Floristic richness remained relatively stable in zone G-2 and G-3 at ~22–24 species.

3.3.3. Ordination result

The first two DCA ordination axes (Fig. 4) explain the greatest variance (23%) in the overall pollen record, with ericaceous heathland taxa ordinated in the positive area of both axes and most significantly ($p < 0.01$) related to sea-level change ($r^2 = 0.48$) and SWW-driven effective precipitation ($r^2 = 0.29$), followed by fire ($r^2 = 0.08$) and winter insolation (low summer insolation; $r^2 = 0.08$). Conversely, scrub and woodland taxa are ordinated in the negative area and most significantly ($p < 0.01$) related to increasing summer insolation ($r^2 = 0.09$) and ENSO ($r^2 = 0.05$). Temperature change is insignificantly ($p > 0.05$) related to the overall pollen record, as well as individual site pollen records, while winter insolation and ENSO are insignificantly related to BRL and tECL pollen records, respectively (see Fig. S6 in Appendix S2 for individual site ordinations).

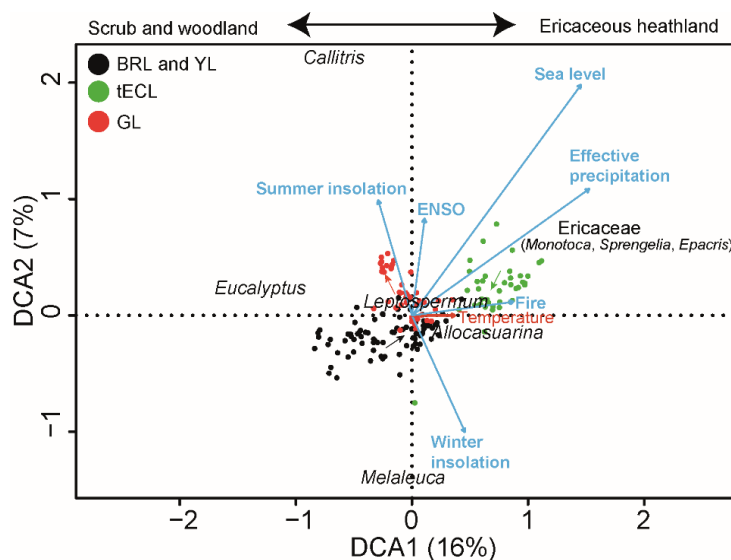


Figure 4: DCA ordination plot of all pollen records from truwana/Cape Barren Island, Bass Strait, fitted with environmental drivers. Significant ($p < 0.01$) environmental drivers are in blue and insignificant ($p > 0.05$) in red (temperature). Small arrows show direction of pollen records for each site from older–younger dates and length of long arrows reflect correlation between each environmental driver and changes in pollen assemblage. Green-shaded area represents maximum heathland development. Fire is the composite (z-score) of CHAR across sites.

3.4. Discussion

3.4.1. Lateglacial and Holocene vegetation development on truwana/CBI

Lateglacial–early Holocene woodland development (~14,000–9000 cal yr BP)

Results show the prevalence of open woodland on truwana/CBI during the lateglacial (~14,000–11,700 cal yr BP) and this period is thought to have been characterized by cool, dry conditions (Petherick et al., 2013). An abundance of Poaceae before ~13,000 cal yr BP suggests a more open landscape during this period, which is also reflected by the slightly higher magnetic susceptibility during this period. An increasingly wet climate (Fletcher and Moreno, 2012) in the early Holocene (~11,700–10,000 cal yr BP) may have contributed to *Eucalyptus* woodland expansion at the expense of herbaceous vegetation. *Allocasuarina* expansion between ~10,500 and 9000 cal yr BP may be related to increasing soil salinity linked to sea-level rise and increased fire activity (possibly driven by increased Indigenous burning) during this period (Thomas and Kirkpatrick, 1996; Sloss et al., 2007; McWethy et al., 2017). *Allocasuarina* is commonly found in scrub and forest today on the island, and the abundance of both *Allocasuarina* and *Melaleuca* between ~10,500 and 9000 cal yr BP may suggest mixed scrub development. However, pollen influx data (see Fig. S1c in Appendix S2) also show continuous presence of *Eucalyptus* during this period as well as herbaceous taxa, suggesting woodland refugia were present.

Early–late Holocene heathland and scrub development (9000 cal yr BP–present)

Shrubby vegetation prevailed at the expense of woodland in BRL at least after ~9000 cal yr BP, starting with a brief increase in *Leptospermum*, followed by an expansion of Ericaceae–Restionaceae heath between ~8200 and 7000 cal yr BP. Ericaceous heathland likely expanded throughout truwana/CBI in the mid-Holocene, as seen in tECL and GL before ~6000 cal yr BP and Restionaceae expansion in most sites during this period suggests the heathlands were mostly wet (Gullan, 2017). Floristically rich scrub developed across sites at least after ~6000 cal yr BP, as recorded for other Bass Strait islands and surrounding coastal sites (e.g., Mackenzie and Moss, 2017; McWethy et al., 2017). Increasing scrub and woodland elements including *Callitris* in BRL and GL and *Allocasuarina* in tECL in the last ~2000 years, although earlier in BRL, suggest increasing scrub density and/or

woodland encroachment. *Xanthorrhoea* heathland, which still persists around BRL and YL today also persisted in some areas in the last ~200 years as seen in the YL record.

3.4.2. Drivers of heathland development

DCA analysis identified sea-level change, climate, and fire as key drivers of the Bass Strait islands' temperate oceanic heathland development during the Holocene. Each of these drivers are discussed below in the context of previous studies.

Sea-level change

The reconstruction of postglacial sea-level changes in southeast Australia is currently inconclusive due to insufficient local proxy-based studies, especially in Bass Strait (e.g., Lewis et al., 2013). Existing records suggest major inundation of the Bass Plain (now Bass Strait) started around 14,000 years ago, reaching a maximum between 8000 and 7000 years ago (e.g., Lambeck and Chappell, 2001; Sloss et al., 2007; Williams et al., 2018). Some records suggest a sustained sea-level high stand until present (Donner and Junger, 1981) and others suggest steady decline to the present level from ~2000 years ago (Sloss et al., 2007).

Results (Fig. 4 and 5) show sea-level rise is the most significantly ($r^2=0.58$, $p<0.01$) related to maximum heathland expansion on truwana/CBI from the early to mid-Holocene (~8500–6000 cal yr BP; see appendix S8 for more details on Holocene sea-level change in Bass Strait). Increased wind-driven storm surges, salt- and sand-blasting with high ocean waves currently constitute a major disturbance on the small islands of eastern Bass Strait (McInnes and Hubbert, 2003) and this may have markedly marginalized tree growth in favour of heathland on truwana/CBI, a shrinking island at this time due to sea-level rise. This also explains the expansion of coastal vegetation at other nearby oceanic sites during the mid-Holocene (Thomas and Kirkpatrick, 1996; Mackenzie and Moss, 2017; McWethy et al., 2017). Also, soils in coastal areas are mostly saline and nutrient-poor and unfavourable for tree growth (Reid et al., 1999), but coastal heathland species including ericaceous species can tolerate these conditions, and this may have contributed to ericaceous heathland expansion on the shrinking island of truwana as sea level rose (Howells, 2012; Lambers et al., 2010).

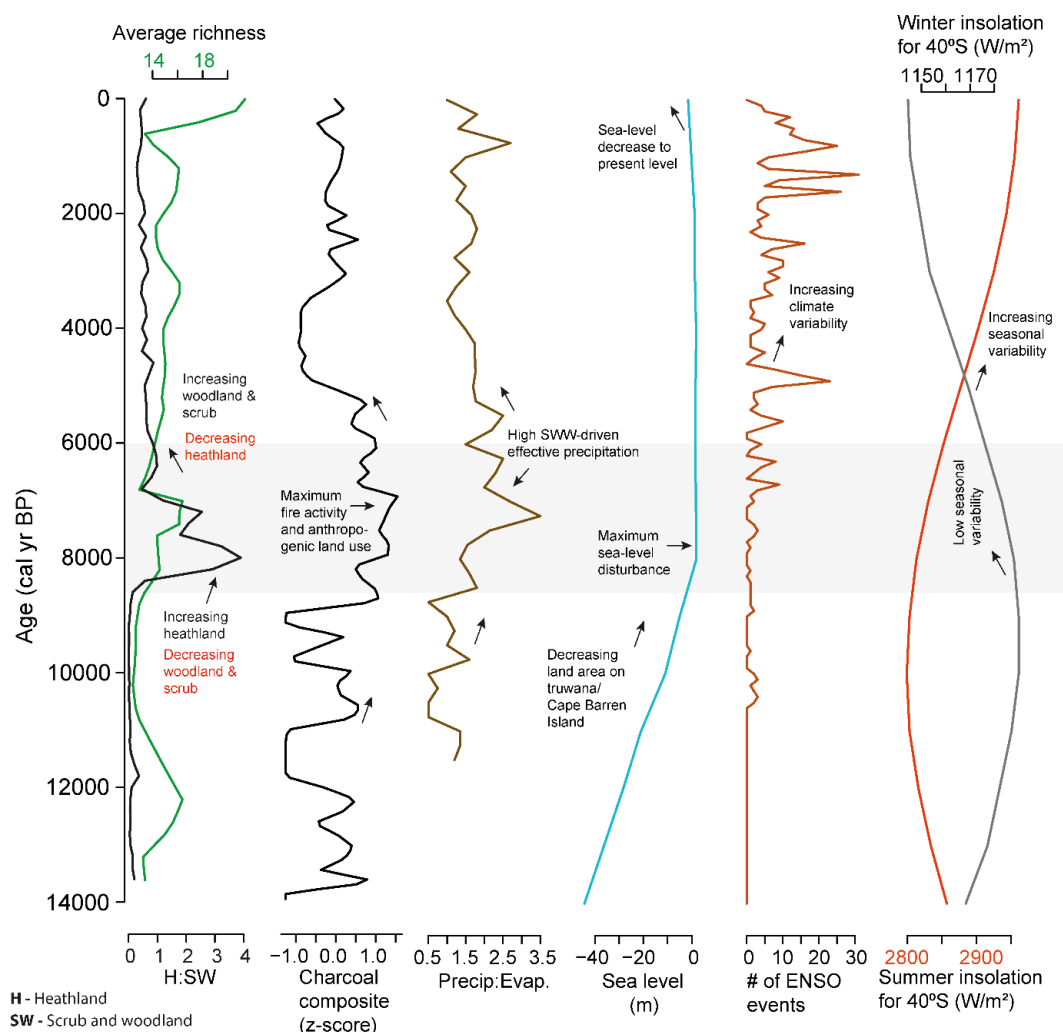


Figure 5: Summary of heathland development on truwana/Cape Barren Island, Bass Strait, southeast Australia, and potential drivers, which include fire (charcoal composite), SWW-driven effective precipitation (Wilkins et al., 2013), sea-level change (Sloss et al., 2007), ENSO (Moy et al., 2002), insolation (Berger and Loutre, 1991) and temperature (Stenni et al., 2001). The ratio of heathland to scrub and woodland is based on composite heathland and scrub and woodland pollen of all sites. Grey-shaded interval (~8500–6000 cal yr BP) shows period of maximum heathland expansion on truwana/Cape Barren Island, which is significantly ($p < 0.01$) driven by high fire activity possibly related to Aboriginal land use, high effective precipitation, sea-level disturbance, and low seasonal variability.

The development and maintenance of ericaceous heathland may have been driven by nutrient-poor waterlogged soils, promoted by a raised groundwater table during sea-level high stand (Nuttall and Portnoy, 1992). Soil waterlogging generally limits plant growth, especially trees, by inhibiting biological activity and nutrient uptake in the root zone

(Lambers et al., 2010). Most heathland species have developed adaptive features to survive this unfavourable condition such as the formations of cluster roots and mycorrhizal association to facilitate nutrient uptake and conservation (Lambers et al., 2010). High magnetic input in BRL from ~9000 cal yr BP may reflect the open vegetation and unstable soil conditions at the site and increasing magnetic input in tECL is likely partly due to the site's proximity to the coast, with constant marine influence contributing to soil podzolization and persistence of *Monotoca* heathland (Howells, 2012; Fig. 2 and 3c).

The expansion of shrub and woodland on truwana/CBI in the last ~6000 years is at least partly related to sea-level stabilization and decline to present level. The eastern part of the island has the lowest elevation and the expansion of *Allocasuarina* at the expense of *Monotoca* in low-lying tECL around 1500 years ago may be related to coastline retraction, with minimal wind disturbance and improved soil drainage, allowing the expansion of tall *Allocasuarina* trees, as found around the site today. This may have also favoured *Callitris* woodland/scrub expansion on the south coast (GL).

Climate

Long-term vegetation change on truwana/CBI has been shown to be significantly ($p < 0.01$) related to climate changes related to SWW-driven effective precipitation, insolation, and ENSO (Fig. 4). This result is consistent with the key climate drivers of Mediterranean heathland development identified in Europe during the Holocene, such as climate-induced soil degradation and reduced seasonal variability (Fletcher and Sánchez Goñi, 2008).

High moisture availability associated with strong SWW flow and low seasonal variability associated with low summer insolation may have promoted favourable conditions, such as longer periods of waterlogged soil conditions, for heathland development on truwana/CBI during the mid-Holocene (Lamont and Keith, 2017; Lambers et al., 2010; Fig. 5).

Conversely, increasing summer insolation and seasonal variability, ENSO-driven climate variability and weakening of SWW-driven precipitation likely favoured scrub development in the last ~6000–5000 years (Fig. 6). Increasing seasonal variability and reduced effective precipitation may have favoured scrub development, especially in inland areas (e.g., BRL), by improving soil conditions through reduced periods of soil waterlogging, increase in soil organic decomposition and greater thermal variability (Kirkpatrick and Harris, 1999;

Howells, 2012). Also, the overall increasingly dry conditions during this period as result of greater seasonality and decrease in precipitation, may have promoted drought-tolerant species such as *Callitris*, increasing floristic richness (Harris and Kirkpatrick, 1991).

Fire

Fire regulates interspecific interactions and resource availability in heathlands and is important in maintenance of heathland structure and composition (Bargmann and Kirkpatrick, 2014). Frequent fires help to prevent the conversion of heathland to scrub and forest by suppressing tree establishment and in some cases, especially in wet climates, reducing soil nutrients required for tree growth by inducing soil erosion/leaching (Jackson, 1977, 1978). A lack of fire can promote dense, taller vegetation and suppress viable seed germination, as most heath species' life histories are dependent on fire (Kirkpatrick and Harris, 1999; Bargmann and Kirkpatrick, 2014; Freestone et al., 2015).

Biomass structure in terms of arrangement on the landscape (dense vs open vegetation) and biomass moisture (wet vs dry) are major factors that shape fire regimes (Pausas and Paula, 2012; Bradstock, 2010; Cochrane and Ryan, 2009). Particularly in temperate Australia where truwana/CBI is located, fire activity is mainly determined by the availability of biomass to burn (dry biomass) in wet productive zones, while vegetation structure (fuel connectivity/dense vegetation) determines fire activity in dry unproductive zones (Bradstock, 2010; Adeleye et al. 2021c). truwana/CBI falls within the dry unproductive zone of temperate Australia.

The early Holocene is thought to be relatively wet in southeast Australia, with *Eucalyptus* woodland expansion and increasing Indigenous land use evident on truwana/CBI and neighbouring Flinders Island (Fig. 3a; McWethy et al., 2017; Sim, 1998). Increased fire activity during this period, despite climatic conditions unsuited for fire spread, may be associated with increased Indigenous burning. Indigenous land management practices likely maintained open woodlands—reduced fuel connectivity/density (McWethy et al., 2017; Gott, 2005) and may have facilitated the expansion of other open vegetation communities, such as heathlands, as also recorded in the coast of northeast Tasmania in the Holocene (Thomas and Kirkpatrick, 1996). Similar transformations from forest to

heathland cover are documented in historic records of ecosystem change in many parts of Europe (Fagúndez, 2013).

Local fire (CHAR) results show decreased fire activity across sites at least in the last ~5000 years until ~230 cal yr BP, likely due to reduced or changing Indigenous land use on the island (Sim, 1998). This likely contributed to scrub and woodland expansion during this period. Although microscopic charcoal accumulation across sites (see Fig. S2 in Appendix S2) suggests continuous regional fire, possibly low-to-moderate fire activity under dry conditions during the late Holocene may have promoted overall expansion (woody thickening) and greater floristic richness in the scrub at this time (Fig. 5). An increase in fire in the last ~200 years likely favoured heathland expansion in some areas with increasing floristic richness, such as the consistent presence of fire-tolerant *Xanthorrhoea* heathland (Bellette et al., 2015). This suggests that continuation of controlled or cool-burning practices will have a positive impact on diversity if enacted over long timescales, especially as droughts become more frequent and severe in the future.

Overall, high fire activity during the early Holocene and the recent past appears to have contributed to the expansion of heathland on truwana/CBI by suppressing taller vegetation. Conversely, low levels of fire from the mid-Holocene allowed the transition of heathland to taller scrub vegetation. This pattern suggests infrequent fire on the island may promote nutrient accumulation and tree/tall shrub expansion in present heathlands. On the other hand, frequent controlled burning can help prevent this from occurring, by suppressing taller vegetation growth to maintain heathland structure and composition on the island, as previously recommended for other parts of Tasmania (Bargmann and Kirkpatrick, 2015; Kirkpatrick and Harris, 1999). Understanding heathland species responses to different fire frequencies and intensities on the island via future ecological studies will further inform efficient controlled burning strategies.

3.4.3. Assessing the applicability of Iversen's cycle to vegetation development on truwana/CBI

The overall vegetation development on truwana/CBI generally fits into Iversen's interglacial phases, but with different timing and drivers of development. The lateglacial–early Holocene woodland development fits into the Protocratic–Mesocratic phase, while the early–late

Holocene scrub and heath development fits into the Telocratic phase (Fig. 6). This is similar to Northern European interglacial vegetation development in Iversen's model, which features increasing woodland cover and productivity during the Protocratic–Mesocratic in response to increasing temperature and soil fertility, and decreasing woodland cover and productivity, with heathland expansion during the Telocratic in response to decreasing temperature and soil fertility (Iversen, 1958; Kuneš et al., 2011). Conifers such as *Picea* also expanded in Northern Europe during the Telocratic, which corresponds with *Callitris* expansion on truwana/CBI in the same phase (Fig. 3a and d).

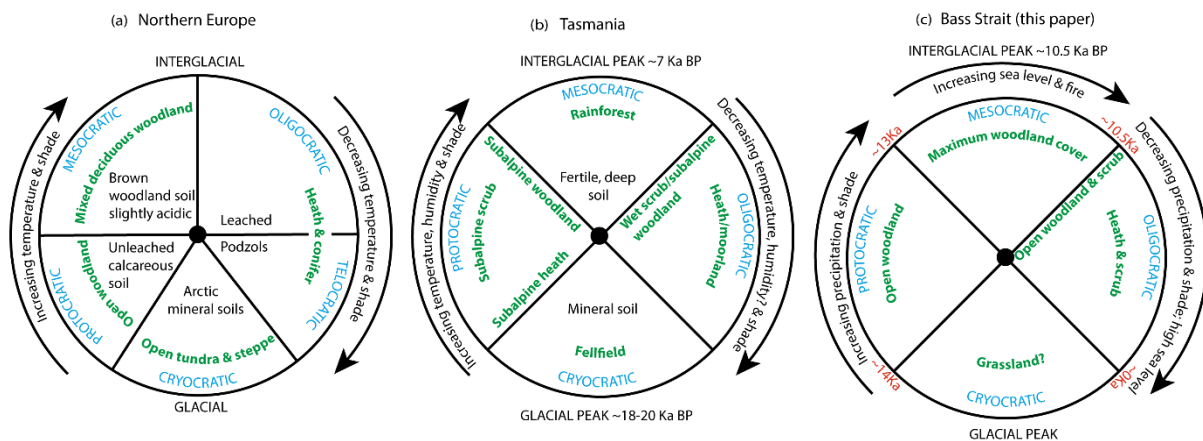


Figure 6: (a) Iversen's glacial-interglacial cycle for Northern Europe; (b) modified Iversen cycle for western Tasmania after Colhoun, 1996; and (c) proposed Iversen cycle for Southern Hemisphere temperate oceanic settings (truwana/Cape Barren Island, Bass Strait, this study).

Temperature change is considered as a key driver of vegetation change in the classic Iversen model for Northern Europe; however, results from this study suggest temperature change ($p > 0.05$) was not a major factor in the overall vegetation development on truwana/CBI. Sea-level change ($r^2 = 0.48$, $p < 0.01$), as discussed in the preceding section, appears to be the most important factor (Fig. 4 and 5). The overall prevalence of scrub and heathland on the island in the Telocratic is associated with high sea level-related disturbance (e.g., storm surges and strong winds, salt blasting), which may have contributed to poor/unstable soil conditions, promoting plants with competitive nutrient-acquisition strategies, such as the formation of mycorrhiza associations common in ericaceous and myrtaceous shrubs (Kuneš et al., 2011; Weijtmans et al., 2007; Brundrett, 2008). On the basis of sea-level change being the key driver of vegetation change, a modified Iversen's model applicable to truwana/CBI (see Fig. 6d) that may be broadly

applicable to Southern Hemisphere temperate oceanic settings is proposed. Since temperature change is the least important factor, the 'Oligocratic' is also substituted for the 'Telocratic' to describe early–late Holocene shrubby vegetation development on the island, following previous studies in western Tasmania and Europe (Colhoun, 1996; Birks et al., 2016b; Andersen, 1994; Fig. 6b–d). Other important factors in the overall vegetation development on truwana/CBI include effective precipitation ($r^2=0.29$, $p<0.01$) and fire ($r^2=0.13$, $p<0.01$).

The Mesocratic phase is known to have the longest duration in Iversen's interglacial model for Northern Europe. In contrast, the Telocratic/Oligocratic has the longest duration (the last 10,500–9000 years) on truwana/CBI, which is likely a result of the earlier influence of postglacial sea-level rise on vegetation on the small island and the low nutrient status of the island's sandy soils (Fig. 5). The extended Oligocratic at truwana/CBI is also longer than the previous estimate (the last 7000 years) for western Tasmania (Colhoun, 1996). This disparity in timing shows sea-level change is capable of accelerating vegetation shifts to a new phase in Iversen's model.

Although sea-level change was not previously identified as driver of Mesocratic–Oligocratic vegetation change in past applications of Iversen's model, result from this study suggests sea-level change should be included as a driver of vegetation change in this phase when applying the model to Southern Hemisphere temperate oceanic settings. As in Northern Europe, nutrient-poor soil and anthropogenic fire were also recognized as major drivers of vegetation change in the Oligocratic in western Tasmania (Colhoun, 1996). However, pollen records from the coastal lowlands of western Tasmania reflect potential sea level-driven moorland/heathland development during the mid–late Holocene (Thomas and Kirkpatrick, 1996; Fletcher and Thomas, 2010b), which fits within the Oligocratic. Sea-level change may have been disregarded as a potential driver of vegetation change in Colhoun's (1996) study due to the prevalence of high-elevation sites (mostly >500 m asl) in his study. Therefore, future studies are recommended in south-eastern Australia (Tasmania and mainland) to test the impact of past sea-level changes on vegetation, especially in lowland areas. Such a study would expand on the study of Colhoun (1996) and to provide further insights into the applicability of Iversen's conceptual model in temperate coastal zones for comparison with present study.

3.5. Conclusion

In this study, drivers of Holocene heathland development in a Southern Hemisphere temperate oceanic setting (truwana/Cape Barren Island, Bass Strait) were identified, and the applicability of Iversen's conceptual model of interglacial vegetation development to the area was also assessed.

Results show major heathland expansion occurred in conjunction with sea-level rise, high effective precipitation, less seasonality and increased (anthropogenic) fire activity during the early-to-mid Holocene. Conversely, increasing seasonality, low effective precipitation, stable sea level, ENSO intensification and low-to-moderate fire activity drove scrub development since the mid-Holocene, and a minor increase in fire activity in the last ~200 years favoured heathland development in inland areas. Overall, disturbance such as salt stress, wind damage and soil impoverishment, which accompanied a reduction in island size during Holocene sea-level rise mainly drove heathland development on truwana/CBI. However, increased Indigenous burning and reduced seasonality, which are also key drivers of heathland development in the Northern Hemisphere, contributed to development on truwana/CBI, reflecting some level of homogeneity in heathland developments in both hemispheres.

The overall vegetation development on truwana/CBI fits poorly with the classic Iversen conceptual model of interglacial vegetation development in the Northern Hemisphere, due to the significant role of interglacial sea-level rise on the island's vegetation development, which was not taken into account in the classic and previously modified Iversen models. Therefore, a new modified model, which takes into account the role of sea-level change on vegetation developments, is proposed for Southern Hemisphere-temperate-oceanic settings.

This study suggests a lack of fire and increasingly dry conditions may favour scrub/woodland expansion on truwana/CBI in the future, while projected sea-level rise may favour heathland expansion on the island. Hence, the use of frequent managed burning strategies is recommended to suppress scrub and woodland expansion on truwana/CBI to promote and maintain heathland diversity. Further ecological studies are also recommended to investigate heathland species responses to different fire frequency and intensity regimes on the island, as this will further inform efficient managed burning strategies.

Chapter 4 MYRTACEAE POLLEN MORPHOLOGY STUDY FROM BASS STRAIT ISLANDS, AUSTRALIA, IS EFFECTIVE IN SEPARATING REGION-SPECIFIC FOSSIL MYRTACEAE POLLEN TYPES

As observed in studies presented in previous chapters, the Australian landscapes, including the Bass Strait islands are dominated by the members of the Myrtaceae plant family and they occupy different habitats, ranging from forest to shrubby vegetation and dry to wet areas. However, separating Myrtaceae plant species pollen in fossil records is problematic due to the high degree of overlap in their pollen morphologies, and this limits palaeoecological interpretations. Previous studies into Myrtaceae pollen morphology have attempted to address this problem on a continental scale (Thornhill et al., 2012a, 2012b, 2012c). However, the more restricted flora of islands, such as Bass Strait's, offers the possibility of identifying individual plant species in the fossil record on the basis of pollen alone. This chapter presents a closer look at Myrtaceae pollen morphology of the Bass Strait area to provide further insights into the lateglacial and Holocene vegetation development discussed in the previous chapter. This additional insight was further developed after publication and is highlighted in the addendum section of this chapter (section 4.6).

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with
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I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

Title: Myrtaceae pollen morphology study from Bass Strait islands, Australia, is effective in separating region-specific fossil Myrtaceae pollen types _____

Authors: Matthew Adeleye, Feli Hopf and Simon Haberle _____

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Matthew Adeleye _____



Candidate – Print Name

Signature

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Endorsed

Prof. Simon Haberle _____

Primary Supervisor – Print Name

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Delegated Authority – Print Name

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Date

4.0. Myrtaceae pollen morphology study from Bass Strait islands, Australia, is effective in separating region-specific fossil Myrtaceae pollen types

Abstract

The identification of Myrtaceae pollen to species level in fossil records has challenged palynologists due to the similarity of pollen grains produced by species in this family. Here, a pollen morphological study of the Myrtaceae species found in a specific region of southeastern Australia, the islands of the Furneaux Group in Bass Strait, is presented and applied to fossil pollen records from the same region to confirm its utility in differentiating Myrtaceae pollen to type level. 23 species of Myrtaceae, belonging to six genera, were examined and 11 distinct types identified. The observed Myrtaceae pollen taxa can be confidently separated to genus level, apart from *Euryomyrtus*, which is indistinguishable from *Leptospermum*. Specifically, separation to species level is most achievable within the genus *Melaleuca*, as well as *Kunzea* and *Calytrix*, which are each represented by a single species. Conversely, *Eucalyptus* could only be separated into major types, while *Leptospermum* species could not be clearly separated, although differences in exine patterns exist. It is also demonstrated that the pollen morphological types in this study can be applied to Holocene and Pleistocene fossil records from the Furneaux Group. Studying the Myrtaceae of a specific area is recommended in identifying fossil Myrtaceae pollen from that area than using general Myrtaceae pollen morphological descriptions or keys that are not site- or region-specific.

4.1. Introduction

The Myrtaceae family is the ninth largest Angiosperm group worldwide and is widely distributed across the Southern Hemisphere on landmasses associated with Gondwana, constituting a key component of Australian floral diversity (Johnson and Briggs, 1981). There are over 2,500 species of Myrtaceae in Australia belonging to 107 genera (Atlas of Living Australia - <https://www.ala.org.au/>) and this diversity extends to its habit (shrubs, small trees and tall trees) as well as distribution, which ranges from tropical to temperate ecosystems to arid areas in central Australia (Beardsell et al. 1993; Howells, 2012). Myrtaceae species can be found growing in various habitats, including woodlands,

rainforests, heathlands, swamps and riverine sites (Howells, 2012) and species composition is mostly determined by soil fertility (Myerscough, 1998; González-Orozco et al., 2014). Also, many species are sclerophyllous and well adapted to Australia's recurrent fires, droughts and poor soils (Gill, 1981).

Plant morphological similarity among species in the Myrtaceae family is high, which results in complex taxonomy and difficulty in plant identification (Govaerts et al. 2008), further complicated by hybridization amongst some *Eucalyptus* species (Kirkpatrick and Backhouse, 1985; Larcombe et al., 2014). This difficulty in identification also extends to their pollen due to the high degree of similarity in their pollen morphologies, which makes separation in fossil records difficult and limits ecological interpretations (considering the high diversity of habitats in which the plants occur). The localized nature of pollen dispersal of Myrtaceae also reinforces why detailed identification of their pollen in fossil records is of great value, as they better reflect local vegetation of the study area, especially Myrtaceae shrub pollen grains (e.g., *Melaleuca*, *Leptospermum*, *Kunzea* and *Calytrix*) (Semeniuk et al., 2006; Deng et al., 2006; Luly, 1990).

Myrtaceae pollen are generally medium (<20 µm) to large sized (~30 µm), angulaperturate, tricolporate, triangular in polar view, oblate in equatorial view, and have an apocolpial island (Thornhill et al., 2012a). Previous studies have analysed Myrtaceae pollen morphology on a large spatial scale and have made an effort to separate pollen types into species, with particular focus on *Eucalyptus* pollen (e.g., Thornhill et al. 2012a, 2012b; Picketts and Newsome, 1997). Despite these studies, the difficulty of separating Myrtaceae pollen into species or types in fossil records remains a major challenge and matter of debate (Picketts and Newsome, 1997; Thornhill, 2010), mostly due to the overlap in many of the pollen morphological features (e.g., Pike, 1956; Thornhill et al., 2012a, 2012b, 2012c).

The complexities surrounding natural pollen formation and the effect of chemical pollen processing procedures in the laboratory contribute significantly to the morphological variation observed, notably also within species. Studies show that intraspecific pollen variation can be caused by natural factors, such as genetic variation, environmental conditions (e.g., altitude), pollen formation, and polymorphism, as well as laboratory factors, including chemical treatments (e.g., acetolysis and KOH), mounting medium type and slide preparation processes (Bonhomme et al., 2013; Meltsov et al., 2008; Kriebel et al., 2017;

Mäkelä, 1996; Huysman et al., 2003; Cushing, 2011; Cushing, 1961; Lindbladh et al., 2002; Sluyter, 1997; van Wyk and Dedekind, 1985; Schüler and Behling, 2011).

The Myrtaceae is a major component of fossil pollen records in Australia, which date back as far as the Eocene (Beardsell, 1993) and their highly diverse ecological significance underpins the importance of high pollen taxonomical resolution in palaeoecological studies (Howells, 2012; Williams and Potts, 1996). Pickett and Newsome (1997) suggest that studying extant *Eucalyptus* plant pollen of an area can aid in separating the fossil pollen of that area into species types to better understand woodland dynamics, especially during the Holocene. The aim of this research is to study the pollen morphology of modern Myrtaceae plants related to a specific region of Australia, the Furneaux Group in Bass Strait, and to explore the possibility of using the morphology of modern Myrtaceae pollen to identify fossil Myrtaceae pollen from the same area to species level or types.

4.2. Methods

4.2.1. Study area

The Furneaux Group is comprised of approximately 78 islands located along the eastern margin of Bass Strait, northeast of Tasmania, with Flinders Island, truwana/Cape Barren Island and lungtalanana/Clarke Island being the three largest islands in the group (Fig. 1). truwana and lungtalanana are the Aboriginal names of Cape Barren and Clarke Islands, respectively. These islands represent the summits of a chain of low, predominately granitic, mountains that protrude above the flooded Bassian Plain. During glacial periods, low sea levels (up to a maximum of ~130 m below present), created a land bridge from mainland Australia to Tasmania. Sea-level rise in the Holocene drowned the 'Bassian Plain', leaving an archipelago of small islands across Bass Strait (Harris et al., 2001; Lambeck and Chappell, 2001; Sloss et al., 2007; Williams et al., 2018). The Furneaux Group is characterized by widespread coastal heaths and scrub rich in Myrtaceous shrubs/small trees, especially species of *Leptospermum* and *Melaleuca* (Kirkpatrick and Harris, 1999; Perrin, 1988; Harris and McKenny, 1999; Harris and Reimer, 1994; Harris and Kitchener, 2005; Fig. 1), while dry *Eucalyptus* forest and woodland has a more restricted distribution on the larger islands (Harris and Kitchener, 2005). The Furneaux Group has a large number

of wetlands suitable for palaeoecological studies, although only few palaeoecological studies have been carried out in the region (McWethy et al. 2016; Ladd et al. 1992).

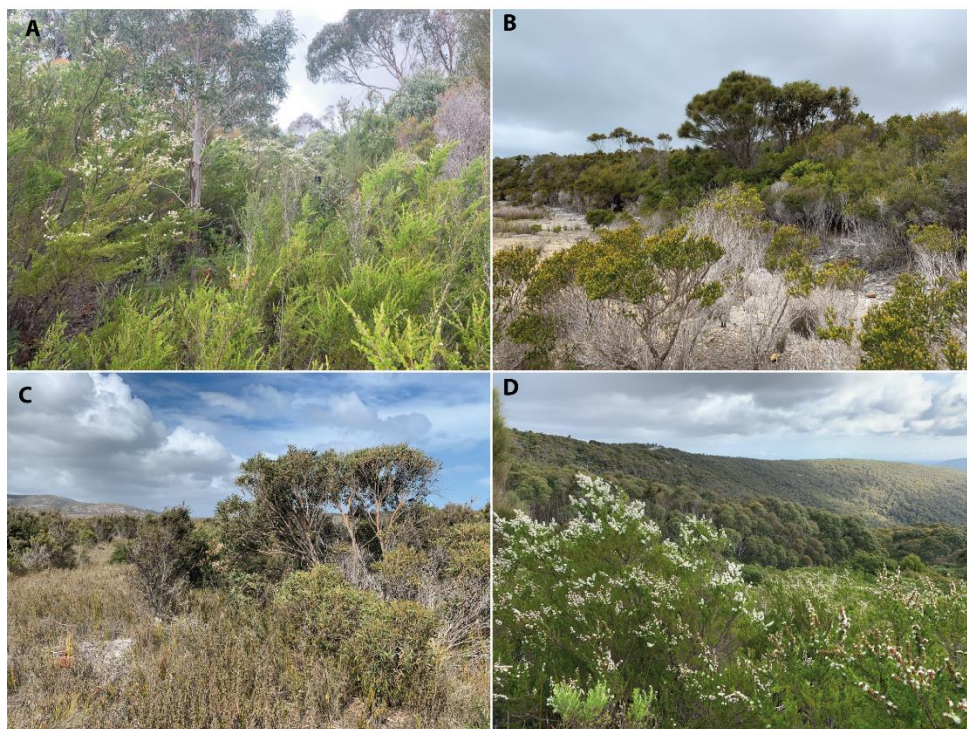
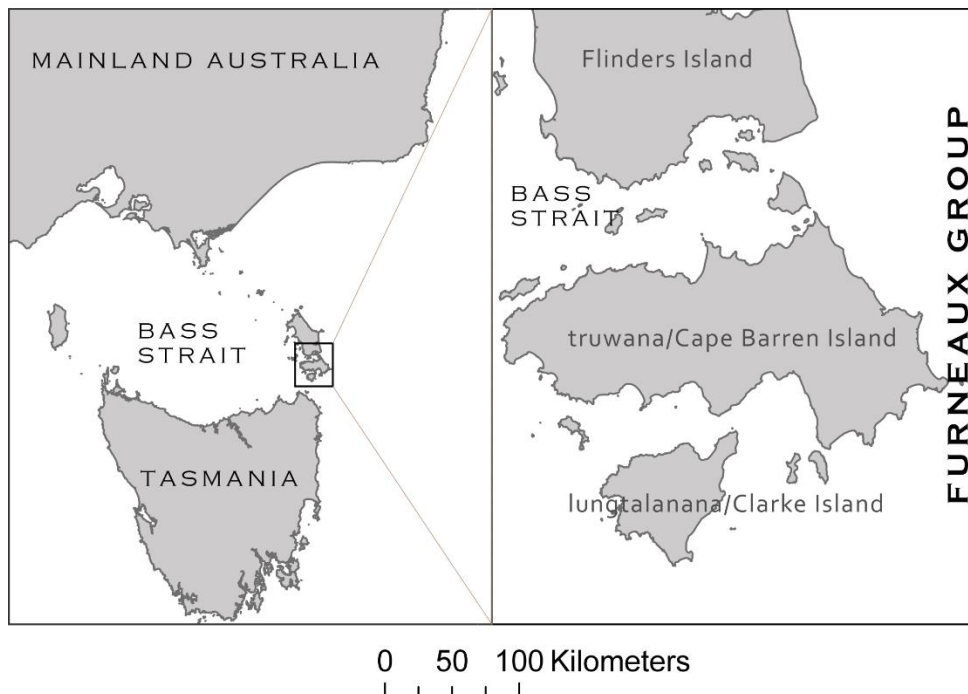


Figure 1: Location map of the Furneaux Group in Bass Strait, southeast Australia, showing major member islands, which include Flinders Island, truwana/Cape Barren Island, and lungtalanana/Clarke Island. Also shown are examples of vegetation types characterized by Myrtaceae in the Furneaux Group, which include (A) open *Eucalyptus* forest with shrubby understorey, (B) scrub, (C) heathland with scattered

thickets of taller shrubs and small *Eucalyptus* (D), *Kunzea* heaths with *Eucalyptus* forest on the background.

The plant species present in the Furneaux Group have been documented alongside plant species from other parts of Tasmania (e.g., Harris et al., 2001; Howells, 2012; Kirkpatrick and Backhouse, 1985; Williams and Potts, 1996; Page, 1998). The Myrtaceae genera found in the Furneaux Group include *Eucalyptus*, *Melaleuca*, *Leptospermum*, *Kunzea*, *Calytrix*, and *Euryomyrtus*, and the ecological distributions of these species on the islands are documented in detail in Harris et al. (2001). Myrtaceae are indicator species of dominant vegetation types on the islands of the Furneaux Group, including forests/woodland and coastal scrub. Coastal heathland and scrub on infertile soils (well drained and wet, acidic soils) are the most dominant vegetation types and are mainly dominated by species of *Leptospermum* (e.g., *Leptospermum glaucescens* and *L. scoparium*) and *Melaleuca* (e.g., *Melaleuca squarrosa*) (Fig. 1). They occupy lowlands, ridge tops and slopes and can also include scattered mallee form *Eucalyptus*. *Eucalyptus* forest and woodland are mainly restricted to Flinders Island, truwana/Cape Barren Island and lungtalanana/Clarke Island, and are mainly dominated by *Eucalyptus nitida* (peppermint), which grows on granitic substrates on slopes and ridges. Other *Eucalyptus*-dominated forests and woodland types are also present, but with limited distributions. An example is *Eucalyptus viminalis* (Symphomyrtus) forest and woodland, which can also occur as wet sclerophyll forest. *Eucalyptus viminalis* forest and woodland occur on moist soils in upper slopes and deep valleys and can also be found growing on coastal back dunes. Other *Eucalyptus*-dominated vegetation present with more limited distribution include *E. ovata* and *E. globulus* forests/woodland (Harris and Kitchener, 2005).

4.2.2. Sample collection and treatment

Pollen from 23 Myrtaceae species were obtained from herbarium specimens at the Australian National Herbarium, Canberra, ACT (Council of Heads of Australian Herbaria-CHAH), whereby specimens from the Furneaux group were targeted, but most specimens were from the wider Tasmanian region and a few samples came from South Australia, Victoria and New South Wales. To evaluate the degree of intraspecific morphological variation, pollen samples were obtained from three to four different plant specimens for each species (Table 1). Pollen samples were subjected to KOH (10%) for 10 minutes at

80°C and acetolysis treatment for three minutes at 90°C, following standard pollen preparation techniques (Faegri and Iversen, 1975; Traverse, 1988). Pollen samples were mounted in glycerol for examination and measurement using a Zeiss Axiolmager microscope at 63× magnification.

Table 1: Myrtaceae plants sampled for pollen in this study at the Australian National Herbarium, Canberra (Council of Heads of Australian Herbaria - CHAH), including location of plant collection and herbarium information.

Genus	Species	Sample id	Herbarium	Accession #	Latitude	Longitude
<i>Eucalyptus</i>	<i>amygdalina</i>	1a	CBG	33691	-43.13	147.8
<i>Eucalyptus</i>	<i>amygdalina</i>	1b	CBG	34983	-42.83	146.13
<i>Eucalyptus</i>	<i>amygdalina</i>	1c	CANB	433390	-42.53	147.46
<i>Eucalyptus</i>	<i>amygdalina</i>	1d	CANB	433402	-42.4	146.3
<i>Eucalyptus</i>	<i>diversifolia</i>	2a	CBG	3870	-38.43	141.55
<i>Eucalyptus</i>	<i>diversifolia</i>	2b	CBG	9306050	-38.41	141.55
<i>Eucalyptus</i>	<i>diversifolia</i>	2c	CANB	444599	-38.43	141.55
<i>Eucalyptus</i>	<i>globulus</i>	3a	CANB	428216	-42	146.75
<i>Eucalyptus</i>	<i>globulus</i>	3b	CANB	429251, 429252	-39.7	147.91
<i>Eucalyptus</i>	<i>globulus</i>	3c	CANB	466953	-33.43	138.95
<i>Eucalyptus</i>	<i>nitida</i>	4a	CANB	454506	-39.48	147.35
<i>Eucalyptus</i>	<i>nitida</i>	4b	CANB	463722	-42.61	145.28
<i>Eucalyptus</i>	<i>nitida</i>	4c	CANB	270213		
<i>Eucalyptus</i>	<i>tenuiramis</i>	5a	CANB	453503	-43.1	147.8
<i>Eucalyptus</i>	<i>tenuiramis</i>	5b	CANB	739302	-43.23	147.41
<i>Eucalyptus</i>	<i>tenuiramis</i>	5c	CANB	800444	-42.825	147.208
<i>Eucalyptus</i>	<i>ovata</i>	6a	CANB	423346	-37.91	147.25
<i>Eucalyptus</i>	<i>ovata</i>	6b	CANB	6644	-42.9	147.31
<i>Eucalyptus</i>	<i>ovata</i>	6c	CANB	720045	-37.13	142.51
<i>Eucalyptus</i>	<i>viminalis</i>	7a	CANB	430032	-41.06	146.8
<i>Eucalyptus</i>	<i>viminalis</i>	7b	CANB	814139	-39.65	144.736
<i>Eucalyptus</i>	<i>viminalis</i>	7c	CANB	551810	-42.043	145.27

<i>Eucalyptus</i>	<i>willisii</i>	8a	CANB	494945	-38.23	146.875
<i>Eucalyptus</i>	<i>willisii</i>	8b	CANB	430175	-37.71	140.61
<i>Eucalyptus</i>	<i>willisii</i>	8c	CANB	418249		
<i>Melaleuca</i>	<i>armillaris</i>	9a	CANB	411315	-38.417	144.183
<i>Melaleuca</i>	<i>armillaris</i>	9b	CANB	346641	-39.231	146.387
<i>Melaleuca</i>	<i>armillaris</i>	9c	CANB	242021	-37.58	149.75
<i>Melaleuca</i>	<i>ericifolia</i>	10a	CANB	480637	-40.05	147.75
<i>Melaleuca</i>	<i>ericifolia</i>	10b	CANB	480640		
<i>Melaleuca</i>	<i>ericifolia</i>	10c	CANB	483636	-40.13	148.13
<i>Melaleuca</i>	<i>gibbosa</i>	11a	CBG	8808370	-39.98	148.21
<i>Melaleuca</i>	<i>gibbosa</i>	11b	CBG	8412039	-42.13	148.31
<i>Melaleuca</i>	<i>gibbosa</i>	11c	CBG	15184	-43.28	147.3
<i>Melaleuca</i>	<i>squamea</i>	12a	CANB	242988	-42.08	146.16
<i>Melaleuca</i>	<i>squamea</i>	12b	CANB	340359	-40.01	148.03
<i>Melaleuca</i>	<i>squamea</i>	12c	CANB	340356	-40	148.2
<i>Melaleuca</i>	<i>squarrosa</i>	13a	CANB	340360	-39.98	148.18
<i>Melaleuca</i>	<i>squarrosa</i>	13b	CANB	346597	-41.1	146.81
<i>Melaleuca</i>	<i>squarrosa</i>	13c	CANB	18883	-41.33	148.25
<i>Melaleuca</i>	<i>pallida</i>	14a	CBG	7613	-42.96	147.31
<i>Melaleuca</i>	<i>pallida</i>	14b	CBG	7631	-43.41	146.86
<i>Melaleuca</i>	<i>pallida</i>	14c	CANB	121363	-41.38	146.16
<i>Leptospermum</i>	<i>glaucescens</i>	15a	CANB	452644	-40.06	148.03
<i>Leptospermum</i>	<i>glaucescens</i>	15b	CBG	8311301	-42.1	148.2
<i>Leptospermum</i>	<i>laevigatum</i>	16a	CANB	481016	-40.3	147.86
<i>Leptospermum</i>	<i>laevigatum</i>	16b	CANB	481013	-40.063	147.759
<i>Leptospermum</i>	<i>laevigatum</i>	16c	CANB	481579	-40.516	148.141
<i>Leptospermum</i>	<i>lanigerum</i>	17a	CBG	7705823	-41.76	146.21
<i>Leptospermum</i>	<i>lanigerum</i>	17b	CBG	8310764	-41.2	148.01
<i>Leptospermum</i>	<i>lanigerum</i>	17c	CANB	483227	-40.1	148
<i>Leptospermum</i>	<i>nitidum</i>	18a	CANB	511048	-42.51	146.18
<i>Leptospermum</i>	<i>nitidum</i>	18b	CANB	829750	-41.485	145.159
<i>Leptospermum</i>	<i>nitidum</i>	18c	CANB	825781	-41.25	145.2
<i>Leptospermum</i>	<i>scoparium</i>	19a	CBG	8704137	-43.204	147.963

<i>Leptospermum scoparium</i>	19b	CBG	8900411	-41.13	146.71
<i>Leptospermum scoparium</i>	19c	CBG	14178	-43.221	147.409
<i>Leptospermum squarrosum</i>	20a	CBG	9010197	-35.15	150.7
<i>Leptospermum squarrosum</i>	20b	CANB	263374	-32.7	152.1
<i>Leptospermum squarrosum</i>	20c	CANB	263376	-33.66	151.3
<i>Kunzea ambigua</i>	21a	CANB	554904	-40.05	148.08
<i>Kunzea ambigua</i>	21b	CANB	553738	-40.4	148
<i>Kunzea ambigua</i>	21c	CANB	885899	-43.08	147.255
<i>Calytrix tetragona</i>	22a	CBG	26785	-42.21	148.33
<i>Calytrix tetragona</i>	22b	CBG	28928	-40.85	145.5
<i>Calytrix tetragona</i>	22c	CBG	30149	-42.21	148.26
<i>Euryomyrtus ramosissima</i>	23a	CBG	7094	-43.03	147.93
<i>Euryomyrtus ramosissima</i>	23b	CBG	19036	-36.56	144.33
<i>Euryomyrtus ramosissima</i>	23c	CBG	7095	-36.7	146.83

4.2.3. Pollen morphological features

At least 20 pollen grains were photographed and measured for each plant specimen.

Features measured include pollen length, pollen width, colpi length, wall thickness and pore height (Fig. 2). Pollen grains were measured as soon as possible after chemical treatment (mostly within a few days up to one week) to limit potential changes in pollen morphology when stored or mounted in glycerol. Measurements and other pollen morphological features such as aperture type, colp and pore morphology, and exine ornamentation were used to create a character table for all pollen grains. Cluster analysis was undertaken using Ward's hierarchical clustering method in R using the 'vegan' package (R core team, 2020; Oksanen et al., 2018).

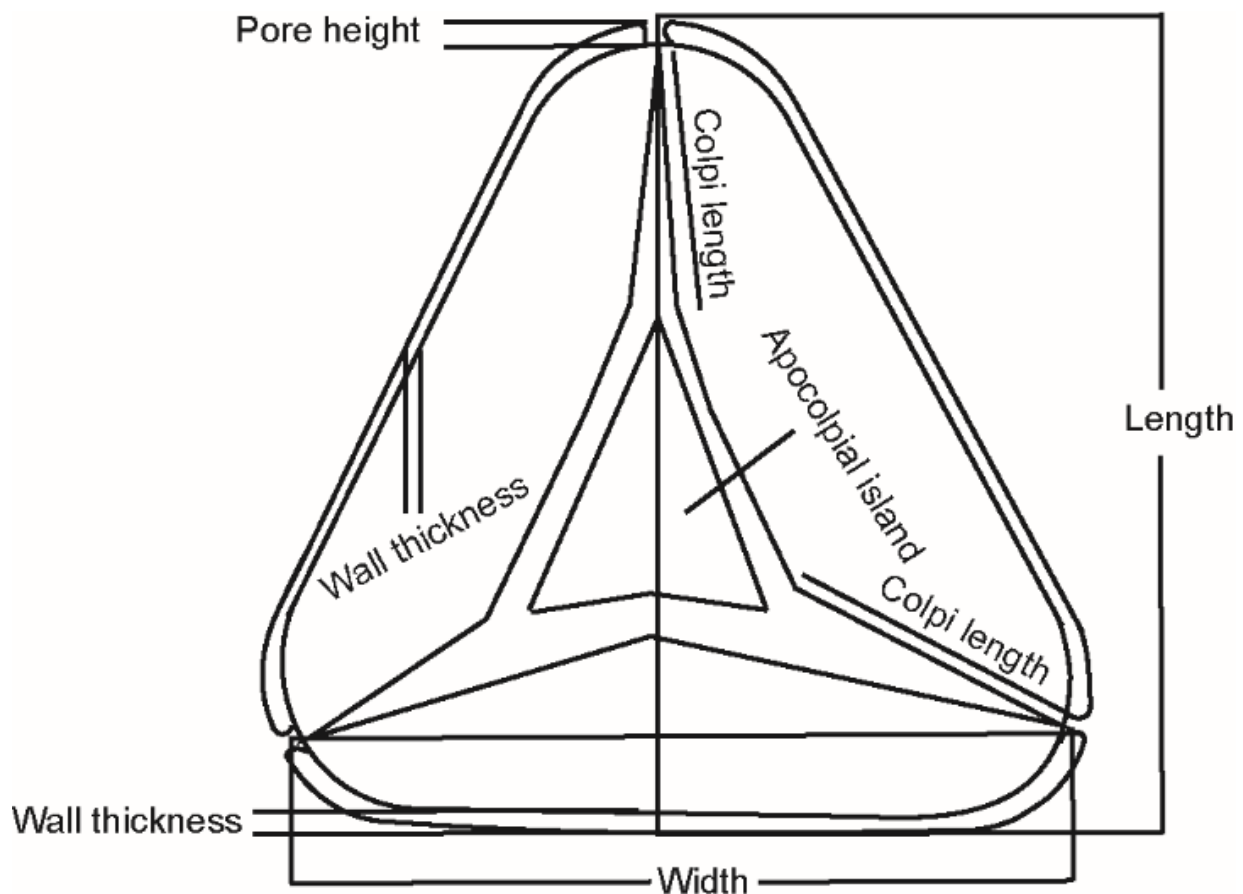


Figure 2: Illustration of pollen measurements undertaken in this study.

All pollen grains were observed in their polar view and morphological descriptions follow Myrtaceae pollen descriptions of Chalson and Martin (1995) as highlighted in Thornhill et al. (2012a). Colpal morphology is defined as primarily syncolpate and parasyncolpate. The syncolpate pollen grains have their colpi joined at the pole, while parasyncolpate pollen grains have colpi that do not meet at the pole thus, forming a triangle (apocolpial field) at the centre of the pole. Exine ornamentation varies between psilate, scabrate and verrucate; however, as the exine patterns of some of the Myrtaceae observed is not clear. Pollen sides are defined as straight, convex or concave.

4.2.4. Fossil Myrtaceae pollen analysis

The observed morphological characters of modern Myrtaceae pollen taxa were applied to unpublished pollen records from the Furneaux Group for possible identification of Myrtaceae pollen to species level or types. The pollen records were extracted from

radiocarbon-dated sediment cores from Big Reedy Lagoon on truwana/Cape Barren Island and Remy Boy Lake on lungtalanana/Clarke Island and span from Marine Isotope Stage (MIS) 3 through the late Glacial and Holocene periods (the last ~40,000 years).

4.3. Results

4.3.1. Reference images and measurement data

Summary images and measurement data of Myrtaceae pollen grains examined in this study including fossil pollen are presented in Plates I–IX, Table 2–3, and Fig. 3–5. Also, a full image catalogue of examined Myrtaceae pollen (with over 3000 images) and raw measurement data used for this study can be accessed and downloaded from the Australian National University Data Commons at <https://dx.doi.org/10.25911/5e82cc833d278>.



Plate I: Modern pollen from the Furneaux Group. *Eucalyptus globulus* (Symphomyrtus). (1-4), *E. ovata* (Symphomyrtus) (5-8), *E. viminalis* (Symphomyrtus). (9-12), *E. diversifolia* (13-16), *E. amygdalina* (Peppermint) (17-20). See supplementary material for more pollen images at <https://dx.doi.org/10.25911/5e82cc833d278>.

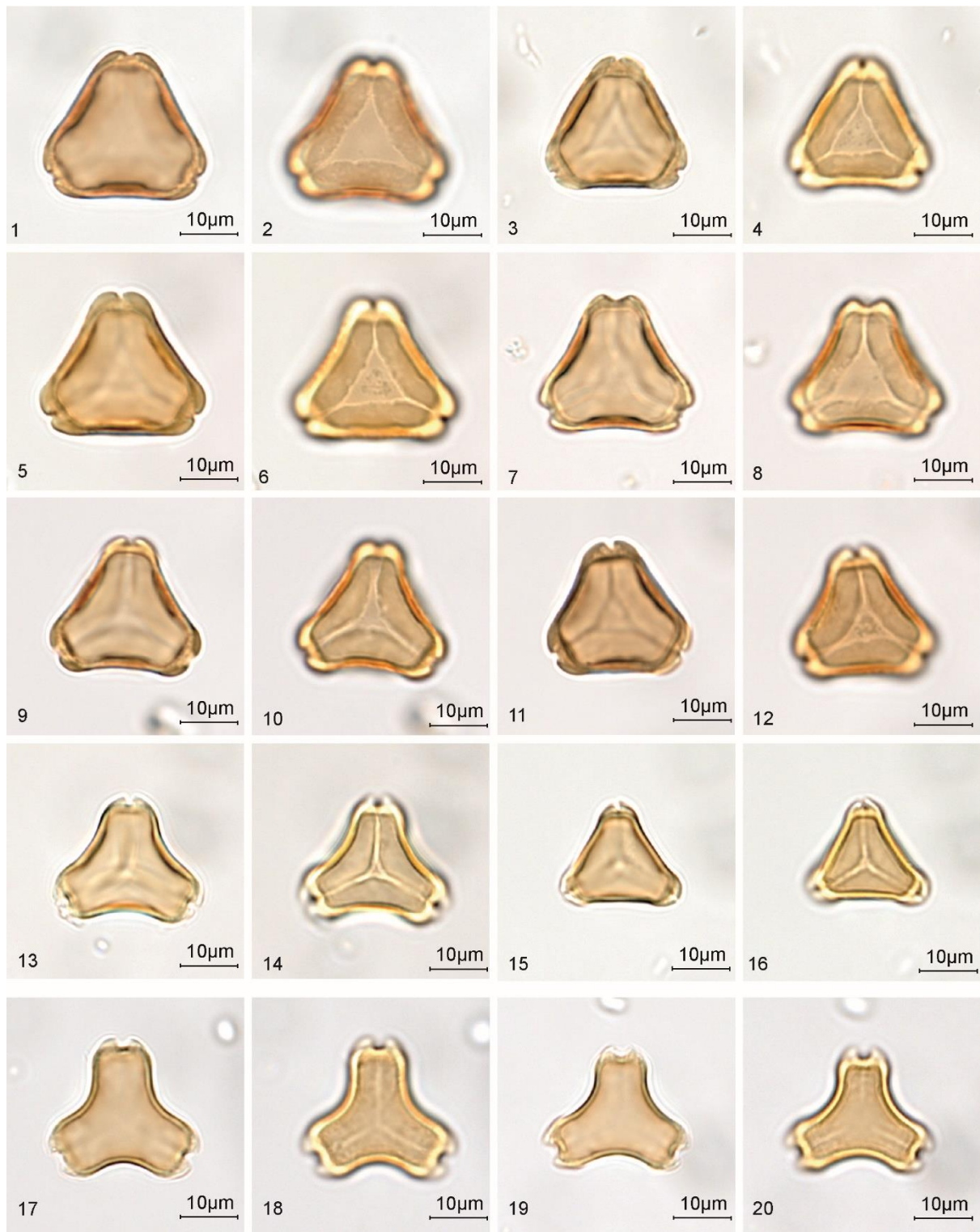


Plate II: Modern pollen from the Furneaux Group. *Eucalyptus nitida* (Peppermint) (1-4), *E. tenuiramis* (Peppermint) (5-8), *E. willisii* (Peppermint) (9-12), *Kunzea ambigua* (13-16), *Calytrix tetragona* (17-20). See supplementary material for more pollen images at <https://dx.doi.org/10.25911/5e82cc833d278>.

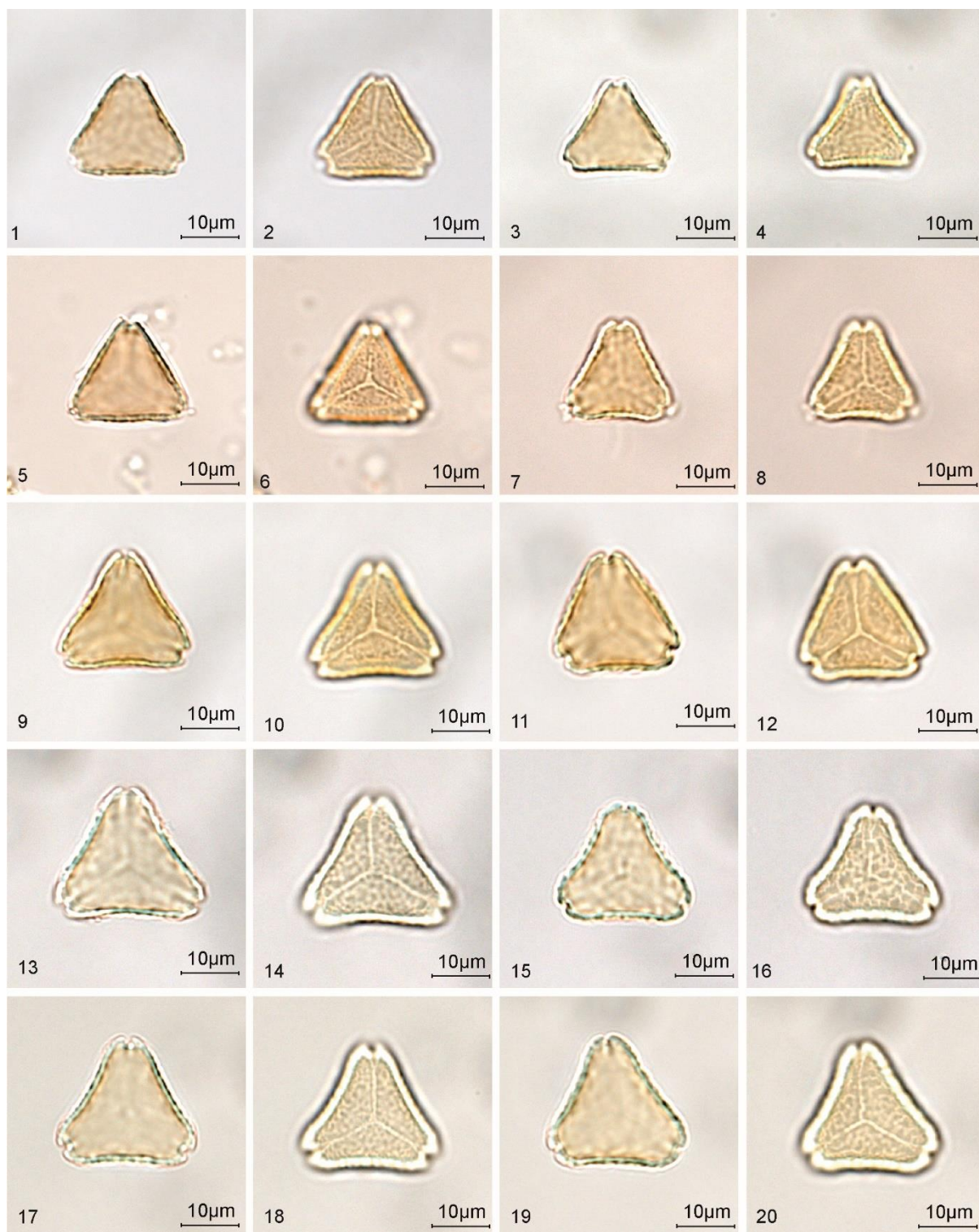


Plate III: Modern pollen from the Furneaux Group. *Euryomyrtus ramosissima* (1-4), *Leptospermum glaucescens* (5-8), *L. laevigatum* (9-12), *L. lanigerum* (13-16), *L. nitidum* (17-20). See supplementary material for more pollen images at <https://dx.doi.org/10.25911/5e82cc833d278>.

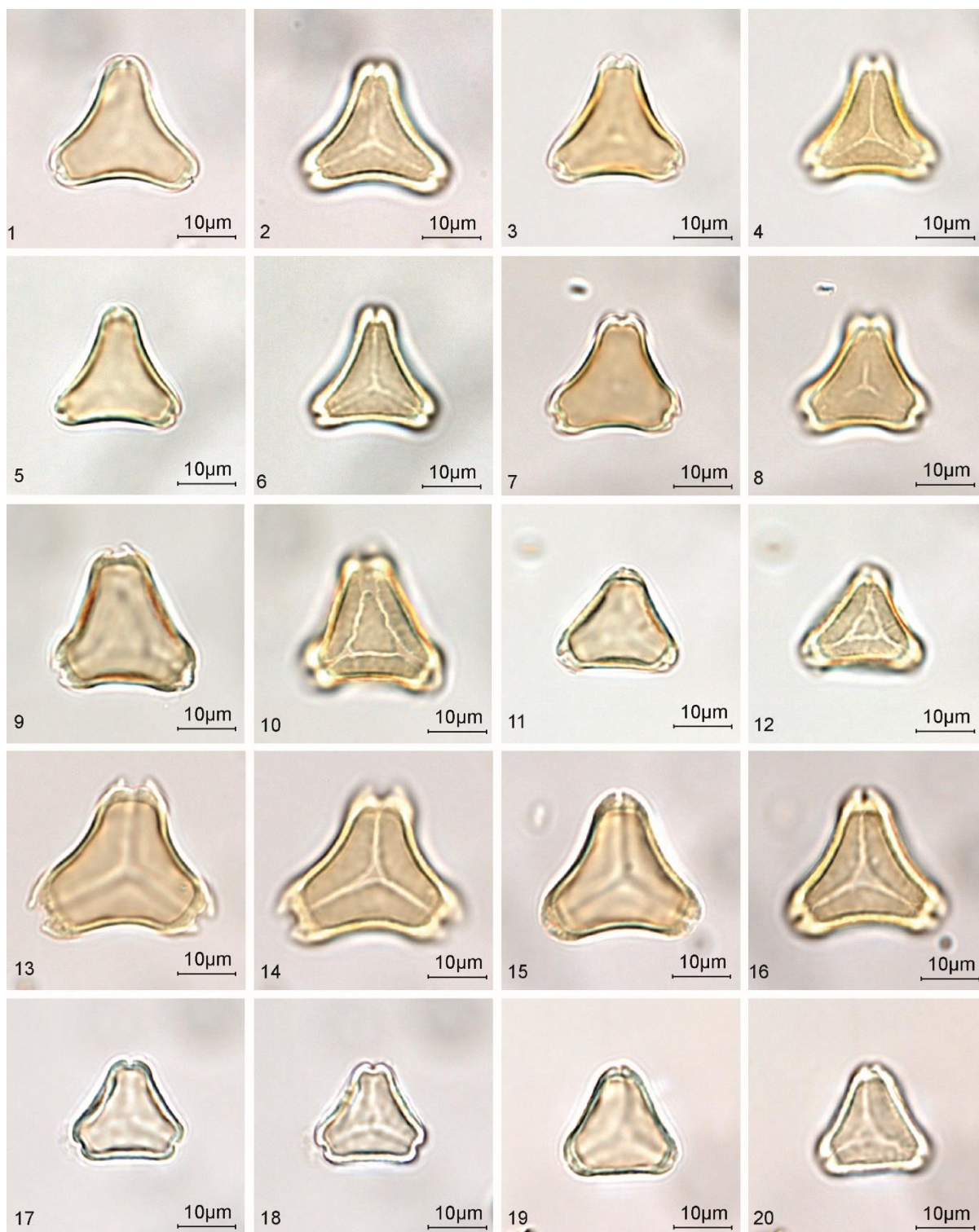


Plate IV: Modern pollen from the Furneaux Group. *Leptospermum scoparium* (1-4), *L. squarrosum* (5-8), *Melaleuca pallida* (9-12), *M. armillaris* (13-16), *M. ericifolia* (17-20). See supplementary material for more pollen images at <https://dx.doi.org/10.25911/5e82cc833d278>.

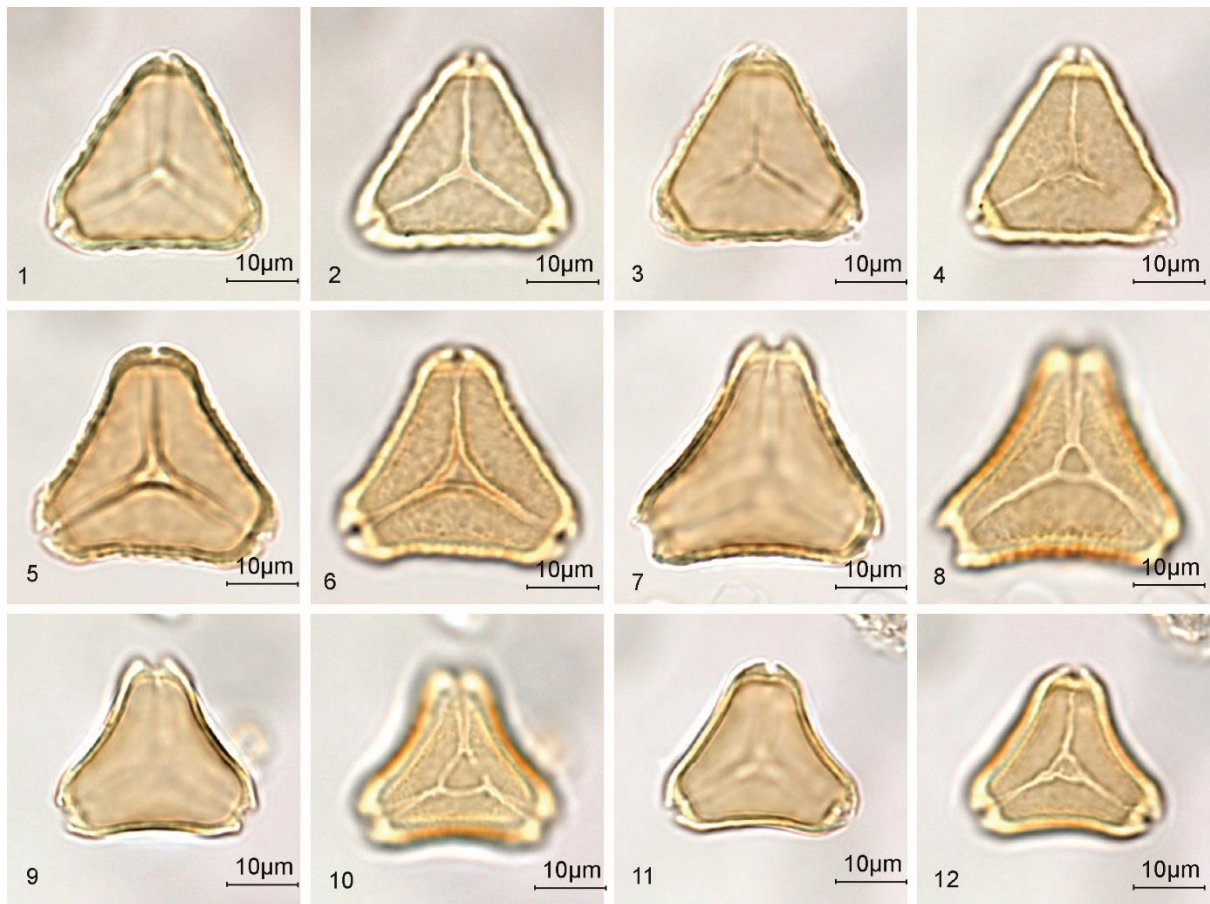


Plate V: Modern pollen from the Furneaux Group. *Melaleuca gibbosa* (1-4), *M. squamea* (5-8), and *M. squarrosa* (9-12). See supplementary material for more pollen images at <https://dx.doi.org/10.25911/5e82cc833d278>.

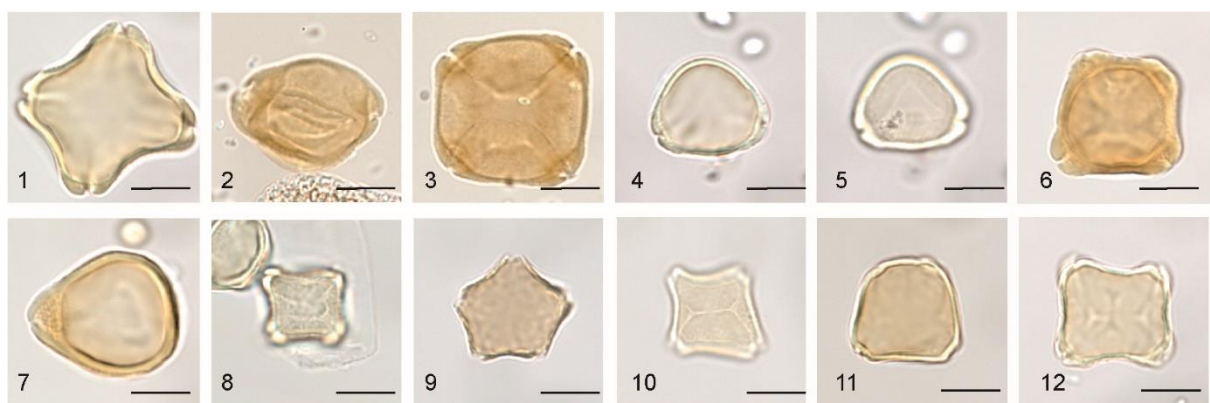


Plate VI: Myrtaceae pollen with pore aberration. *E. viminalis* (1), *E. globulus* (2 and 3), *E. willisii* (4 and 5), *E. ovata* (6 and 7), *M. pallida* (8), *Euryomyrtus ramosissima* (9), *L. scoparium* (10), *L. squarrosus* (11), *M. armillaris* (12).

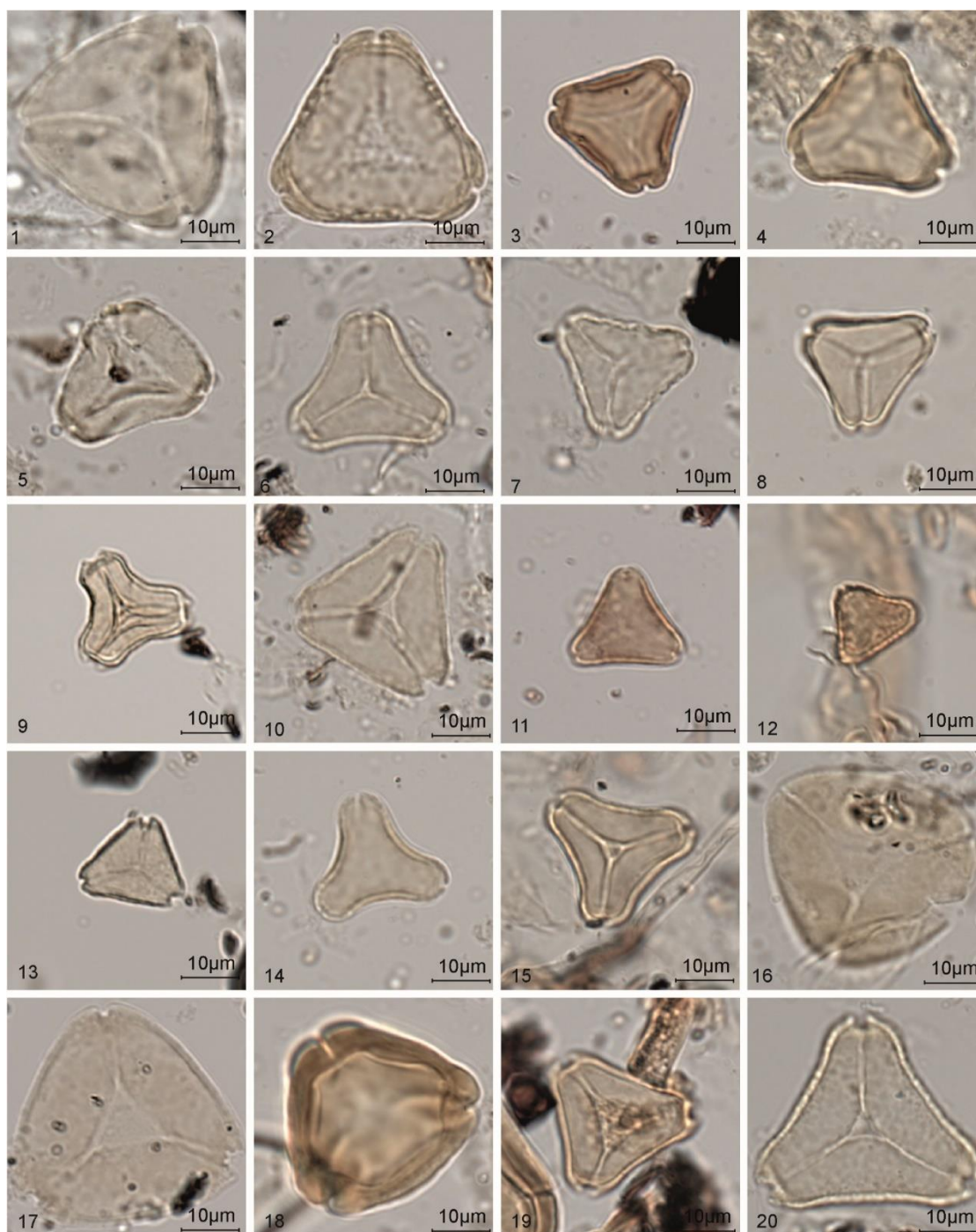


Plate VII: Some examples of fossil pollen from Big Reedy Lagoon samples on truwana/Cape Barren Island. Symphomyrtus type (1-2), peppermint type (2-4), *Melaleuca pallida* (5), *Kunzea ambigua* (6), *M. gibbosa* (7), *M. ericifolia* (8), *Calytrix tetragona* (9), *M. squarrosa* type (10), *Leptospermum*/*Euryomyrtus* (11-13), *Leptospermum grandiflorum*? (14), *Melaleuca* sp? (15), swollen Symphomyrtus type? (16-17), Symphomyrtus type? (18), *M. squarrosa* type? (19-20). Big Reedy Lagoon spans the Late Glacial to Holocene (the last ~14000 years).

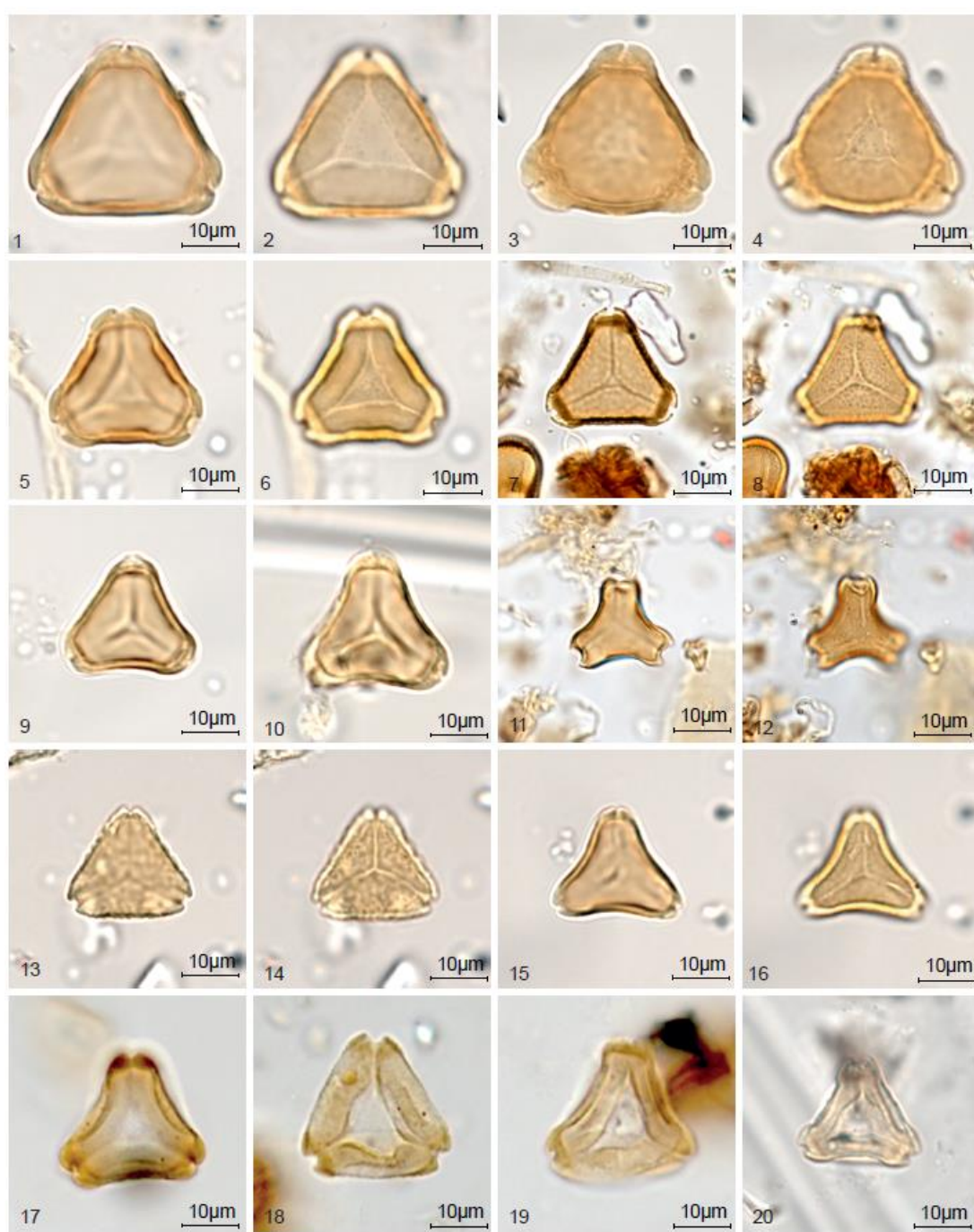


Plate VIII: Some examples of fossil Myrtaceae pollen from Remy Boy Lake on Iungtalanana/Clarke Island. *Eucalyptus* S-type 1 (1-2), *Eucalyptus* S-type 2 (3-4), *Eucalyptus* P-type (5-6), *Melaleuca squarrosa* (7-8), *Kunzea ambigua* (9-10), *Calytrix tetragona* (11-12) *Leptospermum*/*Euryomyrtus* (13-14), *Leptospermum scoparium*/*Leptospermum squarrosum* (15-16). Images 1-16 exhibit well preserved grains from organic, MIS3 aged sediments. Images 17-20 exhibit poorly preserved grains from inorganic, LGM/late glacial aged sediments.

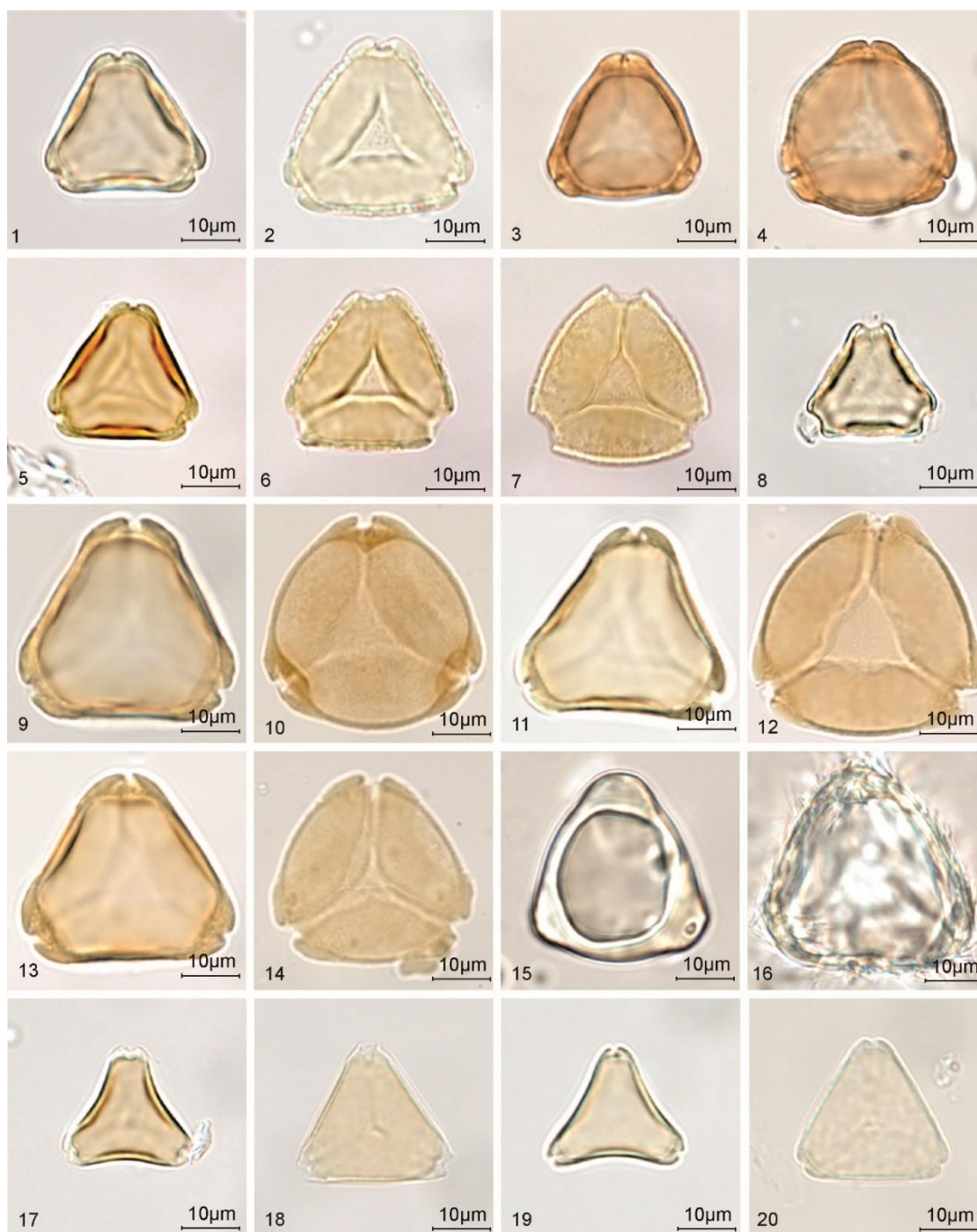


Plate IX: Examples of variability in Myrtaceae pollen shape and size. *E. amygdalina*: sample 1c (1), sample 1c after 5 days (2), sample 1d (3,4), sample 1b (5-7), APSA sample 225-3-242 (8), *E. globulus*: sample 3b (9), APSA sample 225-3-49 (10), *E. ovata*: sample 6c (11-12), *E. viminalis*: sample 7b (13), APSA sample 255-3-1b (14), 255-3-1 (15-16), *L. scoparium*: sample 19a (17-18), *L. squarrosus*: sample 20a (19-20). *after number indicates grain is of suggested natural shape.

Table 2: Myrtaceae pollen sample measurements, showing maximum values (left), averages (in brackets), and minimum values (right). Pollen pore area shape (pore amb) include notched (N), pointed (P), round (R), and flat (F).

Species	Length (µm)		Width (µm)		Colpi length (µm)	Wall		Pore height (µm)	Pore amb		
						thickness (µm)					
<i>C. tetragona</i>	17.5 (15.2)	12.7	18.7 (16.1)	12.8	10.7 (8.6)	6.4	1.3 (0.9)	0.6	2.1 (1.4)	0.9	R
<i>Eucalyptus amygdalina</i>	25.1 (19.6)	15.7	22.4 (18.7)	15.5	8.2 (5.6)	3.3	2.4 (1.4)	0.6	3.5 (2.4)	1.4	R, F
<i>E. diversifolia</i>	24.9 (21.0)	17.4	22.8 (20.4)	18.4	8.9 (7.1)	4.9	2.4 (1.3)	0.6	2.8 (2.1)	1.0	R
<i>E. globulus</i>	29.9 (24.5)	18.3	29.4 (23.7)	16.8	10.4 (7.3)	5.5	2.0 (1.3)	0.7	5.1 (3.2)	0.7	R, F
<i>E. nitida</i>	21.1 (18.6)	16.6	19.5 (18.0)	14.9	6.4 (5.1)	4.1	1.6 (1.4)	0.9	2.6 (2.0)	1.4	R, F
<i>E. ovata</i>	25.5 (22.7)	19.4	24.9 (21.9)	18.2	8.7 (6.8)	4.8	2.4 (1.5)	1.0	5.5 (3.8)	2.1	R, F
<i>E. tenuiramis</i>	22.1 (18.7)	15.7	21.3 (18.5)	14.7	7.7 (5.6)	3.9	2.4 (1.4)	0.7	3.6 (2.2)	1.3	R, F
<i>E. viminalis</i>	26.7 (22.6)	18.9	27.7 (22.1)	17.6	9.2 (6.9)	4.8	2.6 (1.4)	0.6	5.9 (3.5)	1.7	R, F
<i>E. willisii</i>	20.8 (17.2)	14.9	21.3 (16.7)	14.6	6.8 (5.4)	2.2	2.0 (1.3)	0.7	6.5 (2.5)	1.4	R, F
<i>Euryomyrtus ramosissima</i>	17.5 (13.4)	11.2	16.9 (13.6)	11.7	9.9 (6.9)	4.2	1.2 (0.7)	0.3	1.5 (0.9)	0.5	N, P
<i>K. ambigua</i>	19.1 (15.9)	11.3	20.4 (16.3)	10.8	10.7 (8.1)	5.2	1.7 (1.0)	0.6	2.8 (2.0)	1.1	P
<i>L. glaucescens</i>	14.5 (12.9)	11.3	14.9 (13.1)	10.7	8.6 (7.4)	6.4	0.9 (0.7)	0.6	1.9 (1.1)	0.8	N, P
<i>L. laevigatum</i>	17.0 (14.8)	12.6	18.4 (14.9)	13.0	9.3 (7.7)	2.3	1.4 (0.8)	0.5	1.9 (1.2)	0.7	N, P
<i>L. lanigerum</i>	18.6 (15.2)	12.2	19.6 (15.7)	13.0	11.0 (8.0)	1.7	1.5 (0.8)	0.5	1.7 (1.0)	0.7	N, P
<i>L. nitidum</i>	17.3 (15.2)	12.5	18.3 (15.8)	12.7	9.5 (8.2)	6.0	1.5 (0.8)	0.5	1.9 (1.2)	0.7	N, P
<i>L. scoparium</i>	19.4 (15.7)	13.2	19.7 (16.5)	13.4	11.7 (8.4)	5.4	1.5 (0.9)	0.5	2.3 (1.3)	0.6	N, P
<i>L. squarrosum</i>	19.0 (14.9)	12.1	19.7 (15.9)	12.8	11.4 (8.2)	5.4	1.5 (0.9)	0.1	2.2 (1.5)	0.9	N, P
<i>M. armillaris</i>	21.3 (17.0)	12.9	21.9 (17.6)	12.7	10.8 (7.8)	5.1	1.5 (0.9)	0.5	3.5 (2.1)	1.2	R
<i>M. ericifolia</i>	15.7 (13.7)	12.0	16.3 (13.4)	10.9	7.2 (5.7)	3.9	1.6 (0.9)	0.5	2.3 (1.5)	0.8	R
<i>M. gibbosa</i>	21.4 (18.8)	14.9	22.4 (18.8)	15.2	12.2 (9.2)	5.8	1.6 (0.9)	0.5	2.9 (2.0)	1.1	R
<i>M. pallida</i>	18.7 (14.7)	12.7	18.1 (14.8)	11.7	6.2 (4.5)	2.7	1.2 (0.9)	0.5	2.0 (1.5)	1.0	R
<i>M. squamea</i>	24.0 (20.5)	17.1	24.9 (21.8)	17.8	11.3 (8.9)	7.3	1.7 (1.0)	0.5	3.3 (2.2)	1.0	R

Table 3: Table showing percentage ratios of Myrtaceae pollen sample measurements from table 2, wall patterns (exine), aperture types (Apert.), and size of apocolpial field (Apo.Field). 'V', 'P', and 'S' represent verrucate, psilate and scabrate exine/wall, respectively. 'Syn' and 'Para' represent syncolpate and parasyncolpate apertures, respectively. 'L' and 'S' represent large and small apocolpial fields, respectively.

Species	Colpi : Length (%)	Pore : Length (%)	Wall : Length (%)	Exine	Apert.	Apo.Field
<i>C. tetragona</i>	64.9 (55.9) 42.7	13.5 (9.2) 5.9	8.6 (5.5) 3.8	VPS	Syn	-
<i>Eucalyptus amygdalina</i>	36.3 (28.4) 13.9	18.3 (12.2) 8.0	13.7 (7.6) 4.3	S/P	Para	L
<i>E. diversifolia</i>	43.2 (33.4) 12.4	13.4 (10.2) 4.6	12.1 (7.1) 3.8	S/P	Para	L
<i>E. globulus</i>	41.3 (30.1) 23.1	28.2 (14.2) 7.4	9.2 (5.6) 2.7	S/P	Para	L
<i>E. nitida</i>	40.4 (27.6) 16.9	16.9 (10.8) 6.8	13.5 (8.2) 5.3	S/P	Para	L
<i>E. ovata</i>	39.6 (29.9) 21.2	27.3 (16.8) 9.0	10.7 (7.0) 4.0	S/P	Para	L
<i>E. tenuiramis</i>	38.5 (29.7) 20.7	21.9 (12.0) 6.6	12.5 (8.9) 5.5	S/P	Para	L
<i>E. viminalis</i>	38.4 (30.5) 21.9	27.2 (16.0) 6.3	12.0 (6.1) 2.4	S/P	Para	L
<i>E. willisii</i>	38.9 (30.7) 12.5	36.3 (15.0) 6.5	13.4 (8.6) 6.2	S/P	Para	L
<i>Euryomyrtus ramosissima</i>	62.7 (52.0) 29.2	11.0 (6.6) 3.7	8.5 (5.1) 2.2	V	Syn	-
<i>K. ambigua</i>	61.6 (51.1) 33.3	22.3 (12.6) 6.3	10.4 (6.4) 3.9	S/P	Syn	-
<i>L. glaucescens</i>	65.5 (57.1) 50.5	13.5 (8.7) 5.6	7.7 (5.6) 4.5	V	Syn	-
<i>L. laevigatum</i>	66.4 (52.3) 15.9	11.9 (8.2) 4.3	8.0 (5.1) 3.5	V	Syn	-
<i>L. lanigerum</i>	70.3 (52.1) 12.3	12.1 (7.0) 4.3	10.3 (5.0) 3.1	V	Syn	-
<i>L. nitidum</i>	60.0 (54.3) 39.7	12.3 (7.8) 4.3	10.3 (5.0) 3.5	V	Syn	-
<i>L. scoparium</i>	64.6 (53.9) 37.4	9.5 (8.1) 3.0	9.5 (5.6) 3.0	V/S/P	Syn	-
<i>L. squarrosus</i>	63.4 (55.3) 38.7	15.9 (10.2) 5.4	9.1 (5.9) 0.5	V/P	Syn	-
<i>M. armillaris</i>	56.7 (46.1) 33.1	19.3 (12.7) 7.0	7.2 (5.2) 2.6	P/S	Para	S
<i>M. ericifolia</i>	52.6 (41.9) 28.3	16.9 (10.8) 5.0	11.6 (7.2) 3.7	V/P	Para	S
<i>M. gibbosa</i>	60.9 (48.5) 36.2	14.3 (10.3) 6.1	8.1 (5.6) 3.5	V/S	Syn	-
<i>M. pallida</i>	41.6 (31.2) 15.5	14.6 (10.5) 6.9	8.6 (6.0) 3.5	V/P	Para	L
<i>M. squamea</i>	64.6 (43.6) 34.0	17.0 (10.9) 4.4	8.1 (5.6) 2.4	V	Para	S
<i>M. squarrosa</i>	51.8 (43.9) 33.5	18.1 (10.2) 3.4	7.5 (4.8) 2.6	V/S/P	Para	S

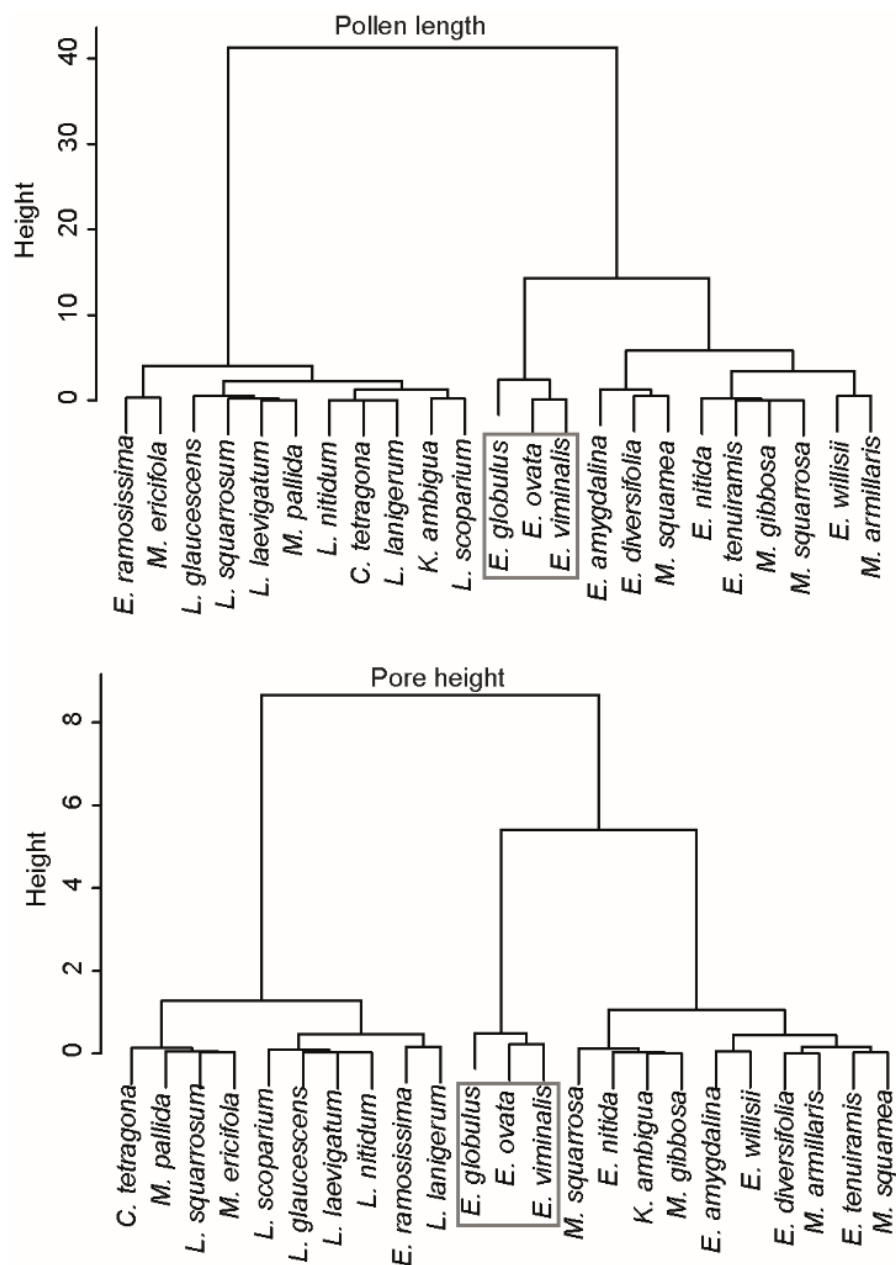


Figure 3: Cluster dendrogram using Ward's clustering method based on pollen length and pore height, showing distinct clusters separating *Symphomyrtus Eucalyptus* types from other *Eucalyptus* types as well as other Myrtaceae pollen grains.

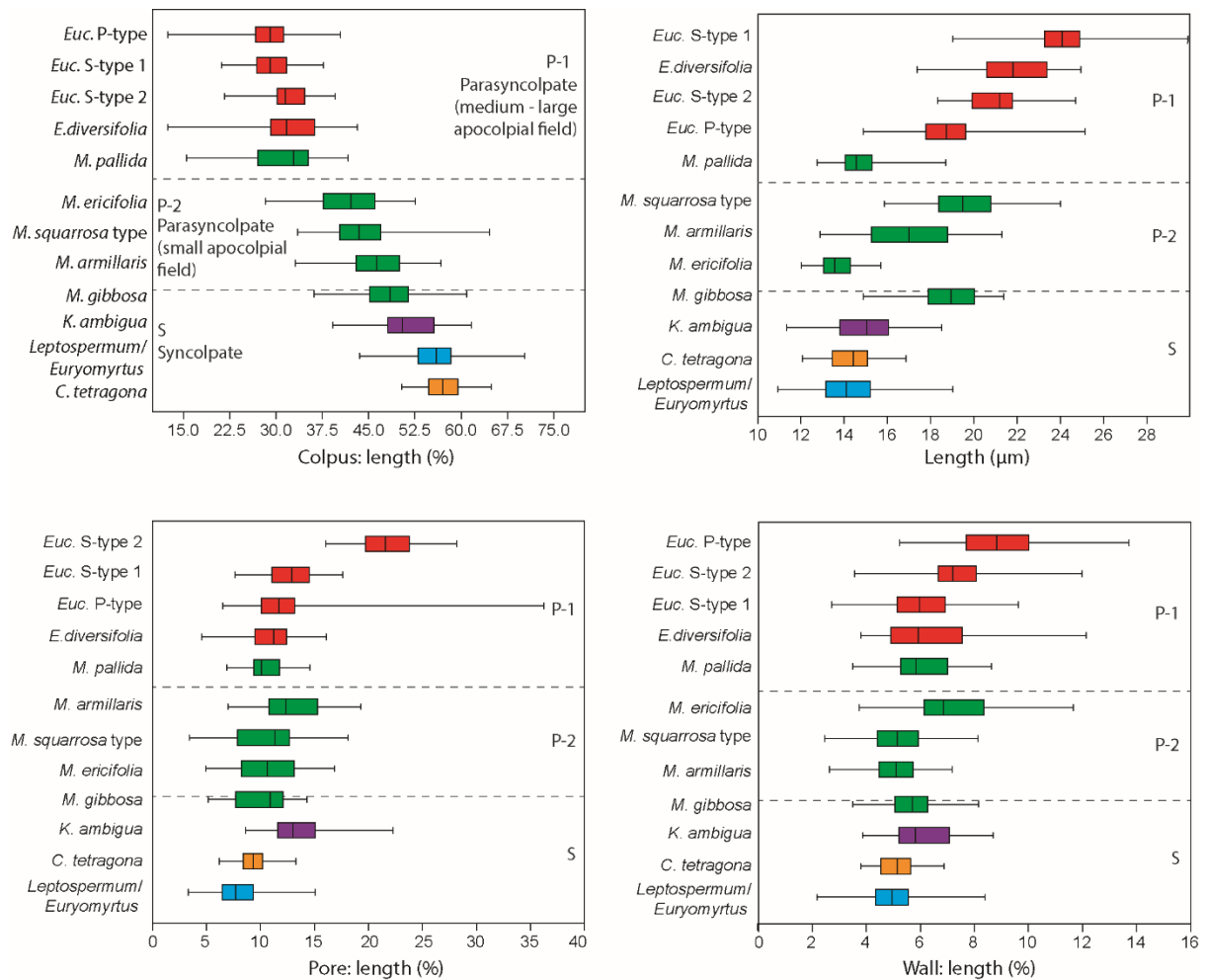


Figure 4: Box plots showing summary distribution of measured morphological characters (colpi length, length, wall thickness and pore height) of Myrtaceae pollen types. *Eucalyptus* types are in red, *Melaleuca* in green, *K. ambigua* in purple, *Leptospermum/Euryomyrtus* in blue, and *C. tetragona* in orange. S-type 1 and 2 refer to the two *Symphomyrtus Eucalyptus* types, while P-type refers to the peppermint *Eucalyptus* type. The pollen types are sorted within three groups based on their colpal morphology: 'P-1' and 'P-2' are parasyncolpate types with large and small apocolpial fields, respectively, while 'S' represents the syncolpate group.

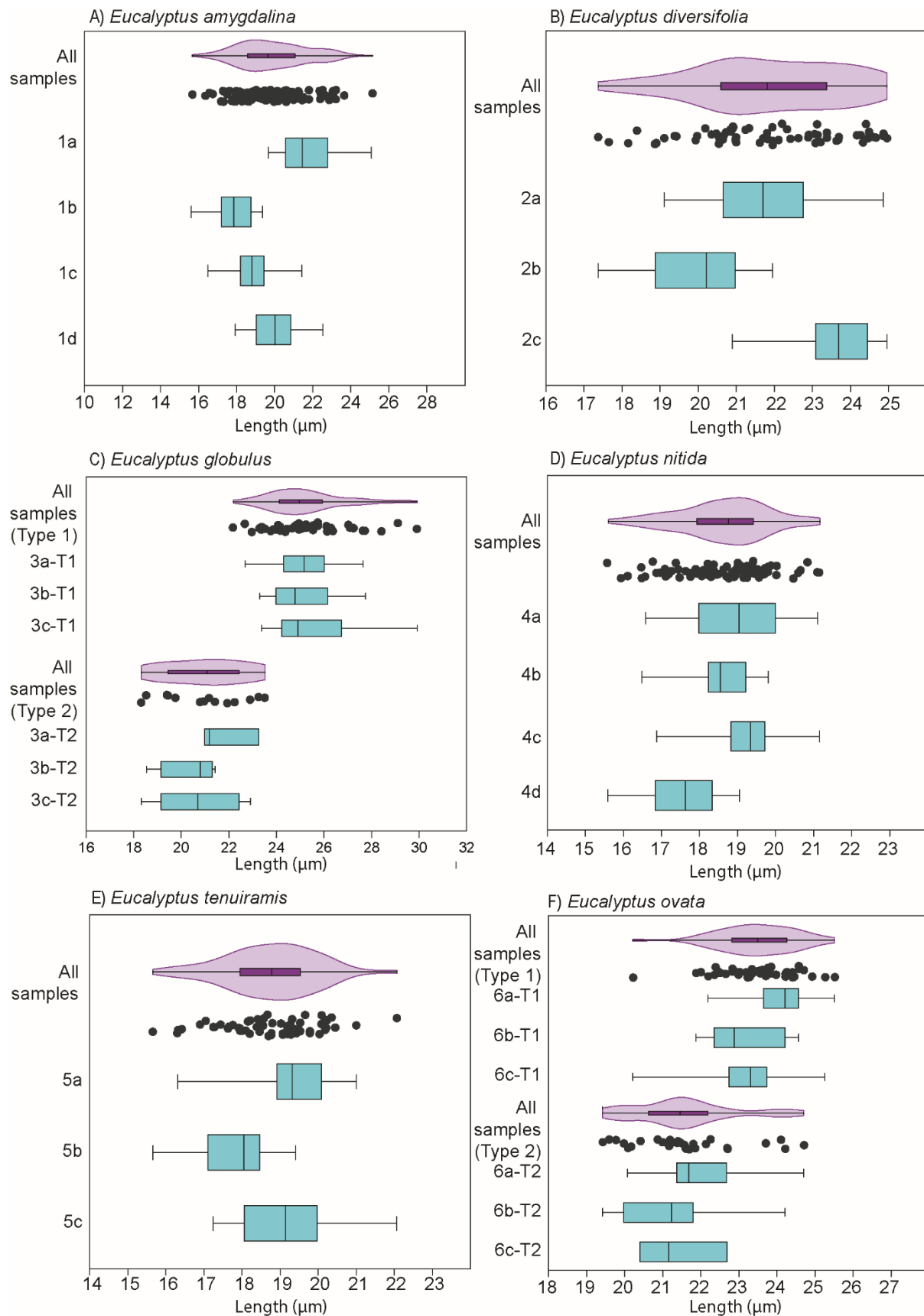


Figure 4a: Size (length) distribution of individual Myrtaceae species sample (*Eucalyptus*).

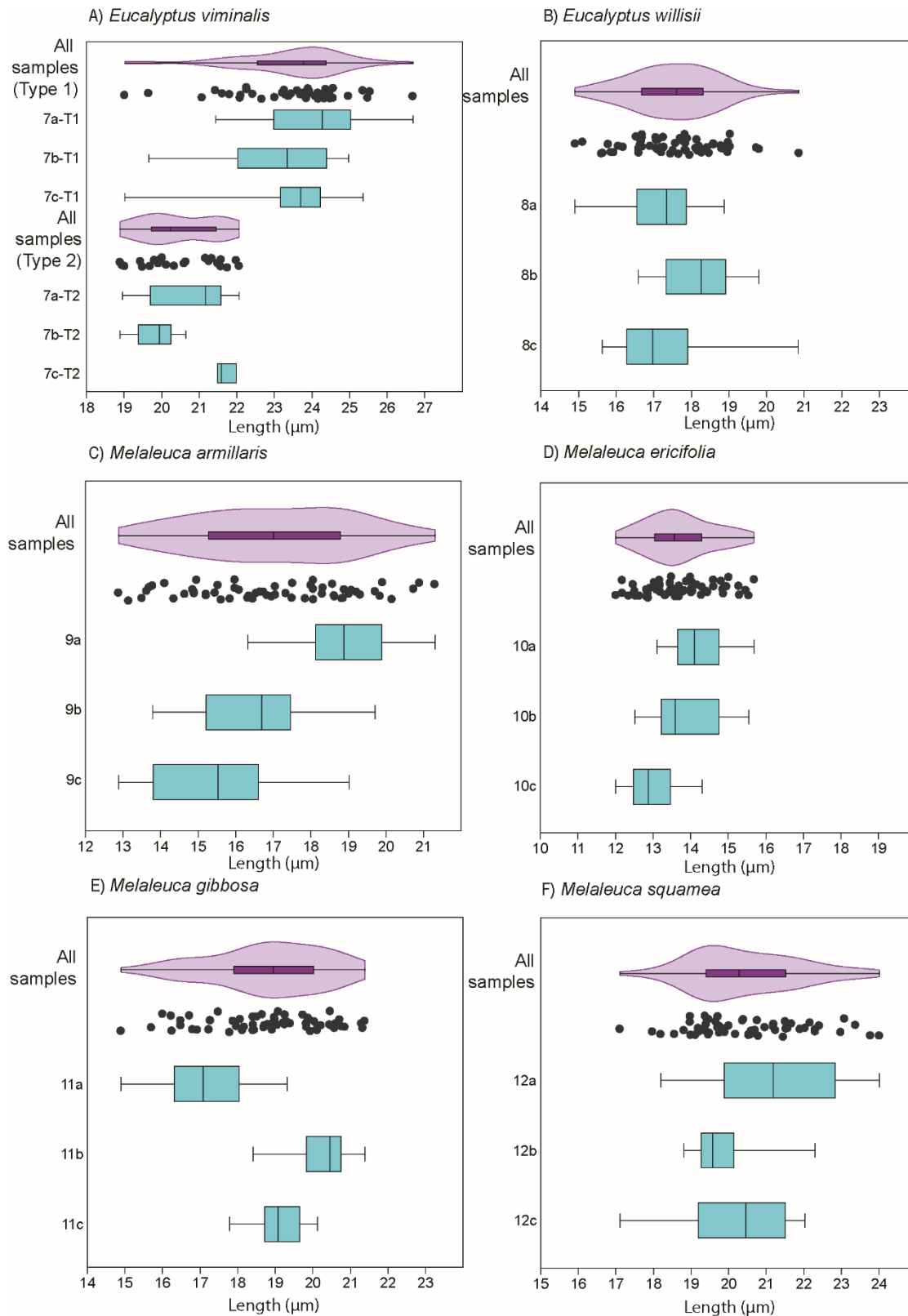


Figure 4b: Size (length) distribution of individual Myrtaceae species sample (*Eucalyptus* and *Melaleuca*) continues. 'T1' and 'T2' represent 'Type 1' and 'Type 2', respectively.

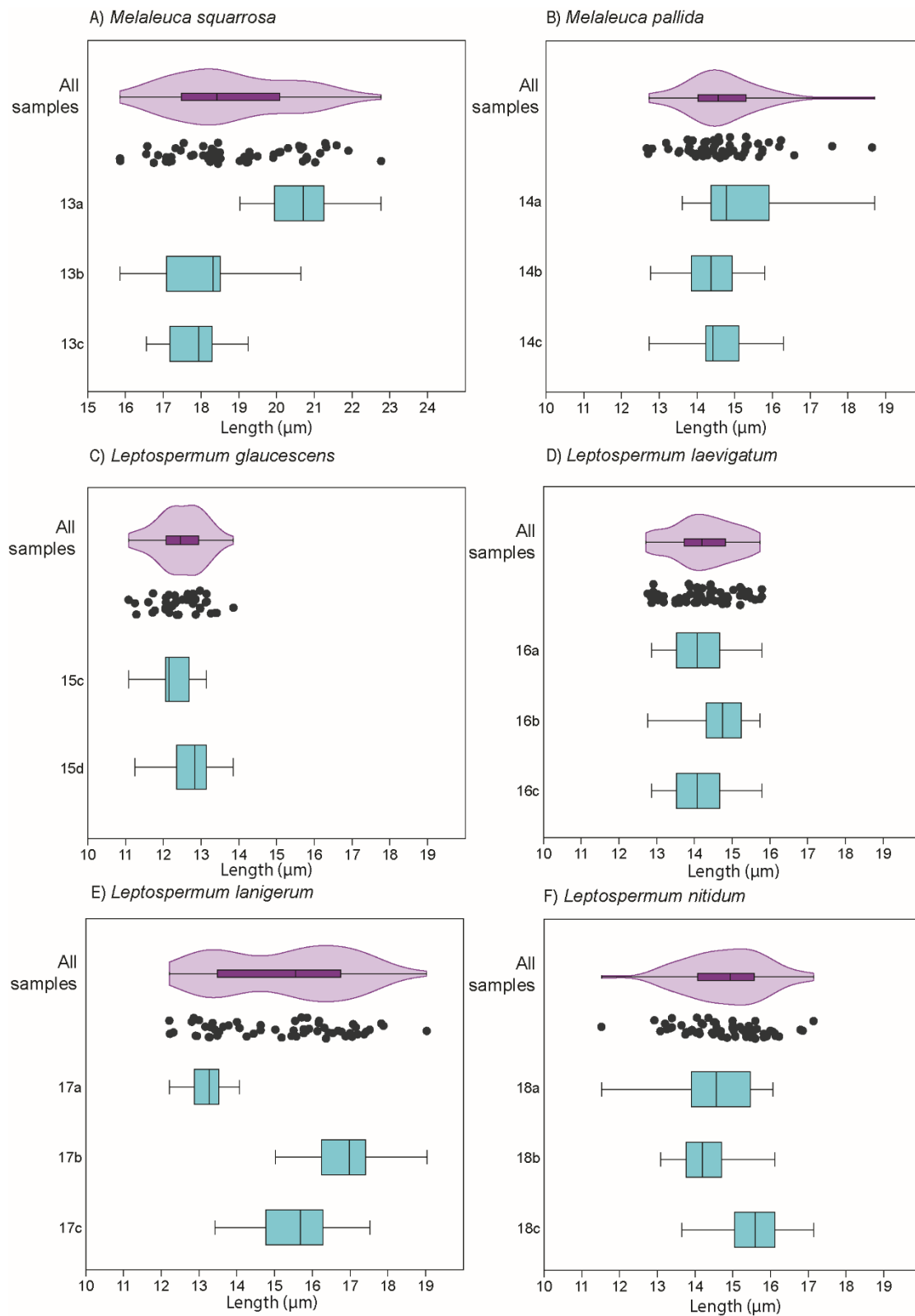


Figure 4c: Size (length) distribution of individual Myrtaceae species sample (*Melaleuca* and *Leptospermum*) continues.

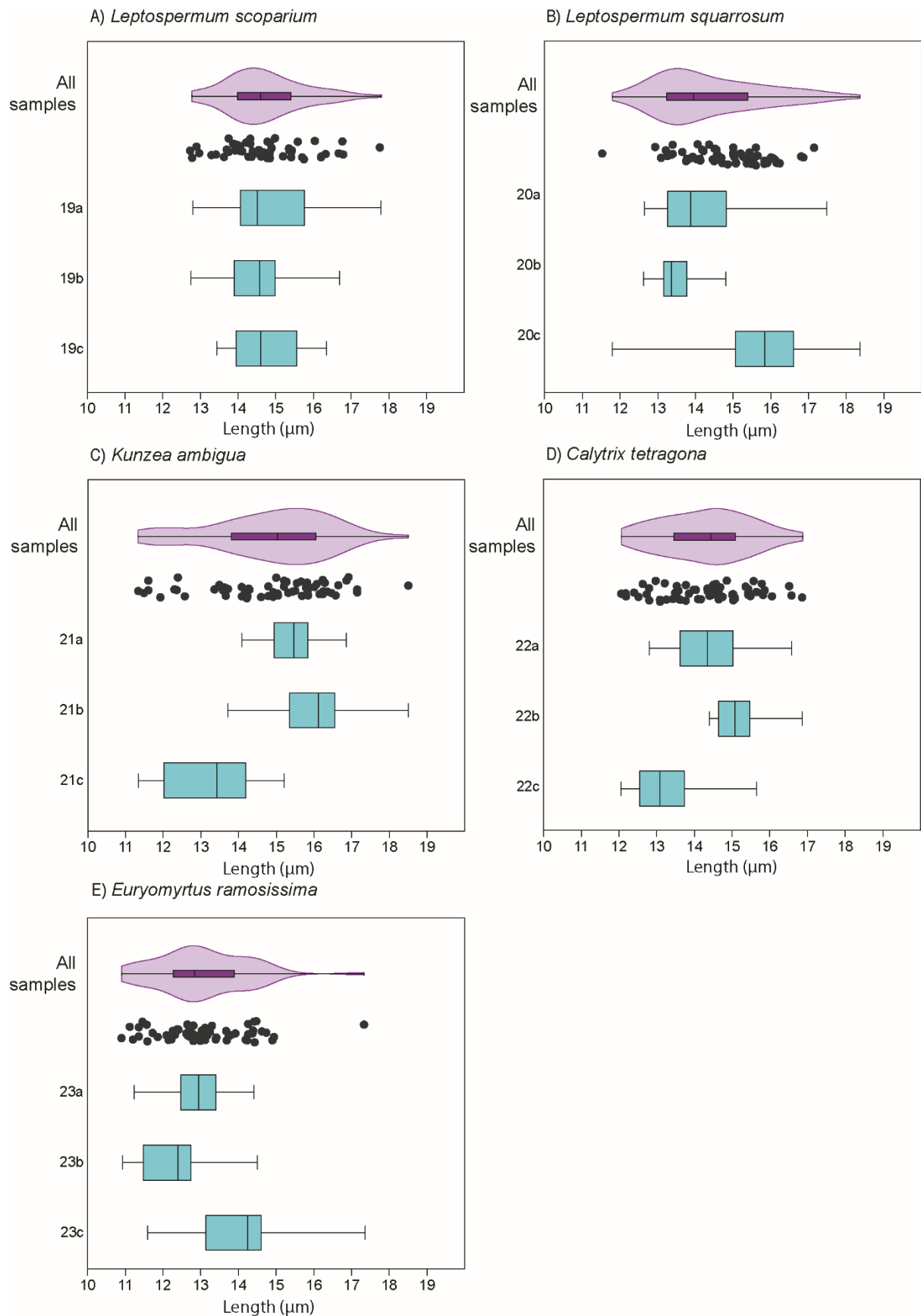


Figure 4d: Size (length) distribution of individual Myrtaceae species sample (*Leptospermum*, *Kunzea*, *Calytrix* and *Euryomyrtus*) continues.

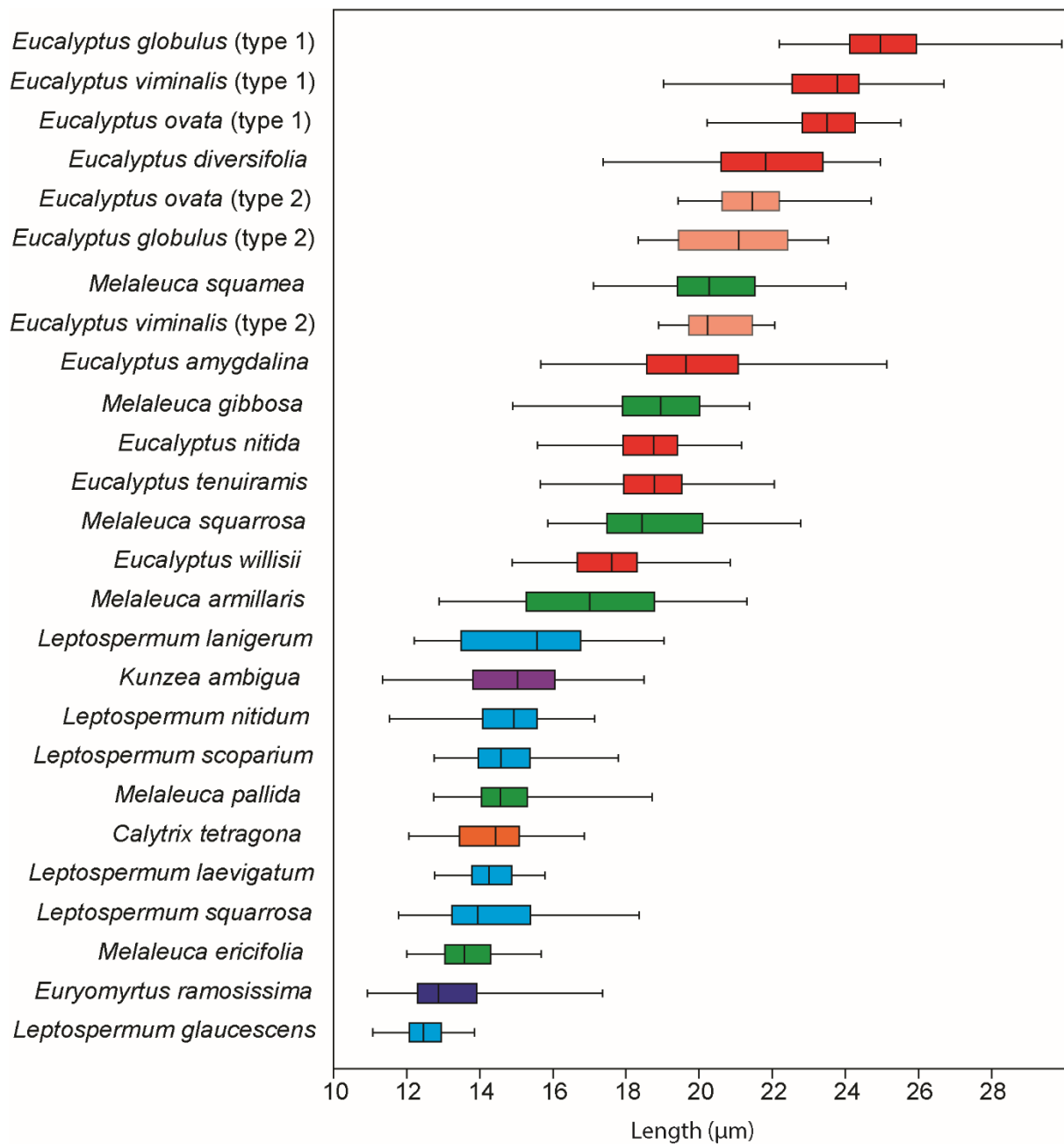


Figure 4e: Size (length) summary of all Myrtaceae species pollen grains.

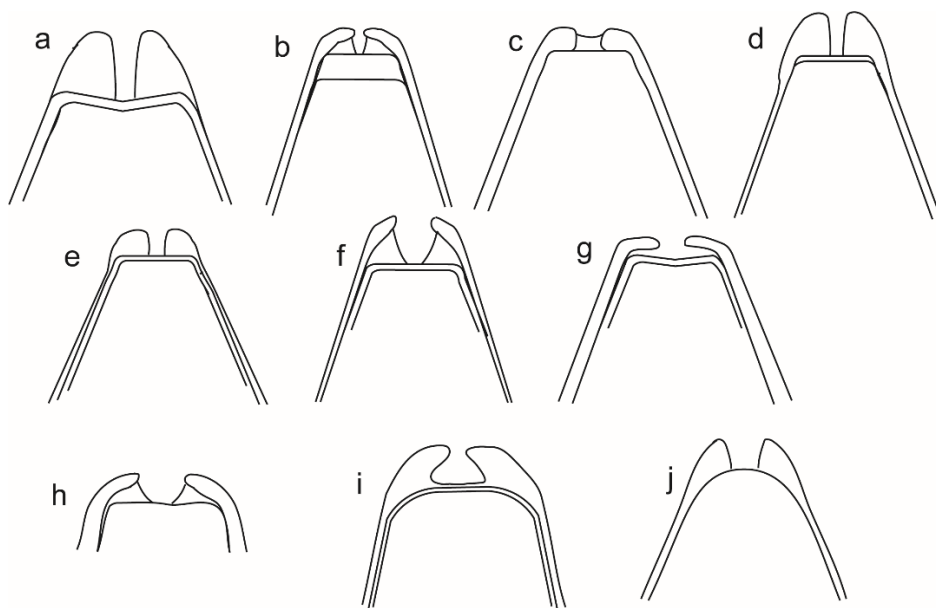


Figure 5: General illustration pore sketches for *Eucalyptus* (a – d), *Melaleuca* (e – g), *Calytrix* (h), *Kunzea* (i), and *Leptospermum*/*Euryomyrtus* (j).

4.3.2. Description of pollen grains of taxa

Eucalyptus

All *Eucalyptus* pollen grains have flat and rounded pore areas, more or less scabrate walls, pores which are generally thicker than the wall and are tricolporate, however, two to four-pored grains also occasionally occurred among *Eucalyptus* and other Myrtaceae pollen grains (Fig. 5, Plate I, II, and VI). *Eucalyptus* pollen grains generally have globular or closely fitted apocolpial islands, while some grains lack an apocolpial island (e.g., *E. tenuiramis*). Observed *Eucalyptus* pollen length ranges from 14.9 – 29.9 μm , colpi length ranges from 2.2 – 10.4 μm , wall thickness ranges from 0.6 – 2.6 μm and pore height ranges from 0.7 – 6.5 μm . Most *Eucalyptus* pollen colpi lengths and pore heights are about 20 – 40% and 5 – 30% of the grain length, respectively, in contrast with the other Myrtaceae taxa, which range mostly from ~30 – 70% and 4 – 20%, respectively (Table 2 and 3; Fig. 4). *Eucalyptus* pollen sides are a mixture of straight, convex and concave. In addition, ~90% of *E. amygdalina*, *E. nitida*, *E. tenuiramis* and *E. willisii* pollen have a thickened mid-wall area.

Some morphological changes in terms of pollen size and sides of *E. diversifolia* and *E. amygdalina* were also observed. Some pollen of *E. diversifolia* (~30%) and *E. amygdalina* (~10%) increased in size and changed in shape (became convex/swollen) after leaving in

glycerol for about five days, pollen length increased from an average of 21 to 24 μm and 20 to 21 μm , respectively.

Leptospermum

All pollen grains are tricolporate and generally syncolpate, however, unclear parasyncolpate (~5%) exists in some of the observed pollen (Plate III and IV). Pollen length ranges from 11.3 – 19.4 μm , colpi length ranges from 1.7 – 11.7 μm , wall thickness ranges from 0.1 – 1.5 μm and pore height ranges from 0.6 to 2.3 μm (Table 2; Fig. 4).

Leptospermum pollen grains generally have straight to slightly concave sides, verrucate and scabrate exine pattern, as well as notched and pointed pore areas (Table 3 and Fig. 5).

Melaleuca

Melaleuca pollen grains mostly have rounded pore areas and are tricolporate with verrucate/scabrate exines. The pollen length ranges from 13 – 24 μm , colpi length ranges from 2.7 – 10.9 μm , wall thickness ranges from 0.5 – 1.7 μm and pore height ranges from 0.7 – 3.5 μm (Table 2 and 3; Fig. 4). Most grains have straight sides and are parasyncolpate except for *M. gibbosa*, which is syncolpate (Plate V) and *M. armillaris*, which can have distinct concave sides. The apocolpial island of the grains is generally small excluding *M. pallida*. *M. pallida* has the widest apocolpial field with a closely fitted island and has the most visible verrucate wall pattern along with *M. gibbosa* and *M. squamea*. *M. ericifolia* is the smallest of the pollen grains with pollen length ranging from 12 – 15.7 μm . *Melaleuca squamea* and *Melaleuca squarrosa* are the largest with pollen length ranging from 17.1 – 24 μm and 15 – 22.8 μm , respectively.

Euryomyrtus, Calytrix and Kunzea

Euryomyrtus ramosissima grains are syncolpate, straight-sided with verrucate exines and notched pore areas (Table 3). The pollen grains are generally tricolporate, but some of the grains have four pores. Pollen length ranges from 11.2 – 17.5 μm , colpi length from 4.2 – 9.9 μm , wall thickness from 0.3 – 1.2 μm and pore height from 0.5 – 1.5 μm . *Calytrix tetragona* has a rounded pore area, pollen grains are tricolporate with psilate exines, and

deeply concave pollen sides. Pollen length ranges from 12.7 – 17.5 μm , colpi length ranges from 6.4 – 10.7 μm , wall thickness ranges from 0.6 – 1.3 μm and pore height ranges from 0.9 – 2.1 μm . *Kunzea ambigua* grains mostly have pointed pore areas, scabrate/psilate exines and are tricolporate with straight to concave sides (Table 3). Pollen length ranges from 11.3 – 19.1 μm , colpi length ranges from 5.2 – 10.7 μm , wall thickness from 0.6 – 1.7 μm and pore height from 1.1 – 2.8 μm (Table 2; Fig. 4).

4.3.3. Intraspecific variation

Many of the species of Myrtaceae studied exhibited considerable morphological variability within the species. Intraspecific variability was most pronounced in the Symphomyrtus *Eucalyptus* pollen types, *E. diversifolia* and *L. scoparium*, whereas *M. ericifolia*, *M. pallida*, and peppermint *Eucalyptus* species such as *E. nitida* and *E. tenuiramis* exhibited more uniform morphology.

Most species of Myrtaceae studied exhibited notable size ranges, with *E. amygdalina* ranging by up to 10 μm in size, while *M. ericifolia*, *L. laevigatum* and *L. glaucescens* exhibit the narrowest size range of ~ 3 μm (see Fig. 4 and 4a – 4e). A closer look at the size ranges between individual samples from the same species shows that within some species there are notably smaller or larger size groups (see Fig. 4a – 4d and supplementary material at <https://dx.doi.org/10.25911/5e82cc833d278>).

Shape variability is also pronounced in Symphomyrtus *Eucalyptus* pollen types and *E. diversifolia*, such that the grains of these species present with both straight and convex sides. Most *K. ambigua* pollen and some *Leptospermum* species also show a degree of variation in their concave sides, although most *Leptospermum* species have more or less straight sides (Plate I, see supplementary material for more images showing shape variation). *Melaleuca* and *Calytrix* pollen grains are generally more uniform in shape with little to no variation within species.

Variability in pore height is more evident in the Symphomyrtus *Eucalyptus* species and *E. willisii* with a height range of ~ 4 μm , while *M. pallida*, *E. ramosissima*, and *L. lanigerum* have the narrowest pore height variability with a range of ~ 1 μm (Fig. 4). The Symphomyrtus *Eucalyptus* generally separates into groups (<0.15 μm and >0.15 μm) based on pore height (see Fig. 4). Four-pored grains occurred mostly within *E. ramosissima*. Although, this

anomaly was also noticed in some other Myrtaceae pollen grains (see Plate VI). Variation in wall thickness and pore ambis were most observed in *Eucalyptus* species. Conversely, wall thickness and pore ambis are generally more consistent within *Leptospermum* and *Melaleuca* species (see Plate I to IV and Fig. 4).

Apocolpial/colpal morphology also varied within some *Eucalyptus* and *Leptospermum* pollen grains. For example, *L. lanigerum* has a mixture of pollen grains with syncolpate, brevicolpate, syndemicolpate, and acolpate apertures. *Calytrix tetragona* and *E. ramosissima* also have some brevicolpate grains (Plate I to V; supplementary material). There is also a mixture of wall patterns (psilate, scabrate, and verrucate) in most pollen grains, especially in *Eucalyptus*, *Leptospermum* and *Kunzea*. In general, intraspecific variations were less observed in *Melaleuca* and *Calytrix* pollen grains.

4.3.4. Interspecific variation

Morphological separation of pollen types

Cluster analysis results based on pollen length and pore height show clear separation of Symphomyrtus *Eucalyptus* types from other *Eucalyptus* types and other Myrtaceae types (Fig. 3). The Symphomyrtus group has bigger pollen grains (up to ~30 µm), thicker pores (up to ~6 µm) and longer colpi (up to ~10 µm) and the group includes *E. globulus*, *E. ovata* and *E. viminalis*. Conversely, the peppermint type generally consists of smaller grains (mostly <25 µm), with thicker mid-wall area, pore height mostly < 4 µm and shorter colpi (mostly <8 µm), and this group includes *E. amygdalina*, *E. nitida*, *E. tenuiramis* and *E. willisii*. Furthermore, two types of Symphomyrtus *Eucalyptus*: type-1 pollen grains were observed and are generally larger and mostly >23 µm in length with thinner pores and walls, while type-2 grains are generally smaller and mostly <23 µm in length with very thick pores and thicker walls (Fig. 4). Both types exist within each of the three Symphomyrtus species. *Eucalyptus diversifolia* generally falls in between Symphomyrtus and peppermint *Eucalyptus* types and cannot be clearly distinguished.

Results also show separation of all Myrtaceae pollen into three broad groups using the colpi length/pollen length ratio (Fig. 4). The three groups include: (1) parasyncolpate pollen types with large apocolpial fields (colpi/length ratio ~<40%), (2) parasyncolpate pollen types with small apocolpial fields (colpi/length ratio ~40 – 55%) and (3) syncolpate pollen types

(colpi/length ratio $\sim >55\%$). The parasyncolpate pollen types with large apocolpial fields include all *Eucalyptus* pollen and *M. pallida*. The parasyncolpate pollen types with small apocolpial fields includes all *Melaleuca* pollen, excluding *M. gibbosa*. The syncolpate pollen types include *M. gibbosa*, *Kunzea ambigua*, *Calytrix tetragona*, *E. ramosissima* and all *Leptospermum* pollen grains. Variability within these species results in a significant degree of morphological overlap.

4.3.5. Myrtaceae fossil pollen analysis

Over 50% of fossil Myrtaceae pollen types were identified, using the morphological character of modern Myrtaceae pollen types. Fossil peppermint *Eucalyptus* pollen matched the modern types to a great extent, while the Symphomyrtus *Eucalyptus* species vary in shape and were identified based on pollen length, colpi length and pore height. Fossil *Melaleuca*, *Leptospermum*, *Kunzea* and *Calytrix* pollen also matched the modern pollen types (Plate VII-VIII).

4.4. Discussion

4.4.1. Morphological variability within species (Intraspecific variation)

Many of the Myrtaceae studied exhibited considerable morphological variability within the species. Intraspecific pollen variation can be caused by natural factors or sample processing techniques (Bonhomme et al., 2013; Meltsov et al., 2008; Kriebel et al., 2017; Mäkelä, 1996; Huysman et al., 2003; Cushing, 2011; Cushing, 1961; Lindbladh et al., 2002; Sluyter, 1997; van Wyk and Dedekind, 1985; Schüler and Behling, 2011). While the causes of these morphological variations may be difficult to pin down, intraspecific variation in the number of pores (see Plate VI), in particular *E. ramosissima*, which frequently presented with 4-pored grains, is likely due to natural factors (e.g., genetic variation). Considerable variability in size ranges between samples of some species was also observed, which likely reflect natural size variability (Fig. 4a – 4e). The presence of two apparent ‘morphotypes’ within the Symphomyrtus eucalypts was found and termed *Eucalyptus* S-type 1 and S-type 2. The type 2 grains are smaller with distinct, large pores (Plate I, images 3-4, 7-8 and 11-12) and were represented in all three specimens of each Symphomyrtus and were also widely found in the fossil record (Plate VIII, images 3-4). This

variability in *Symphomyrtus* pollen grains is most likely of natural origin, as similar occurrence exists within the Haloragaceae family where a single flower produces two morphologically different pollen grains, depending on the extent of pollen wall cohesion during pollen formation (Pragowski, 1970). A few examples of similar aberrations in other Myrtaceae species (e.g., *M. pallida*, *Euryomyrtus ramosissima*, *L. scoparium*, *L. squarrosus* and *M. armillaris*) was also observed, suggesting this may not be a trait exclusive to *Symphomyrtus* eucalypts, however, the other occurrences were rare.

In contrast, observations of variations in size and shape, in species such as *E. diversifolia* and *E. globulus* in this study, are more likely to be due to the influences of chemical treatment, mounting medium or slide preparation. Plate IX illustrates the variability in size and shape observed in a selection of samples from this study compared with examples of reference pollen from the Australian Pollen and Spore Collection (APSA-<http://apsa.anu.edu.au/>). Those grains believed to exhibit their characteristic shape are marked with an asterisk, the other grains all appear to exhibit alteration of some type whether by swelling due to the mounting medium or sealant effects, presence of water, crushing by slide cover pressure or more severe alteration due to long term storage (Plate IX, images 15-16). From observations in this study, *Symphomyrtus Eucalyptus* pollen appeared to be most often affected, where enlarged grains due to possible swelling exhibit thinner walls, which become convex in shape. However, it is possible that genera such as *Leptospermum* are just as likely to be affected as can be seen in Plate IX (images 17-20). Clear effects of swelling in *E. amygdalina* (sample 1c) grains was observed after leaving in glycerol for five days (see Plate IX, image 1 vs 2). Studies have shown that the largest percentage swelling in pollen occur within the first four to five days after chemical treatment (Andersen, 1979; Bolbochan and Salgado-Labouriau, 1983), with some even recommending measurement of pollen the same day after chemical treatment to minimize alteration in pollen sizes (e.g., Schöler and Behling, 2011; Mäkelä, 1996). Possible changes in size and shape due to cover slip pressure in *E. amygdalina* was also observed (Plate IX: sample 1b, images 5-7), where 'flattened' grains (Plate IX: image 7) were focused along the slide edges. The addition of sand grains to pollen slides during pollen morphological studies has been suggested to prevent flattening of grains due to cover-slip pressure (e.g., Lindbladh et al., 2002; Hansen and Engstrom, 1985). Spot checks of other samples revealed that samples/species were inconsistently affected. A targeted study would be required to explore these processes, along with the influence of other factors such

as variable sporopollenin content and hybridisation (e.g. Kirkpatrick and Backhouse, 1985; Larcombe et al., 2014).

Comparison of *E. amygdalina* samples stored in glycerol in this study with a sample stored in silicone oil in APSA (Plate IX, image 8) showed that the pollen grains stored in silicone oil were well preserved and exhibited an apparently normal shape, however, were notably smaller. Median grain length of the glycerol samples were 1.35× larger than those in silicone oil, which is similar to the findings of Moore and Webb (1978) who reported that glycerol swells pollen grains 1.25× compared to silicone oil.

In general, it is important to be aware of intraspecific variability that occurs within Myrtaceae pollen and it is recommended to compare pollen with multiple images/samples for more accurate identification. Nevertheless, it was found that pollen size (length and width), colpal morphology, and pore height can be used to separate Myrtaceae pollen into different species types.

4.4.2. Morphological similarities and distinct pollen groups/types (Interspecific variation)

Colpal morphology was found to be the best morphological feature to use for an initial separation of the Furneaux Group modern Myrtaceae into three groups: 1. parasyncolpate (medium to large apolcolpial field), 2. parasyncolpate (small apocolpial field) and 3. syncolpate (figure 4). Other morphological characters, in particular size (length and width) and pore height, can then be used to further separate the pollen into types and species. Based on these, a summary key is developed (see Appendix S3), which can be used alongside this study's pollen catalogue of over 3000 images (<https://dx.doi.org/10.25911/5e82cc833d278>) to facilitate identification of Myrtaceae from the Furneaux Group.

Parasyncolpate colpal morphology generally separates *Eucalyptus* and *Melaleuca* pollen from all other Myrtaceae pollen grains with the exception of *M. gibbosa*, which was observed to be mostly syncolpate or with a very small apocolpial field without polar island. *Melaleuca gibbosa* can only be identified as a distinct type if observed grains are clearly syncolpate, it otherwise falls into *M. squarrosa* type. *Eucalyptus* pollen can be identified by their medium to large apocolpial fields, thick walls and pores, small colpi/pollen length ratios

and large pore/length ratios. Symphomyrtus type-2 pollen are most distinct due to their very thick pores, whereas the Symphomyrtus type 1 at the upper end of their size range ($> 25 \mu\text{m}$) can be distinguished from the other eucalypts based on their large size. The peppermint eucalypts are best distinguished by their walls, which are thicker on average and frequently have a diagnostic thickened mid-wall. Size can be used to distinguish the peppermints at the lower end of the size range ($<17.5 \mu\text{m}$); however, a large overlap in size otherwise exists between all of the eucalypts. *Eucalyptus diversifolia* falls within the overlap in terms of size and morphologically overall is most likely to be absorbed by the Symphomyrtus type 1. The very rare occurrence of *E. diversifolia* in the Furneaux Group (a single occurrence on Cape Barren Island) makes its indistinctiveness of limited significance, although it cannot be ruled out that the species distribution was more widespread in the past. *Melaleuca pallida* is the only *Melaleuca* species with a medium to large apocolpial field, which is an overlapping feature with *Eucalyptus*, especially the peppermint types. However, the species can be distinguished by the thinner wall ($<1.3 \mu\text{m}$) and pores ($<2.0 \mu\text{m}$), as well as the verrucate exine pattern, but most importantly by the presence of a distinct, closely fitted polar island in all observed grains.

Parasyncolpate pollen types with small apocolpial fields include *M. armillaris*, *M. squamea*, *M. squarrosa* and *M. gibbosa*. Although *Melaleuca* was found to be the genus where the highest degree of separation to species level may be achieved, the large variability in morphology within each species means that most of the species may overlap to some degree depending on the morphology presented by a particular pollen grain. *Melaleuca armillaris* may be distinguished if the pollen sides are concave and the grains are large; however, there is considerable morphological overlap with *Kunzea ambigua*, discussed in the next section. *Melaleuca ericifolia* is the smallest of the *Melaleuca* pollen grains. It does overlap in size with *M. armillaris* and *K. ambigua*; however, in many cases it can be distinguished by its larger apocolpial field with polar island, thinner pores and its straight to slightly concave sides. The morphologies of *M. squamea* and *M. squarrosa* are very similar, hence both are included in the *M. squarrosa* type, which can be separated from *M. ericifolia* based on its larger size ($16 - 24 \mu\text{m}$) and from straight sided *M. armillaris* when a slightly larger apocolpial field with polar island is present. *M. gibbosa* also falls within *M. squarrosa* type when it presents with a small apocolpial field.

The syncolpate pollen types include *M. gibbosa*, *K. ambigua*, *C. tetragona*, *Euryomyrtus ramosissima* and all *Leptospermum* species. *Melaleuca gibbosa* is the only syncolpate

Melaleuca pollen grain and has a distinct verrucate/scabrate wall pattern. This distinguishes it from the psilate/scabrate *K. ambigua*, which presents with both straight and concave sides, and on occasion may have a very small apocolpial field, sometimes with polar island. *Calytrix tetragona* is another distinct pollen grain and can be identified based on its strongly concave sides and, even when slightly less concave, may be distinguished by its psilate exine and very wide pore area. Some *C. tetragona* grains also present as brevicolpate, which is unique amongst this Myrtaceae suite. Also, *Leptospermum* pollen grains (*L. lanigerum*, *L. laevigatum*, *L. glaucescens*, *L. scoparium*, *L. nitidum*, and *L. squarrosum*) and *Euryomyrtus ramosissima* have similar or overlapping morphological features, making them difficult to separate; hence they are grouped as *Leptospermum/Euryomyrtus*. They can be distinguished from other Myrtaceae by their small size in combination with their notched pores and verrucate/scabrate exines. In many cases, *L. scoparium* and *L. squarrosum* can be separated as a separate type based on their weak exine ornamentation (scabrate/psilate) and slightly thicker, concave sides, and they can be distinguished from *K. ambigua* by their pores.

4.4.3. Ecological significance and application to fossil records

Overall, most Myrtaceae pollen from both Holocene and Pleistocene fossil records from the Furneaux Group (Plates VII-VIII) were matched with modern Myrtaceae reference pollen, although previous morphological studies have suggested that modern Myrtaceae pollen are more similar to Holocene Myrtaceae pollen, especially late Holocene ones (Pickett and Newsome, 1997; Thornhill, 2010).

Separation of *Eucalyptus* into types in this study is in line with the study of modern and fossil *Eucalyptus* pollen in southwest Australia by Pickett and Newsome (1997). *Eucalyptus* species included in this study can be classified into two ecological groups based on dominant ecological requirements from the literature (Table 4a). The Symphomyrtus types (*E. globulus* and *E. viminalis*) are more likely to have a tree habit (medium to tall), and prefer very wet to moderately wet conditions and fertile soil, while the peppermint types (*E. amygdalina*, *E. nitida*, *E. tenuiramis* and *E. willisii*) usually grow as shrubs or small trees, preferring drier conditions, sunny sites, infertile soil and are associated with heaths (Williams and Potts, 1996; Howells, 2012; Page, 1998; Kirkpatrick and Harris, 1999). *Eucalyptus ovata*, the swamp gum, is an exception as it is a Symphomyrtus eucalypt that can be found

growing with a multi-stem shrub habit in wet heaths (Kirkpatrick and Harris, 1999). However, changing ratios of *Symphomyrtus* to peppermint eucalypt types overall could reflect changing proportions of wetter, closed forest vs dry, open heathlands in the fossil record. The conclusion of Thornhill (2010), that fossil *Eucalyptus* pollen do not consistently match modern pollen, likely stems from observations based on *Eucalyptus* pollen specimens, which exhibited altered size and shape as a consequence of long-term storage. It was found that diagnostic morphological features of *Eucalyptus* pollen, in particular, were diluted as a result of chemical alteration (Plate IX).

Table 4a: Table showing Furneaux Group Myrtaceae species' growth forms and habitats based on Williams and Potts (1996), Page (1998), Kirkpatrick and Harris (1999), Howells (2012) and Atlas of Living Australia (<https://www.ala.org.au/>). Note arrangement of taxa in order of species number/representation including subsequent tables.

Species	Habit/growth form	Ecology/habitat
<i>E. globulus</i> ^s	Medium to tall tree	Wet and dry soil, deep soil, low fire frequency.
<i>E. ovata</i> ^s	Medium tree	Dry and poorly drained soil, wet heaths and forests, high fire frequency.
<i>E. viminalis</i> ^s	Tall tree	Well-drained soil, deep soil, moderately wet to dry soil.
<i>E. diversifolia</i>	Mallee	Rare, alkaline coastal sites
<i>E. amygdalina</i> ^p	Medium tree	Dry soil, open sunny sites, infertile and deep soil.
<i>E. nitida</i> ^p	Mallee to small to tall tree	Open heathy forest and woodlands, infertile soil, can grow in tall wet forests, infrequent fires.
<i>E. tenuiramis</i> ^p	Small to medium tree	Rare, sunny sites, dry sclerophyll coastal vegetation, open heaths.
<i>Eucalyptus willisii</i> ^p	Mallee to small to tall tree	Rare, poor sandy soils
<i>M. squarrosa</i> ^{Ms}	Shrub to small tree	Rare, heaths, wet or damp areas or swamps.
<i>M. squamea</i> ^{Ms}	Small to medium shrub	Wet heaths, swamp, coastal sites.
<i>M. armillari</i>	Large shrub to small tree	Rare, coastal heaths, other dense heaths, sensitive to fire.
<i>M. pallida</i>	Large shrub to small tree	Moist areas, well drained sites, rocky slopes.
<i>M. gibbosa</i>	Small to medium shrub	Wet heaths, damp heaths, swamp heaths.
<i>M. ericifolia</i>	Large shrub to small tree	Swampy areas, stream banks, sand dunes, coastal swamp heaths, dry sclerophyll forests.
<i>L. scoparium</i> ^L	Medium to large shrub	Scrub and dry coastal sites.
<i>L. laevigatum</i> ^L	Large shrub to small tree	Widespread in coastal sites.
<i>L. lanigerum</i> ^L	Medium shrub to small tree	Wet and coastal heaths.
<i>L. nitidum</i> ^L	Medium shrub	Wet heaths, swamp, coastal sites.
<i>L. glaucescens</i> ^L	Medium shrub to small tree	Widespread, dry heath with some rainfall, moist coastal sites.
<i>L. squarrosun</i> ^L	Medium shrub	Rare, well drained or damp sites.
<i>Calytrix tetragona</i>	Small shrub	Dry to moist coastal heaths.
<i>Kunzea ambigua</i>	Shrub	Moist coastal heaths, sandy heaths, dry heaths.
<i>Euomyrtus ramosissima</i>	Small shrub	Widespread in heaths.

s = Symphomyrtus *Eucalyptus* type, p = peppermint *Eucalyptus* type, Ms = *Melaleuca squarrosa* type, Ll = *Leptospermum laevigatum* type

Findings from this study that fossil and modern pollen of *Melaleuca*, *Leptospermum*, *Kunzea* and *Calytrix* are comparable and separable in fossil records (Plate VII-VIII) supports the conclusion of Thornhill (2010). The *Melaleuca* species in this study indicate wet conditions and are all components of wet heaths; however, *M. ericifolia* and *M. squarrosa* can also exist in the understory of dry sclerophyll forests (Howells, 2012; Kirkpatrick and Harris, 1999), where *M. ericifolia* is also adapted to recurrent fires and may be an indication of high fire frequency (Kirkpatrick and Harris, 1999). The *Leptospermum* species studied are members of dry and wet heath communities and some are widespread (Howells, 2012; Kirkpatrick and Harris, 1999) (Table 4a and 4b). *Kunzea ambigua* and *C. tetragona* are also members of moist–dry heaths, whereas *Euryomyrtus ramosissima* is a widespread species in the Furneaux Group.

Table 4b: Table showing distribution of this study's Myrtaceae species in Australia according to the Atlas of Living Australia (<https://www.ala.org.au/>). 'Mainland' in the table refers to the Australian landscape excluding Tasmania and the Bass Strait islands.

Species	Occurrence/Distribution
<i>E. amygdalina</i>	Widespread in Tasmania (including Bass Strait)
<i>E. diversifolia</i>	Restricted to the south coast and central mainland
<i>E. globulus</i>	Common in Tasmania (including Bass Strait) and southeast (SE) mainland
<i>E. nitida</i>	Widespread in Tasmania (including Bass Strait)
<i>E. ovata</i>	Common in Tasmania (including Bass Strait) and SE mainland
<i>E. tenuiramis</i>	Restricted to Tasmania
<i>E. viminalis</i>	Common in Tasmania (including Bass Strait) and SE mainland
<i>E. willisii</i>	Restricted to SE mainland coast
<i>M. armillaris</i>	Restricted to SE mainland
<i>M. ericifolia</i>	Common in SE mainland and Tasmania (including Bass Strait)
<i>M. gibbosa</i>	Common in Tasmania (including Furneaux Group) and south mainland
<i>M. pallida</i>	Common in Tasmania (including Furneaux Group) and eastern (E) mainland
<i>M. squamea</i>	Common in Tasmania (including Bass Strait) and SE mainland
<i>M. squarrosa</i>	Common in Tasmania (including Bass Strait) and SE mainland coast
<i>L. glaucescens</i>	Common in Tasmania and east coast mainland
	Common in SE, southwest (SW), E mainland and Tasmania (including Bass Strait)
<i>L. laevigatum</i>	
<i>L. lanigerum</i>	Common in SE mainland and Tasmania (including Bass Strait)
<i>L. nitidum</i>	Common in Tasmania and Furneaux Group
<i>L. scoparium</i>	Common in SE mainland and Tasmania (including Bass Strait)
<i>L. squarrosus</i>	Restricted to SE mainland coast
<i>C. tetragona</i>	Widespread in E, SE, and SW mainland
	Common in eastern mainland and eastern Tasmania (including the Furneaux Group)
<i>K. ambigua</i>	
<i>Euryomyrtus ramosissima</i>	Common in Tasmania (including Bass Strait) and SE mainland

The inseparable fossil Myrtaceae pollen in this study may be explained by: 1. the presence of other Myrtaceae species in the fossil record, which are not growing on the Furneaux Group islands today; 2. taphonomic processes affecting the morphology of fossil pollen; or 3. inability to clearly match fossil pollen due to natural morphological variability causing overlap in types. Diagenetic processes as well as those occurring during transport of sediment to a site can variably degrade pollen grains and include oxidation, desiccation, wet-dry cycles (repeated swelling and shrinking of pollen grains) and microbial activity (Holloway, 1989, Campbell, 1991, Campbell and Campbell, 1994, Sangster and Dale, 1961). Plate VIII illustrates the difference in Myrtaceae preservation at Remy Bay Lake from excellent preservation in organic-rich, MIS3 aged sediments (images 1-16) and poor preservation in inorganic, LGM-Late Glacial aged sediments (images 17-20).

Several studies from different parts of Australia have been able to separate Myrtaceae pollen in fossil records, although to varying degrees (Rowes, 2019; Mackenzie and Moss, 2017; Stahle et al., 2016). Most studies are able to separate Myrtaceae fossil pollen at least into *Eucalyptus*, *Melaleuca* and *Leptospermum* types (e.g., Moss et al., 2005; Mackenzie and Moss, 2017; Stahle et al., 2016), while other studies are able to further separate fossil pollen into species types (e.g., Rowes, 2019; Dodson, 1975; Ladd, 1979), even in records with poor pollen preservation (e.g., Dodson, 1975). Studies from semi-arid parts of Australia (sites with generally poor biological preservation) were also able to separate Myrtaceae pollen in fossil records into the three aforementioned genus types (e.g., Cupper, 2005). In regions where the diversity of modern and fossil Myrtaceae is high the identification of fossil Myrtaceae pollen to species is problematic and in many cases not attempted (e.g., Dodson, 1974a, 1975; Donders, 2000). Nonetheless, in study sites where the diversity of Myrtaceae species is low, our approach of using modern Myrtaceae pollen to separate fossil Myrtaceae pollen may be applicable. The fact that poor pollen preservation can increase pollen morphology overlap (e.g., between *Eucalyptus* and *Melaleuca*, between *Melaleuca* and *Kunzea*) is also acknowledged, making Myrtaceae fossil pollen separation difficult, if not impossible, in some sites.

4.5. Conclusion

A morphometric analysis of 23 species of Myrtaceae, belonging to six genera, found throughout the Furneaux Group islands of the Bass Strait, southern Australia, identified eleven distinct pollen types. In general, the Myrtaceae pollen types can be confidently separated to genus level, except *Euryomyrtus*, which cannot be separated from *Leptospermum*. Specifically, six taxa were identified to species level. Separation to species level was more achievable in *Melaleuca*, as well as *Kunzea* and *Calytrix*, with only one representative species each. Conversely, *Eucalyptus* could only be separated into two major types, while *Leptospermum* could not be confidently separated. This study also shows that not just Holocene fossil Myrtaceae pollen but also Pleistocene fossil Myrtaceae pollen in the Furneaux Group are similar to modern Myrtaceae pollen in this area. In addition, the refined identification of fossil Myrtaceae pollen in sedimentary records from the islands of the Furneaux Group provided a greater understanding of past vegetation types, ecosystem succession and prevailing moisture regimes in this area. This detailed study of Myrtaceae pollen grains in Bass Strait significantly increased our understanding of morphological variability in Myrtaceae pollen grains, enabling their separation in the fossil record to a considerable extent. Studying the modern Myrtaceae pollen of a specific area is recommended in identifying fossil Myrtaceae pollen of that area rather than the use of a generalized Myrtaceae pollen morphological descriptions or keys. Pollen analysts should also be aware of the degree of intraspecific variability within the Myrtaceae that may be a result of natural and laboratory processes. Caution should be taken against relying on a single reference specimen for identification, considering the variation in size and shape. Best practice would be to collect reference specimens from the field area and process them in the same way as the fossil material. Finally, considering the variability recorded within Myrtaceae species in this study, the use of more than one representative specimen (source plant) for a species in future pollen morphology studies is recommended. In addition, exploring the potential influence of environmental conditions (e.g., stress) on pollen morphology will provide more insight on intraspecific variability (e.g., two – four pored pollen grains), which may also enhance palaeoecological interpretations in the future.

4.6. Addendum: Revisiting truwana/Cape Barren Island, Bass Strait vegetation history

Following publication of the foregoing chapter, the Myrtaceae pollen morphological description presented in this study was applied to a 14,000-year record (Big Reedy Lagoon) from truwana/CBI to separate fossil Myrtaceae pollen into types, which will help to better understand the lateglacial and Holocene vegetation change on the island. The result shows that *Symphomyrtus Eucalyptus* types were more represented in the lateglacial samples (~14,000–13,000 cal yr BP), while samples from the end of the lateglacial–early Holocene (~13,000–9000 cal yr BP) were dominated by peppermint *Eucalyptus* types (Plate VII). *Leptospermum/Euryomyrtus* type, *M. armillaris*, *M. squamea*/*M. squarrosa* and *K. ambigua*, were abundant in the mid- to late Holocene samples (~6000–700 cal yr BP). The peppermint *Eucalyptus* types, *M. ericifolia* and *M. gibbosa* were also present in the late Holocene samples (~3000–700 cal yr BP) (Fig. 6).

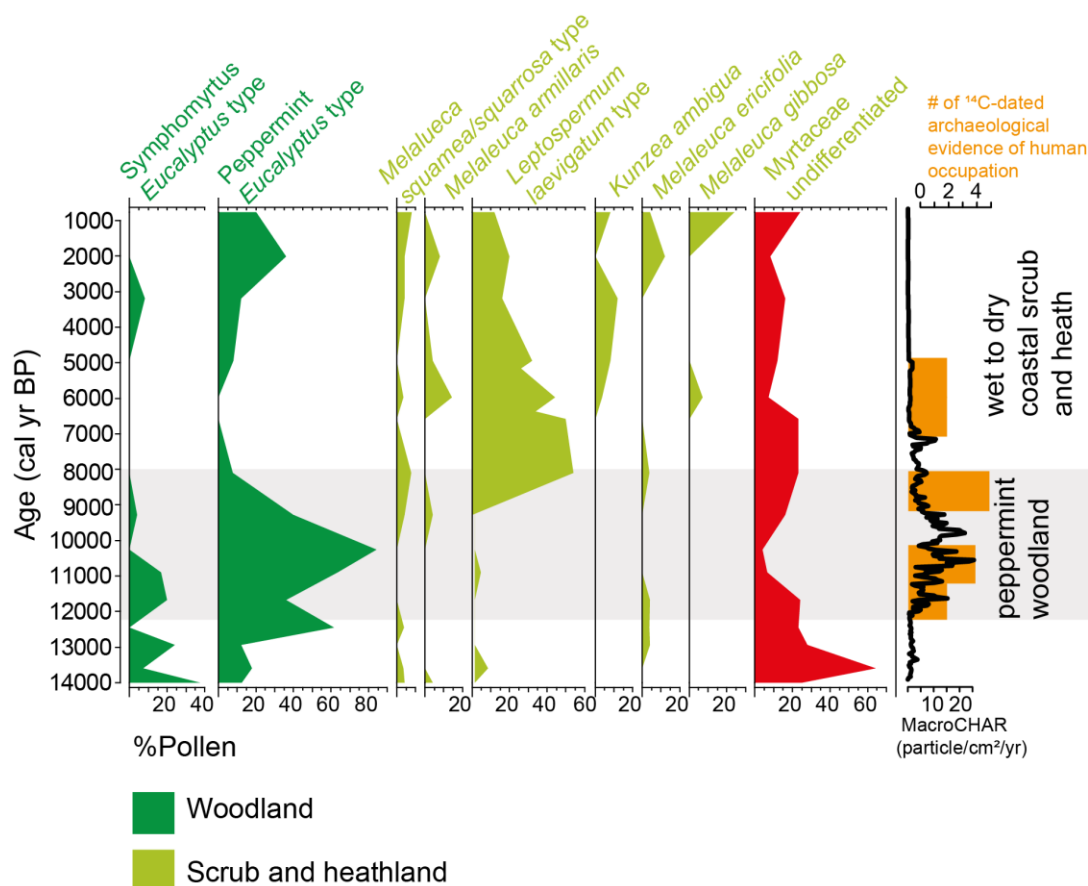


Figure 6: Lateglacial and Holocene Myrtaceae pollen record for Big Reedy Lagoon, truwana/Cape Barren Island, Bass Strait. Also shown is macroscopic charcoal record (fire history) and archaeological evidence of human occupation from eastern Bass Strait islands (orange bars), including truwana/Cape Barren Island. Grey-shaded area indicates the period of major human occupation and land use.

As presented in the previous chapter, *Eucalyptus* woodland prevailed on truwana/Cape Barren Island in the early Holocene and was replaced by heathland and scrub after about 9000 cal yr BP. However, a closer look at the fossil Myrtaceae pollen record suggest this vegetation change can be further understood, especially in terms of the dynamics of *Eucalyptus* woodland.

The abundance of peppermint *Eucalyptus* types between ~12,000 and 9000 cal yr BP suggest the woodland that prevailed on the island at this time was open, not too tall, and dry (Fig. 6). Subsequently, the low representation of peppermint *Eucalyptus* types between ~9000 and 5000 cal yr BP may be related to increased wetness, as climate became increasingly wet in southeast Australia during the early–mid- Holocene due to stronger Southern Westerly Winds (Fig. 6; Wilkins et al., 2013). *Leptospermum* may have occupied heathland and scrub in wet/moist sites during this interval. the modest increase in peppermint *Eucalyptus* types after ~5000 cal yr BP may be explained by the onset of drier conditions due to ENSO intensification and increased seasonality (increased summer insolation) in the late Holocene.

The overall changes in fossil Myrtaceae pollen assemblages also corroborates the idea of Indigenous land-use change on truwana/Cape Barren Island during the Holocene. Indigenous cultural burning to maintain open woodlands may have favoured the peppermint *Eucalyptus* types in the early Holocene, and decreasing land use may have contributed to the relatively low occurrence of peppermint *Eucalyptus* after ~9000 cal yr BP. This reflects the role Indigenous cultural burning practices likely played in maintaining biodiversity in Bass Strait in the past (Adeleye et al., 2021b), highlighting why traditional knowledge is critical to sustainable ecosystem management in Australia.

The results also highlight another critical ecological observation – that pollen records from southeast Australia may appear to show relative stability in terms of overall Myrtaceae pollen abundance, but in fact there has been considerable ecological turnover occurring within the Myrtaceae. This turnover is only revealed by careful pollen-morphological analysis. This study shows the great potential for pollen-morphological studies in other key regions to quantify the true extent of past floristic change.

Chapter 5 ASSESSING LONG-TERM ECOLOGICAL CHANGES IN WETLANDS OF THE BASS STRAIT ISLANDS, SOUTHEAST AUSTRALIA: PALAEOECOLOGICAL INSIGHTS AND MANAGEMENT IMPLICATIONS

While previous chapters focus on the terrestrial vegetation of Bass Strait, this chapter uses original data to track past wetland developments in the region. These are discussed in relation to past changes in terrestrial vegetation and fire regimes from earlier chapters. This chapter presents one of the most detailed analyses and photographic catalogues of non-pollen palynomorphs in Australia and their relevance for palaeoenvironmental reconstruction in the region. The implications of past wetland changes for present and future wetland management and conservation are also highlighted.

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with
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I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

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5.0. Assessing long-term ecological changes in wetlands of the Bass Strait islands, southeast Australia: palaeoecological insights and management implications

Abstract

Understanding long-term ecological development of wetlands is critical to effective management. The islands of Bass Strait, southeast Australia, have several biologically diverse natural wetlands, including Ramsar sites, yet little is known about their ecology. Here, through a multi-proxy palaeoecological approach, we seek to understand how wetland floristic composition and hydrology has changed on truwana/Cape Barren Island (CBI), and how changes in fire regimes have affected wetland integrity and ecological dynamics. We use wetland fossil pollen, non-pollen palynomorphs and sediment geochemistry to reconstruct wetland development and compare it to existing records of terrestrial vegetation and fire regimes from the island. Our results suggest periods of moderately saline–brackish conditions and moderate fire activity supported high floristic richness in wetlands, while floristic richness reduced during periods of extremely high or low salinity or high fire activity. Past changes in precipitation regimes primarily drove water-level changes in wetlands; however, changes in wetland and surrounding terrestrial vegetation cover also contributed to wetland water level dynamics. We recommend long-term monitoring of wetland salinity and water-level changes to track potential changes in wetland floristic richness on truwana/CBI. Controlled fires could also be used to manage wetland biodiversity after careful consideration and experimentation to determine appropriate fire levels that maximize wetland floristic richness and biocultural values.

5.1. Introduction

Australia is home to some of the world's most significant ecologically valuable wetlands ("Ramsar Convention on Wetlands of International Importance Especially as Waterfowl Habitat" also known as Ramsar wetlands), covering more than 8.3 million hectares and spanning tropical to temperate habitats. These wetlands range from permanently inundated to ephemeral and freshwater to saltwater types (Department of Agriculture, Water, and the Environment—DAWE 2013; Ramsar List, 2020). They host many rare and threatened plant species, and are critical stop-off points for migratory birds as they traverse the globe. The

wetlands of the Bass Strait islands, southeast Australia, are renowned as relatively undisturbed habitats for seabirds and waders, while the extensive undisturbed sandy beaches are used by beach-nesting shorebirds, many of which are currently dependent on these wetlands for population maintenance (DAWE 2012; 2013; Blackhall 1986; Hirst et al. 2006; Harris and Harris 2002; Department of Primary Industry and Water 1996; Harris and Magnus 2004). Under the influence of changing climate and sea-level rise, these wetlands, and biota that depend upon them, will be subject to dynamic habitat shifts that are likely to have consequences for current and future wetland management (DAWE, 2019).

Understanding the long-term development of wetland ecosystems through the lens of applied palaeoecology can provide a critical perspective on past, as well as future threats to ecologically and culturally significant wetlands (Froyd and Willis 2008; Clarke and Lynch 2016).

Contemporary ecological appraisals are commonly used to inform ecosystem management decisions; however, these assessments typically do not provide any in-depth understanding of the long-term ecosystem processes and development due to the short period (months–years–decades) covered by ecological surveys and monitoring (Davies and Bunting 2010). Palaeoecological data can provide long-term ecosystem information, revealing centurial–millennial scale processes and developments under different climatic, fire and anthropogenic regimes. This historical knowledge of ecosystem changes has been recognized to be an invaluable complement to ecological research in building a reliable baseline for informing management strategies (Clarke and Lynch, 2016; Williams, 2011; Wingard et al., 2017; Słowiński et al., 2019; Saunders and Taffs, 2009; Roos et al. 2021; Barr et al., 2013).

Wetlands are excellent natural experimental sites for palaeoecological investigations, considering the range of micro- and macro-fossils of botanical and zoological origin archived in the sedimentary deposits (Gray et al. 2013). These fossils provide information on past ecological conditions in wetlands, and a combination of different fossil proxies (e.g., pollen and non-pollen palynomorphs) and other wetland geochemical proxies provide a more robust understanding of long-term processes and development, as well as biodiversity changes through time (e.g., Birks and Birks 2006; Davidson et al. 2013; Lacourse et al., 2019). Geochemical proxies (e.g., ITRAX scan data) are effective in capturing inherent changes and processes in wetlands, such as decomposition and carbon sequestration, as

well as changes in wetland physicochemical properties in general (Croudace and Guy Rothwell, 2015).

A previous ecological assessment/survey (DAWE 2012) of truwana/Cape Barren Island (CBI) wetlands have identified some critical unanswered questions, which are key to managing and conserving wetlands and associated biodiversity on the island. The questions include, (1) how have wetland floristic composition and hydrology changed on the island? and (2) how do changes in fire regimes affect wetland integrity and ecological dynamics? Answering these questions requires long-term data of wetland development and fire regimes from the island. Here, we aim to use a multi-proxy palaeoecological technique to answer these critical ecological questions. We use wetland fossil pollen and non-pollen palynomorphs and sediment geochemistry from multiple sites on the island to reconstruct an island-wide wetland development history and compare it to existing records of terrestrial vegetation and catchment-scale fire regimes from the island (Adeleye et al. 2021a). In addition to answering the above-established questions, we also aim to understand other intrinsic changes in truwana/CBI wetlands, such as rates of terrestrialization, changes in decomposition and rates of carbon accumulation/loss under different climatic regimes in the past. Results from this study will provide insights into potential drivers of wetland development and dynamics, contributing to the baseline knowledge for future management strategies on truwana/CBI and the wider surrounding regions in southeast Australia.

5.2. Study area

The second largest island in eastern Bass Strait, truwana/CBI is situated about 44 km off the coast of northeast Tasmania and south of Flinders Island, with an area of ~480 km² (Fig. 1). Most of the island is underlain by granitic rocks that have intruded, and consequently contact-metamorphosed, older sedimentary rocks (Mathinna beds of Siluro-Devonian age). The granite is extensively exposed and has resulted in broad aprons of colluvial siliceous gravels around higher parts of the landscape. The Mathinna beds crop out in limited areas such as on the north coast of the island near Apple Orchard Point. Pre-Quaternary Cenozoic deposits are made up of calcareous sandstone, limestone, and basalt (Cocker 1980), and the Quaternary deposits are made up of aeolian, marine, and alluvial sediments (McClenaghan et al. 2011). The island's elevation ranges from sea level to about 700 m asl on Mt Munro, and the vegetation is characterized by heathlands, scrubland, and sclerophyll

forests, sedgeland and small areas of grassland and mesophyllous cloud forest. The island also hosts various fresh and saltwater wetlands (dune-bounded on granitic bedrock) in good condition and of high conservation value, especially on the east coast (Ramsar wetlands— DAWE 2012; Fig. 1).

A temperate oceanic climate characterizes the island, with an average annual rainfall of 710 mm, maximum daily temperatures of about 23°C in February and minimum of about 13°C in July (Australian Bureau of Meteorology). The Southern Westerly Winds (SWW) and El Niño Southern Oscillation (ENSO) controls rainfall and interannual fires on the island and across southeast Australia (Mariani et al 2016; Australian Bureau of Meteorology, 2010). The probability of summer rainfall is higher (low winter rainfall) on the island when SWW are in their southernmost positions, and the reverse holds when the SWW move northward. Positive ENSO years (La Niña) are associated with high annual rainfall, while negative years (El Niño) are associated with low annual rainfall on the island (Australian Bureau of Meteorology, 2010). SWW positions also contribute to controlling the teleconnection between ENSO and rainfall (Cleverly et al., 2016). Strong interannual rainfall variability has a major impact on water levels in the shallow wetlands on truwana/CBI (DAWE 2012).

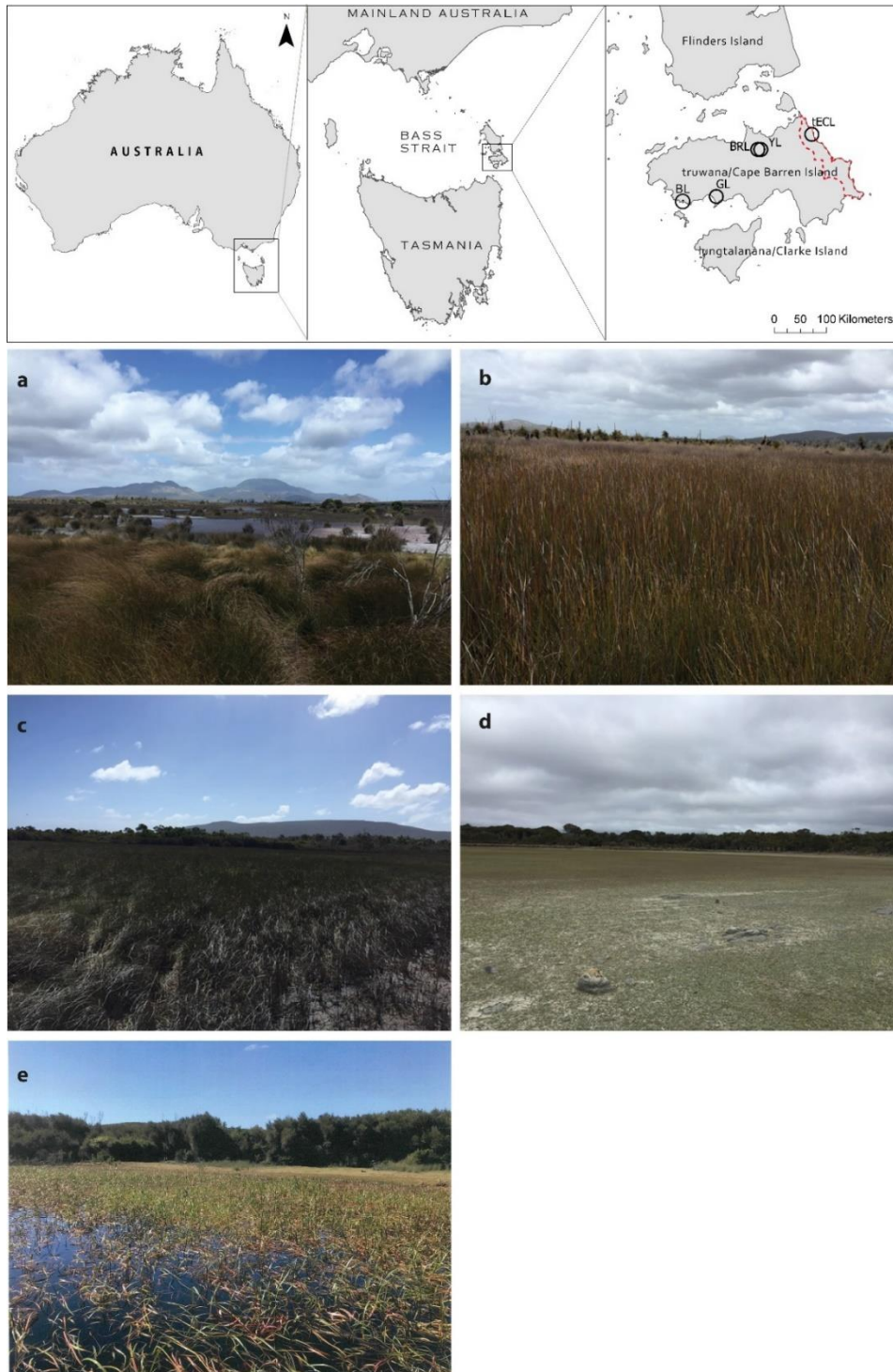


Fig. 1: Top: Location of coring sites (black dots) on truwana/Cape Barren Island, Bass Strait, southeast Australia. Coring sites include Big Reedy Lagoon (BRL), Yakka Lagoon (YL), truwana East Coast Lagoon (IECL), Bumpy Lagoon (BL) and Green Lagoon (GL). Red broken line represents area of Ramsar sites on the island. Bottom: Images of coring sites (wetlands), which include, Big Reedy Lagoon (a), Yakka Lagoon (b), Green Lagoon (c), truwana East Coast Lagoon (d), and Bumpy Lagoon (e). Photos by Matthew Adeleye except Bumpy Lagoon by Feli Hopf.

5.3. Methods

5.3.1. Selected wetlands, core collection and ITRAX geochemical scanning

Five wetlands distributed across truwana/CBI were selected for coring, including wetlands in coastal and inland areas, as well as a Ramsar wetland (truwana East Coast Lagoon) on the east coast of the island, which houses some of Tasmania's rare and threatened plant species (e.g., *Myriophyllum muelleri*, *Wilsonia* spp).

Big Reedy Lagoon (BRL) is the largest wetland (widest diameter ~1 km) on truwana/CBI, a semi-dry/ephemeral shallow swamp (<1 m water depth) in the north-central part of the island. BRL is bounded by dune formations in the eastern–southern edges in which smaller Yakka Lagoon (YL) has formed (Fig. 1b). The surface of BRL is dominated by sedges, with shrubs growing on patches of higher ground and the wetland is only inundated during wetter months (June–September). YL is a small shallow swamp (<1 m water depth), with dense sedgeland and standing water in most part of the year. Of the remaining sites, truwana East Coast Lagoon (tECL) is an infilled coastal lagoon on the east coast (Ramsar site), while Green Lagoon (GL) and Bumpy Lagoon (BL) are shallow swamps (< 1 m water depth) on the south and southwest coast, respectively (Fig. 1). tECL has bedrock close to the surface and is dominated by herbs, GL is dominated by *Triglochin procera* (syn. *Cychnogeton procera*) and *Myriophyllum* sp., and BL is dominated by *Triglochin procera*. tECL is mostly dry, with patches of surface standing water during the wetter months, while GL has standing water all year round. See Table 1 for coring site information and detailed wetland floristic composition for each site.

Table 1: Coring site information and wetland floristic composition for each site (see Fig. 1 for site codes).

All taxa are herbaceous and voucher specimens of many of the plant species collected from the sites have been deposited in the Tasmanian Herbarium (HO).

Site code	Core depth (m)	Location	Elevation (m)	Wetland floristic composition
BRL	2	-40.3589°, 148.2381°	26	<i>Lepidosperma concavum</i> , <i>Lepidosperma laterale</i> , <i>Baumea juncea</i> , <i>Empodisma minus</i> , <i>Centella cordifolia</i> , <i>Selliera radicans</i> , <i>Gahnia</i> sp, <i>Schoenus nitens</i> , <i>Juncus</i> sp, <i>Gahnia filum</i> , <i>Gahnia grandis</i> , <i>Lilaeopsis polyantha</i> , <i>Juncus pallidus</i> , <i>Juncus kraussii</i> , <i>Hydrocotyle muscosa</i> , <i>Isolepis platycarpa</i> , <i>Leptocarpus tenax</i> , <i>Centrolepis strigosa</i> , <i>Drosera pygmaea</i> , <i>Epilobium billardioreanum</i> , <i>Selaginella uliginosa</i> .
GL	1.35	-40.4430°, 148.1438°	10	<i>Triglochin procera</i> , <i>Baumea juncea</i> , <i>Utricularia dichotoma</i> , <i>Drosera pygmaea</i> , <i>Xyris</i> sp., <i>Schoenus nitens</i> , <i>Selliera radicans</i> , <i>Centrolepis fascicularis</i> , <i>Selaginella uliginosa</i> , <i>Leptocarpus tenax</i> , <i>Baumea arthropphylla</i> , <i>Distichlis distichophylla</i> , <i>Eurycordia complanatus</i> , <i>Lepidosperma concavum</i> , <i>Lepidosperma longitudinale</i> , <i>Myriophyllum</i> sp, <i>Hypolaena fastigiata</i> , <i>Ficinia nodosa</i> .
tECL	0.73	-40.3311°, 148.2381°	1	<i>Angianthus preissianus</i> , <i>Wilsonia backhousii</i> , <i>Eryngium vesiculosum</i> , <i>Samolus repens</i> , <i>Lobelia anceps</i> , <i>Schoenus nitens</i> , <i>Sarcocornia quinqueflora</i> , <i>Juncus kraussii</i> , <i>Baumea juncea</i> , <i>Distichlis distichophylla</i> , <i>Gahnia</i> sp, <i>Drosera pygmaea</i> ,
BL	0.44	-40.4515°, 148.0710°	11	<i>Triglochin procera</i> .
YL	0.45	-40.3589°, 148.2447°	30	<i>Lepidosperma longitudinale</i> , <i>Lepidosperma filiforme</i> , <i>Leptocarpus tenax</i> , <i>Selaginella uliginosa</i> , <i>Patersonia fragilis</i> , <i>Xyris operculata</i> , <i>Drosera pygmaea</i> , <i>Gonocarpus micranthus</i> , <i>Baumea acuta</i> , <i>Empodisma minus</i> , <i>Samolus repens</i> .

Terrestrial pollen and charcoal records from BRL, GL, tECL and YL have been published in a separate study, including chronologies and age-depth models (see Adeleye et al. 2021a), while BL's age-depth model is provided in appendix S4 (Table S1 and Fig. S1). The age-depth models suggest a basal age of ~14,000 cal yr BP (calendar years before present, i.e. 1950 CE) for BRL, ~7500 cal yr BP for GL, ~7000 cal yr BP for tECL, ~4060 cal yr BP for BL and ~650 cal yr BP for YL. Cores BRL, tECL and BL were scanned for trace metals using ITRAX at the Australian Nuclear Science and Technology Organisation. Iron (Fe) counts normalized by counts per second (cps) were used to infer palaeo-oxidation (decomposition) and terrigenous inputs in wetlands (Croudace and Rothwell 2015).

5.3.2. Pollen and non-pollen palynomorph analysis

Subsamples (1.25 cm³) were taken from sediment cores at 1–4-cm intervals and processed following standard pollen preparation procedures, which include HCl, KOH and acetolysis treatments (Faegri and Iversen 1975). Aquatic/wetland pollen and spores and NPPs were counted and percentages calculated based on the pollen sum (at least 300) of terrestrial taxa. Non-pollen palynomorphs were identified through various publications by van Geel (e.g., van Geel 1978, 2001; van Geel et al. 1981, 1983, 1989), as well as other literature such as Bakker and van Smeerdijk (1982), Cook et al. (2011), Jarzen and Elsik (1986), Cugny et al. (2010), Botting and Muir (2013), Walker (2007), Ekrem (2004), Komárek and Jankovská (2001), Jankovská and Komárek (2000), Wolowski et al. (2002), Grospietech (1958), Harnisch (1959), Mousinho et al. (2018), Mudie et al. (2010), Montoya et al. (2012) and Schlütz and Shumilovskikh (2017). Other works consulted are included in Table II in appendix 2. Type numbers are designated to indeterminate NPPs following the standard system, which involves the use of an acronym for the laboratory where the NPP analysis was conducted (Miola 2012). In this case, indeterminate NPPs carry the acronym 'ANH' for the Archaeology and Natural History Laboratory at the Australian National University.

Since HF treatment was not used in sediment sample preparation, diatom frustules were retained in samples. Therefore, the frustules were also counted in pollen slides and identified using guides such as Jovanovska et al. (2015) and Sonneman et al. (1999).

Palynomorph images were taken in bright field at 400× magnification, using the Zeiss Axion Imager.M1. Palynomorph (wetland pollen and NPP) diagrams for each site were produced

using Tilia 3.0.1 and diagram zonations were determined using CONISS after square root transformation of palynomorph percentages (<https://www.tiliait.com/>). Wetland palynological richness was also estimated by rarefying wetland pollen data (based on the minimum sum for each site) in 'R' (R Core Team 2020) using the 'rarefy' function in the 'vegan' package (Oksanen et al. 2018). Rarefied palynological richness reflects floristic richness in terrestrial vegetation (Adeleye et al. 2021b; Felde et al. 2016) but here we apply it to wetland pollen assemblages only. Detrended Correspondence Analysis (DCA) was also performed on palynomorph records (wetland pollen and NPPs) using the 'vegan' package. The first DCA axis was extracted to identify the major trend in palynomorph assemblages across sites and the trend was interpreted in the context of palynomorph compositional change and ecological significance to infer wetland water-level changes.

5.4. Results

5.4.1. Recorded palynomorphs

A total of 96 NPP types (Plate I–IV) was documented, which includes algal, fungal, and zoological remains. The ecological significance of each is interpreted in Table S2 in appendix S4. The aquatic/wetland pollen assemblages across sites are dominated by *Myriophyllum* species, Restionaceae and Cyperaceae.

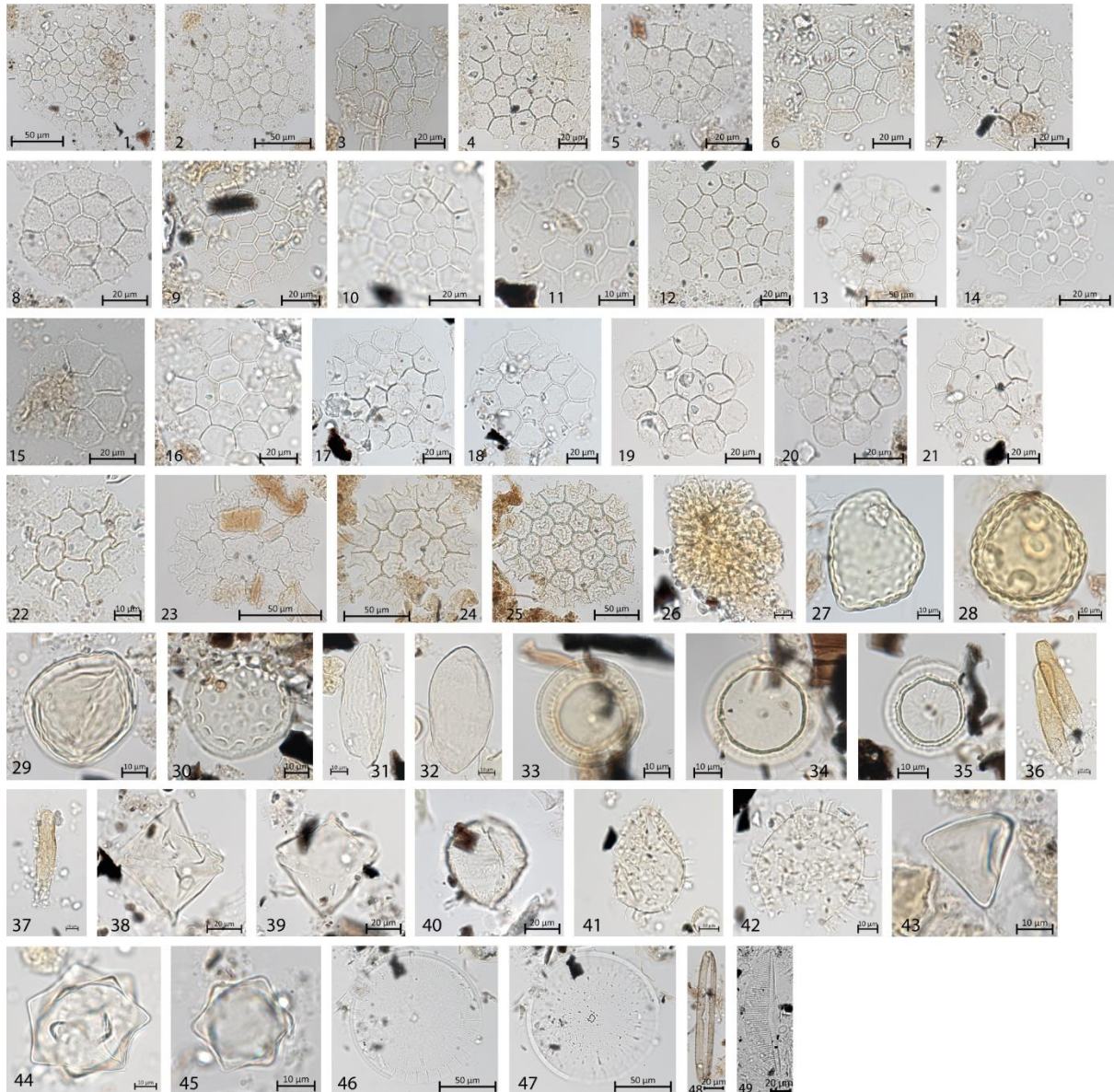


Plate I: Algal types recorded for all sites on truwana/Cape Barren Island, Bass Strait, southeast Australia. *Pediastrum* (HdV-760) types include, *P. integrum* type 1 (1–18); *P. integrum* type 2 (19–20); *P. boryanum* types (21–22); and *P. angulosum* types (23–25). Other alga types include, *Botryococcus*: HdV-766 (26); *Zygnema*: HdV-141 (27–30); *Spirogyra*: HdV-130 (31–32); *Debarya*: HdV-214 (33–35); *Gloeotrichia*: HdV-146 (36–37); *Protoperidinium* cf. *abei* (38); *Protoperidinium* sp (39–40); *Operculonidium centrocarpum* (41–42); type A2 (43); HdV-333 (44); HdV-209/66 (45); centric diatom: *Actinocyclus octonarius* (46–47); pennate diatom: *Pinnularia* cf. *viridiformis* (48); and pennate diatom: *Diploneis* cf. *elliptica* (49).

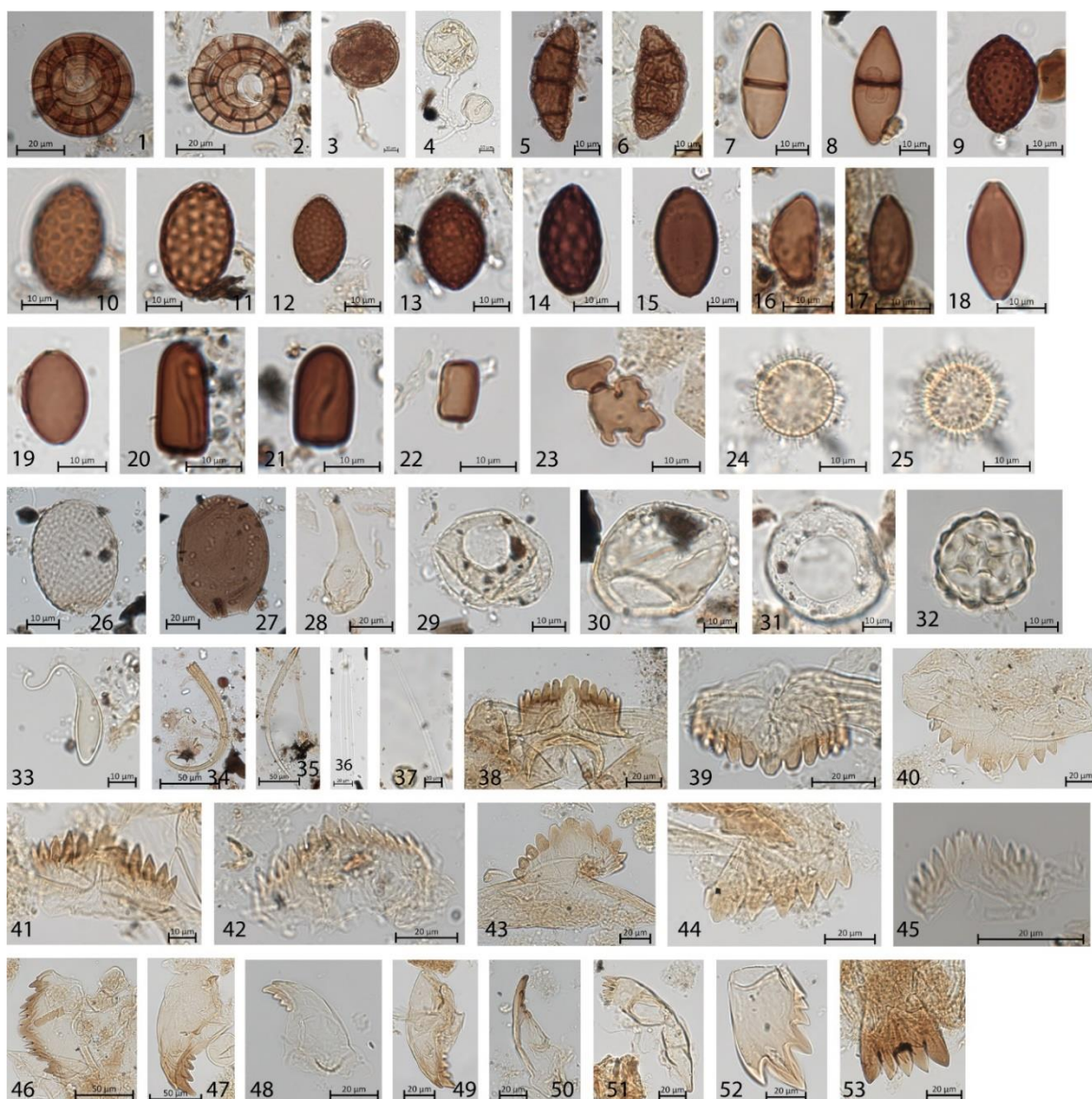


Plate II: Fungal and zoological types recorded for all sites on truwana/Cape Barren Island, Bass Strait, southeast Australia. Fungal types include, *Helicoon*: HdV-30 (1–2); *Glomus*: HdV-207 (3–4); *Bysothecium circinans*: HdV-16 (5–6), HdV-18 (7–8); *Gelasinospora*: HdV-1 (9–14); *Podospora decipiens* type: HdV-368 (15), cf. *Podospora*: HdV-368 (16–17); *Sordaria*: HdV-55 (18–19); *Sporomiella*: HdV-113 (20–22); *Gaeumannomyces hyphopodia*: HdV-126 (23); and *Lycoperdon* (24–25). Zoological types include *Assulina muscorum* (26); *A. semelinum* (27); *Habrotrocha angusticollis* (28); *Centropyxis* type (29–30); cf. *Centropyxis*/cf. *Cyclopyxis arcelloides* type (30); HdV-233 (32); copepod spermatophore (33); animal hair (34–35); sponge spicules (36–37); Chironomidae types; which include *Tanytarsus* types (38–42); cf. *Tanytarsus* types (43–45); *Cladopelma lateralis* type (46); cf. *Tanytarsus* mandible types (47–49); cf. *Cladopelma lateralis* mandible type (50); other chironomid remains (51–52); and cf. Tanypodinae ligula (53)



Plate III: Other sparsely recorded and indeterminate NPP types in core records. NPPs with sparse occurrence include *Neorhabdocoela* oocytes: HdV-353 (1–3); HdV-20 (4); conidium of *Alternaria*: HdV-3 (5); HdV-179 (6); HdV-229 (7); Testate amoebae (cf. *Nebela*)? (8); *Arcella*: HdV-35 (9); *Tilletia* type: HdV-27 (10); *Closterium* (11); and *Entorrhiza* (12–13). Indeterminate NPP types with designated laboratory number include, ANH-1 (14–15); ANH-2 (16–17); ANH-3 (18); ANH-4 (19); ANH-5 (20); ANH-6 (21); ANH-7 (22–23); ANH-8 (24); ANH-9 (25); and ANH-10 (26–28). ‘ANH’ is the acronym for the Archaeology and Natural History laboratory at the Australian National University where the NPP analysis was carried out. See appendix 3 for notes and comments on NPPs

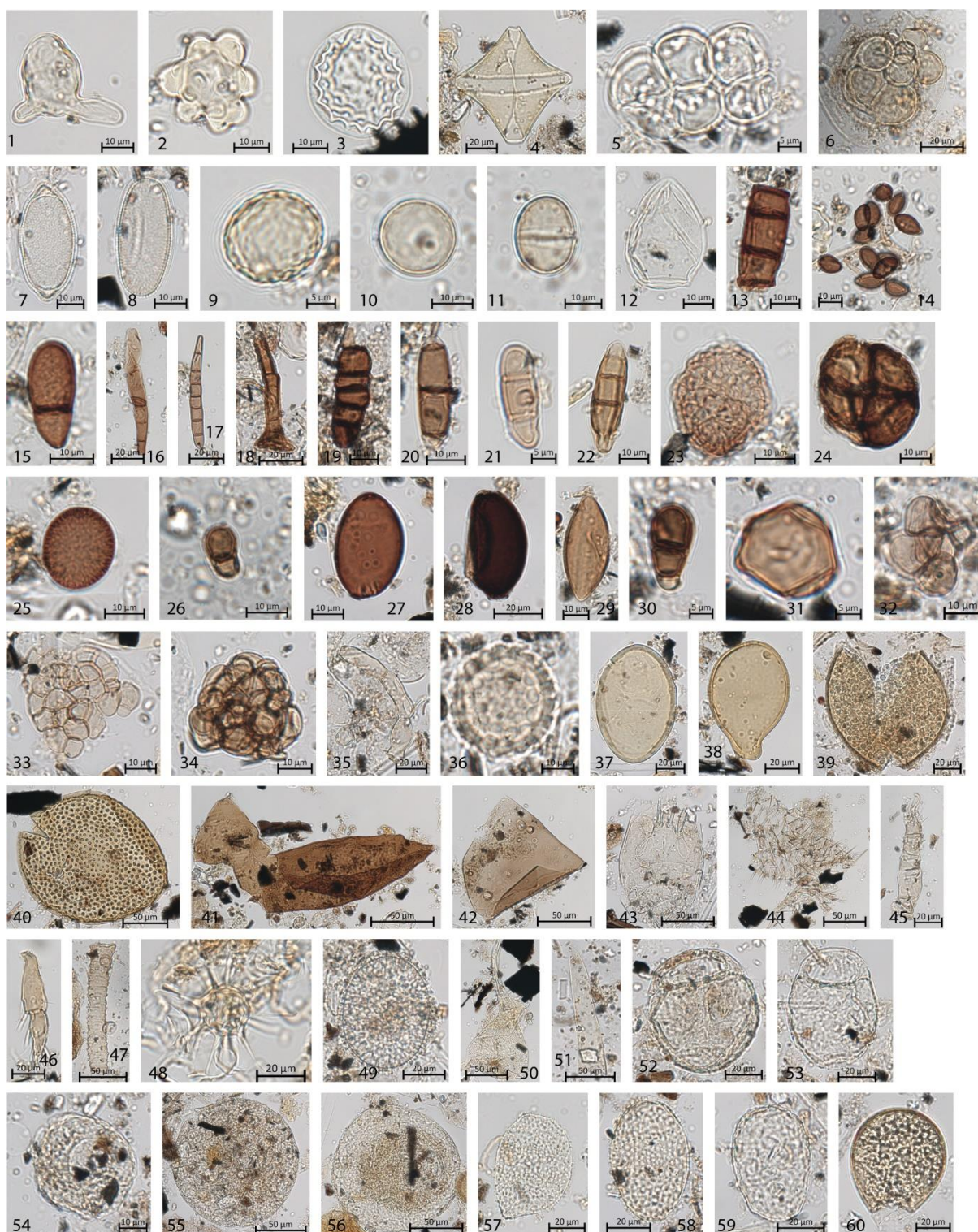


Plate IV: NPPs recorded in Big Reedy Lagoon surface samples excluding types already represented in Fig. 2–IV such as *Botryococcus*, *Zygnema*, *Assulina* and *Arcella*. ANH-11: alga or invertebrate remains (1); ANH-12: cf. Desmidiaceae (2); ANH-13: algal remains? (3); ANH-14: *Zygnema* type? (4); ANH-15: cf. *Aecidium* (5–6); ANH-16: cf. HdV-60 (7); ANH-17: HdV-60 type (8); ANH-18: algal remains? (9); ANH-19: algal remains? (10–11); ANH-20: algal remains? (12); ANH-21: uniseriate ascospore (13); HdV-203 (14); ANH-22: cf. *Trichocladium* conidim: HdV-572 (15); cf. *Geoglossum sphagnophilum*: HdV-77 (16),

Geoglossum sphagnophilum: HdV-77 (17), HdV-96 (18); HdV-324 (19); cf. *Coniochaeta* (20); ANH-23: fungal ascospore (21); ANH-24: fungal ascospore (22); ANH-25 (23); ANH-26: fungal cell cluster (24); ANH-27: fungal spore? (25); ANH-28: cf. HdV-95 fungal spore (26); *Podospora*: HdV-368 (27); ANH-29: fungal spore? (28); ANH-30: fungal spore (29): HdV-359 type (30); cf. HdV-361 (31); ANH-31: fungal cluster cell (32); ANH-32: fungal cluster cell (33); ANH-33: fungal cluster cell (34); ANH-34: invertebrate appendage (35); ANH-35: cf. HdV-233 (36); ANH-36: invertebrate remains? (37–38); cf. turbellaria oocyte (39–40); HdV-52d (41–42); ANH-37: invertebrate remains (43); HdV-52c (44); *Hydrozetes* – an oribatid Acari: HdV-36b (45–46); ANH-38: invertebrate remains (47); ANH-39: also recorded by Montoya et al. (2012), but unidentified (48); cf. Tardigrade egg (49); ANH-40: invertebrate remains (50); ANH-41: invertebrate remains, also recorded by Montoya et al. (2012), but unidentified (51); *Centropyxis aerophila* (52–53); cf. *C. ecornis* or *Cyclopyxis arcelloides* (54); *Trignopyxis* (55–56); cf. *Placocista spinosa* (57); cf. *Heleopera petricola* (58–59); *Nebela* cf. *tincta*. See appendix 4 for Notes and comments on NPPs

5.4.2. Wetland palynomorph assemblage zones, wetland floristic richness, geochemistry, and lithology

The BRL sedimentary record is divided into four major palynomorph zones (Fig. 2a). Zone BR1 (~14,000–12,800 cal yr BP) is mostly composed of silty grey clay, with high Fe counts. Algal types, which include *Botryococcus*, *Pediastrum*, *Operculonidium centrocarpum*, HdV-209/66 and type A2, dominate the NPP assemblage. Wetland pollen diversity (wetland floristic richness) is also high in zone BR1, with an abundance of *Myriophyllum* species and *Lepilaena australis*. Zone BR2 (~12,800–9100 cal yr BP) is characterized by fibrous peat and low Fe counts, with a minor increase in fungal and algal types. Chironomid remains (mandible and mentum) also increased in this zone. *Isoetes* and Cyperaceae dominate the aquatic/wetland pollen assemblages, but with a decreasing trend in wetland floristic richness. Zone BR3 (~9100–7200 cal yr BP) is characterized by dark decomposed peat, with an increase and peak in Fe counts. HdV-18 fungal type and copepod spermatophores dominate the NPP assemblages and Restionaceae increased greatly at the expense of *Isoetes* and Cyperaceae, with wetland floristic richness reaching a minimum. Fibrous peat also characterized zone BR3 (~7200–1000 cal yr BP), with a minor decline in Fe counts. *Botryococcus* and sponge spicules increased in this zone, and Cyperaceae increased at the expense of Restionaceae, with a steady increase in wetland floristic richness. BRL surface is dominated by *Botryococcus*, Cyperaceae and Restionaceae (see Fig. S2 in appendix S4).

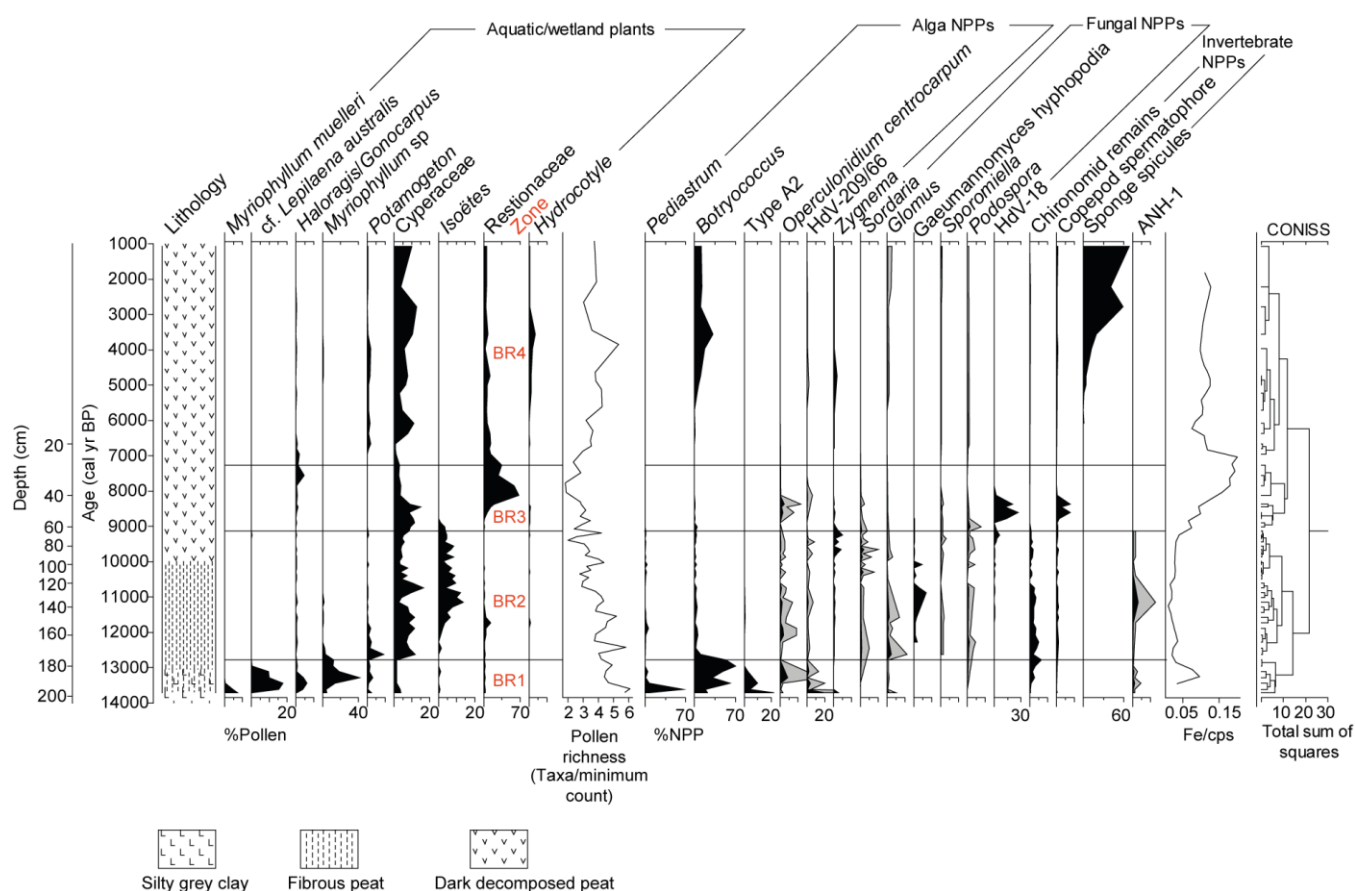


Fig. 2a: Wetland palynomorph percentage diagram, including sediment lithology, major taxa, wetland floristic richness (pollen richness) and CONISS zones for Big Reedy Lagoon (BRL). Also shown is the Fe count normalized by counts per second (cps).

The tECL record exhibits three major zones (Fig. 2b). Zone tEC1 (~7000–5100 cal yr BP) is composed of silty grey clay and dominated by *Pediastrum* (mostly *P. integrum* type 1) and *Botryococcus* algae, while Restionaceae dominates the aquatic/wetland pollen assemblages, with low pollen richness. Zone tEC2 (~5100–1700 cal yr BP) is composed of reddish and grey silty clay and dominated by sponge spicules, alga type A2 and fungal types (*Lycoperdon*, *Sordaria* and *Glomus*). *Myriophyllum* and *Utricularia* also increased in this zone, with increased wetland floristic richness, and Restionaceae continues to be present. Conversely, *Pediastrum* and *Botryococcus* decreased in the zone, but *Botryococcus* later rebounded gradually. Reddish and grey silty clay also characterized zone tEC3 (~1700 cal yr BP–present) and *Botryococcus*, *Zygnema*, *Gloeotrichia*, *Sordaria* and *Glomus* dominate the NPP assemblage. *Myriophyllum muelleri*, Cyperaceae and

Wilsonia dominate the aquatic/wetland pollen assemblage, and wetland floristic richness decreased to its lowest level in the record.

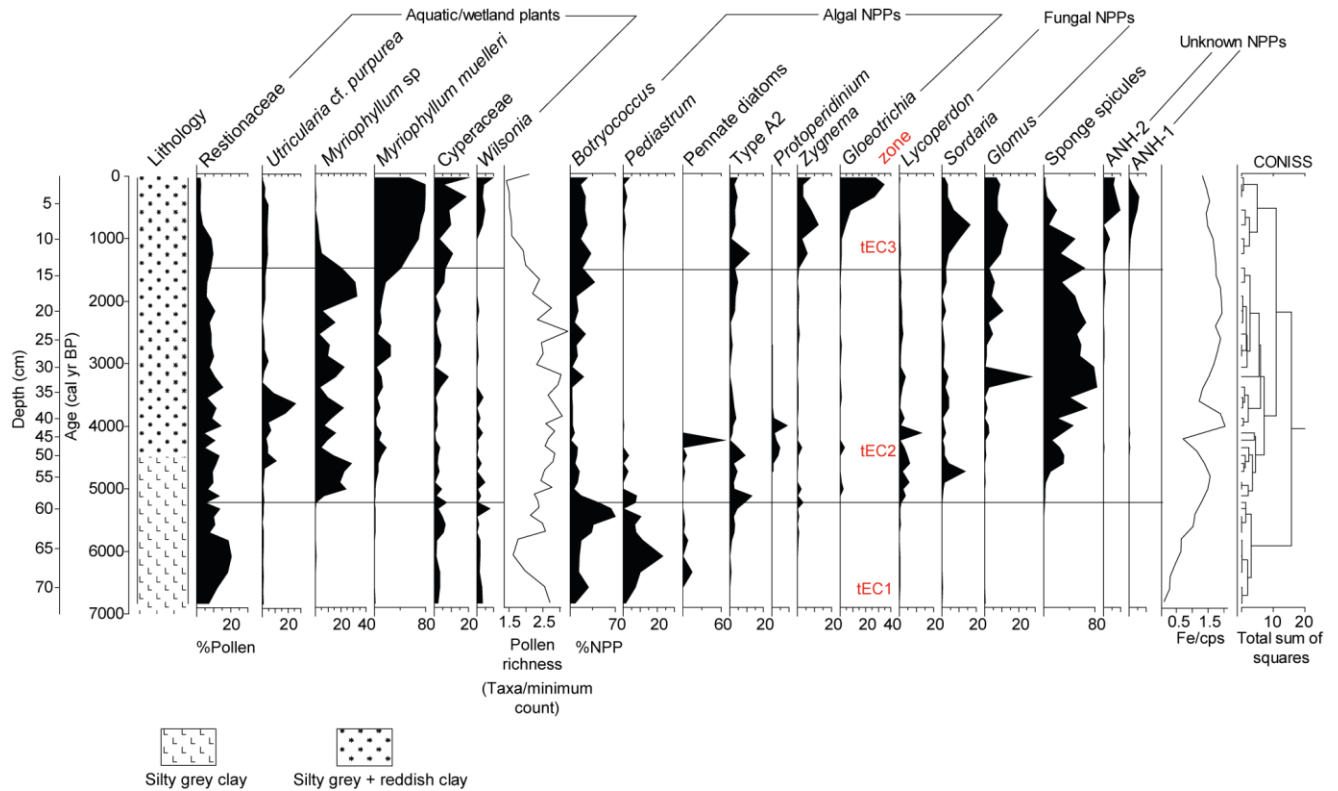


Fig. 2b: Wetland palynomorph percentage diagram, including sediment lithology, major taxa, wetland floristic richness (pollen richness) and CONISS zones for truwana East Coast Lagoon (tECL). Also shown is the Fe count normalized by counts per second (cps).

The GL record is divided into four major zones (Fig. 2c) and wetland floristic richness generally oscillates throughout the record. Zone GL1 (~7500–6000 cal yr BP) is composed of fibrous peat and dominated by pennate diatoms (mostly *Pinnularia*) and Restionaceae. Pennate diatoms are replaced by centric diatoms (mostly *Actinocyclus octonarius*) in the sandy peat part of zone GL2 (~6000–4200 cal yr BP), while *Myriophyllum* and *Triglochin* (syn. *Cycnogeton*) increased toward the end of the zone, which is characterized by dark decomposed peat. Cyperaceae also gradually increased through the zone. Zone GL3 (~4200–2300 cal yr BP) is composed of decomposed peat and features few NPPs, with the highest occurrence recorded for *Botryococcus* and *Spirogyra*. Cyperaceae and *Triglochin* are abundant in this zone, while *Myriophyllum* decreased. Pennate diatoms increased in the

topmost zone GL4 (~2300–0 cal yr BP), *Zygnema* and *Botryococcus* increased in the last 1000 years, which is characterized by fibrous peat, and Cyperaceae and *Triglochin* maintained their abundance.

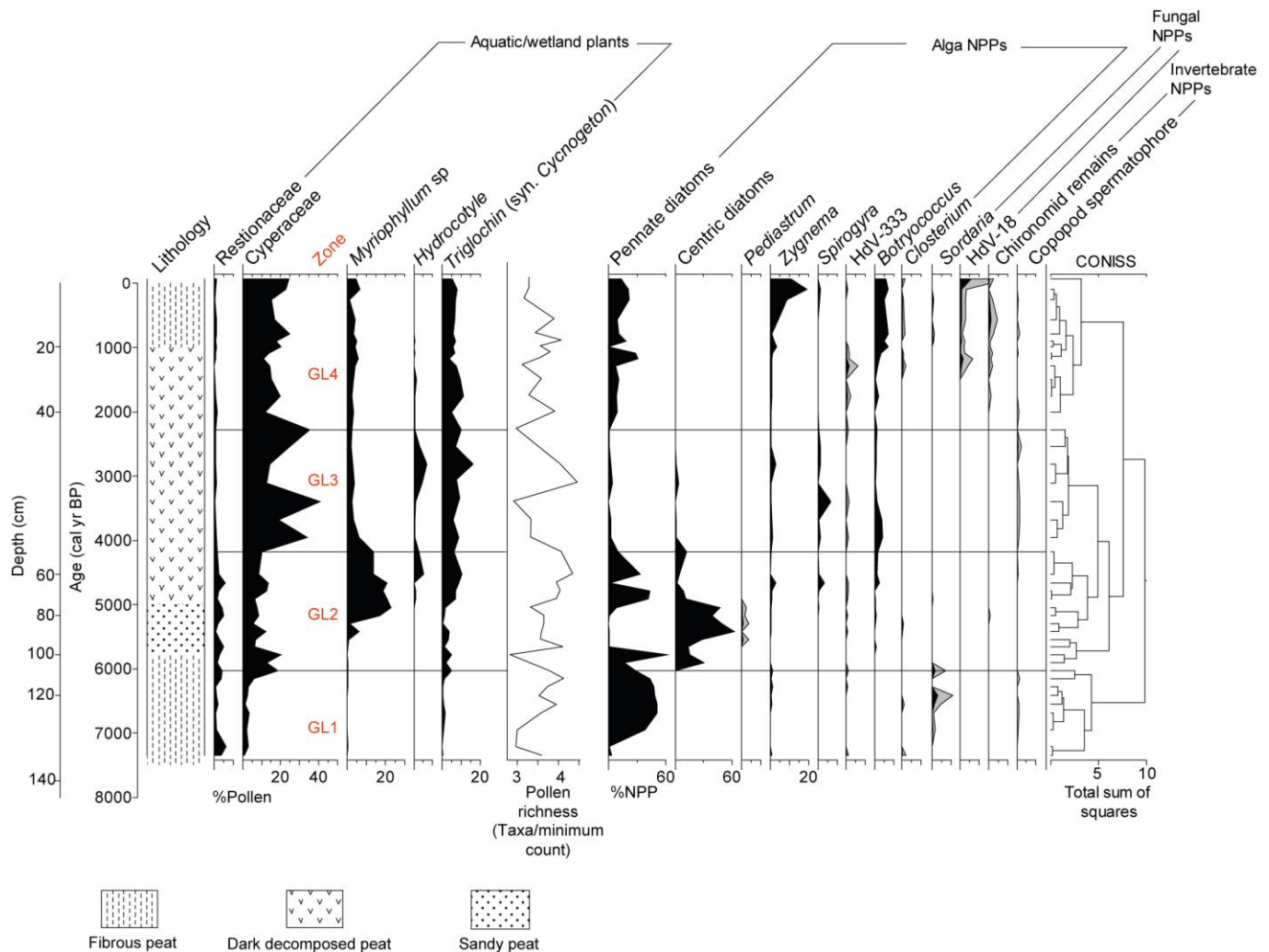


Fig. 2c: Wetland palynomorph percentage diagram, including sediment lithology, major taxa, wetland floristic richness (pollen richness) and CONISS zones for Green Lagoon (GL).

The BL record is divided into two major zones and the entire core is composed of sandy clay (Fig. 2d). A pollen record is not available for Bumpy Lagoon due to extremely low pollen concentration in samples. Zone B1 (~4000–2600 cal yr BP) is generally characterized by high Fe counts and dominated by pennate diatoms (mostly *Pinnularia* and *Diploneis* cf. *elliptica*), *Protoperidinium*, HdV-209/66 and *Zygnema*. Fe counts decreased in zone B2 (~2600–present), as well as *Zygnema* and HdV-209/66, with increase in sponge

spicules and HdV-333. *Protoperidinium* abundance also dropped in this zone but increased again in the last ~500 years.

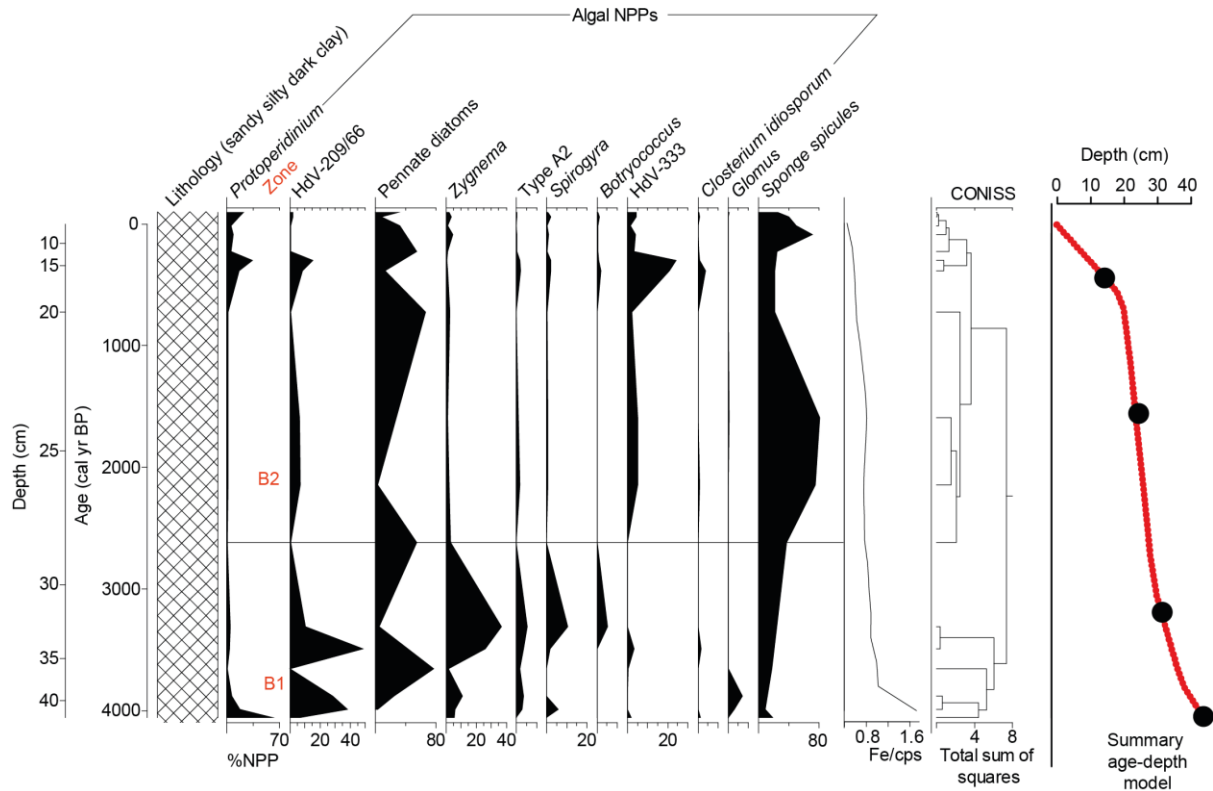


Fig. 2d: Major non-pollen palynomorph taxa percentage diagram, including sediment lithology, and CONISS zones for Bumpy Lagoon (BL). Also shown is the Fe count normalized by counts per second (cps) and summary age-depth model for BL (red curve), including calibrated ^{14}C dates (black solid circles). See Fig. 8 in Appendix 1 for BL full Bacon age-depth model. Aquatic/wetland pollen are not available for BL due to extremely low pollen concentrations.

The YL record is divided into three major zones (Fig. 2e), and wetland floristic richness generally oscillates throughout the record. Zone YL1 (~650–370 cal yr BP) is composed of decomposed peat and is characterized by the Zygnemataceae alga types (*Zygnema*, *Spirogyra* and *Debarya*), Restionaceae and Cyperaceae. The first half of zone YL2 (~370–175 cal yr BP) sees increases in fungal types *Bysothecium circinans*, *Gelasinospora*, and *Sordaria*, as well Restionaceae and Cyperaceae, while the pennate diatoms (mostly *Pinnularia*) and *Botryococcus* joined the assemblage in the second half (~175–35 cal yr BP). Pennate diatoms and *Botryococcus* abundance dropped in zone YL3 (~35 cal yr BP–present), while other fungal (e.g., *Helicooon*) and zoological (e.g., *Centropyxis*, *Habrotrocha*

angusticollis, copepod spermatophores, sponge spicules) types increased, with a minor decrease in Restionaceae.

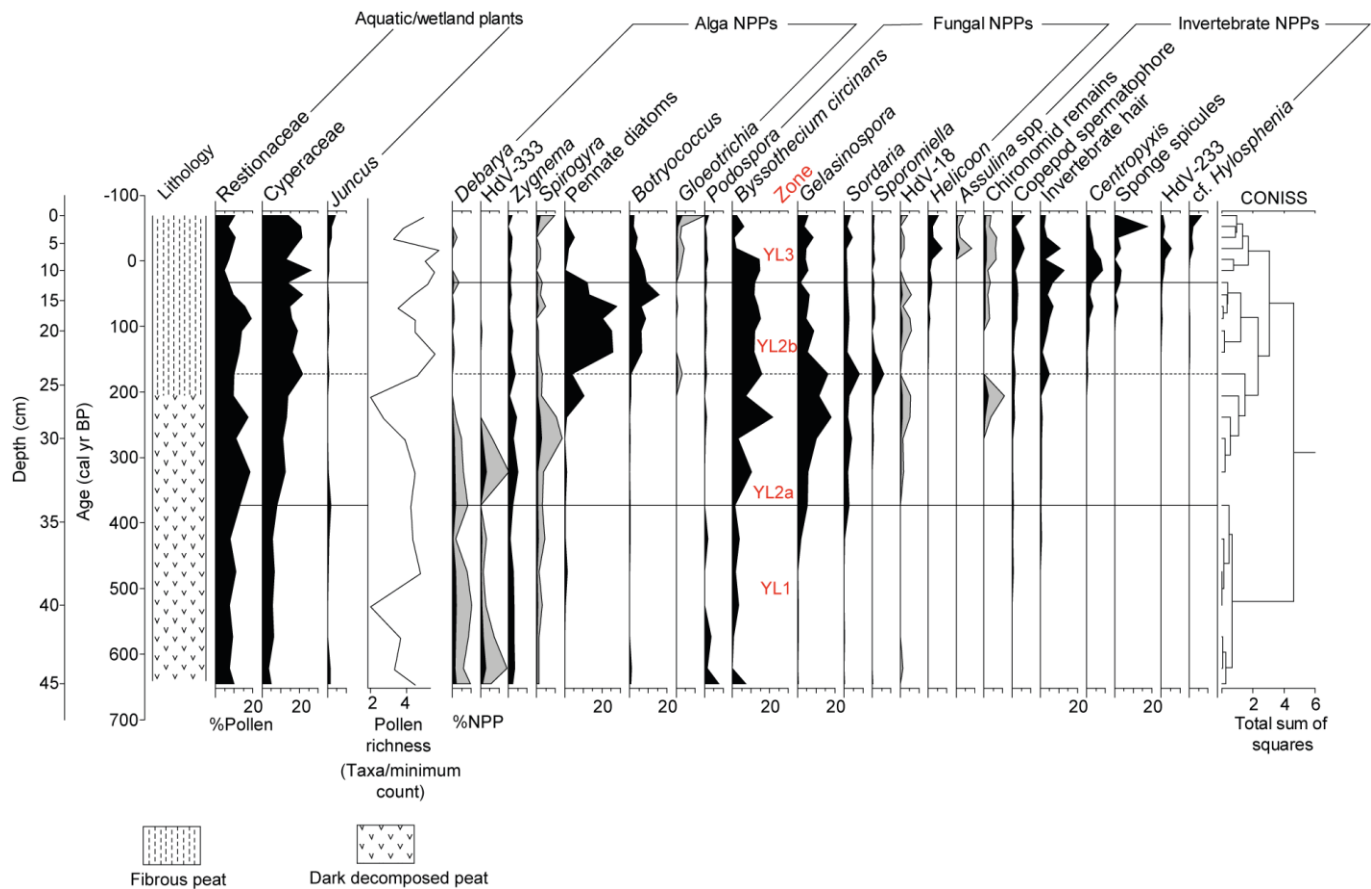


Fig. 2e: Wetland palynomorph percentage diagram, including sediment lithology, major taxa, wetland floristic richness (pollen richness) and CONISS zones for Yakka Lagoon (YL).

5.5. Discussion

The use of non-pollen palynomorphs (NPPs) in palaeoecological reconstructions is increasingly gaining attention and has proven useful in detecting local environmental changes in palaeoecological studies, complementing pollen-based reconstructions (e.g., Montoya et al., 2012; Lacourse et al., 2012; van Geel et al., 1989; van Geel, 1972, 1977, 1981; Cook et al., 2011, 2009). Not only are NPPs cosmopolitan in various ecosystems and well preserved in fossil records (as demonstrated by our study), they are also resistant to chemical treatments during pollen preparation, making them readily available on pollen slides for inclusion in multi-proxy palaeoecological analysis (van Geel, 2001; Tunno and Mensing, 2017). NPPs are sensitive to changes in local conditions, such as changes in

hydrology, temperature, nutrients, salinity, conductivity, and pH, while some are also associated with terrestrial and/or aquatic vegetation changes, making NPP-based palaeoecological reconstructions interpretable ecologically (e.g., López-Vila et al., 2018; Tunno and Mensing, 2017; See Table III in appendix 2 for the ecological interpretations of NPPs recorded in this study). Previous studies have used NPPs to support pollen-based vegetation reconstructions, and to reconstruct human land-use/occupation and wetland development history (e.g., Lacourse et al., 2019; van Geel, 2011; Cugny et al., 2010; Ejarque et al., 2011; Menozzi et al., 2010; Kiage et al., 2019; Fesser and O'Connell, 2010; Montoya et al., 2011). Our study also demonstrates that the use of NPPs can provide in-depth information about past wetland development and provides one of the most detailed records of NPPs so far in Australia, with about 100 NPP types documented and photographed, which will be useful for identifications and interpretations in future palaeoecological studies in Australia and other parts of the world.

Wetland pollen and NPP assemblages presented in this study reveal changes in wetland development on truwana/CBI, Bass Strait, over the past ~14,000 years (Fig. 2–3). Changes in wetland palynomorph composition and abundance, as reflected by the first DCA axis across sites, as well as changes in wetland sediment lithology and geochemistry may reflect the influence of long-term changes in climate and fire regimes on wetlands on the island (Fig. 3). Understanding the roles of these regional and local factors in wetland ecological processes and development is key to the long-term management of wetland ecosystem quality, services, and biodiversity on truwana/CBI. Based on our palaeoecological results, we discuss the long-term roles of these factors and highlight their potential implications for management and conservation.



Fig. 3: Changes in fire regimes (MacroCHAR), oxidation and terrigenous inputs (Fe/cp), climate and terrestrial vegetation in relation to changes in wetland floristic richness (taxa/minimum count) and inferred water-level changes based on the DCA (first axis) of palynomorph assemblage. Also shown is organic

content accumulation rates—OcAR (Oc/cm²/yr) in Big Reedy Lagoon and the record of human land use inferred from ¹⁴C-dated archaeological evidence of human occupation in eastern Bass Strait (Williams et al., 2014) and coprophilous fungal spore record. Climate regimes are adapted from reconstructed SWW-driven changes in precipitation:evaporation ratio for southern Australia (Wilkins et al., 2013) and Laguna Pallcacocha lake sedimentation-based ENSO events reconstruction (Moy et al., 2002). The multi-millennial shifts in these climatic modes in southeast Australia are discussed in detail in Fletcher and Moreno (2012). Terrestrial vegetation, fire regimes and organic content accumulation rates are adapted from Adeleye et al. (2021a), and organic content estimate is based on molybdenum incoherence/coherence scattering ratios in the sediment core from ITRAX scanning (see Woodward and Gadd, 2019 for method details). Note the different axis scales for each record.

5.5.1. Long-term climate-driven wetland changes on truwana/CBI

truwana/CBI wetlands are generally shallow (<1 m-deep) and are therefore sensitive to climatic shifts. The dry lateglacial (~14,000–13,000 cal yr BP) and mid-late Holocene (~6000–0 cal yr BP) climate in southeast Australia (Wilkins et al., 2013; Fletcher and Moreno, 2012) likely drove decreases/variability in wetland water levels on the island, with increases in salinity indicated by the abundance of *Pediastrum integrum*, *Botryococcus*, sponge spicules, *Myriophyllum*, and Cyperaceae at most sites (Komárek and Jankovská, 2001; Jankovská and Komárek, 2000; Wolowski et al., 2002). Herbland dominated by *Myriophyllum* and sedgeland dominated by Cyperaceae likely occupied the shallow wetlands during these dry climatic intervals (Harris and Kitchener 2005; Fig. 2–3).

In contrast, regional precipitation increases during the early Holocene (Wilkins et al., 2013) likely increased wetland water supply, supporting an open water body in BRL, with reduced wetland vegetation, at least between ~13,000 and 9000 years ago, as reflected by the abundance of chironomid remains, *Isoetes* and *Potamogeton* in BRL (Cook et al. 2011; Garrett and Kantvilas 1992; Edwards et al. 2000; Hughes 1990; Mariani et al. 2018b; Chappuis 2015; Danielsen 2010; Fig. 2a and 3). There is currently limited information on the ecology of *Isoetes* in the Bass Strait area and wider Tasmanian region. However, we do know that *Isoetes* species in Tasmania are mostly aquatic and grow in mud or silt in lentic and lotic rivers and lakes, and permanent water is a critical requirement for most species except *Isoetes drummondii* (Garrett and Kantvilas 1992). Chironomid remains recorded in BRL during this interval are predominantly mentum of *Tanitarsus* types (Plate 2_{38–45}) and few occurrences of *Cladopelma laterali* type (Plate. 2₄₆), which are all mostly found in

permanent open, oligotrophic, and warm waters (>1 m deep) (Eggermont et al. 2008; Engels and Cwynar 2011; Dimitriadis and Cranston 2001; Gandouin et al. 2016; Chen et al. 2014).

The interval ~9000–6000 cal yr BP is dominated by Restionaceae at most sites and may reflect a transitional phase from an early Holocene wetter phase in wetlands to mid–late Holocene drier phase (Fig. 2–3). Members of the Restionaceae on truwana/CBI mostly occupy moist/wet, but not permanently inundated sites. Hence, they are indicative of decline in water level between ~9000 and 6000 cal yr BP, with Restionaceae rushland or wet heathland expansion on the island (Harris et al. 2001; Harris and Kitchener 2005). Weakened Southern Westerly Wind-driven precipitation in eastern southeast Australia during this period (Fletcher and Moreno 2012) may explain the decreasing wetland water level and rushland/wet-heathland expansion on truwana/CBI. An increase in copepod spermatophores, HdV-18 in BRL, *Pediastrum integrum* in tECL and *Pinnularia* in GL suggests that open water was intermittently present during this transitional phase.

Climate-driven changes in terrestrial vegetation on truwana/CBI may have contributed to wetland changes in the past by controlling terrigenous input into the wetlands. Considering the major influence of strong maritime winds (storm surges) on the island (McInnes and Hubbert, 2003), open vegetation (scrub and heathland) on the island, especially during the mid–late Holocene when sea level rose, may have promoted landscape erosion (soil instability), with increased terrigenous input in wetlands (terrestrialization), contributing to the lowering of wetland water levels (Fig. 3). During the early Holocene, in contrast, increased vegetation cover would have increased soil stability, reducing erosion across the island, and slowing down wetland terrestrialization (Ellison et al., 2012).

The overall low–variable wetland water levels from ~9000 years ago, combined with elevated Fe counts and core lithologies, especially in BRL (decomposed peats) and tECL (reddish clay), suggest a loss of accumulated-organic matter in wetlands due to increased soil oxidation and decomposition (Fig. 2–3). Reduced accumulation of organic material in wetlands at this time, especially in the larger BRL, is likely associated with regional climatic shifts (increasing climate variability and dry conditions) facilitated by the weakening of the SWWs, intensification of ENSO and increasing summer insolation, which increased seasonality (Fletcher and Moreno 2012; McGlone et al. 1992; Fig. 3).

Salinity changes related to climate change (precipitation/evaporation changes) during the lateglacial and Holocene may partly explain the observed changes in wetland floristic composition and richness on truwana/CBI. Precipitation to evaporation ratio was low during the lateglacial and mid-late Holocene (Wilkins et al., 2013; Mackenzie and Moss, 2017), and the abundance of *Myriophyllum* in BRL, tECL and GL suggests the prevalence of moderately saline-brackish (oligohaline) conditions during periods of reduced effective precipitation may have contributed to high floristic richness in wetlands between ~14,000 and 12,000 cal yr BP and between ~6000 and 2000 cal yr BP (Harris and Kitchener, 2005; Kirkpatrick and Harwood, 1983; Sharpe and Baldwin, 2009; Engels and Jensen, 2009). In contrast, declining wetland floristic richness in the last ~2000 years may be associated with extreme levels of salinity in response to drier conditions associated with major declines in effective precipitation during the late Holocene (Herbert et al., 2012; McGlone et al. 1992), as presently seen in southeast Australian wetlands (Goodman, 2002; Hart et al., 1990). This drying trend is most evident in tECL, which sees an expansion in drought-tolerant *Myriophyllum muelleri* (Threatened species section 2020) over the last ~1500 years. On the other hand, extremely low wetland salinity is indicated by the abundance of *Isoetes* (Hart et al. 1991) in BRL between ~12,000 and 9000 cal yr BP under a much wetter climate (precipitation>evaporation; Wilkins et al., 2013). This may have also contributed to the low wetland floristic richness during this period (Fig. 6a and b; Engels and Jensen, 2009).

5.5.2. The roles of fire and Indigenous land use in wetland changes on truwana/CBI

Fire

The role of fire has been found to vary in different wetlands and can alter wetland nutrient states, hydrology, and floristic composition (Kotze 2013; Stewart et al., 2020; Moss et al., 2016). High fire activity can remove wetland nutrients (nitrates), especially in granitic landscapes, as well as driving loss of floristic richness on a long-term basis (Whitlow 1985; Salvia et al. 2012). Changes in wetland fire regimes can also alter wetland vegetation density, with frequent burning preventing woody vegetation thickening, especially in mires and infrequent burning promoting woody thickening (Moss et al., 2016; Stewart et al., 2020). Frequent wetland burning (reduced vegetation cover) can also increase freshwater flow in wetlands (Diaz et al. 2007; McGlone 2009; Woodward et al. 2014; McWethy et al. 2017).

The island of truwana/CBI is typical of a granitic landscape and macroscopic charcoal particles (especially particles $>250\text{ }\mu\text{m}$) recorded in the wetlands most likely include charcoal produced in-situ after wetland fires (Whitlock and Larsen, 2001). Notable is the period of abundant macroscopic charcoal particles (high wetland fire activity) in BRL (13,000–9000 cal yr BP) and tECL (~7000–5000 cal yr BP), which corresponds with when wetland floristic richness was lowest (Fig. 3). In contrast, low–moderate wetland fires (reduced macroscopic charcoal particles) evident during other intervals may have promoted nutrient accumulation and availability in wetlands, increasing floristic richness, a similar pattern to that recorded for terrestrial vegetation on the island (Adeleye et al. 2021a and b).

As mentioned earlier, changes in surrounding terrestrial vegetation cover in response to climatic changes may have modulated terrigenous input in wetlands by limiting or facilitating erosional soil deposition (Ellison et al., 2012). Even so, localized changes in wetland vegetation cover associated with wetland fire regime changes may have influenced freshwater flow/distribution pattern within wetlands. Surface water flow in wetlands tends to be more active (fast) in the absence of dense vegetation and less active (slow) with increasing wetland vegetation density (He et al., 2010). Reduced wetland vegetation cover due to high wetland fire activity may have increased the rate of freshwater distribution, which would have been particularly important in a large wetland like BRL. Conversely, increased vegetation density (sedgeland, herbland, rushland intrusion) due to insufficient/infrequent fires may have reduced freshwater distribution, contributing low wetland water levels.

Indigenous land use

Indigenous people have not only shaped the Australian terrestrial vegetation for millennia but have also contributed to the development of wetlands (Pyke et al. 2018). Indigenous people used wetlands, especially for cultural and subsistence purposes (Head, 1987; Pyke et al. 2018). Plant growth in wetlands was physically controlled by cutting/uprooting/harvesting or by the use of small fires, in order to promote open, clear, and drinkable freshwater in wetlands (Pyke et al. 2018).

The archaeological record of human occupation in Bass Strait suggests human population density was pronounced during the early Holocene and reduced from ~5000 cal yr BP due to sea-level encroachment on the islands (Sim, 1998). The early Holocene timing of major human occupation is consistent with the period (~13,000–8000 cal yr BP) of abundant coprophilous fungal spores (*Sordaria*, *Podospora* and *Sporormiella*) in BRL (Fig. 3). Coprophilous fungal spores have been related to the presence of large herbivores and human land use in previous paleoenvironmental studies (e.g., van Geel and Aptroot, 2006; Davis and shafer, 2006; Menozzi et al., 2010; Kiage et al., 2019; Fesser and O'Connell, 2010; Montoya et al., 2011). In addition to the generally wet productive environment that prevailed during the early Holocene, abundant coprophilous fungal spores in BRL may also reflect the contributing role of Indigenous land management to promote grazing large herbivores (e.g., kangaroo, wallaby) for hunting on truwana/CBI. High fire activity and inferred high water levels in BRL record between ~13,000 and 9000 cal yr BP, may partly reflect the frequent fire usage by Indigenous peoples on truwana/CBI to control wetland vegetation density in order to increase freshwater availability and other freshwater resources (McWelthy et al., 2017). Reduced fire usage later in the Holocene may have partly contributed to increased wetland vegetation density and wetland dryness, especially over the last 5000 years (Fig. 3), a land-use change–wetland development pattern also seen in northeast and southeast Australia (Moss et al., 2016; Hamilton and Penny, 2015).

5.5.3. Wetland management and conservation on truwana/CBI

The knowledge of long-term ecosystem changes is becoming critical under the currently changing climate, fire regimes and anthropogenic land use. Understanding ecosystem response to these changes on centurial–millennia scales using palaeoecological data is key to building reliable baselines for future management and conservation goals (Willis et al. 2010; Gillson and Marchant 2014; Wingard et al. 2017; Słowiński et al. 2019; Barr et al., 2013). The lack of knowledge on long-term changes in wetland hydrology and floristic composition, as well as the long-term role of fire regimes, currently hampers wetland management and monitoring plans on truwana/CBI (DAWE, 2012). Our palaeoecological data offer new insights into this critical knowledge gap. Based on our results, we highlight some recommendations to help monitor and preserve wetlands on truwana/CBI.

Our results suggest regional climatic changes governed changes in wetlands on truwana/CBI in the past. However, local factors, such as changes in fire regimes and vegetation (terrestrial and wetland) cover, as well as changes in salinity, also contributed to wetland dynamics. The observed changes in wetland floristic richness in response to fire and salinity suggest controlled fires may be used to manage wetland floristic richness on the island, and salinity monitoring may be incorporated into monitoring plan to help track potential changes in wetland floristic richness. Even so, these management strategies will benefit from additional studies targeted at understanding how wetland nutrients and different wetland plant species respond to varying levels of fire intensity and frequency, as well as varying salinity levels on truwana/CBI.

In addition, the observed pattern of wetland water-level changes and changes in terrestrial vegetation cover in the past may indicate a positive link between the former and latter, i.e., high woody vegetation cover around wetlands promotes high wetland water levels and vice versa (Ellison et al., 2012). However, studying the different contributions of terrigenous/allochthonous and autochthonous processes/activities to wetland sedimentation is important in order to understand whether buffering vegetation has the capacity to reduce erosional inputs and thus, promoting wetlands' persistence or whether dense woody vegetation draws down the water table locally, exposing the wetland sediments to desiccation during dry periods. This is especially critical for wetlands (e.g., tECL; Fig. 1d) that are currently drying out on the island and that are critical stop-offs for migratory birds and habitats for other flora and fauna species, including rare and threatened species (DAWE 2012). Though wetlands on truwana/CBI have been mostly dry at least over the last 5000 years, primarily in response to a drier climate, high wetland water levels during the period of intensive Indigenous land management may also reflect the important role of managed wetland burning in maintaining wetland hydrology on the island.

Myriophyllum muelleri is currently listed as a rare and threatened species on truwana/CBI and wider Tasmanian region (Threatened Species List 2021; DAWE 2012), and the pollen is readily distinguishable from other *Myriophyllum* species due to the higher number of pores (>10) compared to other species, which have 3–6 pores. The low abundance of the plant species compared to other *Myriophyllum* species in tECL before ~1700 cal yr BP suggests it is less competitive in brackish or freshwater wetlands with relatively high water levels. The abundance of *M. muelleri* and decline in other *Myriophyllum* species after ~1700 cal yr BP suggest *M. muelleri* is highly competitive at low-water levels or/and in ephemeral saline

wetlands, and these conditions may prove critical for its survival in tECL, a key Ramsar site on truwana/CBI. This may also be the case with *Wilsonia*, which increased in tECL in the last ~1000 years. *Wilsonia* species are also currently listed as rare and threatened across Tasmania (Threatened Species List 2021; DAWE 2012; Fig. 2a). Therefore, long-term monitoring of tECL's salinity and water-level changes may help in the early detection of potential population declines among these species. Introducing these species to other brackish wetlands on truwana/CBI, especially on the east coast, may also help increase their population on the island and Tasmania in general, reducing their risk of extirpation.

Finally, BRL is the largest wetland on truwana/CBI (widest diameter ~1 km), but not currently listed as a Ramsar wetland due to its inland location, relatively easy accessibility (human disturbance), and other Ramsar criteria highlighted in DAWE (2012). The wetland has about 2-m accumulated peat, which is the deepest peat deposit identified on the island and likely a major carbon sink. High accumulation of peat/organic material in BRL during the early Holocene is consistent with the timing of maximum carbon accumulation in global peatlands, especially Northern peatlands during the Holocene (Yu 2011; Yu et al. 2010; Gallego-Sala et al., 2018; Fig. 3). Additional study with proper quantification of carbon contents and accumulation rates in BRL will provide a better understanding of the wetland's carbon-storage capacity, indicating another potential conservation benefit.

5.6. Conclusion

This study provides insights into long-term changes in wetland hydrology and floristic richness, as well as the role of fire regimes in wetlands of the Bass Strait islands, southeast Australia. Our palaeoecological data suggest that a combination of climate-driven changes (e.g., precipitation) and local factors, such as changes in fire regimes and vegetation (terrestrial and wetland) cover, controlled past changes in water levels, salinity, and ultimately floristic richness in wetlands on truwana/CBI. High wetland floristic richness was maintained in wetlands under moderately saline–brackish conditions and moderate fire activity, while wetland floristic richness was reduced under extremely high or low salinities and high fire activity. Long-term monitoring of water levels and wetland salinity is recommended for tracking changes in wetland floristic richness, while carefully considered fire management options, including Indigenous cultural burning practices, may also be used to manage these important habitats.

Chapter 6 LONG-TERM DRIVERS OF VEGETATION TURNOVER IN SOUTHERN HEMISPHERE TEMPERATE ECOSYSTEMS

While previous chapters have focused more on the Bass Strait area, this chapter places those findings into their regional context by conducting a meta-analysis of overall past ecosystem changes in southeast Australia (including Bass Strait), with a focus on the late glacial and Holocene period. The drivers of vegetation and floristic richness changes are assessed, using a robust quantitative approach. This approach includes an empirical definition of significant vegetation turnover and validation of pollen as a proxy for vegetation and floristic richness for the first time in Southern Hemisphere ecosystems.

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with
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I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

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6.0. Long-term drivers of vegetation turnover in Southern Hemisphere temperate ecosystems

Abstract

Knowledge of the drivers of ecosystem changes in the past is key to understanding present ecosystem responses to changes in climate, fire regimes and anthropogenic impacts. Northern Hemisphere-focussed studies suggest that climate and human activities drove turnover during the Holocene in temperate ecosystems. Various drivers have been invoked to explain changes in Southern Hemisphere temperate vegetation, but the region lacks a quantitative assessment of these drivers. To better understand the regional drivers of past diversity, a quantitative meta-analysis study of turnover and richness during the lateglacial and Holocene in Australian temperate ecosystems is presented here. A meta-analysis study of 24 fossil pollen records across southeast Australian temperate ecosystems was conducted and an empirical turnover threshold was applied to fossil records to identify periods of major turnover for the first time in Australia. Pollen richness was also tested as a proxy for vegetation richness to estimate past richness and this was applied to fossil pollen data. The resulting reconstructions were compared to independent records of climate, sea-level change and fire through generalised linear modelling. Results show changes in available moisture and sea level drove turnover and richness in most parts of SE Australia in the past, explaining up to ~97% deviance. However, fire mainly drove turnover in Bass Strait. Richness reconstructions in this study also support the Intermediate Disturbance Hypothesis, suggesting that high biodiversity was partially maintained by anthropogenic-managed fire regimes. While temperature change is considered key to Northern Hemisphere palaeodiversity, past turnover and richness in Southern Hemisphere temperate ecosystems responded mainly to moisture availability and sea-level change (considering its role in modulating regional oceanic climate).

6.1. Introduction

Temperate ecosystems harbour many of the world's largest biodiversity hotspots and carbon sinks (Forseth, 2010; Dean and Wardell-Johnson, 2010), but are also the most disturbed by human activities (Heath et al., 1993). These ecosystems are dependent on

cool winter temperatures and are sensitive to climatic shifts (Kreyling, 2010; Giesecke et al., 2017). Numerous quantitative regional studies have shown that temperature change was the major regional driver of ecosystem turnover (magnitude of change through time) during the Holocene in the Northern Hemisphere temperate ecosystems (e.g., Seddon et al., 2015; Overpeck et al., 1985; Stivrins et al., 2016), but recent research from the Mediterranean region argues that humans were the major driver of Holocene turnover (Connor et al., 2019). Studies targeted at understanding the drivers of regional ecosystem turnover are hitherto lacking in Southern Hemisphere temperate ecosystems. Quantitatively assessing the rates of long-term regional vegetation turnover and richness, as well as their respective drivers in Australian ecosystems will provide insights into the regional dynamics, degree of resilience/stability and potential for future changes in these ecosystems.

Southern Hemisphere temperate ecosystems are different from the Northern Hemisphere counterparts. Species pools (composition) are vastly different due to the Gondwanan heritage of Southern Hemisphere ecosystems, as well as a climate marked by greater oceanic influence and the limited extent of glaciation during the Last Glacial Maximum compared to the Northern Hemisphere (Markgraf et al., 1995). This explains why the floristic physiognomy (especially of rainforests) in temperate Australia, New Zealand and southern South America is similar (McGlone et al., 2016). Southern Australia is characterized by temperate forest ecosystems dominated by *Eucalyptus* and *Nothofagus* s.l. (Keith, 2017). These temperate ecosystems are resilient and resistant to fires to a large extent (Knox and Clarke, 2012). However, recurrent large fires and a rapidly changing climate are transforming sclerophyllous temperate forests to the point where these ecosystems risk tipping into a new state (Laurance et al., 2011; Fairman et al., 2016).

Australian palaeoecological studies have mostly attributed Holocene vegetation changes in Australia's temperate ecosystems to fire and climate, while anthropogenic impact accelerated since British colonisation in the late 18th century (e.g., Black et al., 2006, 2007; McWethy et al., 2017). On the 'island continent', the sea also modulates regional temperature and moisture, especially in areas with an oceanic climate (Australian Bureau of Meteorology – ABM, 2018). Past sea-level changes are thought to have affected vegetation development in coastal areas, especially on the small islands in Bass Strait during the sea-level transgression around 8000 years ago (Thomas and Kirkpatrick, 1996; McWethy et al., 2017). However, no study has quantitatively assessed the above-mentioned patterns on a regional scale for Australia, even though pollen records elsewhere have proven to be useful

in quantitatively estimating long-term vegetation turnover and richness, especially on a regional scale (e.g., Seddon et al., 2015; Connor et al., 2019; Jacobson et al., 1986; Shuman et al., 2005).

The dynamics of ecosystem floristic richness is largely dependent on interactions between plant functional traits and disturbance regimes (e.g., Dornelas et al., 2014; Vellend et al., 2013). Disturbance can both promote or reduce richness, depending on the ecosystem type and magnitude and nature of disturbance (e.g., Biswas and Mallik, 2010; He et al., 2019). For example, fire may promote richness in fire-adapted woodlands and heathlands through enhanced seed germination, while fire may drive extirpation in fire-sensitive rainforests (Gill, 1996). The idea of disturbance promoting richness is encapsulated in the Intermediate Disturbance Hypothesis (IDH) which theorises that: (1) disturbance significantly affects species richness, (2) competitive exclusion is driven by interspecific competition, and (3) moderate disturbance suppresses interspecific competition (Wilkinson, 1999; Kricher, 2011; Catford et al., 2012). While richness change has been mainly driven by human activity during the Holocene in the Northern Hemisphere's temperate and Mediterranean ecosystems (Giesecke et al., 2017), research into the past richness/diversity dynamics of Australia's temperate ecosystems is lacking. In Australia, diversity was thought to have been promoted by moderate burning by humans in the past (Bowman, 1998; Bird et al., 2016a); however, few studies have directly and quantitatively addressed the role of fire in promoting ecosystem richness/diversity during the Holocene in Australia (Thomas et al., 2001; McWethy et al., 2013).

This study presents a meta-analysis that assesses the drivers and timing of past turnover and richness change in temperate Southern Australia, using a quantitative approach. The SE Australian regions included in this study include the SE mainland (continent), Bass Strait islands (an archipelago, formerly a land bridge) and Tasmanian mainland (continental island, formerly connected to the mainland) (Fig. 1). It is hypothesised that: (1) sea-level change may have driven vegetation turnover and changes in richness during the Holocene in addition to climate and anthropogenic land-use/fire, and (2) intermediate levels of fire (biomass burned) likely promoted floristic richness in the past. To test these hypotheses, palynological richness and rates of vegetation change were estimated using fossil pollen records across SE Australia. Objective measures of turnover and richness were developed by adopting an empirical turnover threshold to identify the timing of major vegetation

turnover and by verifying palynological richness as a proxy for plant species richness. Generalised linear models were used to compare the reconstructions to independent records of fire, climate and sea-level changes to identify possible drivers of regional vegetation turnover and richness during the lateglacial (~13,000–11,700 years ago) and Holocene (the last 11,700 years) in SE Australia.

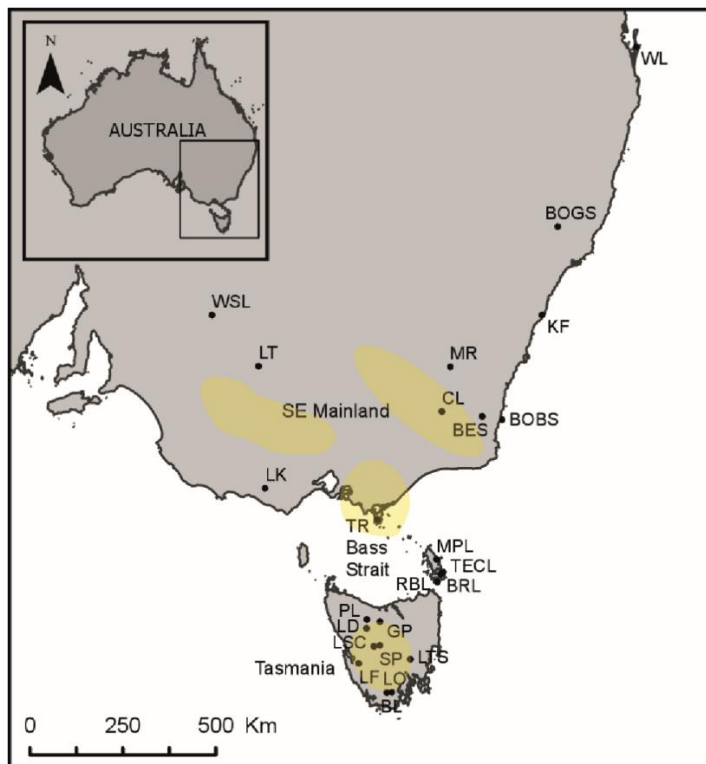


Figure 1: Map showing site location of temporal and spatial data used in this study. Black dots represent sites of fossil pollen records on the mainland, Bass Strait islands and Tasmania. Key to site codes is included in Table S1 in Appendix S5. Yellow shading indicates area where modern vegetation survey and surface pollen were sampled on the mainland and Tasmania (Mariani et al., 2016b).

6.2. Southeast Australian vegetation and climate

Australia's vegetation follows a precipitation gradient, ranging from wet to dry landscapes characterized by forests and non-forest vegetation types (Keith, 2017). The vegetation of the SE Australian mainland is characterized by *Eucalyptus* open forests and woodlands, as well as mallee shrublands. The central to eastern part of Tasmania is dominated by *Eucalyptus* open forests and open woodlands, while the western to southern part is

characterized by cool temperate rainforests, wet sclerophyll forests and moorland (Keith, 2017). The Bass Strait islands' vegetation is characterized primarily by myrtaceous heaths and related scrub, with very little rainforest (Harris and Kitchener, 2005). A large part of the Australian mainland has been transformed into grazing pasture and dryland cropping, as have widespread areas in the central eastern parts of Tasmania. In Bass Strait, however, only King and Flinders Islands have been largely modified into grazing pastures (Department of Agriculture, 2018).

The climate of the southern Australian mainland is controlled by strong Southern Westerly Winds (SWW) during winter, bringing high rainfall, while an anticyclonic influence comes into play during summer, causing dry summers (ABM, 2019). The El Niño Southern Oscillation (ENSO) also drives interannual climatic variability on the SE mainland and in NE Tasmania (Mariani et al., 2016a; Risbey et al., 2009). In contrast, high rainfall in southern to western Tasmania is generally driven by the Pacific–South American mode and SWW (Mariani and Fletcher, 2016; Hill et al., 2009; ABM, 2019; Risbey et al., 2009).

6.3. Methods

6.3.1. Data selection

Pollen records from 117 sites across SE Australia were considered for this study. From these, strict criteria were used to select 24 sites ranging between 1 and 1955 m asl, which include the SE mainland (11 sites), Tasmania (9 sites) and the Bass Strait islands (4 sites; Fig. 1; see Table S1 in Appendix S5 for list of sites and site details). Site selection was made based on at least one pollen sample every 500 years and at least one radiocarbon date every 3000 years. Most pollen data were obtained from a SE Australian pollen database (Herbert and Harrison, 2016), some by contacting individual analysts, and five sites from the Neotoma Paleoecology Database (<http://www.neotomadb.org/>). Four unpublished records were also used with permission, due to the scarcity of high-resolution pollen records.

Overall, 14 sites were used spanning the last 13,000 years, while the remaining 10 sites span the last 9000 years. *Pinus*, introduced to Australia in the 19th century, was used as a dating marker for seven sites by assigning a date of 150 cal yr BP to the first appearance of *Pinus* pollen in the records. The age-depth model for one of the sites (Middle Patriarch

Lagoon – MPL) from the Bass Strait islands was corrected by re-running a Bacon age-depth model (Blauuw and Christen, 2011), using *Pinus* as a marker for ~150 cal yr BP (see Table S2 in Appendix S5 for new age-depth model and age estimates).

6.3.2. Composite charcoal analysis

In order to compare turnover and richness results with an independent record of regional fire activity, 61 and 13 charcoal accumulation datasets from different sites in SE mainland and Tasmania were selected from the Global Paleofire Database, respectively (<https://paleofire.org/index.php>). Four charcoal records (not from the Global Paleofire Database) were added from the Bass Strait region (Adeleye et al., 2021c.; Hopf et al., in prep.). Composite z-scores were then calculated for each region using the ‘paleofire’ package in R (Blarquez et al., 2014b; R Core Team, 2020).

6.3.3. Numerical analysis - turnover

To estimate the rate of vegetation turnover through time at each site, a rate-of-change analysis was conducted, using the Squared Chord Distance (SCD) dissimilarity metric (Overpeck et al., 1985; Seddon et al., 2015; Connor et al., 2019). There are many metrics that can be used to estimate rates-of-change, however the SCD metric has been proven to be the most suitable for palynological data due to its better handling of the signal-noise effect (Overpeck et al., 1985). ‘Rates-of-change’, ‘compositional change’ and ‘temporal turnover’ are often used interchangeably in the literature, as they can all be interpreted from the SCD of fossil pollen spectra; however, the term ‘turnover’ is used in this study to refer to these. After calculating fossil pollen percentages, a binning approach (Connor et al., 2019, after Seddon et al. 2015) was chosen over interpolation due to the risk of artefacts created by interpolation (Birks, 2012). The binning approach involves dividing pollen records from each site into time bins, selecting random samples from adjacent bins, calculating the inter-sample SCD, then repeating this random selection 50 times to obtain an average bin-to-bin SCD score. A bin width of 1000 years was used due to the low dating resolution of most available records. Spores and aquatic/wetland taxa were excluded from the pollen sum. An alternative dissimilarity metric known as Hellinger transformation with Euclidean distance was also tested (Plumpton et al., 2019) for comparison with SCD results.

In order to determine an empirical SCD threshold for significant change in SE Australian vegetation, surface pollen rain and modern vegetation survey data from different sites on the mainland and Tasmania were obtained (Fig. 1). For Tasmania, samples were collected from 27 sites (see Mariani et al., 2016b for more information and sampling methods). Using the same approach, 25 sites were included from the SE Mainland, with 11 sites from the Alpine National Park, 4 sites from Wilson's Promontory National Park and 10 sites from Grampians National Park (Mariani et al., submitted).

SCDs were calculated between modern samples in the two regions and SCDs of vegetation and corresponding pollen data were then compared using a Mantel dissimilarity test (Legendre and Legendre, 2012) to determine whether dissimilarity in vegetation translated into dissimilarity in pollen assemblages. This step was repeated using distance-weighted plant abundance of target taxa, which is the product of each taxon's cover and respective weighting factor (weighted with Lagrangian Stochastic pollen-dispersal model) to verify relationships between modern pollen and vegetation (see Mariani et al., 2016b for details on calculating distance-weighted plant abundance). A numerical SCD threshold was then set based on modern pollen and vegetation SCDs, using the analogue matching technique and a dissimilarity score greater than the 5th percentile was selected as the cut-off for significant dissimilar vegetation groups, i.e. an indicator of ecosystem turnover (Plumpton et al., 2019; Simpson, 2007). Mainland and Tasmanian vegetation were also grouped by SCD, using Ward's clustering method, with similar and dissimilar vegetation groups separated in line with the SCD threshold. Similar assessments of thresholds have been done in the Northern Hemisphere (e.g., Overpeck et al., 1985; Huntley, 1990; Davis et al., 2015).

6.3.4. Numerical analysis - richness

To estimate palaeo-richness for each site, a rarefaction analysis was conducted by randomly resampling each pollen sample (1000 times) to the minimum pollen sum from each pollen record (excluding introduced species). Random resampling reduces the bias effect of pollen taxa with high counts over taxa with low counts (Felde et al., 2016). For this study, pollen richness is taken to reflect floristic richness at a site, though there are complexities surrounding the use of pollen spectra in estimating vegetation richness. These complexities include differential pollen production, dispersal and preservation, as well as pollen taxonomic resolution (Birks et al., 2016). Despite these complexities, pollen records

have proven useful in reconstructing past floristic richness (Giesecke et al., 2017). To verify palynological richness as a proxy of richness in Australian vegetation, plant richness in modern vegetation was compared to surface pollen richness from SE Australia.

6.3.5. Modelling

In order to identify major drivers of turnover and richness, Generalized Linear Modelling (GLM), with Gaussian distribution was applied, with each potential driver (fire, ENSO, temperature, sea level and precipitation:evaporation) as a predictor of vegetation turnover and changes in richness. The effect of temporal autocorrelation was removed by resampling each variable at a lower resolution and re-running each model 1000 times (bootstrapping) (Mellin et al., 2010). All variables were initially included as predictors of turnover and richness, and significant variables were selected for final GLMs using a stepwise variable selection procedure. Corrected Akaike's information criterion (AICc) and delta AICc ($\Delta AICc$) were then used to rank final models, with additional consideration given to the amount of deviance explained by each variable. All data analyses in this study were done in R (R core team, 2020) using the 'vegan', 'analogue', 'TSA', 'stats', 'EnvStats', 'mgcv' and 'MASS' packages (Oksanen et al. 2007; Simpson, 2007; Cryer and Chan, 2012; Millard, 2013; Ripley et al., 2020; Wood, 2020). Composite charcoal results was used as a proxy for fire, sedimentation record of Laguna Pallcacocha lake as a proxy for ENSO events (Moy et al., 2002), EPICA Dome C Antarctic deuterium record as a proxy for temperature (Stenni et al., 2001), precipitation:evaporation reconstruction from southwestern Victoria as a proxy for SWW-driven moisture availability (Wilkins et al., 2014) and biological indicator-based reconstructed sea levels for SE Australia as a proxy for sea-level change (Sloss et al., 2007).

Generalized Additive Modelling (GAM) with non-linear effect was applied to assess the Intermediate Disturbance Hypothesis in SE Australia, using charcoal composite (fire disturbance) and reconstructed palynological richness. Considering that pollen production may have differed under glacial climates (Mariani et al. 2016b), only Holocene samples were used for this assessment.

6.4. Results

6.4.1. Squared Chord Distance (SCD) threshold assessment

SCD and Hellinger transformation results were similar ($r = 0.9$), therefore only the former is presented (see Fig. S4a–S4c in Appendix S5 for examples of SCD versus Hellinger transformation results). Results show a significant positive correlation (based on Mantel test) between Tasmania's ($r = 0.4$, $p < 0.01$) and the mainland's ($r = 0.6$, $p < 0.01$) modern vegetation survey SCD and surface pollen rain SCD, which means sites with similar vegetation tend to have similar pollen assemblages (Fig. 2a–b). Distance-weighted plant abundance results were similar to those of the unweighted vegetation data (Fig. 2c–d). After applying Ward's clustering method, the sites with the most similar vegetation had a pollen assemblage SCD value ranging from 0–0.4 in both regions, while SCD values for the most dissimilar sites mainly ranged from 0.1–1.0 (Fig. 3). Specifically, SCDs within *Eucalyptus* forests ranged from 0.15–0.3, however Tasmanian *Nothofagus* rainforest ranged between 0.3 and 0.8 (see Fig. S2 in Appendix S5).

Analogue analysis produced a dissimilarity threshold (5th percentile) of 0.143 for the mainland and 0.259 for Tasmania (Table 1). To obtain a single representative regional analogue threshold for SE Australia comparable to regional studies from the Northern Hemisphere, the analogue thresholds for the mainland and Tasmania were averaged, yielding a final threshold value of 0.2. Results also show a positive relationship between pollen and plant richness ($r = 0.33$, $p < 0.05$), and excluding high elevation sites across the region, as suggested by Felde et al. (2016), further improved the relationship ($r = 0.53$, $p < 0.05$) (Fig. 3).

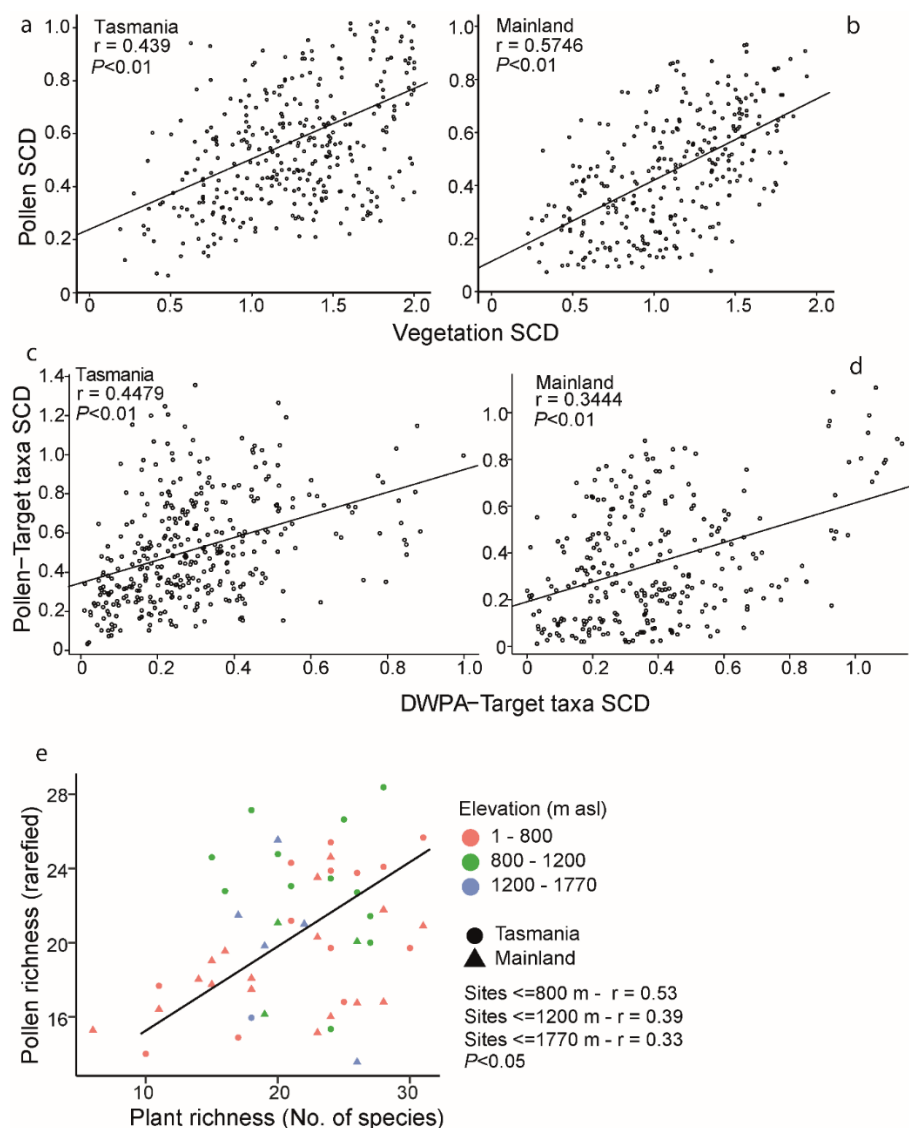


Figure 2: Scatter plot showing positive relationship (based on Mantel test) between dissimilarities of modern vegetation and surface pollen in SE mainland and Tasmania (a–b), and similar pattern is observed using distance-weighted plant abundance (DWPA) of major vegetation and pollen taxa (c–d). Richness comparison (e) between plants and pollen using all samples from mainland and Tasmania, showing relationship distribution along elevation gradients. Regression line shows best relationship ($r=0.53$) with the removal of high-elevation sites >800 m asl (following Felde et al. 2016).

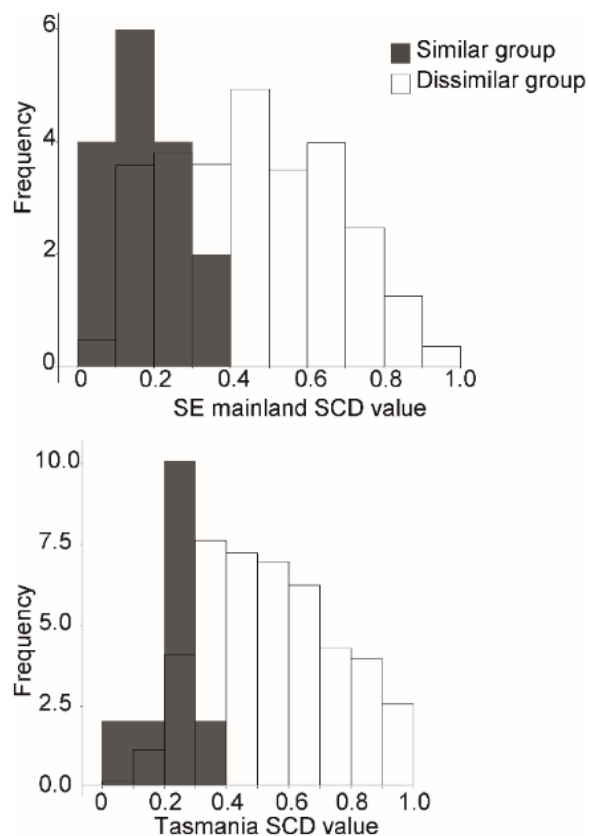


Figure 3: Histogram showing Squared Chord Distances (SCDs) of similar and dissimilar vegetation groups/sites on the SE mainland and Tasmania, used in developing the empirical turnover threshold. In general, similar vegetation types (grey) have an SCD < 0.3, while most dissimilar vegetation groups/sites are above SCD > 0.3. The empirical threshold of 0.2 SCD indicates significant vegetation turnover in pollen assemblages (Table 1).

Table 1: Percentiles of the squared chord dissimilarities for the mainland and Tasmania training set after analogue matching. SCD scores above 5% reflect dissimilar vegetation (Simpson, 2007). Averaged threshold (5%) of both regions represents SCD threshold for SE Australia.

	1%	2%	5%	10%	20%
SE Mainland	0.104	0.109	0.143	0.192	0.268
Tasmania	0.162	0.208	0.259	0.327	0.405
Average threshold	0.201				

6.4.2. Generalized Linear Models (GLM)

For Bass Strait, only fire was significantly ($p < 0.05$) related to turnover during variable selection. Only sea-level change was significant for richness. Hence, fire and sea-level change are taken as the major drivers of Holocene turnover and richness in the region, respectively (Table 2a).

For the mainland, precipitation:evaporation, sea-level change and ENSO were significantly ($p < 0.05$) related to turnover. A combination of these variables best predicted turnover ($AICc=186$, $dAICc=0$, $Rm=50$, Deviance=71%). For richness, a combination of precipitation:evaporation, sea-level change, temperature, and fire most significantly ($p < 0.05$) predict richness ($AICc=61$, $dAICc=0$, $Rm=91$, Deviance=96%) on the mainland. Of these variables, fire appears to be less important, considering the similar deviance explained (95%) by models 2–4 (Table 2a and b).

For Tasmania, a combination of precipitation:evaporation, sea-level change, temperature, and ENSO best predicted turnover ($AICc=141$, $dAICc=0$, $Rm=93$, Deviance=96%). ENSO appears to be the least important variable, considering the similar deviance explained (97%) by model 2 (Table 2). Richness in Tasmania is best predicted by a combination of sea-level change, temperature and ENSO ($AICc=95$, $dAICc=0$, $Rm=49$, Deviance=63%).

Table 2a: Summary GLMs for the selection of significant predictors of turnover (SCD) and richness in Bass Strait (BS), southeast mainland (SEM) and Tasmania (Tas).

	<i>Turnover (SCD)</i>				<i>Richness</i>		
	Variable	Std. Error	t value	Pr(> t)	Std. Error	t value	Pr(> t)
BS	<i>Fire</i>	2.33489	-4.331	5.74E-05*	0.25521	-1.771	0.0816
	<i>P:E</i>	1.79148	0.103	0.918	0.19582	-1.563	0.1233
	<i>Sea</i>	0.09587	0.276	0.7839	0.01048	-6.336	3.35E-08*
	<i>Temp</i>	0.17516	-1.775	0.0809	0.01915	-1.744	0.0863
	<i>ENSO</i>	0.16319	0.22	0.8267	0.01784	-1.812	0.075
SEM	<i>Fire</i>	2.07872	1.516	0.134648	0.340735	4.511	3.06E-05*
	<i>P:E</i>	0.76058	-3.204	0.002173*	0.124671	-4.768	1.22E-05*
	<i>Sea</i>	0.03703	3.545	0.000769*	0.00607	15.909	< 2E-16*
	<i>Temp</i>	0.07251	1.694	0.095512	0.011885	4.455	3.72E-05*
	<i>ENSO</i>	0.06799	2.97	0.004276*	0.011144	0.131	0.896
Tas	<i>Fire</i>	0.67282	0.608	0.545684	0.40109	-0.646	0.520714
	<i>P:E</i>	0.41441	4.292	6.56E-05*	0.24704	-0.967	0.337668
	<i>Sea</i>	0.02777	-12.654	< 2E-16*	0.01655	-2.517	0.014518*
	<i>Temp</i>	0.03488	-4.769	1.22E-05*	0.02079	-2.963	0.004361*
	<i>ENSO</i>	0.03497	2.145	0.035972*	0.02085	3.975	0.000192*

*Significant ($p < 0.05$) variables selected for GLMs in Table 2b.

Table 2b: GLMs relating vegetation turnover (SCD) and richness (Rich) as a function of significant predictors identified for southeast mainland (SEM) and Tasmania (Tas) in Table 2a, which included temperature (temp), ENSO, fire, precipitation:evaporation (P:E) and sea-level change (sea). Models are ranked based on Akaike's information criterion corrected for small sample sizes (AICc) and delta AICc. Also shown are percentage of deviance explained and marginal R^2 (Rm). For Bass Strait, only fire (sea-level change) was significantly ($p < 0.05$) related to turnover (richness) during variable selection in Table 2a. Therefore, fire and sea-level change are taken as the major drivers of turnover and richness in the region, respectively.

	Model	AICc	dAICc	Rm	%Deviance
BS	1 <i>SCD ~ Fire</i>	-	-	-	-
	1 <i>Rich ~ Sea</i>	-	-	-	-
SEM	1 <i>SCD ~ ENSO+P:E+Sea</i>	185.9702	0	49.6	70.6
	2 <i>SCD ~ ENSO+Sea</i>	186.6286	0.658	45.15	62.4
	3 <i>SCD ~ ENSO+P:E</i>	188.6671	2.697	42.2	52.5
	4 <i>SCD ~ Sea+P:E</i>	197.0497	11.079	28.34	63.1
	<i>Null</i>	205.2042	19.234	0	
	1 <i>Rich ~ Sea+Temp+P:E+Fire</i>	61.152	0	90.79	95.8
	2 <i>Rich ~ Sea+Temp+P:E</i>	69.40632	8.254	87.87	94.8
	3 <i>Rich ~ Sea+Temp</i>	69.78211	8.63	86.92	94.1
	4 <i>Rich ~ P:E+Sea</i>	75.81581	14.664	84.79	94.8
	5 <i>Rich ~ Fire+Sea</i>	81.52133	20.369	82.46	87
	6 <i>Rich ~ Fire+Temp</i>	121.4014	60.249	52.47	0
	7 <i>Rich ~ P:E+Temp</i>	129.9882	68.836	41.09	0
	8 <i>Rich ~ Fire+P:E</i>	137.1007	75.949	29.63	0
	<i>Null</i>	146.3388	85.187	0	
Tas	1 <i>SCD ~ Sea+Temp+P:E+ENSO</i>	141.0679	0	93.25	96.4
	2 <i>SCD ~ Sea+Temp+P:E</i>	145.0892	4.021	91.96	96.7
	3 <i>SCD ~ Sea+P:E</i>	150.2798	9.212	90.17	84.2
	4 <i>SCD ~ Sea+Temp</i>	153.851	12.783	89.23	92
	5 <i>SCD ~ ENSO+Sea</i>	164.5718	23.504	85.82	0
	6 <i>SCD ~ Temp+P:E</i>	219.5086	78.441	42.02	
	7 <i>SCD ~ ENSO+Temp</i>	221.9746	80.907	38.23	
	8 <i>SCD ~ ENSO+P:E</i>	235.4719	94.404	12.69	

<i>Null</i>	235.9219	94.854	0	
1 <i>Rich ~ Sea+Temp+ENSO</i>	94.76423	0	49.2	63.2
2 <i>Rich ~ ENSO+Sea</i>	96.20435	1.44	43.59	59.8
3 <i>Rich ~ Sea+Temp</i>	101.6355	6.871	35.16	0
4 <i>Rich ~ ENSO+Temp</i>	110.4195	15.655	18.78	57.3
<i>Null</i>	113.6897	18.925	0	

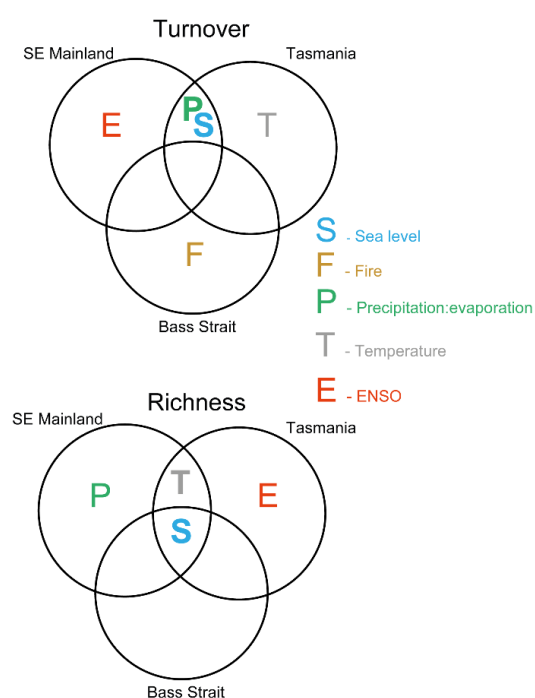


Figure 4a: Summary Venn diagrams showing major predictors of turnover and richness based on GLM results in Table 2b. Predictors in bold explain turnover and/or richness in more than one region.

6.4.3. Rates of vegetation turnover, changes in richness and fire activity

For the SE mainland, significant vegetation turnover occurred in the late Holocene (~4000–present cal yr BP) with average SCDs reaching 0.25. Rarefaction analysis shows richness increased during the lateglacial–early Holocene, remained relatively stable until ~7000 cal yr BP and gradually increased from ~7000 cal yr BP–present (Fig. 4b). Results also show low fire activity on the mainland from the lateglacial to mid-Holocene (~13,000–7000 yr BP) with z-scores below 0, while fire activity increased over the last ~7000 years with z-scores consistently above 0 (Fig. 4b).

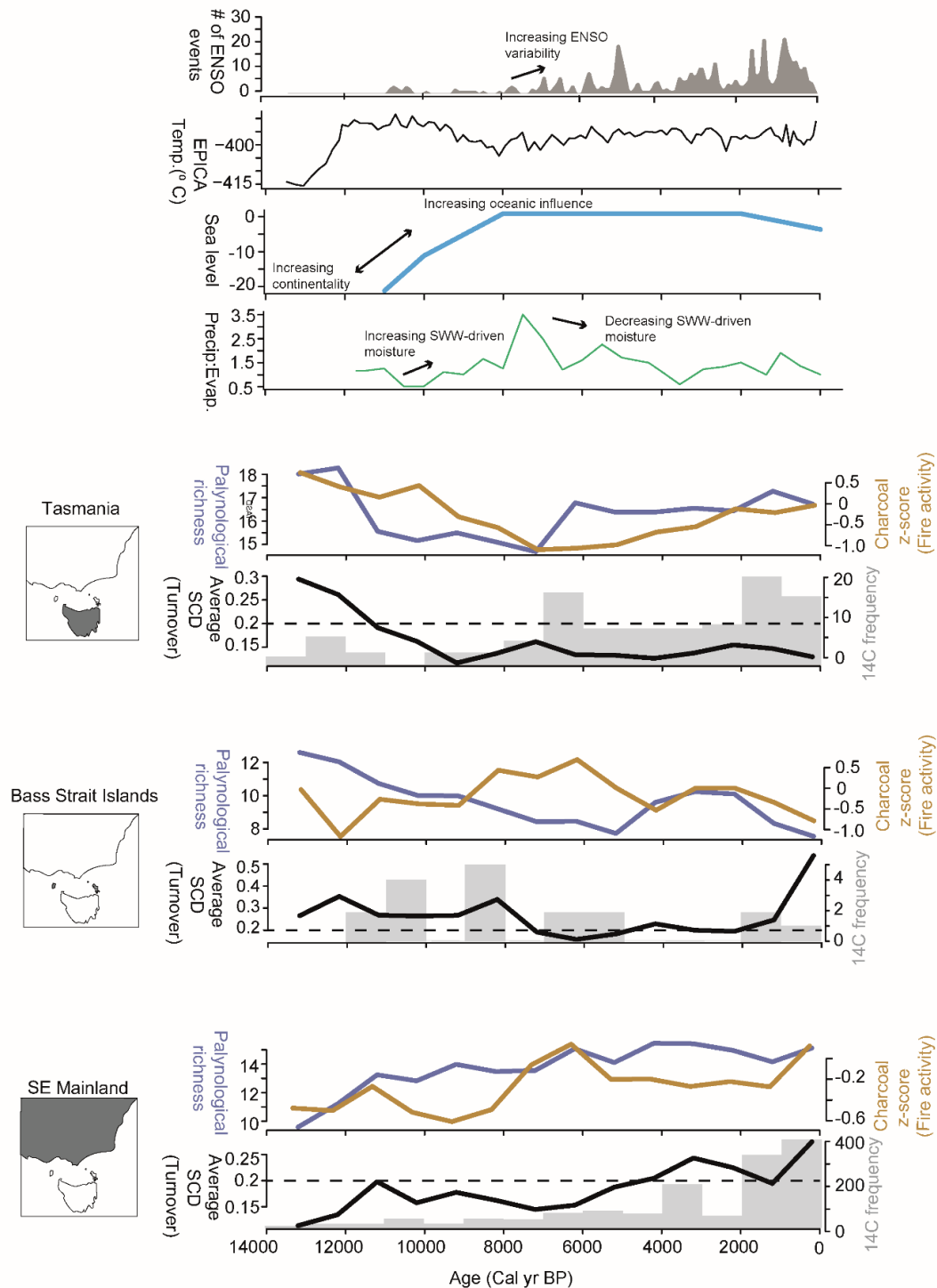


Figure 4b: Lateglacial and Holocene rates of turnover (black) and richness (purple) in SE Australia in relation to composite charcoal concentration z-score (yellow), number of El Niño Southern Oscillation (ENSO) events (Moy et al., 2002), precipitation:evaporation (available moisture)(Wilkins et al., 2013), relative Holocene sea levels of coastal SE Australia (Sloss et al., 2007), and EPICA Dome C temperature (Stenni et al., 2001). Grey histograms represent the number of radiocarbon dates from human occupation sites, drawn from the Australia Archaeology data base (Williams et al., 2014). Black dash line represents the empirical threshold (SCD > 0.2) for significant vegetation turnover. Each average SCD

point represents dissimilarity between adjacent time bins e.g., the average SCD point at ~1000 represents the dissimilarity between 500 and 1500 cal yr BP.

In Bass Strait, results show high rates of vegetation turnover from the lateglacial through the mid-Holocene with SCD values between 0.3 and 0.4 (~13,000–8000 cal yr BP), stabilizing during the mid- to late Holocene (~7000–1000 cal yr BP) with intermittent changes, as reflected in SCD values below 0.2. Turnover increased in the last ~1000 cal yr BP with a return to values >0.2. The highest richness is recorded during the lateglacial, after which it steadily decreased until ~5000 cal yr BP. Richness increased again from ~5000–2000 cal yr BP before finally decreasing during the last ~2000 years. Charcoal z-scores ranged between -1 and 0 from ~13,000 to 9000 cal yr BP, attained a maximum from ~8000 to 6000 cal yr BP with a maximum z-score of up to 0.5, then declined to below 0 for the last 2000 years (Fig. 4b).

In Tasmania, rate of vegetation turnover was highest during the lateglacial–early Holocene (~13,000–11,000 cal yr BP) with average SCDs of up to 0.3, attaining stability by ~10,000 cal yr BP and remaining stable (below threshold) throughout the rest of the Holocene. Richness was highest in the lateglacial–earliest Holocene and mid- to late Holocene (~7000 cal yr BP–present) and lowest from ~11,000–7000 cal yr BP. Tasmanian fire records show the highest fire activity during the lateglacial–early Holocene (~13,000–10,000 cal yr BP) with z-scores above 0, decreasing through the mid-Holocene (~10,000–6000 cal yr BP) and then gradually increasing from ~6000 yr cal BP–present (Fig. 4b). In addition, overall results in all regions show that a high–intermediate level of charcoal corresponds with high richness (Fig. 5).

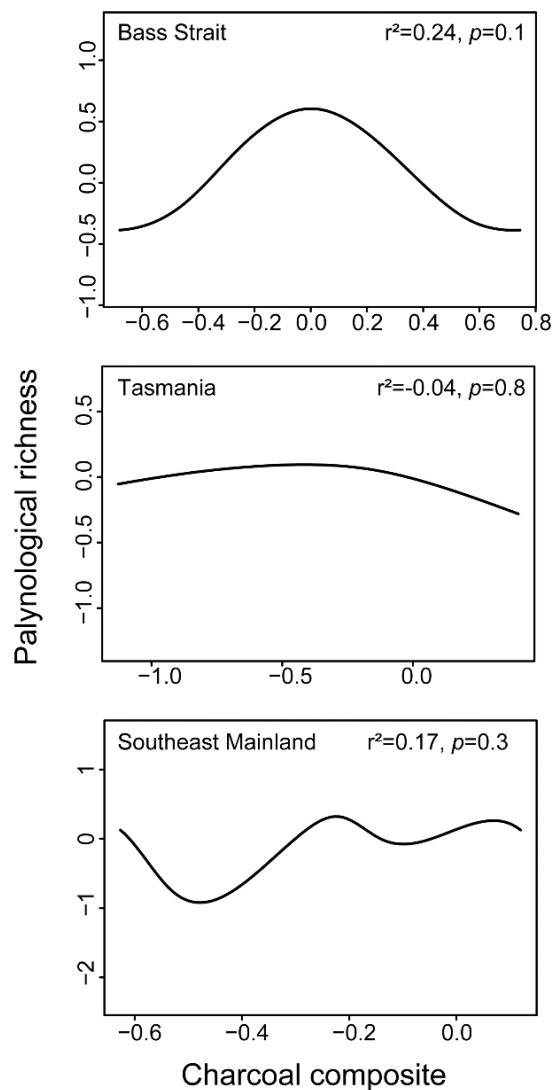


Figure 5: Testing the Intermediate Disturbance Hypothesis: Generalized Additive Model, showing relationships between charcoal composite (fire) and reconstructed richness in Bass Strait, Tasmania, and the southeast mainland.

6.5. Discussion

6.5.1. Richness metrics and potential sources of error

This study presents the first attempt to confirm and apply richness measures to Holocene pollen data in Australia. It is also shown that modern palynological richness has a positive relationship with floristic richness, especially in sites <800 m asl ($r = 0.53$, $p < 0.05$). Inclusion of sites >800 m asl weakened the relationship ($r=0.33$) but remained significant ($p < 0.05$). This increased disparity between modern floristic richness and palynological richness in sites >800 m asl may be due to the openness of the sites (dominated by e.g., heathland,

moorland) with increased extra-local pollen sources (Felde et al. 2016; Markgraf, 1980). Results from this study demonstrate a strong link between modern plant richness and pollen richness in SE Australia. This agrees with the findings of Meltsov et al. (2013) that, palynological richness better reflects floristic richness when a single climatic region is considered, with our study restricted to the SE Australian temperate zone. Limitations that surround the use of rarefied pollen assemblages to estimate floristic richness are acknowledged, especially pollen taxonomic precision and differential pollen production (Birks et al., 2016). These effects were minimized by ensuring consistency in taxonomic resolution of fossil and modern datasets as much as possible. Distance-weighted plant abundance was also used to verify the relationship between surface pollen and modern vegetation, which produced similar results to non-weighted plant abundance (Fig. 2c–d). However, the role of pollen productivity should be investigated in future studies. Also, the use of pollen counts for modern and fossil pollen rarefaction analysis may include potential effects of evenness (Odgaard, 1999; van der Knaap, 2009). While fossil pollen accumulation rates can help to reduce this bias, they tend to incur large errors from sediment accumulation rate estimation (van der Knaap, 2009) and cannot be derived for the modern moss samples used here.

Other potential sources of error in this study include the nature of fossil pollen sites (e.g., swamps, lagoon), the available high-resolution pollen records (e.g., Bass Strait has 4) and site distribution in terms of location and elevation (in Tasmania, mostly mid- to high elevation in western and central parts). These are unavoidable biases due to the scarcity of high-resolution pollen records in SE Australia.

6.5.2. Turnover metric (SCD) verification

The SCD threshold (0.2) verified in this study agrees with Northern Hemisphere studies (Overpeck et al., 1985; Davis et al., 2015). Turnover within *Eucalyptus* forests is low across space on the mainland and Tasmania, which is due to the relative homogeneity in *Eucalyptus* forest structure across SE Australia. Conversely, the relatively high turnover scores for *Nothofagus* rainforests are due to the floristic variety of rainforest communities (high beta diversity) in western Tasmania (Fig. S2 in Appendix S5). For example, several *Nothofagus*-dominated rainforest types were identified in the vegetation and surface pollen data, including *Nothofagus-Eucalyptus*, *Nothofagus-Phyllocladus*, *Nothofagus-Pomaderris*

and *Nothofagus-Eucryphia* associations. *Nothofagus* pollen is strongly over-represented, comprising up to 50% of total pollen even in non-arboreal vegetation and surpassing non-arboreal pollen like *Gymnoschoenus*, which in fact dominates non-arboreal vegetation (Mariani et al., 2016b; Fletcher and Thomas, 2010c; Macphail, 1979).

6.5.3. Drivers of turnover and richness in SE Australian temperate ecosystems

GLM results suggest all predictors contributed to past changes in turnover and richness to some degree across SE Australia. (Table 2b). However, precipitation:evaporation (SWW-driven moisture availability), sea-level change (oceanic influence) and temperature appear to have affected turnover and richness in most regions, considering the lesser contributions of fire and ENSO (Fig. 4a). Human influence is not included as a driver in the GLMs due to the patchiness of the archaeological records but is included in the discussion to infer past anthropogenic land-use and its influence on past turnover and richness. While the proxy records modelled are currently the best for the region, especially in terms of resolution, it is acknowledged that the nature and quality of some of the proxies used as drivers of turnover and richness may have potentially influenced the results of this study.

Turnover drivers: Moisture availability and sea-level change

Moisture availability and sea-level change mainly explained Holocene turnover in most parts of SE Australia, while fire was the major driver of turnover in Bass Strait (Fig. 4a). These drivers are discussed in the following sections.

Changes in SWW flow pattern contribute to precipitation:evaporation changes in temperate Australia and determine available soil moisture, which is critical for plant growth, seed production and seedling recruitment (Keith, 2017; Wilkins et al., 2014). The interactions between precipitation (rainfall) and local factors such as slope and aspect also determine vegetation structure, composition and distribution on a landscape scale (Keith 2017; Enright et al., 1994). Biomass wetness/dryness influences fire regimes by modifying the quantity of fuel available to burn (Bradstock 2010), though anthropogenic activities also control fire regimes, particularly ignitions (Keith, 2017). The fire regime feeds back onto vegetation structure and composition, with high fire activity promoting fire-adapted species (Keith, 2017; Bowman et al., 2016).

Oceanic circulation also modulates temperature and available moisture for plant growth/productivity in temperate Australia, especially in mid–higher latitudes such as Tasmania (Duran et al., 2020; Keith 2017). Sea-level changes can also directly shape vegetation structure and composition, especially in coastal areas or small islands by filtering certain species and growth forms (Kirkpatrick and Harris, 1999; Keith, 2017).

Low SWW-driven moisture availability, an increase in ENSO events and higher sea levels are associated with turnover on the mainland (Table 2a; Fig. 4b). Significant turnover in the region after the mid-Holocene can be linked to decreasing moisture availability due, in part, to ENSO intensification, which overrode SWW-driven precipitation during this period (Fletcher and Moreno, 2012). Increasing drought and fire is thought to have promoted the expansion of sclerophyllous woodland on the mainland during this period. This may have also driven changes in understorey composition in woodlands, resulting in a major vegetation turnover (Kershaw et al., 1991). Furthermore, the increasingly oceanic climate (cool summer, mild winter) that gets established with sea-level rise would have also promoted longer growing seasons, a factor that has been linked to turnover in some Southern Hemisphere ecosystems (Lord, 2019).

Direct salt spray and wind damage driven by sea-level rise may have also driven vegetation changes by supressing trees to promote shrubby and herbaceous vegetation on the mainland, at least at sites exposed to direct oceanic influence (e.g., Hope, 1974; Martin, 1994). High soil salinity limits available soil moisture for tree growth and causes tree die-back, reducing competition in favour of shrub and herb communities (Cramer et al., 2004; Briggs and Taws, 2003). Similarly, ocean-driven strong winds are capable of removing trees in woodlands/forests further inland, increasing understorey composition in woodland/forest gaps (Smart et al., 2014).

Conversely, lower sea levels, high moisture availability and low temperature are linked to high turnover in Tasmania (Table 2a; Fig. 4b). Major turnover before ~11,000 years ago may be mostly linked to increasing moisture during the lateglacial–Holocene climate transition, which featured increases in forest cover. The Tasmanian landscape was generally open prior to the Holocene under a cooler climate and lower sea level (Hopf et al., 2000). The overall decreasing turnover trend in the region may reflect vegetation stabilisation as climate transitioned from a continental, cool lateglacial climate, characterized by open vegetation, to an oceanic climate, characterized by increasing forest

cover, as Tasmania became separated from the Australian mainland due to rising sea-level around 14,000 years ago (Lambeck and Chappell, 2001; Fig. 4b). High-resolution pollen records spanning beyond the ~13,000-year records considered in this study are required to better understand turnover in Tasmania during the glacial period.

In Bass Strait, low fire activity is associated with turnover, and the coherence between turnover and human occupation patterns suggests Aboriginal burning at least partly drove turnover in the region before the mid-Holocene (Table 2a; Fig. 4b). Aboriginal people may have used low-intensity fire to shape vegetation in Bass Strait for country keeping during this period. Low turnover after the mid-Holocene may be related to reduced Aboriginal fire usage in the region (McWethy et al., 2017; Sim, 1998), with occasional natural fires resulting in stable vegetation. Contrastingly, Romano and Fletcher (2018) concluded that intensive Aboriginal land usage stabilized vegetation in northwest Tasmania during the late Holocene. This disparity may reflect the heterogeneous nature of Aboriginal land use in southeast Australia in the past.

Richness drivers: Sea-level change, temperature, and moisture (SWW and ENSO)

Sea-level change primarily explains richness variations across the three regions (Fig. 4a; Table 2a). As discussed for mainland turnover, higher sea levels are also associated with high richness on the mainland (Table 2a) and can be related directly to sea-level disturbance (salt spray and wind damage) and indirectly to the prevalence of an oceanic climate (extended growing seasons).

Conversely, low sea level is associated with high richness in Bass Strait. This can be explained by the increase in salt stress/damage to plants as Holocene sea levels rose in this low-lying coastal region. Increased salt stress/damage (e.g., leaf necrosis) can suppress growth of shrubby/short vegetation, selecting for salt-tolerant species, especially in coastal sites, reducing richness by promoting only salt-adapted species (Griffiths, 2006). This would have been pronounced on the Bass Strait islands (which are more exposed to direct salt-laden winds), as sea level rose through the lateglacial–mid- Holocene, contributing to the decreasing richness trend in the region during this period (Fig. 4b). As a more oceanic climate developed, temperate forest and woodland cover spread rapidly in Bass Strait and Tasmania (McWethy et al., 2017; Hopf et al., 2000). This expansion may have suppressed

open vegetation communities (grasslands and heathlands), resulting in the overall trend in richness decline in the two regions during the early Holocene.

Holocene richness trends can also be interpreted in the light of ecosystem-level responses to drought. Ecological studies in Asia have shown that resource partitioning is more effective in saplings of drought-tolerant trees during periods of drought, which in turn promotes tree diversity (Sugden, 2020). High diversity also reduces the impact of drought in drought-prone environments such as SE Australia (Grossiord et al., 2014). High richness is associated with low moisture availability, which might relate to weakened SSW and/or ENSO intensification in this region (Table 2a). Increasing drought under a warmer climate, likely promoted species-rich drought-tolerant sclerophyllous woodland, especially on the mainland from the mid-Holocene (Hopf et al., 2000; Jones et al., 2017; Kershaw et al., 1991; Yuan et al., 2017; Pickett et al., 2004). Aboriginal managed burning is thought to have also promoted vegetation richness in Australia in the past (Bird et al., 2016b; Bowman, 1998) and the overlap between richness trends and human occupation patterns across regions suggests Aboriginal land-use may have also promoted/maintained richness, especially on the mainland and Tasmania in the past (Fig. 4b).

6.5.4. Fire regime and Intermediate Disturbance Hypothesis (IDH) in SE Australia

Fire plays an important role in Australian ecosystems, providing opportunities for on-plant and in-soil seed bank germination for species continuity and colonization of new habitats (O'Bryan et al., 2009; Williams et al., 2012). In line with the IDH, a lack of fire promotes competitive exclusion, decreasing richness (Keith et al., 2002), whereas too much fire selects for pyrophytes, also decreasing richness (Wilkinson, 1999; Kricher, 2011; Catford et al., 2012).

The GAM-based IDH assessment for SE Australia is not statistically significant at the $p < 0.05$ level (Fig. 5), and this is due to the low resolution of pollen records (few data points).

Further study to improve sampling resolution is recommended to investigate fire–richness relationships (IDH) in temperate Australia. Nonetheless, the IDH model shows a hump-shaped trend, especially in Bass Strait and Tasmania, suggesting moderate fire promoted richness in these regions during the Holocene, while decreases in richness are associated with low or high levels of biomass burning. This is in agreement with previous tests of the

IDH in temperate and tropical forest ecosystems (e.g., Colombaroli et al., 2013; Molino and Sabatier, 2001). It is important to note that charcoal records for Tasmania and Bass Strait are of high resolution (contiguously analysed), while few contiguous records are available for the mainland. Fire episodes (charcoal peaks) are likely to be missing in mainland records. For this reason, the IDH pattern for the mainland is considered less robust than that of the other regions. The overlap between periods of increased human occupation and increase in richness across regions also suggests Aboriginal-managed burning may have at least partly promoted richness in SE Australia during the Holocene (Bowman, 1998; Bird et al., 2016b; Fig. 4b and 5).

6.6. Conclusion

This is the first comprehensive meta-analysis study of long-term vegetation turnover in Australia, which provides insight into drivers of change in temperate ecosystems using a quantitative approach.

This study has successfully established an empirical turnover threshold ($SCD = 0.2$), comparable to pollen-based thresholds developed in other temperate ecosystems globally. Results from this show different interacting drivers were responsible for vegetation turnover and changes in richness in SE Australian temperate ecosystems during the lateglacial and Holocene. Overall, turnover and richness were driven by a combination of moisture availability, sea-level change, temperature, fire and ENSO. However, moisture availability/variability (related to SWW and ENSO) and sea-level change appears to be the primary drivers in most regions. This contrasts with the Northern Hemisphere, where temperature change was a major driver of turnover during the Holocene.

The Holocene richness reconstructions support the Intermediate Disturbance Hypothesis, especially in Bass Strait and Tasmania, promoting the notion that high biodiversity was at least partially maintained by (managed) fire regimes.

Overall, moisture availability (both in terms of amount and variability) and sea-level change (considering its role in modulating regional oceanic climate) should be recognized as key drivers of ecosystem turnover and richness in Southern Hemisphere temperate ecosystems. These long-term drivers may prove critical in shaping future turnover and richness changes in SE Australian ecosystems.

Chapter 7 INDIGENOUS FIRE-MANAGED LANDSCAPES IN SOUTHEAST AUSTRALIA DURING THE HOLOCENE— NEW INSIGHTS FROM THE FURNEAUX GROUP ISLANDS, BASS STRAIT

One of the primary aims of this thesis is to assess the role of human activities in shaping the vegetation and fire regimes of the past. In this chapter, the drivers of past fire regimes across southeast Australia are assessed quantitatively in terms of fire frequency and the amount of biomass consumed by fire. In particular, insights are drawn from Bass Strait on the role of humans and climate in past fire regimes, showing that human-managed fires have quite different palaeoecological signatures from climate-driven fires. This key finding allows future researchers to disentangle human and climatic signals from palaeoecological records with a degree of confidence. Implications for future fire management in southeast Australia are also highlighted.

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with
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I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

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Date

7.0. Indigenous Fire-Managed Landscapes in Southeast Australia during the Holocene— New Insights from the Furneaux Group Islands, Bass Strait

Abstract

Indigenous land use and climate have shaped fire regimes in southeast Australia during the Holocene, although their relative influence remains unclear. The archaeologically attested mid-Holocene decline in land-use intensity on the Furneaux Group islands (FGI) relative to mainland Tasmanian and SE Australia presents a natural experiment to identify the roles of climate and anthropogenic land use. We reconstruct two key facets of regional fire regimes, biomass (vegetation) burned (BB) and recurrence rate of fire episodes (RRFE), by using total charcoal influx and charcoal peaks in palaeoecological records, respectively. Our results suggest climate-driven biomass accumulation and dryness-controlled BB across southeast Australia during the Holocene. Insights from the FGI suggest people elevated the recurrence rate of fire episodes through frequent cultural burning during the early Holocene and reduction in recurrent Indigenous cultural burning during the mid–late Holocene led to increases in BB. These results provide long-term evidence of the effectiveness of Indigenous cultural burning in reducing biomass burned and may be effective in stabilizing fire regimes in flammable landscapes in the future.

7.1. Introduction

Fire has been part and parcel of the Australian landscape for millions of years, with fire-adapted plant species widespread across the continent (Crisp et al., 2011; Gill, 1975; Beadle, 1981; Miller and Murphy, 2017). On a regional scale, moisture variability and vegetation type are the major biogeographic drivers of fire regimes in Australian landscapes (Miller and Murphy, 2017; Murphy et al., 2013; Bradstock, 2010; Mooney et al., 2011). Localized factors, such as human activity, topography and herbivory are also key drivers of fire regimes globally (Whitehair et al., 2018; Archibald et al., 2013). Indigenous land use is thought to have shaped the landscape for tens of thousands of years through traditional managed burning practices that create fire mosaics, especially in central and northern Australia (Miller and Murphy, 2017; Bowman, 1998; Gammage, 2008; Bird et al., 2020; Bowman et al., 2004).

During the Holocene, Indigenous land use has driven fire regimes *sensu lato* since at least the last 6000 years (Black et al., 2006; Black and Mooney, 2006; Fletcher et al., 2013, 2018; Stahle et al., 2016, 2017; McWethy et al., 2013) and ecosystem changes associated with Indigenous fire use is thought to have been greatest in fire-sensitive ecosystems such as temperate rainforests (McWethy et al., 2013). While efforts have been made to separate the effects of Indigenous fire use from climate as cause of vegetation change (e.g., Romano and Fletcher, 2018; Mooney et al., 2007), the regional-scale aspects of fire regimes (amount of biomass burned and recurrence rate of fire) that are influenced by past Indigenous land use remain unclear. Similarly, the role of climate change in past fire regimes is not fully understood and confounded by persistent anthropogenic land use during the Holocene (Williams et al., 2014; Lourandos, 1983).

Archaeological records from the eastern Bass Strait islands (Furneaux Group) in southeast Australia suggest a reduction in the islands' occupation densities since their separation from the surrounding land masses by mid-Holocene sea-level rise (Sim, 1998). These islands provide a rare natural laboratory to explore the different roles of climate and anthropogenic land use in past changes in fire regime, given their history contrasts with land-use intensification evident on the mainland at the same time (Lourandos, 1983; Hargrove et al., 1992). Understanding the individual roles of long-term anthropogenic and climatic drivers in past changes in fire regime in southeast Australia will better inform predictions of fire regime change in the region.

Sedimentary charcoal records in catchments (e.g., peatlands, lakes, swamps) have been empirically proven to reflect vegetation biomass burned within 50 km source area(s) (Vachula, 2020). In particular, total sedimentary charcoal influx has been shown in many cases to reflect amount of vegetation biomass burned regionally (Duffin et al., 2008; Tinner et al., 1998; Ali et al., 2012; Carcaillet et al., 2002, 2007; Blarquez et al., 2014). Charcoal influx peaks have also been validated empirically as a proxy for recurrence rate of fire episodes above the regional background rate of biomass burned (Tinner et al., 1998; Ali et al., 2012; Higuera et al., 2010; Adolf et al., 2018). In this study, we use these proxies to decompose Holocene fire regimes of the Furneaux Group Islands (FGI) of southeast Australia into biomass burned (BB) and recurrence-rate-of-fire-episodes (RRFE). We then compare these two facets of fire regimes of the FGI to independent records of climate and anthropogenic land-use using generalized linear models, to identify the major drivers of change. We also compare these reconstructions to those from surrounding landmasses of

southeast mainland Australia and Tasmania to compare the role of Indigenous land-use practices and climatic changes in past changes in fire regime in southeast Australia more generally. Our aim is to identify the roles of climate and anthropogenic land use in the southeast Australian fire regimes during the Holocene, and also draw insights from the FGI, especially regarding the role of anthropogenic land use in modulating biomass burned and the recurrence rate of fire episodes.

7.2. Study Region

7.2.1. Dominant climatic modes in Bass Strait and southeast Australia

The southeast Australian climate is influenced by El Niño Southern Oscillation (ENSO), Indian Ocean Dipole (IOD) and the Southern Annular Mode (SAM) (CSIRO, 2012; Abram et al., 2020; Fierro et al., 2014; Risbey et al., 2009; Australian Bureau of Meteorology; Fig. 1). ENSO and SAM are the dominant modes in the FGI, Bass Strait and the wider Tasmanian region. ENSO drives rainfall variability in winter, spring and summer. SAM, which is the pattern of Southern Westerly Winds (SWW), drives shifts in rainfall variability between western and eastern southeast Australia (CSIRO, 2012; Risbey et al., 2009; Australian Bureau of Meteorology; Hendon et al., 2007). Variability in wet-dry conditions influences fire occurrence driven by the aforementioned climatic modes, especially ENSO, which governs interannual fire variability across southeast Australia (Risbey et al., 2009; Mariani et al., 2016a, 2018a; Mariani and Fletcher, 2016). Zonal shifts in SWW flow were the dominant climatic mode across southeast Australia during the early to mid-Holocene, while ENSO has prevailed since the mid-Holocene (Fletcher and Moreno, 2012). Recent studies also suggest the IOD has played a significant role in driving catastrophic fires, especially on the southeast mainland since European colonisation (Abram et al., 2020; Williamson et al., 2016).

7.2.2. Vegetation

The natural vegetation of the southeast Australian mainland is characterized by various types of fire-promoted sclerophyllous woodlands/forests and shrublands, as well as large areas of grassland (Fig. 1). Western Tasmania, which receives the highest amount of rainfall in the region is characterized by fire-sensitive rainforests and large areas of flammable

sedgeland and moorland, while eastern Tasmania, which is in the rain shadow, supports drier sclerophyllous woodlands (Keith, 2017). The FGI are characterized by coastal scrub and heathlands, with localized sclerophyllous woodlands/forests in some areas (Harris and Kitchener, 2005; Harris et al., 2001; Fig. 1 inset).

Pollen records suggest Casuarinaceae woodland dominated southeast Australian mainland vegetation during the early Holocene, while *Eucalyptus* woodland expanded in many areas, at least since mid-Holocene, as climate became variable (Kershaw et al., 1991). Rainforest communities expanded in western Tasmania through the early to mid-Holocene and *Eucalyptus* woodland also expanded in the region, with increasing climate variability since mid-Holocene (e.g., Fletcher et al., 2018; Stahle et al., 2016, 2017). Conversely, *Eucalyptus* woodland generally expanded in eastern Tasmania throughout the Holocene but was reduced and replaced by coastal heathland and scrub in coastal sites due to the mid-Holocene sea-level transgression (e.g., Mackenzie and Moss, 2017; Jones et al., 2017). Similarly, sea-level rise drove the replacement of *Eucalyptus* woodland by coastal heathland and scrub on the FGI around the same time (McWethy et al., 2017; Adeleye et al., 2021a).

7.2.3. Past human occupation

Indigenous occupation was widespread across southeast Australia during the Holocene, but major expansion occurred from the mid to late Holocene on the mainland and Tasmania (Williams et al., 2014; Lourandos, 1983). Conversely, widespread human occupation on the Bassian Plain and today's islands, especially the FGI, was concentrated during the early to mid-Holocene and markedly reduced since the mid-Holocene (Sim, 1998). Bass Strait was previously a plain and a connecting landbridge for human movements between Tasmania and the Australian mainland before its inundation by postglacial sea-level rise between ~14,000 and 6000 years ago (Cosgrove, 1995; Lambeck and chappell, 2001; Sloss et al., 2007; Williams et al., 2018). Human occupation (and land use) is thought to have declined on the FGI by ~5000 years ago, possibly as a result of sea-level encroachment and declining resource availability as the islands shrank (Sim, 1998; Williams et al., 2018).

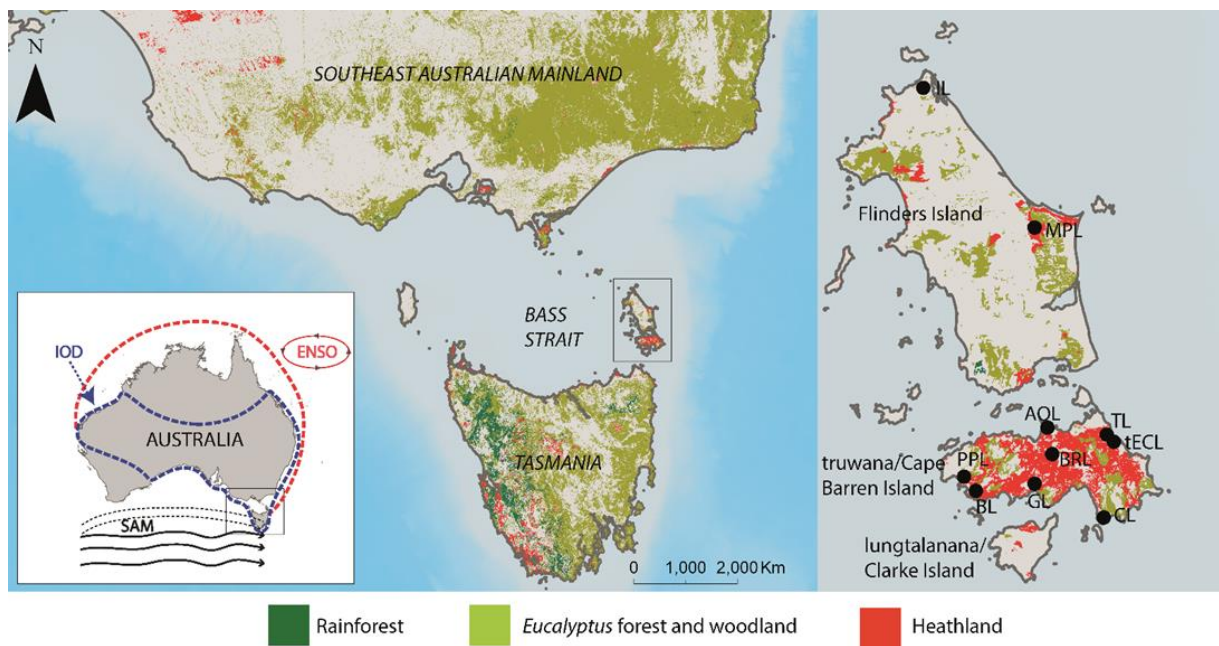


Figure 1: Major climatic modes influencing southeast Australia. A positive Indian Ocean Dipole phase (IOD) generally drives less rainfall, higher temperatures, and extreme fire weather in parts of Australia (blue-broken lines) in winter and spring, while rainfall is significantly higher in winter and spring during negative IOD phases (Australian Bureau of Meteorology). Southern Annular Mode (SAM) is generally a short-lived oscillation and most pronounced in Tasmania (grey-broken lines). A positive SAM phase features increased summer rainfall (but dry winter) in eastern Tasmania, while a negative SAM phase features increased summer rainfall in western Tasmania and increased winter rainfall in both eastern and western Tasmania (Australian Bureau of Meteorology). Positive El Niño Southern Oscillation (ENSO) years (La Niña) generally bring higher annual rainfall to many parts of Australia (red-broken lines), while negative years (El Niño) are associated with low annual rainfall and extreme fire weather (Australian Bureau of Meteorology). Positive El Niño Southern Oscillation (ENSO) years (La Niña) generally bring higher annual rainfall to many parts. Colour-shaded areas represent major vegetation types, which include *Eucalyptus* forest and woodland (olive), rainforest (green) and heathlands (red). Light grey-shaded area outside southeast Australia region margin represents the continental shelf (Geoscience Australia. Australian Bathymetry and Topography, 2016). Major vegetation communities and sites with charcoal records (black circles) in the Furneaux Group islands, Bass Strait (see Table 1 and Fig. 2 for full site names). Vegetation information is adapted from “major vegetation groups” (Department of Agriculture, Water and Environment, 2018a—National Vegetation Information System version 5.1.).

7.3. Methods

7.3.1. Composite charcoal influx as a proxy for vegetation biomass burned (BB)

Composite analysis of multiple records of charcoal influx reflects the amount of vegetation BB in the landscape on a regional to continental scale, with minimal sedimentation and taphonomy-related biases (Ali et al., 2012; Power et al., 2008; Marlon et al., 2016). We applied this method, with z-score transformation, to ten high-resolution (1 cm interval) macroscopic charcoal records (charcoal fragments > 125 μm in size) from the FGI (Flinders Island and truwana/Cape Barren Island) to estimate regional BB during the Holocene (Fig. 2; Table 1). Five out of the 10 sites are published records, while the remaining 5 are newly analysed sites. Charcoal extraction and quantification followed the method of Whitlock and Larsen (2001) (Whitlock and Larsen, 2001). Composite analysis was conducted using the “pfCompositeLF” function (two-way smoothing) in “paleofire” package in “R” (Blarquez et al., 2014; R Core Team, 2020). All chronologies are published age-depth models and Accelerator Mass Spectrometry AMS dates and age-depth models for newly analysed sites are provided in Table S2 and Fig. S2–S5 in Appendix S6. Note: BB is a centennial-scale average of regional charcoal production (influx).

7.3.2. Charcoal influx peak component as a proxy for recurrence-rate-of-fire-episodes (RRFE)

The use of peak components of charcoal influx is an established proxy for RRFE reconstruction, a decadal frequency of above-average charcoal influx events, and commonly analysed using the “CharAnalysis” program (Higuera et al., 2007, 2009, 2010). We applied this method to reconstruct RRFE for individual sites, with the temporal envelope of peak detection set to 500 years. Charcoal peaks were calculated by setting “cPeak” to residuals, which is the difference between total charcoal accumulation rates and background charcoal. The threshold for peak detection was determined using percentile cut-off of noise distribution with a Gaussian mixed model, and minimum count cut-off probability was set to 0.05. The resulting peak frequencies for all sites were interpolated to 200-year intervals for consistency with charcoal composites and the average of all sites’ peak frequencies taken to represent regional RRFE (number of fire episodes per 500 years) for the FGI. Each fire episode represents one or more major fire events per 500 years. RRFE

or charcoal peaks are not taken to reflect fire severity (Higuera et al., 2010). Developing reliable proxies for palaeofire severity is the goal of current research efforts (Gosling et al., 2019).

The overall results (BB and RRFE) for the FGI were compared to reconstructed palaeofire for the southeast mainland and Tasmania. See Fig. S1 and Table S1 in Appendix S6 for site details for the charcoal records used in reconstructing palaeofire for these regions.

7.3.3. Identifying drivers of fire regimes across southeast Australian regions using generalized linear modelling

Generalized linear modelling (GLM) with Gaussian distribution was applied to identify major drivers of BB and RRFE in the past, with ENSO, SWW-driven effective precipitation and anthropogenic land use as the predictors. The effect of temporal autocorrelation was removed from the models by bootstrapping at a lower resolution 1000 times (R Core Team, 2020). Best models were selected based on the corrected Akaike's information criterion (AICc). The analysis was done in "R" (Mellin et al., 2010) using the "TSA", "stats" and "EnvStats" packages [68,69]. The Laguna Pallcacocha lake sedimentation record was used as a proxy for ENSO events (Moy et al., 2002), reconstructed precipitation:evaporation from southwestern Victoria as a proxy for SWW-driven effective precipitation (Wilkins et al., 2013) and the number of radiocarbon dates from archaeological evidence of past human occupation as a proxy for anthropogenic land use (Williams et al., 2014).

Table 1: Site information of charcoal records from the Furneaux Group islands, Bass Strait.

Site Name	Latitude	Longitude	Elevation (m)	Source
Middle Patriarch Lagoon (MPL)	-39.9963°	148.1833°	15	McWethy et al. (2017)
Inlet Lagoon (IL)	-39.7638°	147.9594°	10	McWethy et al. (2017)
Big Reedy Lagoon (BRL)	-40.3589°	148.238°	26	Adeleye et al. (2021a)
truwana East Coast Lagoon (tECL)	-40.33083°	148.3611°	3	Adeleye et al. (2021a)
Green Lagoon (GL)	-40.442967°	148.143840°	10	Adeleye et al. (2021a)
Crystal Lagoon (CL)	-40.4774°	148.351°	8	Adeleye et al. (submitted)
Apple Orchard Lagoon (AOL)	-40.325°	148.2161°	3	New site
Tobacco Lagoon (TL)	-40.3228°	148.3603°	20	New site
Piano Point Lagoon (PPL)	-40.4367°	148.0503°	10	New site
Bumpy Lagoon (BL)	-40.4515°	148.071°	11	New site

7.4. Results

7.4.1. FGI Holocene regional palaeofire reconstruction

Charcoal accumulation rates (CHAR) were high at most sites on the FGI between early and mid-Holocene (~12,000–6000 cal yr BP), with an average CHAR of 2–7 particles/cm²/y and charcoal concentration of 70–300 charcoal particles/cm³. CHAR was low at most sites in the mid–late Holocene (~6000–1000 cal yr BP), with an average CHAR of ~1 particles/cm²/y and charcoal concentration of ~50 charcoal particles/cm³. CHAR and charcoal concentrations increased at most sites in the last 1000 years, reaching an average of 100 particles/cm²/y and 100 charcoal particles/cm³, respectively (Fig. 2; see Fig. S6 in Appendix S6 for average CHAR and charcoal concentration curves). Charcoal peak analysis identified high numbers of significant ($p < 0.05$) peaks across sites in the early–mid Holocene and fewer peaks after this period.

A non-linear relationship was observed between RRFE and BB on the FGI, confirming that total charcoal influx and influx peaks are measures of different aspects of fire regimes on the landscape; in other words, high RRFE is not always associated with high levels of biomass burning (Fig. 3). Charcoal composite results show a low–gradual increase (z-score < 0) in BB on the FGI at the beginning of the Holocene, with a major increase after ~9000 cal yr BP (z-score > 0). BB later declined (z-score < 0) from ~5000 to 2000 cal yr BP and increased again (z-score > 0) in the last ~1500 years (Fig. 2). Conversely, RRFE was highest (~3 fire episodes/500 years) on the FGI during the early Holocene (~12,000–8000 cal yr BP) and consistently declined to ~1 fire episode/500 years through mid–late Holocene, with a minor increase in the last ~3000 years (Fig. 2). GLM results suggest that a combination of anthropogenic land use, ENSO and SWW-driven effective precipitation-controlled BB on the FGI during the Holocene, while a combination of anthropogenic land use and ENSO drove RRFE (Table 2).

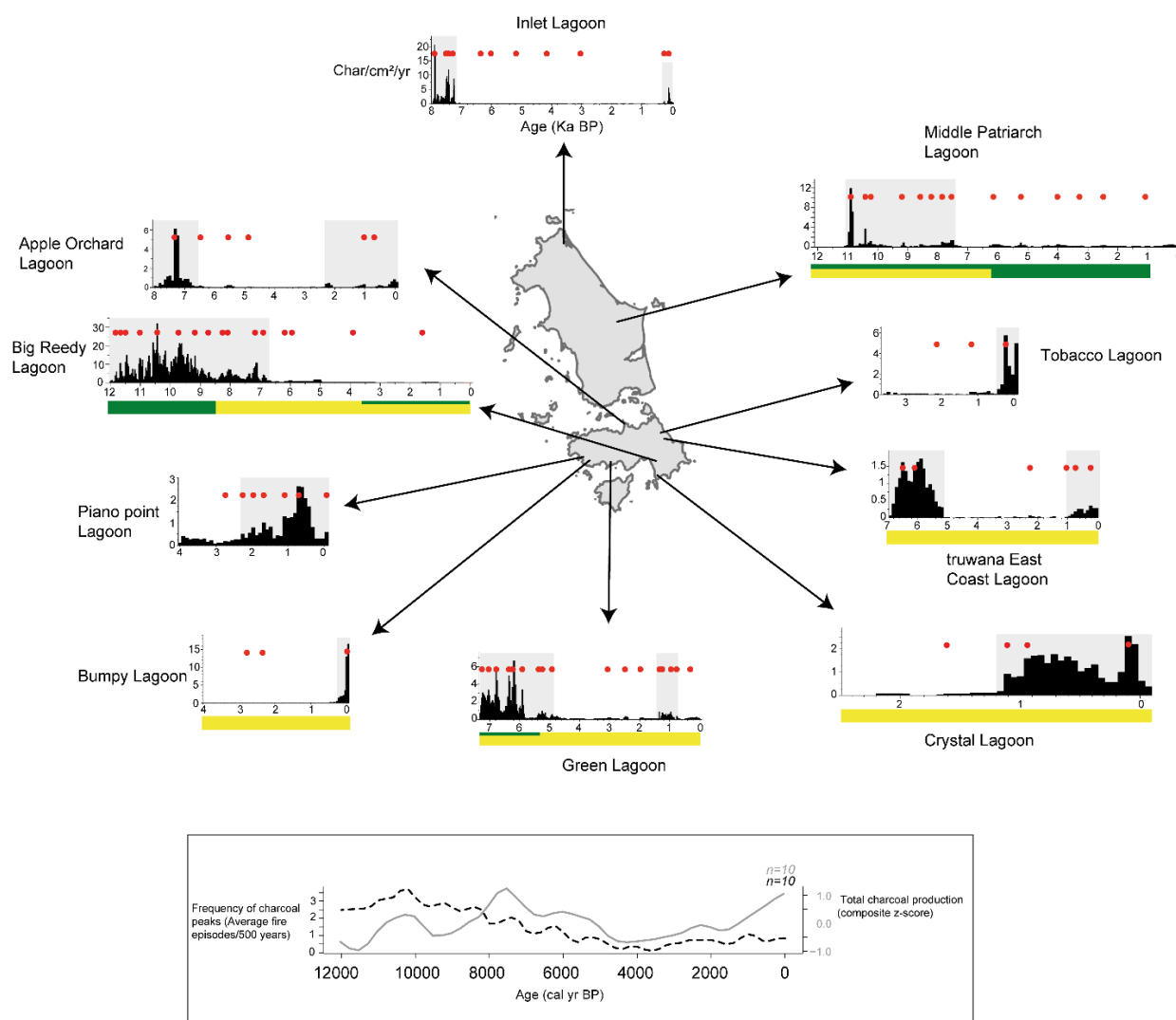


Figure 2: Charcoal accumulation rates with charcoal peaks (red dots) for each site on the Furneaux Group islands, Bass Strait. Periods of major fire activity (high charcoal accumulation) during the early–mid Holocene and late Holocene are shaded in grey. Colour bars represent temporal vegetation types, which include woodland (green) and a combination of heath and scrub (yellow) (McWethy et al., 2017; Adeleye et al., 2021a; Ladd et al., 1992). The horizontal axis in each record represents age (calendar years before present, i.e., 1950 AD). The rectangular box shows the composite of all charcoal records’—regional biomass burned (grey curve) and frequency of charcoal peaks—recurrence rates of fire episodes (black dashed curve) for the Furneaux Group.

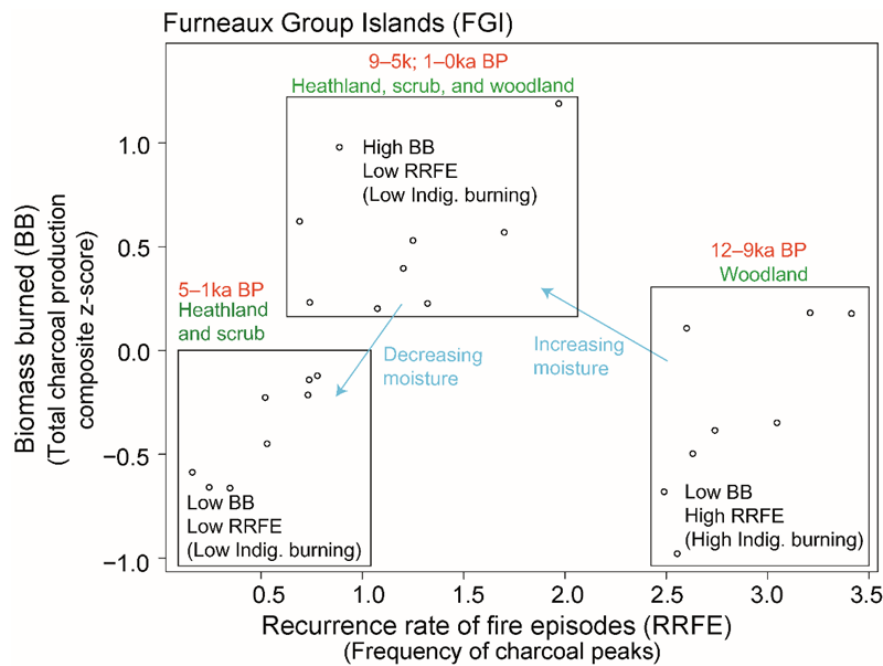


Figure 3: Scatter plot showing a non-linear relationship between RRFE and BB on the FGI during the Holocene in relation to changes in climate and Indigenous (Indig.) land use. Each point represents a 500-year period relationship between BB (total charcoal production) and RRFE (frequency of charcoal peaks).

7.4.2. FGI Holocene palaeofire compared to other southeast Australian regions

As recorded for the FGI, a generally low-gradual increase in BB was also observed on the mainland at the beginning of the Holocene, with a major increase after ~9000 cal yr BP. A similar trend was also observed in eastern Tasmania, which has similar vegetation to the mainland; however, BB reconstruction for the region is considered less robust due to data limitation ($n = 2$) (see Fig. S7 in Appendix S6 for eastern Tasmania BB reconstruction). BB declined markedly on the FGI from ~5000–2000 cal yr BP (Fig. 4) but remained generally high on the mainland (and eastern Tasmania). Conversely, BB was high in western Tasmania at the beginning of the Holocene (~12,000–9000 cal yr BP), decreasing between ~9000 and 4000 cal yr BP, and increasing again in the last ~4000 years.

High RRFE was recorded for the FGI in the early Holocene (~12,000–8000 cal yr BP) but declined through the rest of the Holocene (Fig. 4). RRFE was also relatively high (0.8 fire episodes/500 years) in western Tasmania in the early Holocene (~12,000–10,000 cal yr BP), declined slightly to ~0.4 fire episodes/500 years between ~10,000 and 6000 cal yr BP and then increased in the last ~6000 years, reaching up to 1.2 fire episodes/500 years.

RRFE shifted from 0.8 to 2 fire episodes/500 years on the mainland around 8000 cal yr BP, with a major increase in the last ~200 years, reaching > 4 fire episodes/500 years (Fig. 4).

GLM results show SWW-driven effective precipitation and ENSO mainly explain BB across regions, while anthropogenic land use mainly explains RRFE. Anthropogenic land use also contributed to BB in Bass Strait and Tasmania, while ENSO contributed to RRFE in Bass Strait, SWW-driven effective precipitation in Tasmania, and a combination of ENSO and SWW-driven effective precipitation on the mainland (Table 2).

Table 2 : Generalized linear modelling (GLMs) of biomass burned (BB) and recurrence-rate-of-fire-episodes (RRFE) as a function of ENSO, SWW-driven effective precipitation and anthropogenic land use (human). Models are ranked based on corrected Akaike's information criterion corrected for small sample sizes (AICc), and top models are in bold. Percentage of deviance (%Dev) explained by models and marginal R² (Rm) are also shown.

Region	Model	AICc	dAICc	Rm	%Dev
Furneaux Group	BB~Human + ENSO + Precipitation	32.79763	0	62.11	66.4
	BB~Human + ENSO	34.32317	1.526	56.1	50
	BB~Human + Precipitation	40.59263	7.795	49.27	62
	BB~Precipitation	51.575	18.777	26.56	46.2
	BB~ENSO + Precipitation	53.88739	21.09	26.97	
	BB~Human	56.39019	23.593	17.6	
	BB~ENSO	57.53586	24.738	15.72	
	Null	62.03616	29.239	0	
	RRFE~Human + ENSO	13.20343	0	93.82	95
	RRFE~Human + ENSO + Precipitation	18.09869	4.895	93.9	96
	RRFE~Human + Precipitation	23.2508	10.047	92.42	
	RRFE~Human	30.02591	16.822	89.86	
	RRFE~ENSO + Precipitation	84.77862	71.575	59.28	
	RRFE~ENSO	93.53249	80.329	49.85	
	RRFE~Precipitation	107.6661	94.463	19.07	
	Null	118.7938	105.59	0	
Southeast mainland	BB~ENSO + Precipitation	-3.69868	0	32.2	47.3
	BB~ENSO	-3.28083	0.418	18.89	28.5

	BB~Precipitation	-2.45098	1.248	24.93	41
	BB~Human + Precipitation	-0.73134	2.967	42.12	55
	BB~Human + ENSO + Precipitation	-0.16225	3.536	46.25	61.2
	BB ~ Human + ENSO	-0.03095	3.668	32.97	46.9
	Null	2.751073	6.45	0	
	BB ~ Human	3.805082	7.504	19.04	47.7
	RRFE~Human + ENSO + Precipitation	44.8662	0	86.47	90.6
	RRFE~Human + Precipitation	49.99191	5.126	82.94	86.4
	RRFE~Human + ENSO	56.78118	11.915	79.53	87.4
	RRFE~Human	67.34123	22.475	70.55	
	RRFE~ENSO + Precipitation	100.1835	55.317	36.71	
	RRFE~Precipitation	104.936	60.07	23.39	
	RRFE~ENSO	105.7968	60.931	27.53	
	Null	116.3326	71.466	0	
Western Tasmania	BB~Human + ENSO + Precipitation	-21.034	0	81.59	83.1
	BB~ENSO + Precipitation	-14.9711	6.063	68.64	76
	BB~Precipitation	-1.8434	19.191	52.12	
	BB~Human + Precipitation	3.869802	24.904	56.2	
	BB~ENSO	17.30092	38.335	14.88	
	Null	21.40191	42.436	0	
	BB~Human + ENSO	21.8768	42.911	18.3	
	BB~Human	23.02665	44.061	9.16	
	RRFE~Human + Precipitation	-2.16589	0	66.53	72.1
	RRFE~Human + ENSO + Precipitation	0.499337	2.665	66.7	78.1
	RRFE~Human	10.23483	12.401	43.39	
	RRFE~ENSO + Precipitation	11.81571	13.982	38.75	52.7
	RRFE~Human + ENSO	12.7847	14.951	43.44	66.7
	RRFE~Precipitation	15.75663	17.923	27.43	27.7
	RRFE~ENSO	18.15752	20.323	19.76	
	Null	24.62277	26.789	0	

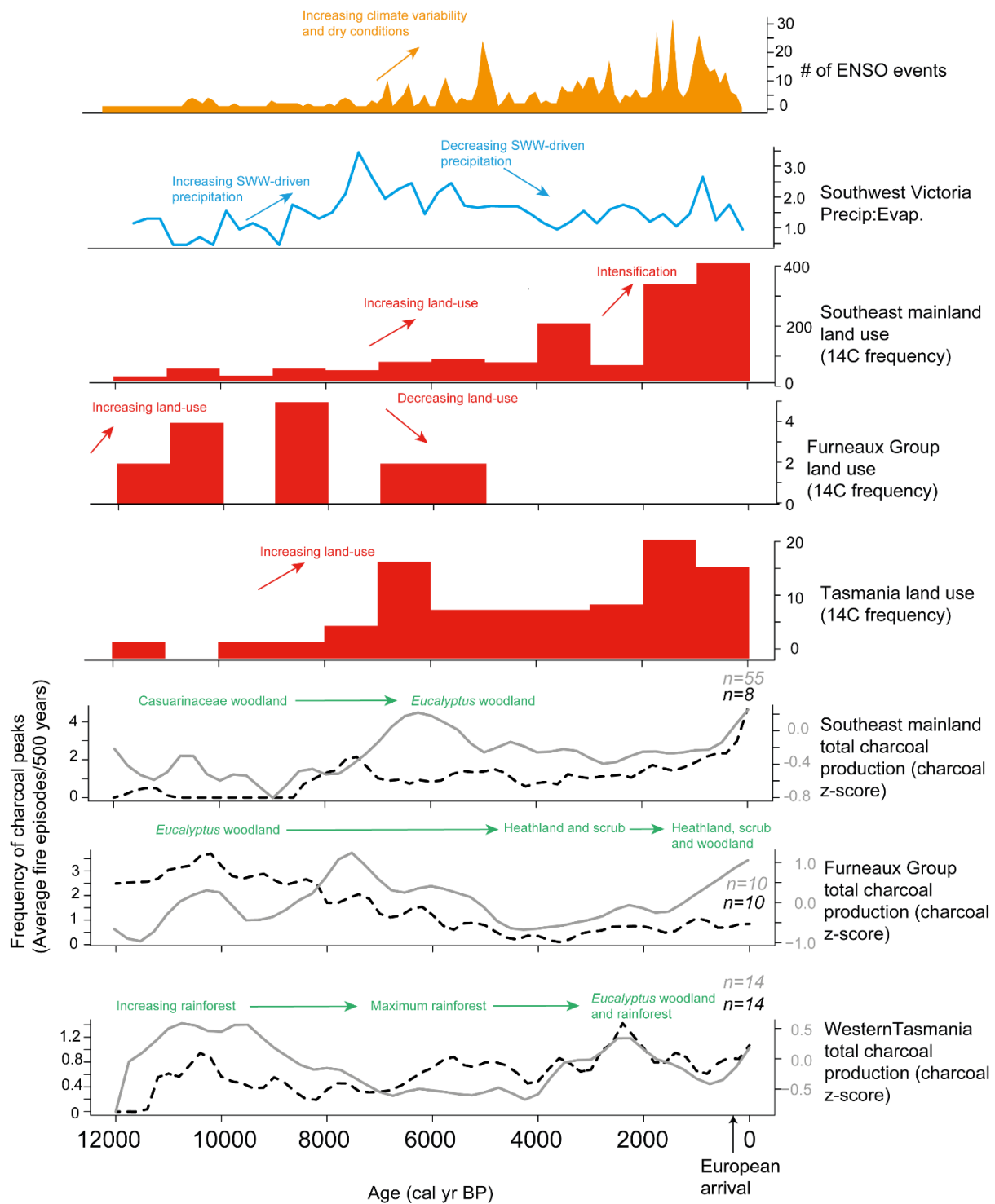


Figure 4: Regional biomass burned—charcoal z-score (solid grey line) and recurrence-rate-of-fire-episodes—average fire episodes/500 years (black dashed line) for the Furneaux Group islands (FGI), western Tasmania and the mainland in relation to vegetation, anthropogenic land use (Williams et al., 2014), SWW-driven changes in precipitation (Wilkins et al., 2013) and ENSO (Moy et al., 2002). Vegetation labels are based on major palaeoecological interpretations in published studies from

respective regions (e.g., Fletcher et al., 2018; Stahle et al., 2016, 2017; McWethy et al., 2017; Adeleye et al., 2021a; Ladd et al., 1992; Hopf et al., 2000). Note the different scales of ^{14}C dates (anthropogenic land use).

7.5. Discussion

This is the first time that long-term drivers of fire regimes in the Australian landscape have been quantitatively assessed, and our GLM results suggest changes in climate and anthropogenic land use are sufficient to explain fire regimes (regional BB and RRFE) in southeast Australia during the Holocene. Nonetheless, we acknowledge that our results may have incurred potential errors due to limitations associated with some of the proxies used.

7.5.1. Potential sources of error

The climatic and anthropogenic proxies considered for our GLMs are currently the best for southeast Australia; however, we acknowledge that the quality of these proxies, especially the use of radiocarbon-dated archaeological evidence of human occupation as an index for regional anthropogenic land use, may have potentially influenced our results. Previous studies have pointed out a number of limitations in the use of radiocarbon-dated archaeological evidence as a proxy for human activity, and biases associated with sampling size, intensity and choice of location have been identified particularly in Australian archaeological records (Williams et al., 2015a, 2015b, 2018; Williams, 2012; Timpson et al., 2014; Crema et al., 2016). These factors may have potentially influenced our GLM results. Furthermore, worthy of mentioning is the generally low R_m and percentage deviation values for BB on the mainland, which is likely as a result of the quality of charcoal data from the region—mostly non-contiguous microscopic charcoal records, which carry the possibility of missing major fire events (Table 2; Fig. S1 in Appendix S6). This bias is less problematic in Tasmania and FGI, where contiguously-sampled records prevail.

7.5.2. Holocene drivers of biomass burned (BB) in southeast Australia: SWW-driven effective precipitation and ENSO

Climate-driven changes in fuel structure and moisture have been widely identified as major drivers of fire regime (Cochrane, 2009; Pausas and Paula, 2012; Bradstock, 2010). However, the operational pattern of these drivers varies in different ecosystems (Pausas and Paula, 2012; Pausas and Bradstock, 2007). In wet ecosystems with high net primary productivity (rainforests), fuel is generally not a limiting factor, the availability of fuel to burn (dry fuel) is the major limiting factor of fire activity. Conversely, a lack of fuel (low biomass accumulation) generally limits the chances of fire in dry, less productive ecosystems (woodland) (Krawchuck and Moritz, 2011). BB in southeast Australia during the Holocene can be explained in the context of climate-driven vegetation growth (biomass accumulation) and changes in biomass moisture. The FGI, mainland and eastern Tasmania generally fall into the category of a less productive dry ecosystem zone, while western Tasmania falls into the category of a wet productive ecosystem zone.

Our GLM results suggest SWW-driven effective precipitation and ENSO were the major drivers of BB across regions during the Holocene. Though anthropogenic land use contributed significantly to BB in Tasmania and FGI regions, we focus on the major climatic drivers in this discussion (Fig. 5).

Southeast Australia is generally thought to have become increasingly wet during the early Holocene, especially between ~9000 and 6000 cal yr BP (Wilkin et al., 2013; Moros et al., 2009, Fig. 4). The generally low BB on the FGI and mainland prior to ~9000 cal yr BP can be associated with reduced biomass accumulation due to low precipitation at this time, and more BB in western Tasmania during this period may be related to biomass dryness and availability to burn (Fig. 4). A major increase in BB on the FGI and mainland between ~9000 and 6000 cal yr BP may be as a result of increased biomass accumulation in woodlands as SWW-driven effective precipitation reached its Holocene maximum. Contrastingly, high precipitation during this period likely increased biomass wetness in western Tasmanian rainforests, with reduced chances of ignitions, leading to a major decline in BB between ~9000 and 5000 years ago (Fig. 4).

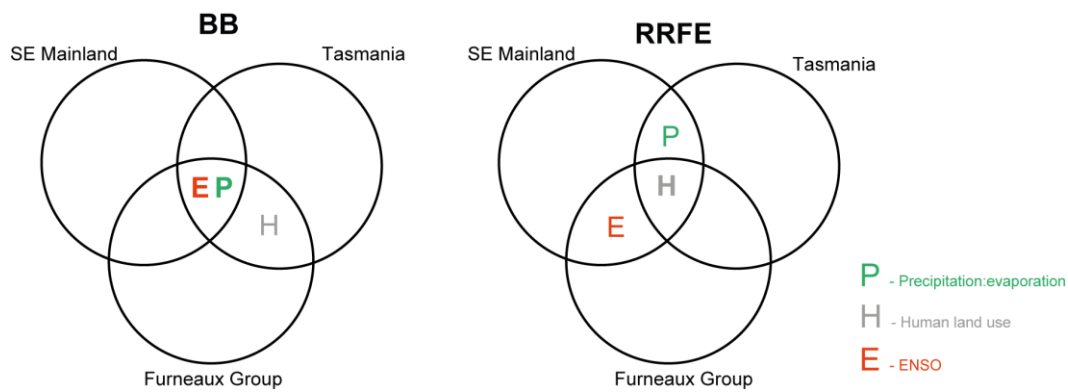


Figure 5: Summary Venn diagrams showing major predictors of Holocene regional biomass burned (BB) and recurrence-rate-of-fire-episodes (RRFE) in southeast Australia, based on GLM results in Table 2. Predictors in bold explain biomass burned/fire frequency across all regions.

Alternatively, the heterogeneous pattern of BB in southeast Australia between ~12,000 and 6000 cal yr BP (Fig. 4) may be as a result of zonal shifts in SWW-driven effective precipitation between eastern and western southeast Australia proposed by Fletcher and Moreno (2012). These authors suggested stronger SWW-driven effective precipitation in eastern southeast Australia and a weaker SWW flow in western areas between ~12,000 and 9000 years ago, which may explain reduced BB (wetter fuel) on the FGI and mainland, and more BB (drier fuel) in western Tasmania during this period (Mariani and Fletcher, 2017). This east–west anti-phased pattern is thought to have switched between ~9000 and 5000 years ago, with less BB in western Tasmania and more BB on the FGI and mainland (Fletcher and Moreno, 2012; Mariani and Fletcher, 2017). Additional proxy-based studies of Holocene dynamics of SWW-driven effective precipitation are certainly required in southeast Australia, especially in eastern areas (FGI, southeast New South Wales, eastern Victoria, and eastern Tasmania), to fully understand this east–west anti-phased pattern and relationship between BB and moisture regimes.

SWW-driven effective precipitation weakened in southeast Australia from the mid-Holocene due to ENSO intensification (Fletcher and Moreno, 2012). Dry conditions associated with ENSO intensification during this period likely promoted drier fuel in western Tasmanian wet forests again, with an increase in BB after ~5000 cal yr BP. Drier fuel may have also contributed to more BB on the mainland during this period. However, the decline in effective precipitation at this time may have reduced biomass accumulation in woodlands on the

mainland and FGI, with some decline in BB after ~5000 cal yr BP. Although the decline in BB on the mainland was relatively minor, BB declined markedly on the FGI after ~5000 cal yr BP, and this may be as a result of a major decline in woodland vegetation on the FGI at this time (McWethy et al., 2017; Adeleye et al., 2021a; Ladd et al., 1992; Fig. 2 and 4). Sea level-related disturbance (e.g., salt spray, wind damage) is thought to have driven the expansion of sclerophyll shrubby vegetation at the expense of woodland on the FGI during the mid-Holocene, due to higher sea levels and the flooding of the continental shelf forming present-day Bass Strait (Adeleye et al., 2021a; Fig. 2). These vegetation changes may also have reduced fuel loads and connectivity for major biomass burning in the region.

Woodland elements gradually increased again on the FGI in the later part of the Holocene, which is thought to be related to a decline in sea level-related disturbance at this time (McWethy et al., 2017; Adeleye et al., 2021a; Fig. 2). Increasing vegetation density may have led to the increase in BB (Fig. 4). Biomass accumulation at this time may have been slow due to the generally dry conditions; however, when biomass burns it will do so with high intensity when enough biomass accumulates, and this may apply especially in the last 200 years after European colonisation (Nicholson et al., 2017).

7.5.3. Holocene drivers of recurrence rate of fire episodes (RRFE) in southeast Australia: anthropogenic land use

Our GLM results show that anthropogenic land use was the primary driver of RRFE across regions (Fig. 5), with a secondary role for SWW-driven effective precipitation and ENSO variability.

The high RRFE on the FGI between ~12,000 and 9000 cal yr BP despite the generally low biomass burned during this period likely reflects recurrent Indigenous fire usage on the FGI (Fig. 4, Table 2). Indigenous people likely used frequent fires to maintain open and accessible woodland conditions in order to promote resource availability during this period (Gott, 2005; McWethy et al., 2017; Adeleye et al., 2021a). The open/mosaic landscapes maintained by Indigenous peoples also corresponded with less biomass burned on the FGI between ~12,000 and 9000 cal yr BP, possibly due to a minimal fuel load and connectivity, decreasing the likelihood of major widespread fire on the landscape. High RRFE associated

with Indigenous land use and open woodland is also evident on the mainland and western Tasmania, especially in the last ~6000 years (Fig. 4).

From the mid-Holocene, RRFE on the FGI markedly diverges from that of the surrounding land masses (Fig. 4). Recurrent fires associated with Indigenous land use continued on the mainland and western Tasmania in the late Holocene, with intensification in the last ~4000–2000 years, possibly in response to increasing ENSO-driven climate variability and dry conditions. Romano and Fletcher (2018) also found that the primary impact of Indigenous land use in north-western Tasmania in the late Holocene was to stabilize the landscape under more variable climates and minimising vegetation changes. In contrast to increasing RRFE on the mainland and western Tasmania, RRFE declined further on the FGI in the last ~5000 years and overlaps with a reduced human population based on archaeological records (Sim, 1998), which suggests reduced land use. The reduced presence of people as recorded by the archaeology is thought to have been due to postglacial sea-level rise and submergence of the Bassian landbridge (Sim, 1998; Lambeck and Chappell, 2001; Sloss et al., 2007; Williams et al., 2018; Fig. 4). A reduction in recurrent Indigenous cultural burning practices due to an infrequent use of the islands may have also allowed biomass to accumulate and burn severely on the FGI during the latter part of the Holocene, a pattern that was exacerbated following European colonisation in the last ~200 years.

7.5.4. Australian fire regime and management

This study broadly reflects the bioclimatic and anthropogenic control of fire regimes across Australia. Biomass accumulation (vegetation types) and availability to burn (dry biomass), fire weather conditions and anthropogenic activities modulate fire regimes in Australia (Bradstock, 2010; Russell-Smith et al., 2007). Long-term dry conditions in particular have been identified to potentially lead to a decline in fire activity in dry woodlands (due to reduced biomass accumulation) and increase fire activity (dry fuel) in temperate forests (Bradstock, 2010). A fire behaviour model for southeast Australia (Matthews et al., 2012) also suggests changes in fuel load (biomass accumulation) are the underlying controlling factor of fire behaviour in dry woodlands. These patterns are in line with our results, which show changes in moisture availability (biomass accumulation and dryness) controlled BB in southeast Australian temperate sclerophyll woodlands and temperate rainforests in the past, and these factors will likely continue to shape the fire regime in the region (Fig. 6).

Indigenous people have managed the Australian landscape for many millennia, with frequent, low-intensity fire usage to maintain open or mosaic landscapes and promote biodiversity (Trauernicht et al., 2015; Ens et al., 2017; Bowman, 1998). Apart from increasing resource availability, Indigenous culturally-maintained open/mosaic landscapes also reduced the probability of extensive fires on the landscape, especially in southeast Australia under increasingly dry conditions (ENSO intensification), where catastrophic and widespread fires can easily become the norm rather than the exception (Fletcher et al., 2021). The suppression of Indigenous cultural land management following European colonisation of Australia has resulted in increased biomass accumulation in forest zone, leading to catastrophic fires in recent times (Rowe, 1983).

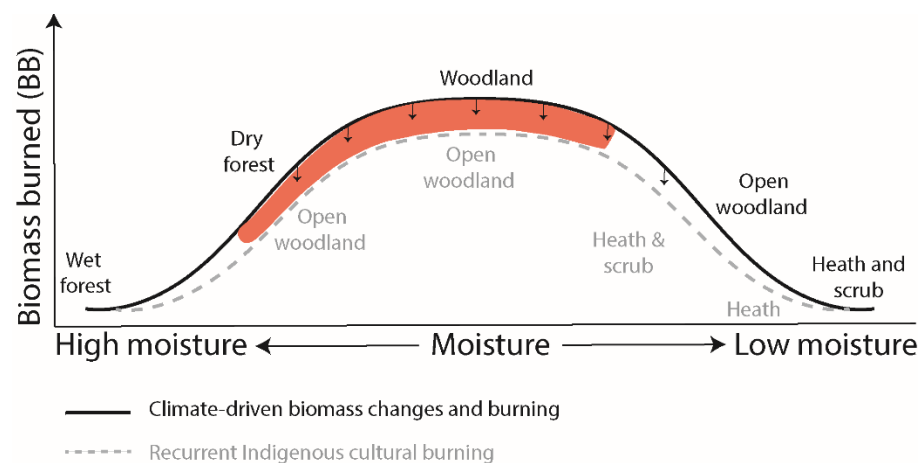


Figure 6: Proposed summary framework (adapted from McWethy et al., 2013) of how climate (black solid line) and recurrent Indigenous cultural burning practices (grey dashed line) modulated fire regimes in southeast Australia during the Holocene. Recurrent Indigenous cultural burning is most important (shaded area) during dry phases in wet forests (drier fuel—dry forest) and during wet phases in woodlands (dense woodland), to reduce biomass accumulation and putting downward pressure on BB. Recurrent Indigenous cultural burning in dry forests and dense woodlands potentially promotes open woodland, with low biomass accumulation and burning. The likelihood of widespread burning in open woodland is low due to reduced fuel connectivity.

Our results suggest Indigenous land use is mainly reflected in changes in RRFE across regions in the past. Given that fire frequency can shape vegetation structure and composition (Noble and Slayter, 1981; Adeleye et al., 2021a), recurrent Indigenous fire-usage likely created open/mosaic diverse vegetation (D'Costa et al., 1989), with reduced fuel loads in many parts of southeast Australia during the Holocene. Results for the FGI in

particular suggest periods of reduced Indigenous burning allowed biomass accumulation, contributing to an increase in BB on the FGI between ~9000 and 5000 years ago and the last ~200 years (Fig. 3 and 4). This implies that continued suppression of Indigenous cultural burning practices and other forms of burning such as coordinated hazard reduction, especially in southeast Australian dry forests/woodlands, will result in increasingly widespread large fires on the landscape. This agrees with previous recommendations to reduce fuel loads in these ecosystems to ameliorate fire behaviour induced by warmer and drier climates (fire weather) in the region (Trauernicht et al., 2015). Preventing future ecosystem biodiversity and habitat loss associated with catastrophic fires in southeast Australia (e.g., 2019/2020 Black Summer bush fires in southeast Australia) may be facilitated by reinstating an Indigenous cultural landscape management approach.

7.6. Conclusions

Climate-driven biomass accumulation and dryness mainly controlled biomass burned (BB) across southeast Australia during the Holocene. Insights from the Furneaux Group Islands (FGI) suggest recurrent Indigenous cultural burning was mainly associated with less biomass accumulation and burning. This result reflects how Indigenous cultural burning worked with the climate to reduce flammable biomass across the landscape in the past. Therefore, reinstating Indigenous cultural burning practices could help reduce the occurrence of catastrophic fire events in southeast Australia's temperate forest ecosystems, thereby minimizing negative impacts on biodiversity, infrastructure and cultural heritage values.

A significant outcome for future research is that the recurrence rates of fire episode (RRFE) estimates are likely a better proxy for anthropogenic burning in sedimentary charcoal records than BB estimates. Considering that high RRFE is not always associated with high levels of biomass burning (as shown on the FGI in the early Holocene), existing Holocene palaeofire records in southeast Australia may primarily reflect a pattern of climate-driven biomass (vegetation) changes rather than Indigenous land use. To avoid potential misinterpretation in future studies, we recommend including both RRFE and BB estimates in future palaeofire studies to better infer anthropogenic land use. In addition to studies of fire severity [66], this will help uncover long-term ecological role of anthropogenic fire and assist

in its reinstatement to restore ecological health and Indigenous cultural values to the landscape.

Chapter 8 EUROPEAN COLONIZATION AND THE EMERGENCE OF NOVEL FIRE REGIMES IN SOUTHEAST AUSTRALIA

To further address the aim of understanding human activity's role in shaping past fire regimes and vegetation, this chapter adopts a similar approach to the previous one. However, here the focus is on the last 700 years to identify the drivers of fire regime changes in southeast Australia before and during European colonisation. Like other parts of the colonised world, the imposition of novel approaches to land management have drastically altered fire regimes in Australia. This chapter was motivated by the southeast Australia 2019–2020 catastrophic summer bushfire ('Black Summer'), in an effort to help provide some longer-term insights into how to reduce the likelihood of similar occurrences in the future.

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with
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I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

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Candidate – Print Name

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Date

Endorsed

Prof. Simon Haberle _____

Primary Supervisor – Print Name

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Delegated Authority – Print Name

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Date

8.0. European colonization and the emergence of novel fire regimes in southeast Australia

Abstract

The rapid increase in severe wildfires in many parts of the world, especially in temperate systems, requires urgent attention to reduce fires' catastrophic impacts on human lives, livelihoods, health and economy. Of particular concern is southeast Australia, which harbours one of the most flammable vegetation types on Earth. While previous studies suggest climate and European activities drove changes in southeast Australian fire regimes in the last two hundred years, no study has quantitatively tested the relative roles of these drivers. Here, we use a Generalized Linear Modelling to identify the major driver(s) of fire regime change in the southeast Australian mainland during and prior to European colonization. We use multiple charcoal and pollen records across the region and quantitatively compare fire history to records of climate and vegetation change. Results show low levels of biomass burned before colonization, when landscapes were under indigenous management, even under variable climates. Biomass burned increased markedly due to vegetation/land-use change after colonization and a major decline in regional precipitation about 100 years later. We conclude that Indigenous-maintained open vegetation minimized the amount of biomass burned prior to colonization, while European-suppression of Indigenous land management has amplified biomass accumulation and fuel connectivity in southeast Australian forests since colonization. While climate change remains a major challenge for fire mitigation, implementation of a management approach similar to the pre-colonial period is suggested to ameliorate the risk of future catastrophic fires in the region.

8.1. Introduction

Catastrophic wildfires are becoming more frequent and severe in many parts of the world and are associated with unprecedented impacts (Filkov et al., 2020; Nauslar et al., 2017; Flannigan et al., 2013; Dutta et al., 2016; Tran et al., 2020; Bowman et al., 2017). This is particularly true in Australia and North America, as demonstrated by recent (2019/2020) catastrophic wildfires in southeast Australia and California (Filkov et al., 2020; CAL FIRE,

2020; Bowman et al., 2017). The 2019/2020 Black Summer wildfires in southeast Australia claimed 34 human lives, at least 2000 homes, 3 billion animals, and 19 million hectares land area (Filkov et al., 2020). The fires have attracted growing concern internationally and locally in southeast Australia, which houses one of the most flammable vegetation types on Earth: dry sclerophyllous woodlands and forests (Crisp et al., 2011; Dutta et al., 2016; Bowman et al., 2017).

Fire regimes are complex and influenced by multiple factors, including vegetation type and moisture (Bradstock, 2010). Recent studies (Clarke et al., 2019; Tran et al., 2020) have shown that fire weather (dry, windy and hot days) significantly influences fire occurrence and is a significant predictor of the occurrence of catastrophic fires in southeast Australia. However, the role of factors associated with vegetation (fuel composition, connectivity and moisture) is not fully understood (Bradstock et al., 2020). Quantitative knowledge of long-term changes in vegetation composition and connectivity, as well as fire regimes, provide a robust baseline that can guide to effective fire management plans (Gilson et al., 2019). Palaeoecological records offer the possibility of undertaking such long-term quantitative studies, tapping into the rich knowledge archives of the past (Fordham et al., 2020).

Palaeoecological studies have shown that increasing climatic variability and anthropogenic land-use change drove centennial-scale shifts in fire activity (biomass burned) in southeast Australia for at least the last ~5000 years (Kershaw et al., 2003; Black et al., 2008; Mooney et al., 2011, 2012). On shorter timescales, agro-pastoral activities following Australia's colonization by Europeans in 1788 AD are thought to have contributed to landscape changes in the last 200 years, especially via the suppression of Indigenous land management, clearance of forests in some areas and promotion of wooded landscapes in others (Lunt et al., 2006; Fletcher et al., 2021). Several authors have sought to understand and quantify changes in fire activity in southeast Australia in the centuries before and after European colonization (e.g., Dodson and Mooney, 2002; Mooney et al., 2012; Dodson et al., 1993, 1994a, 1994b, 1994c, 1995). However, the drivers of past fire regimes in the region are still not fully understood, as no study has quantitatively tested the role of centennial-scale vegetation and climate changes in shaping fire regimes.

Here, we use a robust modelling approach to identify the major driver(s) of fire regimes in the southeast Australian mainland (SEAM) in the centuries before and after European initial colonization. To achieve this, we use multiple charcoal records from the SEAM, spanning

the last 700 years, to reconstruct past biomass burned (an estimate of the amount of vegetation biomass consumed by landscape fire). This SEAM biomass-burned reconstruction was then quantitatively compared to records of vegetation turnover and independent multi-model-based records of past climate in the region. A quantitative estimate of rates of palynological change in pollen records was used to infer regional vegetation turnover (beta diversity), a reflection of vegetation (fuel) compositional change on the landscape. It has been empirically established that palynological rates of change in southeast Australian pollen assemblages are significantly correlated with vegetation compositional change in the region (Adeleye et al., 2021a). The results from this study will help inform management efforts not only in Australia, but also in other fire-prone regions globally.

8.2. Study area

Wildfire seasons vary across Australia, generally ranging from winter-dominated, frequent, low-intensity in northern regions characterized by a monsoon climate, to summer-dominated, infrequent high-intensity in southern regions characterized by a temperate climate (Miller and Murphy, 2017; Archibald et al., 2013). In southeast Australian sclerophyll forests, intense fires primarily occur during late summer–autumn (Australian Bureau of Meteorology, 2021).

The SEAM climate is mainly modulated by El Niño Southern-Oscillation (ENSO), Indian Ocean Dipole (IOD) and the Southern Westerly Winds (SWW; CSIRO, 2012). ENSO and IOD bring drought to the region, especially in El Niño years, which are associated with extreme fire weather and fire events (Mariani et al., 2016a; Abram et al., 2020). SWW have the greatest influence in the southernmost part of the SEAM. Positive phases of SWW are generally associated with high summer rainfall (low winter rainfall), while negative phases are associated with high winter rainfall (low summer rainfall) (Australian Bureau of Meteorology). Vegetation on the SEAM is dominated by *Eucalyptus* forests and woodlands, as well as sclerophyllous shrublands (Department of the Environment and Water Resources, 2007), and many lowland areas have been cleared for farmland (Department of Agriculture, Land and Environment, 2018b; Figure 1).

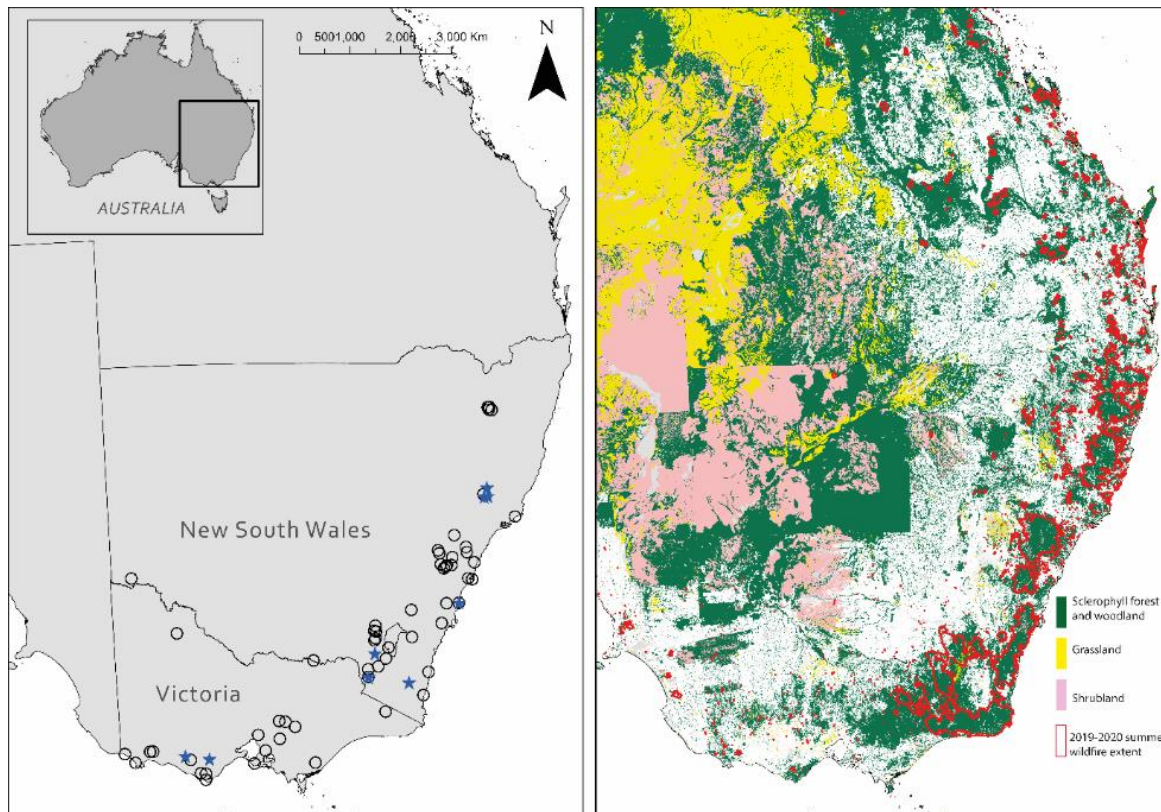


Figure 1: Locations of charcoal (black hollow circles) and pollen records (blue stars) on the southeast Australian mainland used in this study (left panel). Present vegetation distribution and extent of 2019–2020 summer wildfires (right panel). White-coloured areas on the right panel represent cleared areas. (Department of Agriculture, Land and Environment, 2020—National Indicative Aggregated Fire Extent Datasets; Department of Agriculture, Land and Environment, 2018a—National Vegetation Information System version 5.1).

8.3. Methods

Sedimentary charcoal is the most robust indicator of past fire regimes in a given landscape, containing information on past biomass burned and burning frequency (Whitlock et al., 2001; Ali et al., 2012). Sixty-one charcoal records with at least one radiocarbon date every 3000 years were selected across the SEAM from the Global Paleofire database (<https://www.paleofire.org/>; see Table 1 in supplementary material for charcoal data information). Composite charcoal z-scores were then calculated at 50-year resolution using the ‘paleofire’ (‘pfComposite’) package in ‘R’ (Blarquez et al., 2014; R Core Team, 2020) to reconstruct regional biomass burned in the last ~700 years. A Kruskal-Wallis ANOVA test was also performed using the ‘paleofire’ package in ‘R’ to test the dissimilarity in biomass

burned between different time periods (150-year time bin) (Blarquez et al., 2014; R Core Team, 2020).

To reconstruct regional vegetation turnover, nine pollen records spanning the last ~700 years with at least 100-year sampling resolution and at least one radiocarbon/ ^{210}Pb date every 400 years were obtained from a southeast Australian database (Herbert and Harrison, 2016). Pollen records with centennial-scale resolution were required for this study and only nine records met this criterion in the SEAM region (see Table 2 in supplementary material for pollen data information). Pollen records were divided into 100-year time bins and Squared Chord Distances (SCD) calculated between randomly selected samples (resampled 50 $\times$) from adjacent bins to estimate temporal vegetation turnover, using the ‘analogue’ package in ‘R’ (R Core Team, 2020; Simpson and Oksanen, 2020). The average SCD of all nine pollen records was then taken, representing regional vegetation turnover for the SEAM (Adeleye et al., 2021b).

Published pollen and charcoal record chronologies were accepted. Recalibration of published dates using the latest radiocarbon calibration curve (SHCal20: Hogg et al., 2020) made no difference – all published calibrations overlapped with recalibrations at 68 and 95% confidence intervals. Exotic pollen, such as *Pinus*, was also commonly used as a biostratigraphic marker to fine-tune the timing of European settlement in the records (e.g., Dodson et al., 1994a, 1974; Black and Mooney, 2006; Mooney et al., 2007; Kodela and Dodson, 1988).

Generalized linear modelling (GLM) with Gaussian distribution was used to identify major drivers of biomass burned, with vegetation turnover and climatic drivers as predictors. The effect of temporal autocorrelation was removed from the model by multiple resampling of each variable at a lower resolution 1000 $\times$ (Mellin et al, 2010). The best model was selected based on the corrected Akaike’s information criterion (AICc) and delta AICc (ΔAICc) statistics. The climate records used are multi-model averages of ENSO (Nino 3.4 index), temperature and precipitation simulations for eastern Australia based on simulations of the last millennium from a set of climate models: BCC-CSM1.1, CCSM4, CSIRO-Mk3L-1-2, GISS-E2-R, IPSL-CM5A-LR, and MPI-ESM-P (see Brown et al., 2016 and Schmidt et al., 2012 for climate model details). Alongside the fact that these model-based climate simulations were developed for eastern Australia, the simulations were selected due to the model robustness and their high temporal resolution.

8.4. Results

Charcoal composite and vegetation turnover results show a relatively low biomass burned ($z\text{-score} < 0$), with minimal vegetation turnover ($\text{SCD} < 0.2$) before 1788 AD, while biomass burned ($z\text{-score} > 0$) and vegetation turnover ($\text{SCD} > 0.2$) increased markedly after 1788 AD, especially since 1850 AD (Fig. 2). The charcoal composite using a subset ($n=17$) of the charcoal records with at least one radiocarbon date per 700 years shows a similar trend in biomass burned ($r=0.8$, $p=0.002$). Kruskal-Wallis ANOVA test shows a significant ($p < 0.05$) difference between biomass burned before and after 1788 AD (Fig. 2). Generalized linear models (GLMs) show a combination of vegetation turnover and precipitation changes best explain regional biomass burned, judged by the low AICc and dAICc values (Table 1).

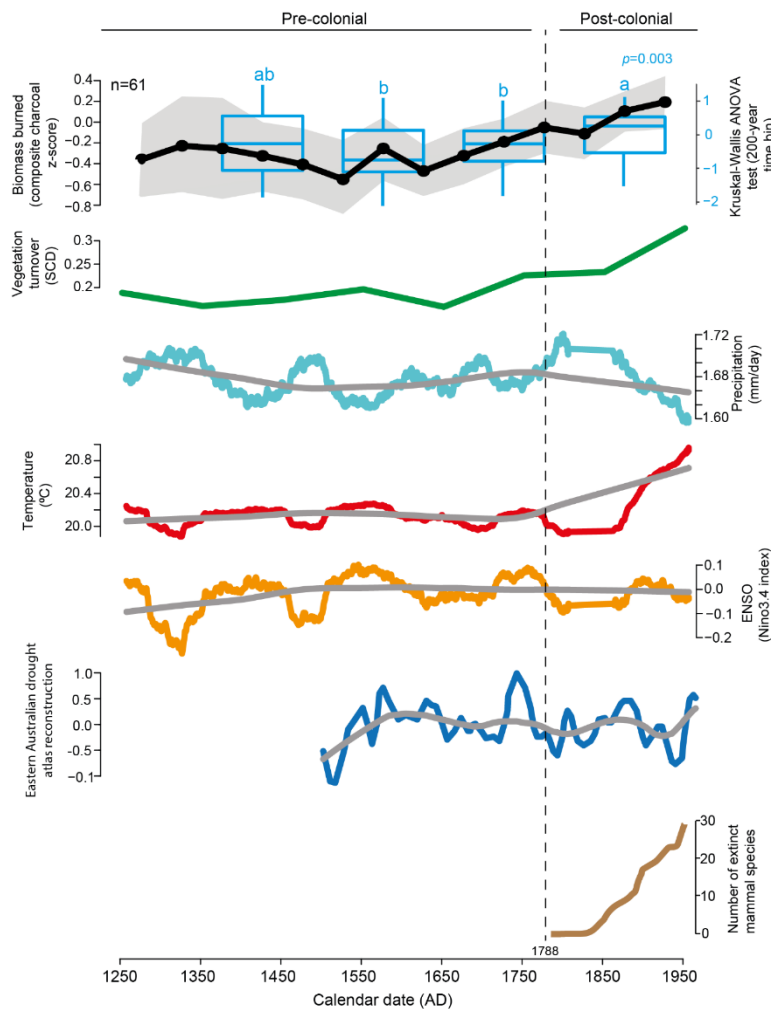


Figure 2: Biomass burned in southeast Australia over the last 700 years before present (present = 1950) with error estimates (grey-shaded area) in relation to vegetation turnover, precipitation, temperature, and ENSO, with loess smoothing (grey curves, span=0.5). Boxplots are the Kruskal-Wallis ANOVA test results, which indicate a significant ($p < 0.05$) difference between biomass burned before and after

European colonization. ENSO (Nino 3.4 index), temperature (°C) and precipitation (mm/day) are based on simulations of the last millennium from a set of climate models for eastern Australia: BCC-CSM1.1, CCSM4, CSIRO-Mk3L-1-2, GISS-E2-R, IPSL-CM5A-LR, and MPI-ESM-P (Brown et al., 2016). Vegetation turnover (SCD) is based on nine pollen records (Herbert and Harrison, 2016) and biomass burned (charcoal z-score) estimate is based on composite of 61 charcoal records from the southeast Australian mainland (Global Paleofire database—<https://www.paleofire.org/>). See Table 1 and 2 in supplementary material for pollen and charcoal data information. Also shown is eastern Australian drought atlas reconstruction, with loess smoothing (span=0.25), which is based on tree rings and coral series (Palmer et al., 2015), as well as the number of extinct mammals in Australia since European colonization (Woinarski et al., 2015).

Table 1: GLMs comparing biomass burned (BB) to vegetation turnover (SCD) temperature (temp), ENSO and precipitation (precip). Models are ranked based on Akaike's information criterion corrected for small sample sizes (AICc) and delta AICc. Also shown are percentage of deviance explained and marginal R² (Rm).

Model	AICc	dAICc	Rm	%Deviance
<i>BB ~ Veg+Precip</i>	-38.1218	0	84.35	91.7
<i>BB ~ Veg+Precip+Temp</i>	-36.8575	1.264	85.93	91.8
<i>BB ~ Veg+ENSO+Precip</i>	-34.8237	3.298	84.5	90.3
<i>BB ~ Veg+ENSO</i>	-34.1719	3.95	81.11	90.2
<i>BB ~ Veg+Temp</i>	-33.6057	4.516	80.59	94.3
<i>BB ~ Veg+ENSO+Temp+Precip</i>	-32.8776	5.244	85.94	89.9
<i>BB ~ Veg+ENSO+Temp</i>	-31.8366	6.285	82.13	95.8
<i>BB ~ Temp+Precip</i>	-25.3593	12.762	71.25	83
<i>BB ~ ENSO+Temp+Precip</i>	-24.1344	13.987	74.21	85.7
<i>BB ~ ENSO+Temp</i>	-7.26838	30.853	31.97	58.4
<i>Null</i>	-5.01251	33.109	0	-
<i>BB ~ ENSO+Precip</i>	0.502465	38.624	1.5	41.9

8.5. Discussion

8.5.1. Potential sources of error

The charcoal and pollen records used in this study are currently the best publicly accessible data sets for the SEAM spanning the time frame considered in this study. We acknowledge that the quality of these data sets (e.g., Dodson et al., 1994a, 1994d; Black and Mooney, 2006; Mooney et al., 2007; Kodela and Dodson, 1988), especially in terms of the generally low resolution and poor chronological control over the targeted time period, may have potentially influenced the timing of shifts in our vegetation turnover and biomass burned reconstructions. Hence, given chronological uncertainties, dates given in the text should be regarded as approximations. Though the overall number of charcoal data sets analysed is high ($n=61$), the majority of the records are non-contiguous microscopic ($<125\text{ }\mu\text{m}$) charcoal records, which have the potential of missing fire events. Despite these limitations, the result presented in this study provides a quantitative insight into the drivers of fire regimes in pre-colonial and colonial landscapes of the SEAM.

8.5.2. Fire regime change driven by vegetation and precipitation changes in southeast Australia

In both Northern and Southern Hemisphere temperate ecosystems, palynological rates-of-change estimates with SCDs >0.2 indicate complete turnover in vegetation types across space and through time (Overpeck et al., 1985; Adeleye et al., 2021b). Our results (Fig. 2) indicate that prior to the 18th century, vegetation was relatively stable and after that time major turnover occurred. Our generalized linear models (GLMs) show that a combination of vegetation turnover and precipitation changes best explain regional biomass burned on the SEAM in the last ~700 years (Table 1).

Vegetation type/structure and moisture, as well as temperature, are major determinants of fire regime (Cochrane and Ryan, 2009; Daniau et al., 2012). However, vegetation type/structure and moisture are more important in dry vegetation types, where fire is often limited by biomass fuel loads and connectivity (Cochrane and Ryan, 2009; Bradstock, 2010; Pausas and Paula, 2012; Daniau et al., 2012). High fuel connectivity in dry woody vegetation is a function of biomass accumulation (increased vegetation growth), which can be caused by one or more of the following: (1) high moisture, (2) high CO_2 , and (3)

insufficient disturbance, such as infrequent fires (Pausas and Paula, 2012; Murphy et al., 2013). A large percentage of the SEAM's forest vegetation falls into the category of dry, contiguous, woody vegetation, making the region one of the most fire-prone places on Earth (Keith, 2017). Also, compared to the pre-colonial landscape, present-day forests on the SEAM are denser and have greater fuel connectivity, while present-day open vegetation has much less tree cover (Mariani et al. in press).

Indigenous population growth and land usage were high and widespread across the SEAM during the last millennium, especially prior to European colonization in 1788 AD (Williams, 2013; Williams et al., 2015c). Scientific studies and ethnographic accounts indicate that Indigenous people regularly and deliberately burned vegetation to keep landscapes open in order to promote resource availability, such as diverse plant-based food and herbivore grazing for hunting, as well as to increase land accessibility and freshwater resources (Bowman, 1998; Gammage, 2005, 2008, 2012; Bird et al., 2020; McWethy et al., 2017; Mulvaney and Golson, 1971). Other fire-related activities carried out by Indigenous people in the past include cooking, ceremonies, and rituals (Mulvaney and Golson, 1971). Existing pollen records suggest European land-use transformations drove tree-cover declines in the partially wooded landscapes on the SEAM following initial colonization (Dodson et al., 1994a, 1994b, 1994c, 1995). A recent land cover reconstruction suggests that forest/woodland understorey shrub density likely increased after colonization at the same time as agro-pastoral landscapes were expanding (Mariani et al., in press). These denser forest understoreys might represent a major increase in forest connectivity over the last two centuries.

Vegetation turnover recorded from 1788 AD (especially since 1850 AD) on the SEAM likely reflects this polarisation in fuel connectivity and woody biomass accumulation following European arrival, which in turn led to increased biomass burned across the landscape. The majority (90%) of pollen records considered in our study show increases in shrubs such as *Kunzea*, *Ericaceae*, *Melaleuca*, and *Leptospermum* after 1788 AD. Shrub expansion would have increased fuel connectivity by creating ladder fuels linking the surface vegetation layer to the tree canopy (Sullivan et al., 2012), facilitating widespread and severe fires and increases in the amount of biomass burned on the landscape. Indigenous peoples used frequent low-intensity fires (cool burning) to promote mosaic landscapes, thus reducing fuel connectivity and fire spread (Bowman, 1998; Gott, 2005). Our data support the hypothesis that European suppression of Indigenous cultural burning helped to drive increases in

vegetation thickening (biomass accumulation and fuel connectivity) on the SEAM (Bradstock et al., 2002; Mariani et al., in press).

A two-way feedback exists between fire and vegetation, such that fire can drive vegetation turnover and vice versa (Marlon et al., 2016; Feurdean et al., 2020). However, fire regimes in most cases are pre-conditioned by vegetation structure and moisture, especially in temperate ecosystems (Feurdean et al., 2020; Pausas and Paula, 2012; Bradstock, 2010). A study of contemporary fire ecology in temperate southeast Australia (Bradstock, 2010) shows that biomass availability (vegetation) is the major factor limiting fire activity. Deliberate reduction of biomass load (to limit fuel connectivity) has been proposed to reduce potential risks of fire weather-driven catastrophic fires in the region (Matthews et al., 2012).

At a regional scale, decreasing precipitation and drought variability are associated with the Interdecadal Pacific Oscillation across eastern Australia since the 1600s (Palmer et al., 2015; Gergis et al., 2012; Mantua and Hare, 2002). This climatic trend is likely to have not only influenced biomass burned as early as ~1650 AD, but also exacerbated biomass burned over the last 200 years by increasing fuel dryness. The unstable/weak connection between ENSO (Nino3.4) and precipitation across eastern Australia on a decadal scale (Palmer et al., 2015; Brown et al., 2016) may explain why our GLMs identified ENSO as a minor driver of fire regimes in southeast Australia over the last ~700 years.

Precipitation was also generally low between ~1450 and 1650 AD, a possible indication of pre-existing climate variability prior to European colonization in 1788 AD (Barr et al., 2014; Fig. 3). However, in contrast to the colonial period, biomass burned during this period was relatively low, and may be explained by the open vegetation maintained by Indigenous peoples through frequent low-intensity patch burning (cool burning), which reduced understorey shrub load and fuel connectivity for landscape-scale fires (Gammage, 2005). Other ecological factors, such as herbivory and changes in soil conditions may have also played a role in maintaining relatively low levels of plant biomass and vegetation density (Eldridge et al., 2017), contributing to the open landscape and low biomass burned during this period. Native mammal populations have crashed in Australia since the 1850s (Woinarski et al. 2015), but prior to this time these herbivores are likely to have played a key role in suppressing biomass (Fig. 2).

Overall, the role of Indigenous people in maintaining diverse and interconnected ecosystems and landscapes appears to have been dismissed or even deliberately suppressed since European colonization (Gammage, 2012; Fletcher et al., 2021). The disruption of Indigenous burning practices has not only elevated the present-day risk of catastrophic fires in southeast Australia but has also led to changes in biodiversity maintained by Indigenous skilful burning for many millennia (Adeleye et al., 2021b, 2021c; Bowman, 1998; Bowman et al., 2011). While climate-change risks remain the primary global challenge for fire mitigation, local-scale management targeted at restoring pre-colonial fire regimes will likely help reduce present fuel connectivity, thus altering fire behaviour and diminishing the potential for widespread wildfires in SEAM forests and woodlands. This conclusion echoes the recommendations of the Australian Royal Commission into Natural Disaster Arrangements on wildfire, which highlighted the urgent need for states and territories to strengthen their engagements with Traditional Owners to further explore Indigenous land and fire management insights throughout the process of public management activities (Royal Commission into Natural Disaster Arrangement, 2020).

Management approaches that draw on traditional knowledge are also now being recommended in South America, North America, and southern Europe to reduce risks and effects of severe wildfires in fire-prone ecosystems (Mistry et al., 2019; Eloy et al., 2019; White et al., 2011; Keane et al., 2002; Fernandes et al., 2002). It is therefore becoming apparent that the knowledge of the past (traditional land management) is key to effective future management of severe wildfires globally. The earlier this is embraced by land managers and policy makers, the lesser the risk of future losses of human lives, properties, cultural heritage, ecosystem functions, and biodiversity associated with severe wildfires (Tran et al., 2020; Filkov et al., 2020; CAL FIRE, 2020).

8.6. Conclusion

Results from this study support the idea that Indigenous peoples maintained a fire regime with low levels of biomass burning on the southeast Australian mainland prior to European colonization, while European suppression of Indigenous cultural land management, exacerbated by increasingly dry conditions, has driven an increase in biomass burned after colonization. Considering the projected increase in fire weather and extreme fire events for southeast Australia, exploring management approaches modelled on Indigenous cultural

burning practices is recommended to reduce the risks of future catastrophic wildfires in the region.

Chapter 9 CONCLUSION

The overall goal of this thesis was to provide insights into how the use of palaeoecology-informed management approach can significantly assist in tackling current environmental challenges in Australia, especially catastrophic fires and associated ecosystem changes. This goal has been achieved by providing a deeper understanding of past links between ecosystem changes, fire, climatic and anthropogenic impacts in southeast Australia, and highlighting the implications of these ecological links for current and future management practices. The following research questions were specifically addressed: (1) What drove vegetation and wetland changes in southeast Australia during the last glacial and Holocene? (2) What was the role of humans in vegetation and fire-regime changes in southeast Australia during the Holocene? (3) How can this deep-time knowledge contribute to better managing the ecosystems and fire regimes of the Bass Strait islands and southeast Australia at large?

Results presented in chapters 2–6 show that vegetation and wetland changes were mainly in response to precipitation, temperature and sea-level changes during the late Pleistocene and Holocene. This suggests that climate was the major driver of ecosystem change in southeast Australia in the past, at least at the relatively large spatial scales represented by combining multiple pollen records. Specifically, temperature change and shifts in Southern Westerly Winds (SWW)-driven precipitation were important drivers of vegetation and wetland changes during the last glacial period, while sea-level change and precipitation changes related to El Niño Southern Oscillation (ENSO) and SWW were more important during the Holocene.

Findings in chapters 2–6 also show a strong connection between past fire regimes and vegetation structure. This lends further support to oral histories that describe how Indigenous people used fire to maintain open woodlands in the past, in places where denser vegetation would have existed in the absence of frequent burning. In terms of fire regimes generally, results in chapter 7 reveal that a combination of climate and anthropogenic land use drove past fire regimes across southeast Australia. On a much finer scale, insights from the Bass Strait islands suggest that frequent Indigenous cultural burning promoted open vegetation and helped to reduce major fires that would have been facilitated by suitable climates in the past. Chapter 8 results further show that European-era suppression of this

cultural burning, combined with climate change, gave rise to recurrent large fires in southeast Australia over the last 200 years.

In light of the results presented in chapter 3, showing that Indigenous burning practices contributed to the development of heathlands between 8000 and 6000 years ago, a carefully managed burning approach is recommended to preserve these rare ecosystems in Bass Strait and the wider region. Results from chapter 5 suggest monitoring of wetland hydrology and salinity will help preserve wetlands of significant ecological value on the Bass Strait islands and the wider region. Finally, as revealed by chapters 7 and 8, the re-instatement of Indigenous cultural burning could help reduce the occurrence of destructive fires in southeast Australian forests, restoring ecosystem health and biocultural heritage in the region.

Islands remain among the world's most productive natural ecological settings in which to research some of the globe's current environmental challenges, including ecosystem degradation and extinction, and are therefore of significant ecological interest. However, understanding long-term ecological patterns and processes on islands is key to preserving their ecological values for future scientific investigations. This thesis provides insights into biogeography of island ecosystems, especially on the critical role sea-level changes play in shaping island vegetation development, providing an understanding of potential vegetation changes that may occur in response to projected sea-level rise. The knowledge of ecological changes on land bridges (today are straits and islands) and their role in past species dispersals are presented as well, an area of research that is currently underrepresented globally. The conservation role of islands as biodiversity hosts is also revealed in this thesis, as reflected by the occurrence of some of the presently rare and endangered plant species (e.g., *Myriophyllum muelleri*) in Tasmania on truwana/Cape Barren Island (CBI) for many millennia in the past.

The findings presented in this thesis reinforce the relevance of temporal factors in ecosystem management planning and strategies. The knowledge of long-term or historical patterns and processes in ecosystems is key for effective, enduring and sustainable present and future management. Acknowledging and understanding the past is one of the major keys to tackling or mitigating some of the current global environmental challenges, which not only pose significant threats to ecosystems, but also to humanity. Environmental managers and policy makers need to start integrating palaeo records/datasets into

management and conservation frameworks to build a more robust and reliable basis for decision making and ecosystem interventions. Palaeoecologists also need to engage more deeply with management/conservation agencies and Indigenous communities to develop robust approaches to translating local palaeo-records into effective, culturally meaningful management outcomes. Engaging Traditional Owners and Custodians in government-funded management planning will also provide opportunities for Indigenous communities to exercise their right to practice traditional burning and apply traditional knowledge and expertise that will in themselves help to inform future management plans and strategies. For instance, understanding how people have used fire and lived with fire for millennia will help to better understand how, when and where fire can be harnessed in the present day to maximize natural biodiversity and biocultural heritage.

Potential future work

The main sampling sites of this thesis were on the eastern Bass Strait islands, increasing the available palaeoecological records for the area from three to twelve, while palaeoecological records from the western area remain sparse (two) and these records have low-temporal resolution. Additional, detailed high-resolution palaeoecological records from the western Bass Strait islands will provide further understanding of the spatio-temporal pattern of human occupation on the Bassian Land Bridge during the last glacial, as well as Holocene paleoclimate of southeast Australia. These sites could also be used to further test and verify the conclusions drawn in this thesis in relation to human-managed vs climate-driven fires and vegetation dynamics. As pointed out in Chapter 2 (section 2.5.2), a preliminary charcoal record from King Island suggests burning in western Bass Strait during the Last Glacial Maximum (LGM), which contrasts with the results from truwana/CBI despite vegetation homogeneity across the land bridge. These divergent patterns may indicate spatial heterogeneity in Indigenous fire usage on the land bridge during the LGM or relate to taphonomic processes related to charcoal sources. Also in Chapter 4 (section 5.5.1), changes in wetland hydrology on truwana/CBI agree in early Holocene precipitation lake/precipitation records from eastern Tasmania and New South Wales. However, western Tasmania and western Victoria exhibit contrasting trajectories at the same time, potentially confirming a non-uniform climatic pattern (millennial-scale zonal shifts in Southern Westerlies position) in southeast Australia during the early Holocene. Though this climatic

pattern has been proposed in a previous study (Moreno and Fletcher, 2012), there is great potential to improve the temporal and spatial resolution of the research design to better pinpoint the dynamics and extent of this climatic system in the past. Additional wetland palaeoecological records from western Bass Strait, combined with the *truwana*/CBI records presented in this thesis, will provide further understanding of the temporal and spatial scale of this key climatic pattern in southeast Australia. Similar to this is the need for additional robust proxy-based palaeoclimatic reconstructions across southeast Australia in general, which will help to further develop and better understand the drivers of vegetation and fire-regime changes presented in Chapters 6 and 7. In Chapter 8, we identified vegetation change as the main driver of large fires in southeast Australia since European colonisation; however, we also suspected the background role of Interdecadal Pacific Oscillation (IPO) in fire-regime changes during this period, as in Tibby et al. (2018). Given the current insufficient knowledge of the role climatic changes may have played in driving environmental changes alongside land-use change after European arrival, further investigation on the role (spatio-temporal) of IPO in post-colonial environmental changes is recommended to better understand how climate–land use interactions have shaped and will shape southeast Australian ecosystems in the future.

Finally, this thesis has developed a number of robust methods for the reconstruction of past biodiversity (richness and turnover) and applied them to island ecosystems, thus contributing to a growing global literature on the key insights that island palaeoecology is uniquely placed to reveal into the future of ecosystems on Earth (Nogué et al., 2021).

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APPENDICES

Part A

10.1. Appendix S1 (for Chapter 2)

Crystal Lagoon detailed Pollen (vegetation) zone description

Zone CL-1 (~35–29 ka) at the base of the core is dominated by *Eucalyptus* (50%), Poaceae (20%), Restionaceae (20%), Asteraceae (15%) and *Monotoca* (5–20 %). *Allocasuarina* and *Amperea xiphoclada* are also abundant reaching over 10%. Other taxa present at about 5–10% include *Melaleuca*, *Pomaderris*, *Plantago*, Cyperaceae, *Lepidosperma*, *Potamogeton*, *Triglochin* and *Myriophyllum propinquum* (Fig. S1).

Zone CL-2 (~29–25.2 ka) sees an increase in Casuarinaceae and Poaceae, reaching 20% and 40%, respectively. Asteraceae and Restionaceae decreased to about 5%, while *A. xiphoclada* gradually disappeared. *Plantago* and Cyperaceae increased from this zone to 15% and 10%, respectively.

Zone CL-3 (~25.2–10.7 ka) begins with a rapid decline in Casuarinaceae (5%) and with a further expansion of herbaceous taxa, especially Poaceae, reaching up to 80% as well as an increase in aquatic/wetland taxa, especially *Myriophyllum sp*, reaching over 40%. There is a minor increase in *Eucalyptus* in the first part of this zone (CL-3a: ~25.2–18.6 ka) and Casuarinaceae later in the second part of the zone (CL-3b: ~18.6–10.7 ka).

Zone CL-4 (~2.5 ka–present) towards the top of the record is dominated by Casuarinaceae (30%) and *Monotoca* (20%). Other taxa present at ~5–10% include *A. xiphoclada*, *Dodonaea*, *Goodenia*, Poaceae, Cyperaceae and Restionaceae. *Pinus* (non-native) is abundant in the topmost sample of the record, reaching over 15%. *Lepilaena australis* dominates that aquatic/wetland communities in this zone at ~40% (Fig. S1).

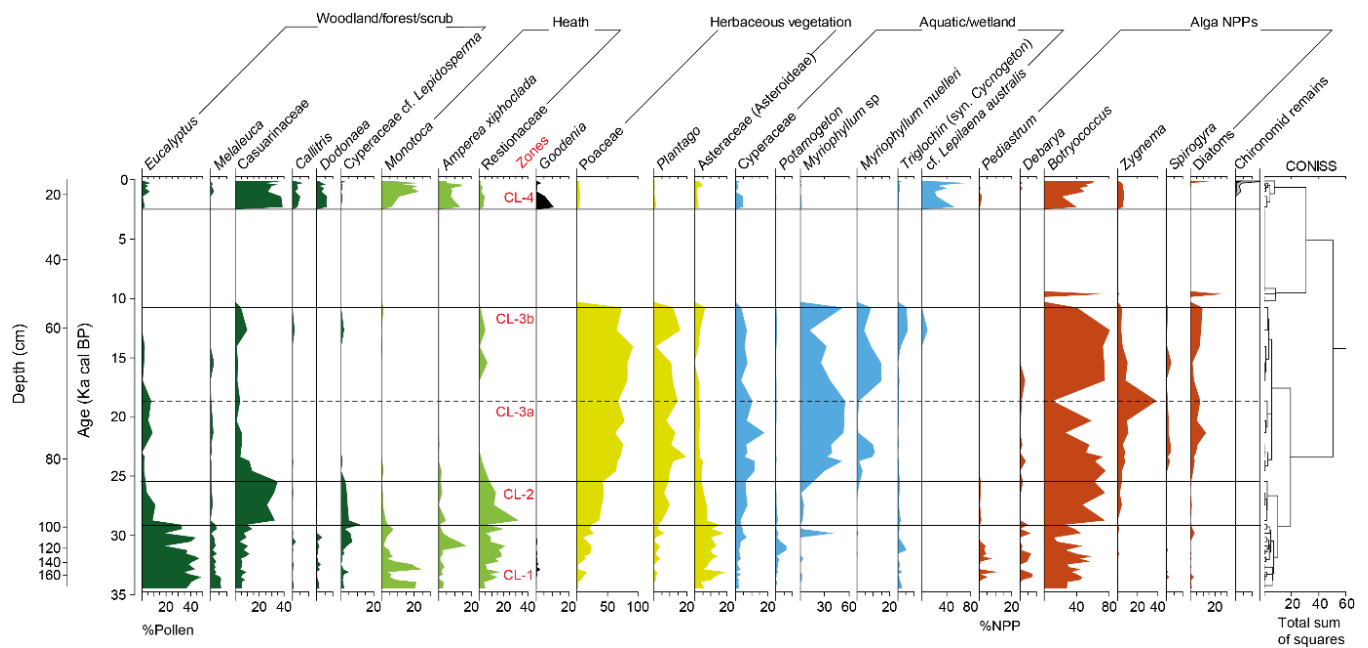


Figure S1: Crystal Lagoon full pollen and NPP record of major taxa (with CONISS zones), spanning ~35 ka to present. The record lacks palynomorphs from ~10.7 to 2.5 ka (sandy zone).

Holocene palaeoenvironmental changes

Coarse sand is present in the Crystal Lagoon record from ~10.7 to 2.5 ka (56–24 cm; Fig. S1) and was likely blown into the lagoon by strong winds and dune transgression associated with the early Holocene sea-level rise (Sloss et al., 2007). The lack of pollen in this interval is likely due to poor preservation in sand. Casuarinaceae abundance in the last ~2000 years may be related to increased dry-land area and soil drainage in coastal sites when sea level dropped to present level (Sloss et al., 2007), as observed on the east and south-west coast of truwana/CBI at the same time (Adeleye *et al.* 2021; Adeleye, unpublished). Sea-level decline in the late Holocene is thought to have contributed to the expansion of scrub and woodland at the expense of heathland on truwana/CBI (Adeleye *et al.* 2021) due to a reduced sea-level disturbance (salt and wind damage, soil instability). Casuarinaceae-dominated scrub likely prevailed on the island's coast, with heathy understories or heathland mosaics in the last ~2000 years.

The abundance of *Botryococcus* and *Zygnema* and aquatic macrophyte *Lepilaena australis* during this period suggests low-fluctuating water level, with increasing salinity in Crystal Lagoon in response to increasingly dry conditions during the late Holocene. An increase in Chironomidae at the top of the record may reflect lake warming in recent times, and shrub

encroachment observed in Crystal Lagoon at the time of coring also reflects present low–fluctuating water level at the site.

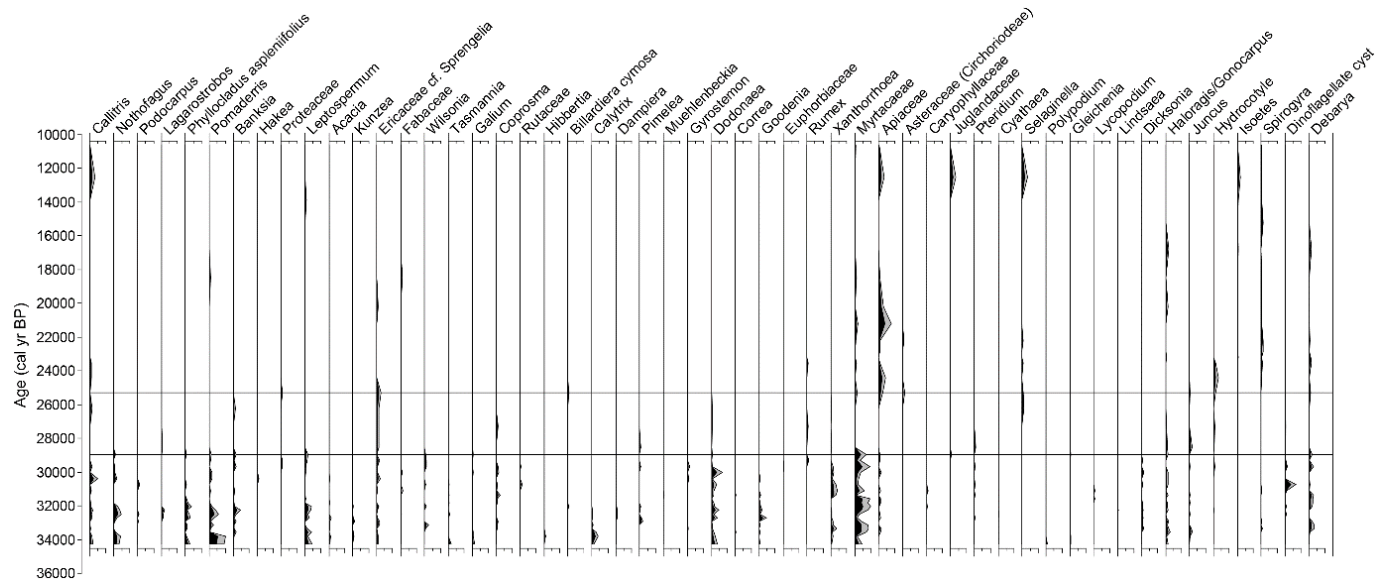


Fig S2: Crystal Lagoon pollen diagram showing taxa <5%, with ×2 exaggeration for visibility.

Table S1: Crystal Lagoon non-pollen palynomorph types and their ecological significance.

NPPs	Ecological significance
<i>Botryococcus</i>	May indicate permanent open or deep fresh water when other alga species (e.g., <i>Pediastrum</i>) are present and used to infer shallow or temporary fresh water if aquatic macrophytes are present (e.g., Davis, 1999; Cook <i>et al.</i> , 2011). <i>Botryococcus</i> is generally abundant in Crystal Lagoon record but most abundant from ~28,000–11,000 cal a BP alongside <i>Myriophyllum</i> and <i>Zygnema</i> , suggesting shallow–variable water level. Likely a wetland system (pond or swamp).
<i>Pediastrum</i>	Although different species can reflect different water depths and physicochemical conditions, <i>Pediastrum</i> in fossil records is generally used to infer open, oligotrophic waters (e.g., Singh <i>et al.</i> , 1981; Dodson, 1974a; Davis <i>et al.</i> , 1977). <i>P. angulosum</i> is the main type recorded in Crystal Lagoon and there is limited ecological information for the species in Australia. Nonetheless, the species is known to be common in lake systems. (Komarek & Jankovska, 2001; Danielsen, 2010). <i>P. angulosum</i> is present in Crystal Lagoon between ~35,000 and 30,000 cal a BP alongside <i>Botryococcus</i> , with low occurrence of aquatic macrophytes, which is indicative of a lake system rather than a wetland.
Zygnemataceae	Members of this family mostly produce their spores in shallow, stagnant, clear, oxygen-rich warm waters and their presence in fossil records is used to infer shallow/temporary standing waters (Hoshaw, 1968; van Geel, 2001). The types recorded in Crystal Lagoon (~28,000–11,000 cal a BP) include <i>Zygnema</i> , <i>Spirogyra</i> and <i>Debarya</i> .
Pennate diatoms	Pennate diatoms recorded in Crystal Lagoon are mostly freshwater types (<i>Pinnularia</i> , <i>Diploneis</i>), except <i>Epithemia</i> , which can also be found in brackish waters (Sonneman <i>et al.</i> , 1999; McCarthy, 2013; Kattel <i>et al.</i> , 2015).

10.2. Appendix S2 (for Chapter 3)

Full vegetation description of coring sites on truwana/Cape Barren Island (CBI), full pollen diagrams and pollen diagram descriptions and individual DCA ordination result.

Reedy (Big Reedy and Yakka Lagoon) vegetation description

At the western edge of Reedy (Plate SIA and B) are fire-killed *Eucalyptus nitida* and the vegetation was likely *Eucalyptus nitida* forest, which is now a sedge land with some emergent shrubs. Also present are areas of *Xanthorrhoea* plants, which have been infested by *Phytophthora cinnamomi*. The swampy area at the site is dominated by herb field and consists of 1 m high stems of fire-killed *Leptospermum scoparium*. A patch of 3 m tall dense scrub is present in the centre of Big Reedy, dominated by *Leptospermum scoparium* intermixed with *Melaleuca gibbosa*, and *Hakea* species. *Gahnia* and *Baumea* dominated sedgeland are present with *Leptospermum* growing emergent in these sedgeland. The eastern edge of Big Reedy, which is where Yakka Lagoon is located, is dominated by *Poa* tussock grassland and *Gahnia* sedgeland above water table, as well as patches of *Melaleuca*, *Pteridium* and *Xanthorrhoea australis*.

Surrounding vegetation includes patches of standing and burnt *Eucalyptus nitida* forests intermixed with *Banksia marginata*, *Leptospermum glaucescens* and *Pteridium esculentum* and a patch of *Callitris rhomboidea* intermixed with *Banksia marginata* and *Leptospermum lanigerum*. Also present in the surrounding vegetation around an open water, is a fringing *Melaleuca squarrosa*-dominated dense scrub and a *Lepidosperma longitudinale* and *Leptocarpus tenax* dominated patch.

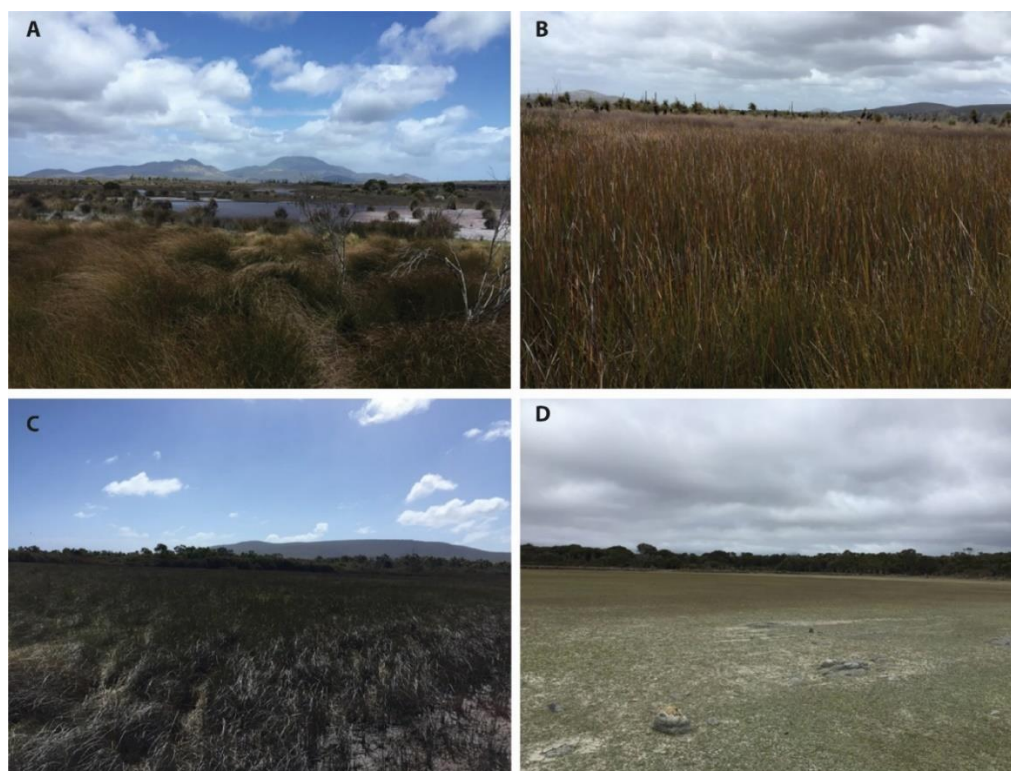


Plate SI: Coring site photos for Big Reedy Lagoon (A), Yakka Lagoon (B), Green Lagoon (C) and truwana East Coast Lagoon (D).

Green Lagoon vegetation description

Green Lagoon (Plate SIC) is an open water body about 50 cm deep occupied by *Cyanogeton procerum* and *Myriophyllum* sp. A fringing beach is also present in a section at the site, which supports *Baumea juncea*, *Utricularia dichotoma*, *Drosera pygmaea*, *Xyris* sp., *Schoenus nitens*, *Selliera radicans*, *Centrolepis fascicularis*, *Selaginella uliginosa*, *Leptocarpus tenax*, *Baumea arthropphylla*, *Distichlis distichophylla*, *Epacris obtusifolia* and *Eurycordia complanatus*. The lagoon is generally surrounded by heathland, scrub, and dense shrubland vegetation. The heathland consists of emergent mallee form *Eucalyptus nitida* up to 2 m with a shrub layer between 90 and 100 cm comprising mainly *Banksia marginata*, *Acacia genistifolia* and *Allocasuarina monilifera*. The heathland grades into dense *E. nitida* scrub about 3 m high mixed with *Banksia marginata*. The heathland also includes species such as, *Correa reflexa*, *Leucopogon ericoides*, *Tetraria capillaris*, *Sprengelia incarnata*, *Gleichenia microphylla*, *Patersonia fragilis* and *Allocasuarina monilifera*. The dense shrubland vegetation is mostly dominated by *Melaleuca* species, while the scrub comprises *Leptospermum glaucescens*, *Leptospermum scoparium*, *Acacia genistifolia*, *Exocarpos* sp., *Acacia mucronata* and *Hakea teretifolia*. The scrub understorey has some *Pteridium esculentum* and *Lepidosperma* sp. Also present around this site is a 3–4 m high scrub dominated by *Eucalyptus globulus* and *Leptospermum laevigatum*, and *Acacia mucronata* and *Callitris rhomboidea* are present in some sections of the scrub.

truwana East Coast Lagoon vegetation description

This site (Plate SID) is surrounded by tall vegetation and mostly about 6–8 m high closed scrub dominated by *Melaleuca*, *Leptospermum*, *Allocasuarina verticillata* and *Callitris*. The lagoon itself is ephemeral and covered by herbfield with fringing *Juncus*. The *Juncus* zone has about 95% vegetation cover, consisting of *Samolus repens*, *Distichlis distichophylla*, *Cotula* sp., and *Baumea juncea*. *Poa* grassland is present on the northern end of the lagoon. Rocky outcrops near the lagoon are colonized by small herbs such as *Angianthus preissianus*, *Wilsonia backhousii* and *Eryngium vesiculosum*. *Samolus repens*, *Lobelia anceps*, *Wilsonia backhousii*, *Schoenus nitens* and *Sarcocornia quinqueflora* are also present in patches in the lagoon floor.

Core Lithologies

The base (200–195 cm) of the BRL core is composed of inorganic clay, which became mixed with fibrous peat from 195–180 cm. The YL core is made up of decomposed peat between 48 and 22 cm and the rest of the core is composed of fibrous peat. The base (73–50 cm) of tECL core is composed of grey inorganic clay, which became yellowish (podzol) from 50–0 cm. The GL core is composed of fibrous peat from 135–103 cm, sandy peat from 103–74 cm, decomposed peat from 74–14 cm, and the top 14 cm is composed of fibrous peat.

Full pollen diagrams and description

Big Reedy Lagoon pollen zone description:

Zone BR-1 (200–177 cm, ~14,000–12,800 cal yr BP) is dominated by *Melaleuca*, *Eucalyptus* and Poaceae at >20%, as well as Asteraceae and Amaranthaceae at ~10%. Although pollen influx shows major expansion of *Melaleuca* started ~9000 cal yr BP. *Lepilaena australis* and *Myriophyllum* are also abundant reaching ~20% and 40%, respectively (Fig. S1a).

Zone BR-2 (177–63 cm, ~12,800–9100 cal yr BP) shows further expansion of *Eucalyptus* to >30% but later drops to ~10% at the end of the zone. Asteraceae and Amaranthaceae decrease early to <5%, while Poaceae remains high and later decreases in the middle of the zone to ~10%. Conversely, *Allocasuarina/Casuarina* (*Allocasuarina*) peaks to about 40% in the middle of the zone when Poaceae decreases. *Isoetes gunnii* is also present in the zone between ~11,500 and 9000 cal yr BP, reaching up to 10%.

Zone BR-3 (63–27 cm, ~9100–7200 cal yr BP) shows increases in *Sprengelia*, *Epacris impressa* and *Selaginella* at about 20%. Although pollen influx shows *Sprengelia* remains well represented until ~4000 cal yr BP (Fig. S1c). *Leptospermum* peaked briefly to over 40% at the beginning of the zone and decreases to <10% between ~9000 and 8500 cal yr BP. *Allocasuarina* fluctuated through the zone and drops to <20% by ~7200 cal yr BP. Restionaceae shows a pronounced increase, reaching >60%, while *Isoetes gunnii* disappears.

Zone BR-4 (27–1 cm, ~7200–1000 cal yr BP), which is the topmost zone, continues to show consistent presence of *Melaleuca* (20%), however, *Leptospermum* representation increases to over 40% in the first half of the zone (~7000–4000 cal yr BP) and decrease to <10%. *Sprengelia*, and *E. impressa* also decrease to <10%. *Monotoca* is present throughout the zone at ~10%, while *Allocasuarina* and *Callitris* increase in the second half of the zone (~4000 – 1000 cal yr BP) to about 20% and 10%, respectively. Restionaceae shows a major decrease through the zone to <10% (Fig. S1a).

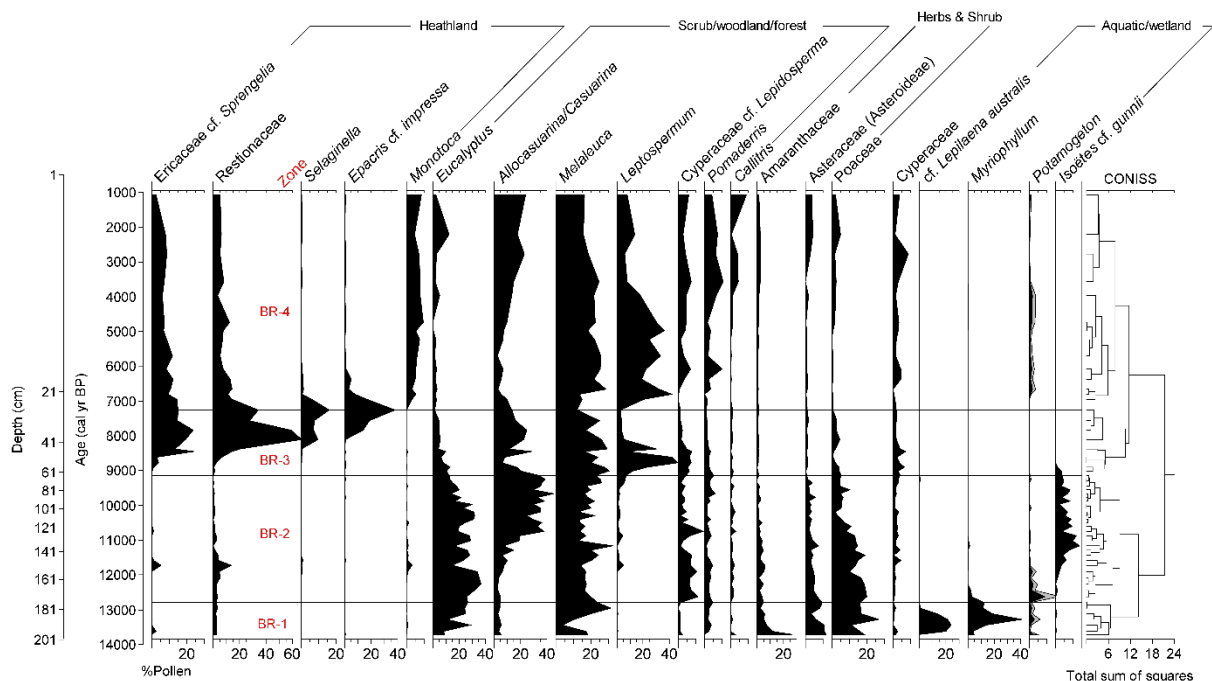
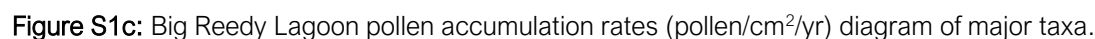
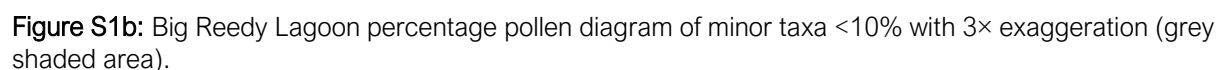


Figure S1a: Big Reedy Lagoon percentage pollen diagram of major taxa with at least 10% representation.



Big Reedy Lagoon macroscopic charcoal accumulation rates (CHAR) are low (<5 particles/cm²/yr) during the Late Glacial (200–156 cm, ~14,000–11,900 cal yr BP) and quickly increase during the early Holocene between ~11,900 and 7000 cal yr BP, reaching over 20 particles/cm²/cal yr. Accumulation rates decrease again to <5 particles/cm²/yr after ~7000 cal yr BP and the rest of the record. Similarly, microscopic CHAR are highest from early to mid- Holocene (~11,000 and 5000 cal yr BP), reaching $>9 \times 10^{10}$ particles/cm²/yr, and low in the rest of the record $<6 \times 10^{10}$ (Fig. S2).

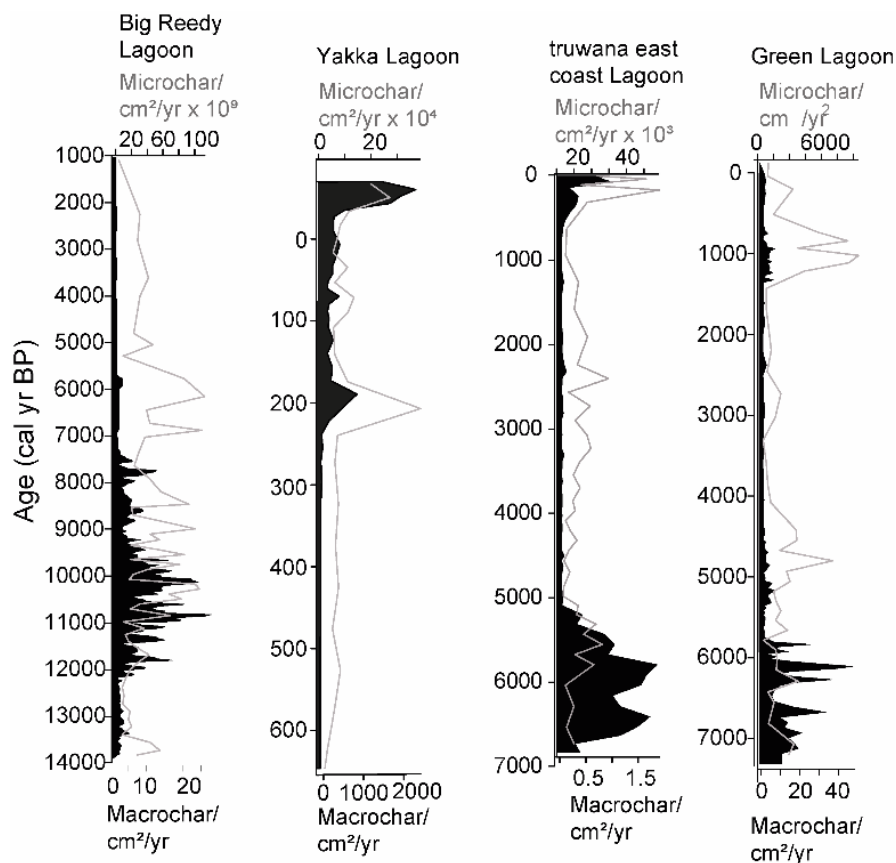


Figure S2: Macroscopic (black) and microscopic (grey) charcoal accumulation rates for all sites.

Yakka Lagoon pollen zone description

Zone Y-1 (45–23 cm, ~630–200 cal yr BP) shows abundance of *Melaleuca* and *Monotoca* at ~20 – 30%, as well as *Eucalyptus* and *Leptospermum* at about 10%. *Allocasuarina* and Restionaceae maintain values of 10-20% throughout. *Xanthorrhoea* and *Selaginella* increase in the second half of the zone (~460–200 cal yr BP) to >10%. Similarly, Cyperaceae also increase in the second half of this zone to >10%.

Zone Y-2 (23–0 cm, ~200 cal yr BP–present) shows increases in Poaceae and *Selaginella* at >10%, while *Melaleuca*, *Monotoca*, *Eucalyptus* and *Leptospermum* decrease to about half of their percentages compared to the previous zone. This zone also marks the appearance and increase in exotic *Pinus* pollen. Cyperaceae increased further in this zone to >20% (Fig. S3a).

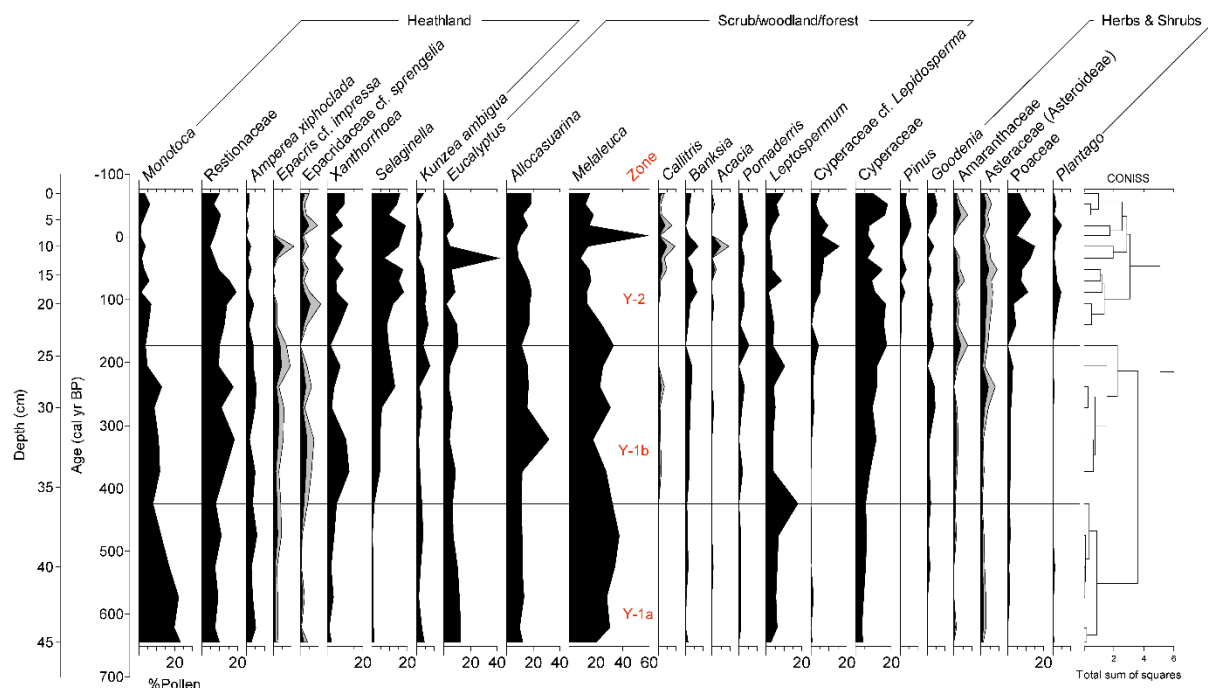


Figure S3a: Yakka Lagoon percentage pollen diagram of major taxa with at least 5% representation, shown with 3× exaggeration (grey shaded area).

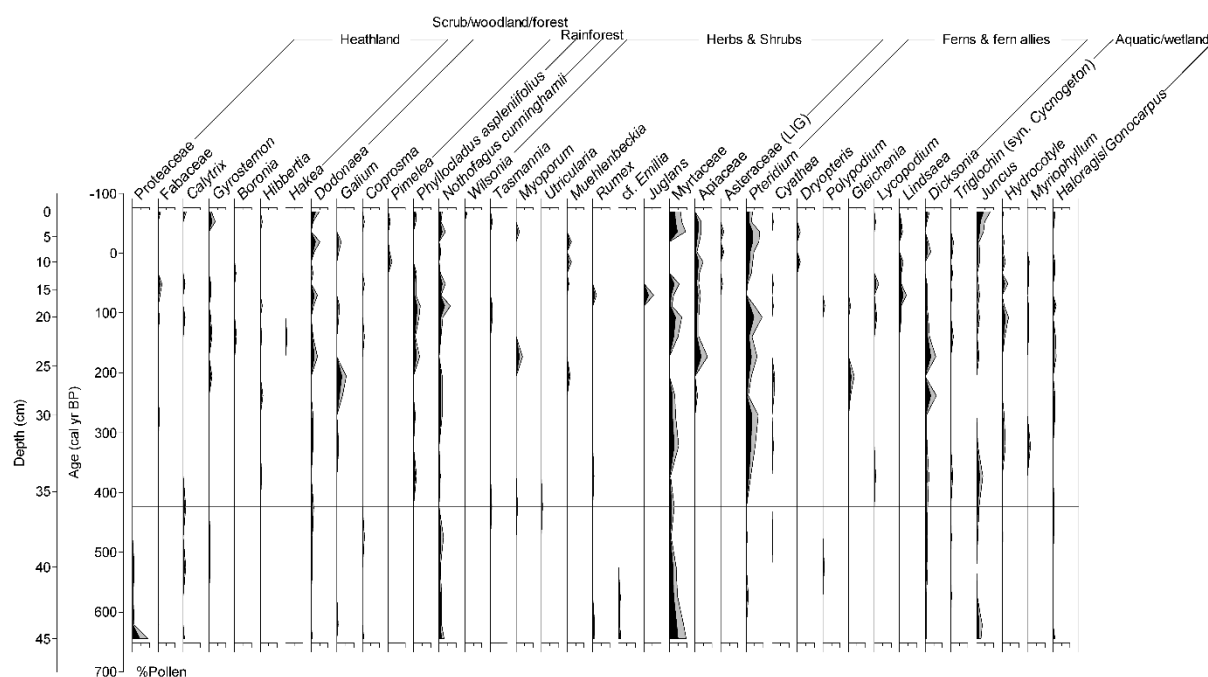


Figure S3b: Yakka Lagoon percentage pollen diagram of minor taxa <5% with 3× exaggeration (grey shaded area).

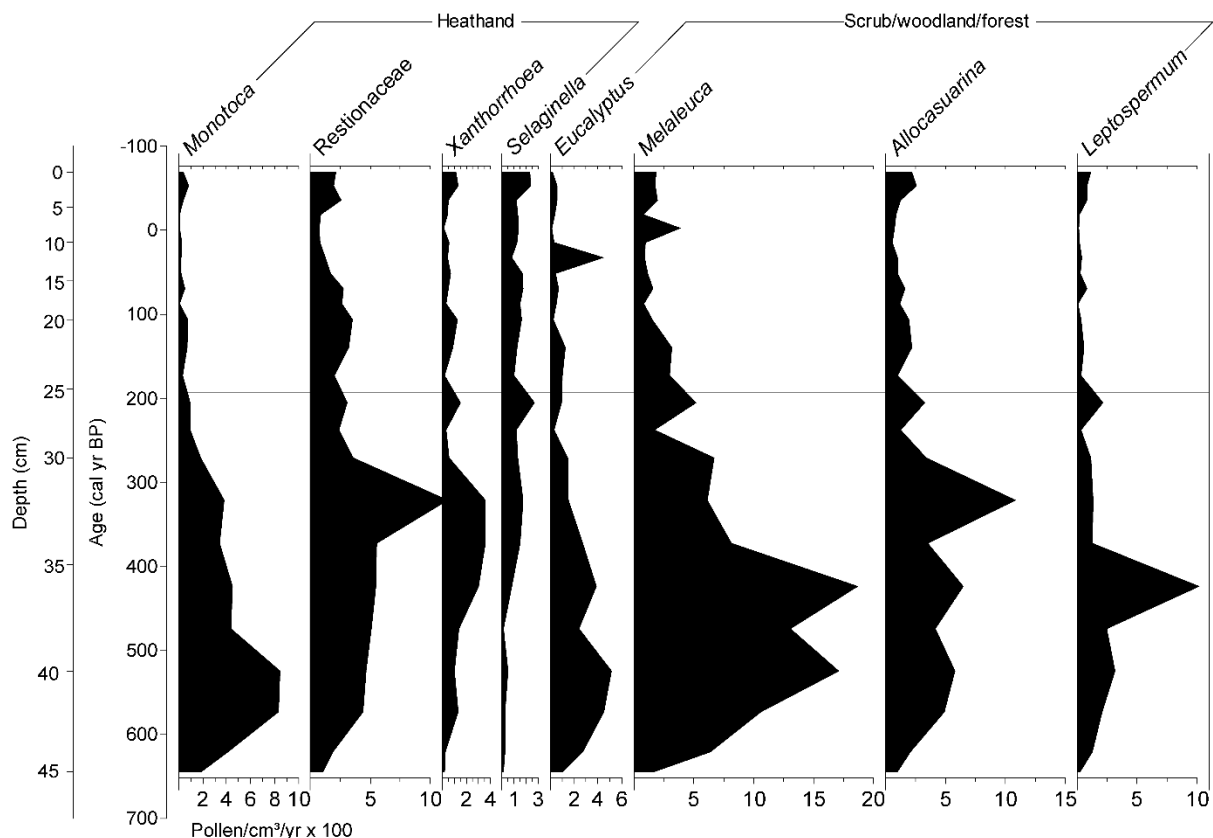


Figure S3c: Yakka Lagoon pollen accumulation rates (pollen/cm²/yr) diagram of major taxa with 3× exaggeration (grey shaded area).

Yakka Lagoon charcoal record

The YL macroscopic charcoal results show high accumulation rates from ~230 cal yr BP to present, ranging from ~300 to >1000 particles/cm²/yr and low rates prior to this time (<100 particles/cm²/yr). Microscopic CHAR are stable throughout the record, ranging between 1×10^4 – 5×10^4 particles/cm²/yr; however, there is a peak ~230 cal yr BP, reaching $>30 \times 10^4$ particles/cm³ (Fig. S2).

truwana East Coast Lagoon pollen zone description

Zone TEC-1 (73–58 cm, ~7000–5100 cal yr BP) is dominated by *Monotoca*, *Amaranthaceae* and *Allocasuarina* at 30 – 40%, 30 – 40% and 10%, respectively (Fig. S4a). *Restionaceae* is also abundant at ~10–20%. Zone TEC-2 (58–17 cm, ~5100–1700 cal yr BP) shows an expansion of *Dodonaea* and *Phyllocladus aspleniifolius*, reaching up to ~30% and major decrease in *Amaranthaceae* to ~2% in the first half of the zone and later increase to ~10% from ~3500 cal yr BP, although pollen influx shows *Dodonaea* is most abundant in the previous zone (Fig. S4c). *Monotoca* also slightly decreases in most samples to about 20%. *Myriophyllum* (10–20%) is generally well represented and *Myriophyllum muelleri* (~10%) gradually increases through the zone. Zone TEC-3 (17–1 cm, ~1700 cal yr BP–present) shows an expansion of *Allocasuarina* (20%), and *Pteridium* (~20%) and *Pinus* (>10%) increase towards to the end of the zone. However, pollen influx shows *Allocasuarina* is highest in zone TEC-1. *Phyllocladus aspleniifolius* declined towards

the end of this around 200 cal yr BP. *Myriophyllum muelleri* increases to ~70%, Cyperaceae increase to ~10%, and *Wilsonia* (>15%) increases towards the end of the zone (Fig. S4a). The overall abundance of *Phyllocladus asplenifolius* in the record may reflect a far regional (possibly mainland Tasmania) rainforest signal via long distance transport. However, the overlap of the decline around 200 years ago with *Pinus* and *Pteridium* increase may also suggest possible presence of a small rainforest/rainforest scrub refugium on truwana/CBI, which disappeared upon European arrival.

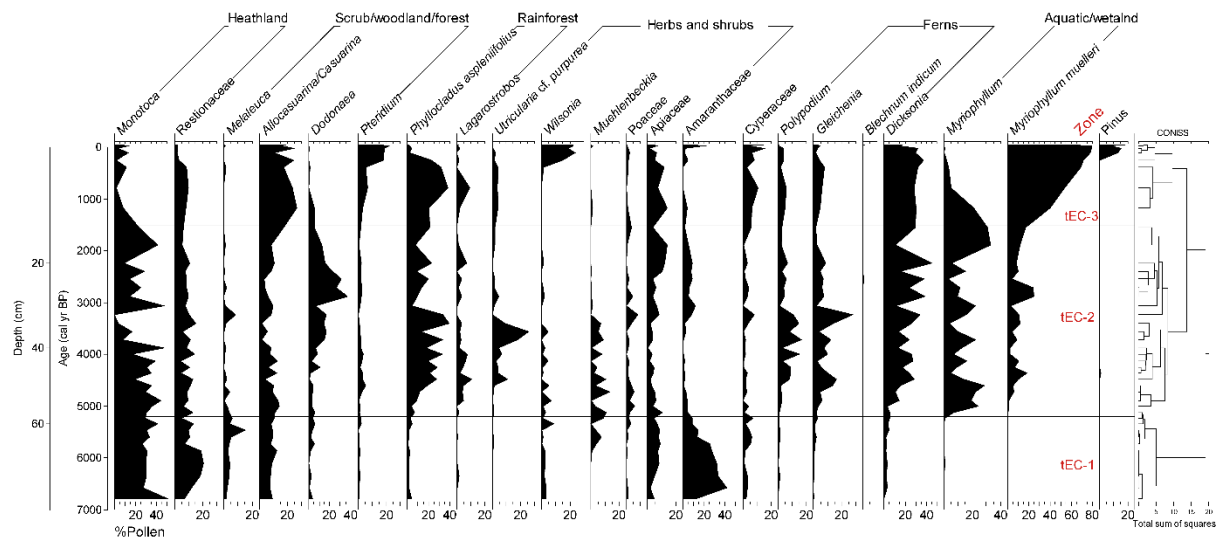


Figure S4a: truwana East Coast Lagoon percentage pollen diagram of major taxa $\geq 10\%$ representation.

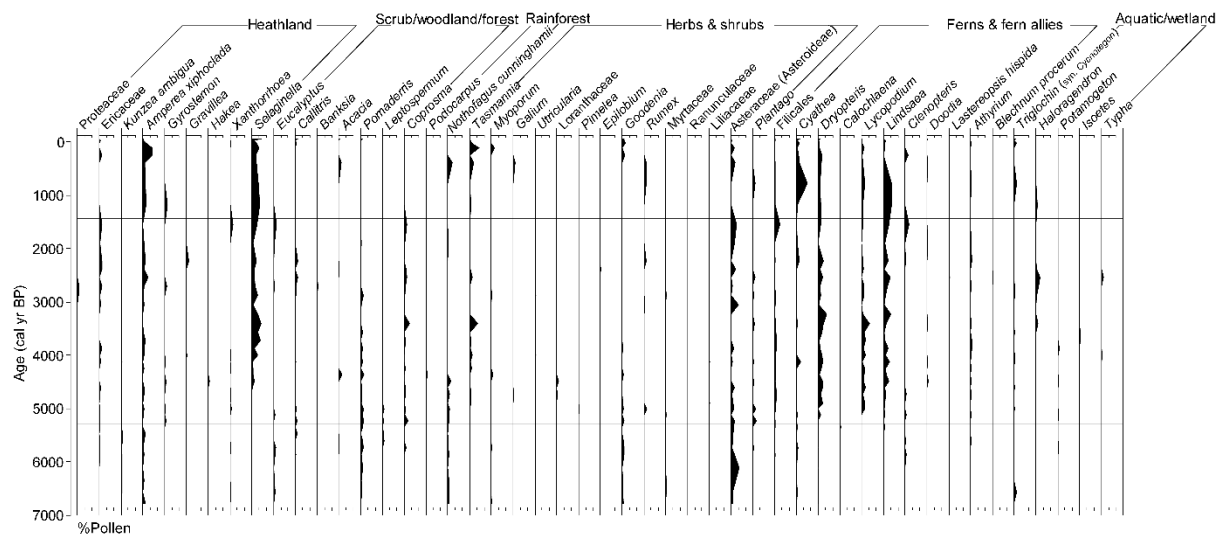


Figure S4b: truwana East Coast Lagoon percentage pollen diagram of minor taxa <10%

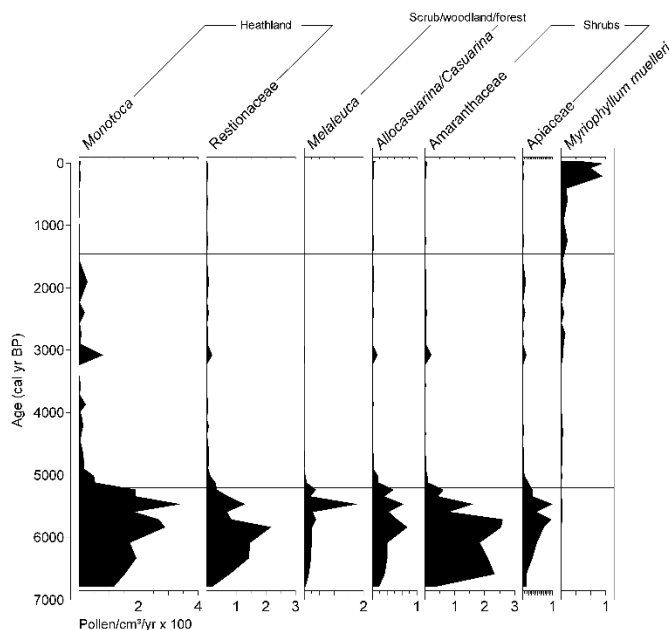


Figure S4c: truwana East Coast Lagoon pollen influx diagram of major taxa with 3× exaggeration (grey shaded area).

truwana East Coast Lagoon charcoal record

TEC Lagoon macroscopic CHAR are consistently high in the base of the record from ~6900 – 5200 cal yr BP (73–59 cm) and the last ~200 years (7–1 cm) with accumulation rates of up to 1.5 particles/cm²/yr and 0.4 particles/cm²/yr, respectively and accumulation rates are low (<0.2 particles/cm²/yr) for the rest of the record. Microscopic CHAR are also high between ~6000 and 5000 cal yr BP (~6×10⁴ particles/cm²/yr), drop to <2×10⁴ particles/cm²/yr from about 5000 to 4000 cal yr BP and gradually increase between ~3200 cal yr BP and present, reaching a peak of >40×10³ particles/cm²/yr (Fig. S2).

Green Lagoon pollen zone description

Zone G-1 (134–107 cm, ~7300–6000 cal yr BP) at the base of the record is mainly characterized by *Monotoca* (15 – 50%), *Leptospermum* (20%), *Eucalyptus* (10%), *Acacia* (10%), *Melaleuca* (10%) and *Sprengelia* (10%). Zone G-2 (107–91 cm, ~6000–5500 cal yr BP) is largely dominated by Amaranthaceae (35%), while the majority of other aforementioned taxa decrease to ~5% or lesser, and *Allocasuarina* is present at ~10%. *Gahnia* is also present at ~12%.

In zone G-3 (91–42 cm, ~5500–2300 cal yr BP), *Monotoca*, *Leptospermum*, *Eucalyptus*, *Acacia* and *Melaleuca* increase again to at least 10% and *Allocasuarina* continues to be present mostly at 10%. There is a major increase in *Gahnia* through this zone reaching >30% and *Myrtophyllum propinquum* is also abundant (up to 20%) between ~5500 and 4000 cal yr BP. Zone G-4 (42–0 cm, ~2300 cal yr BP–present) at the top of the core is characterized by a major increase in *Callitris*, reaching up to 15%. *Lepidosperma* (~10%) also expands to ~10%, while *Gahnia* decreases quickly to <10% (Fig. S5a).

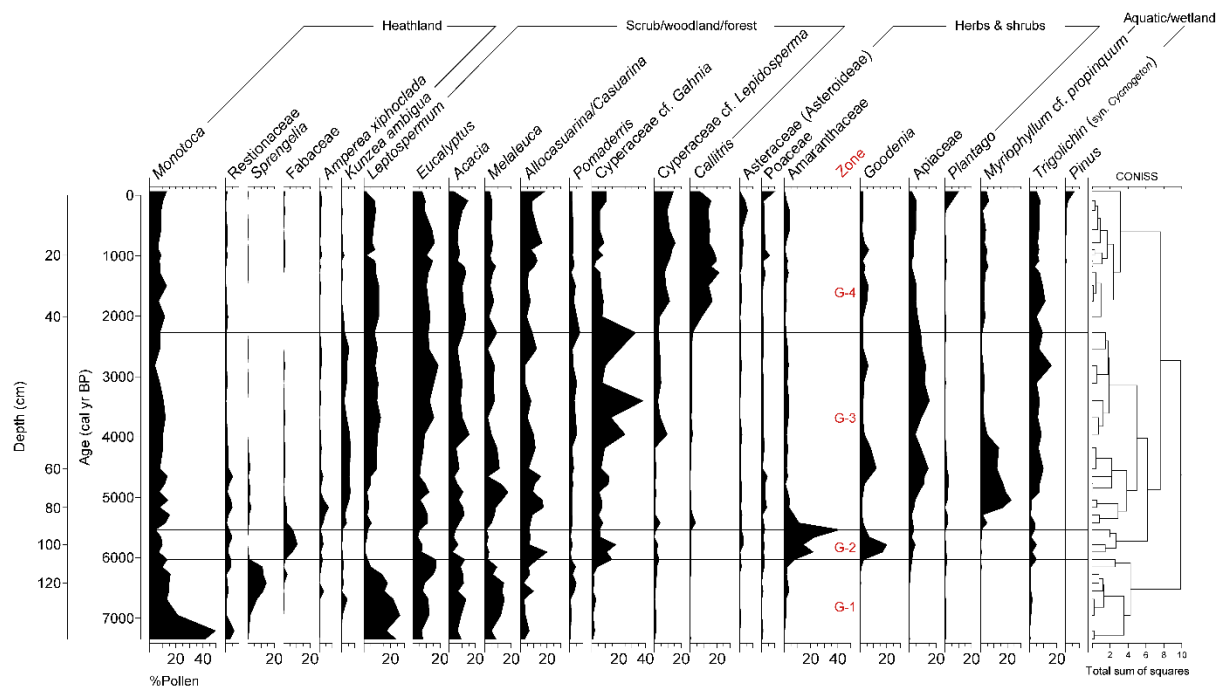


Figure S5a: Green Lagoon percentage pollen diagram of major taxa $\geq 10\%$.

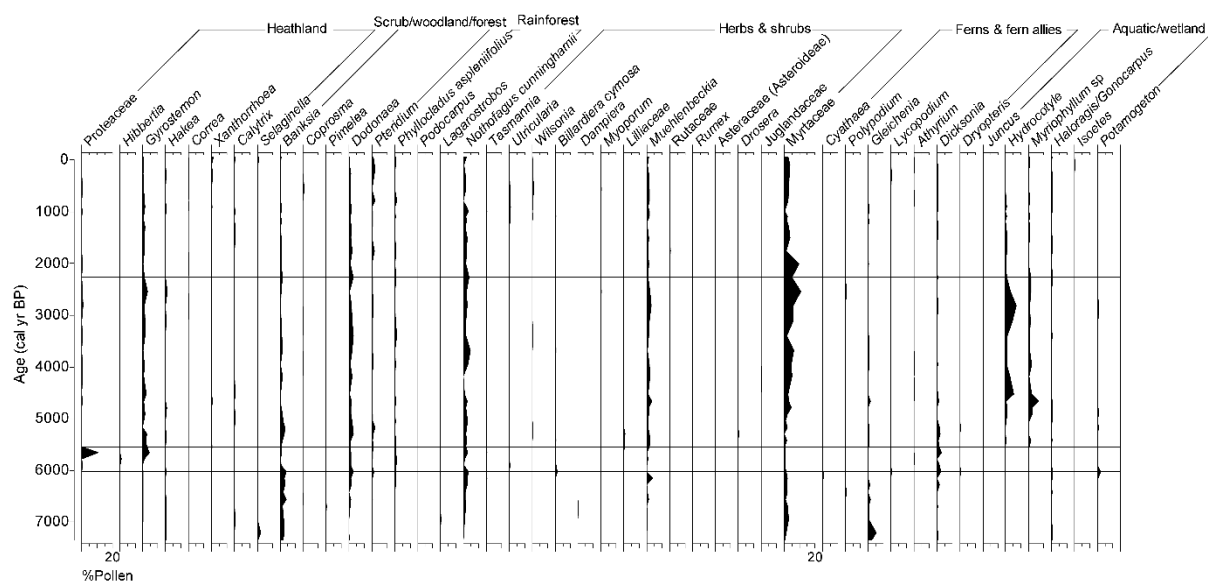


Figure S5b: Green Lagoon percentage pollen diagram of minor taxa $< 10\%$.

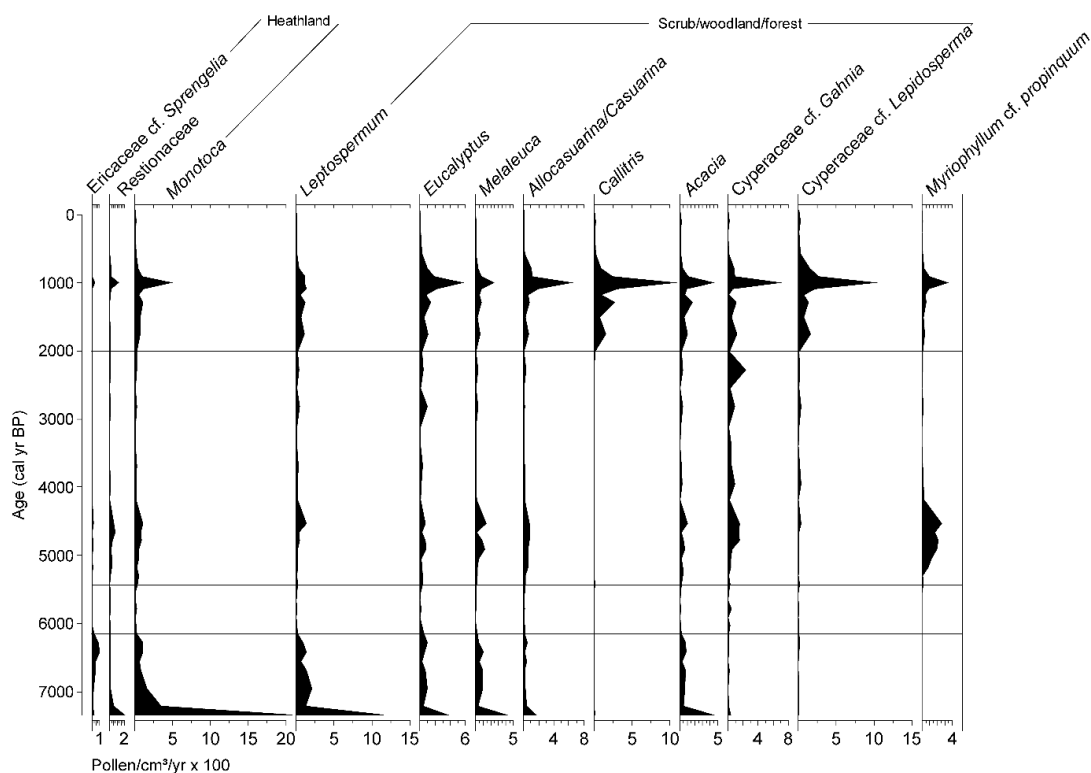


Figure S5c: Green Lagoon pollen accumulation rates (pollen/cm²/yr) diagram of major taxa.

Green Lagoon charcoal records

Green Lagoon macroscopic CHAR are highest in the base of the record, which is dated at mid- Holocene (~7300 and 6000 cal yr BP), ranging between 10 and 20 particles/cm²/yr, and low accumulation (<10 particles/cm²/yr) in the rest of Holocene. Microscopic CHAR are mostly around 4000 particles/cm²/yr between ~7300 and 4600 cal yr BP and between ~1500 and 600 cal yr BP, and the highest rates are observed around 4800 cal yr BP and between ~1200 and 600 cal yr BP, reaching >8000 particles/cm²/yr (Fig. S2).

Individual DCA ordination results

For Big Reedy and Yakka Lagoon, heath and scrub development is mostly significantly ($P<0.01$) related to effective precipitation, sea-level change, ENSO and summer insolation, while fire is most significantly related *Eucalyptus* woodland development (Fig. S6). In truwana East Coast Lagoon, sea-level change and summer insolation are most significantly related to heath and scrub development. For, Green Lagoon, heath development is most significantly related to winter insolation (low summer insolation), sea-level change, fire and effective precipitation, while scrub and woodland development is most significantly related to summer insolation and ENSO (Fig. S6). The differences observed in terms of drivers of vegetation development, especially in tECL record (<7000 cal yr BP) is most likely due to the length of the record compared to BRL and GL, which are >7000 cal yr BP.

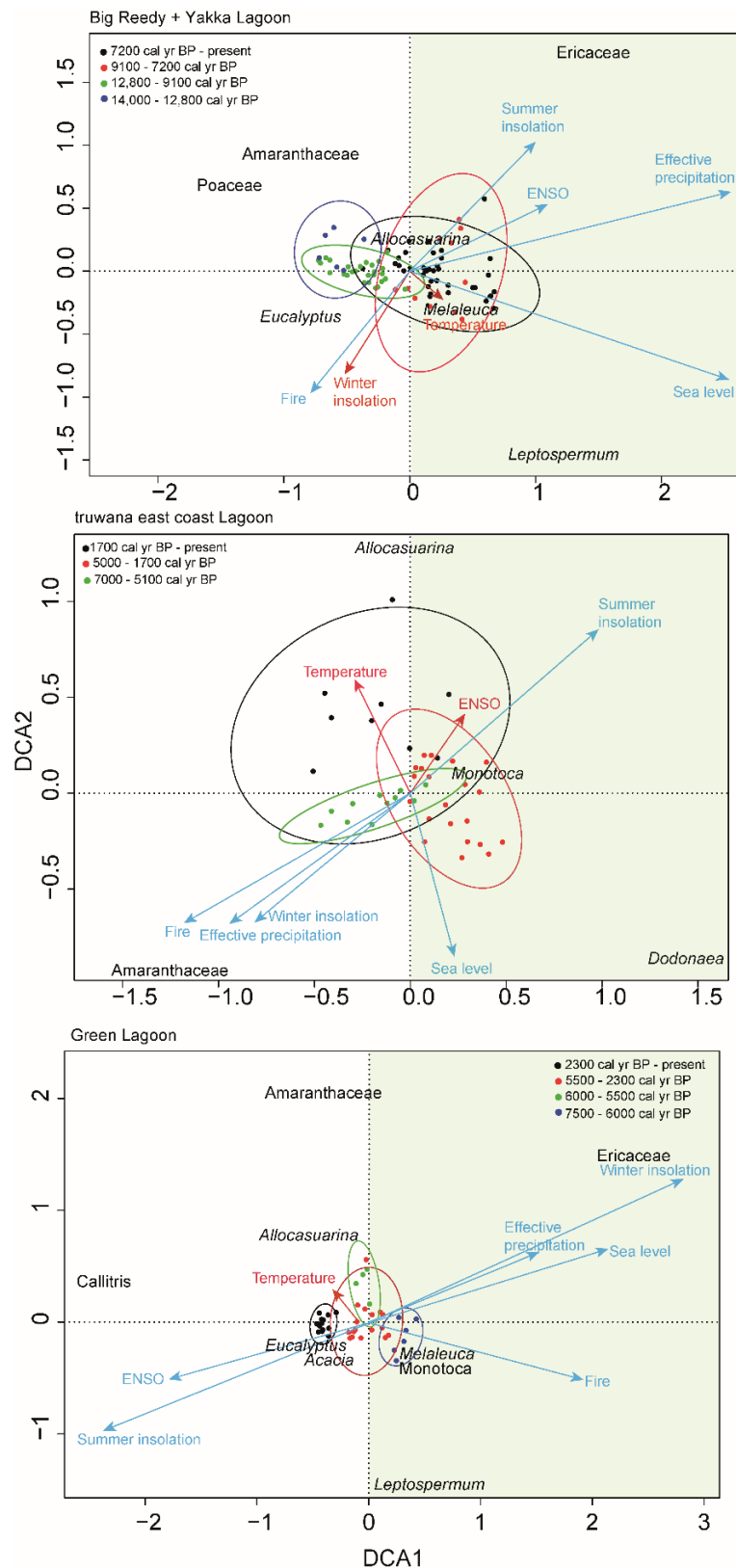


Figure S6: Individual DCA ordination plots for each site fitted with potential environmental drivers, and significant ($P < 0.01$) drivers are in blue and insignificant variables in red. Arrow lengths reflect correlation between each environmental driver and changes in pollen assemblage. Green-shaded area represents heathland and scrub vegetation in the ordination space.

Table S1: Indicator pollen types and their representative plants and major vegetation types on truwana/CBI.

Pollen	Plants	Vegetation
<i>Eucalyptus</i>	<i>Eucalyptus nitida</i> , <i>E. viminalis</i> , <i>E. globulus</i>	Woodland, forests, scrub
<i>Callitris</i>	<i>Callitris rhomboidea</i>	Forest, scrub
<i>Allocasuarina</i>	<i>Allocasuarina verticillata</i> , <i>A. monilifera</i>	Forest, scrub, heathland
<i>Leptospermum</i>	<i>Leptospermum scoparium</i> , <i>L. glaucescens</i> , <i>L. laevigatum</i>	Woodland, scrub, heathland
<i>Acacia</i>	<i>Acacia verticillata</i> , <i>A. genistifolia</i> , <i>A. mucronata</i> , <i>A. terminalis</i> , <i>A. longifolia</i>	Scrub
<i>Melaleuca</i>	<i>Melaleuca squarrosa</i> , <i>M. gibbosa</i> , <i>M. ericifolia</i>	Scrub
<i>Dodonaea</i>	<i>Dodonaea viscosa</i>	Forest, scrub
<i>Pomaderris</i>	<i>Pomaderris apetala</i> , <i>P. intermedia</i> , <i>P. paniculosa</i> , <i>P. pilifera</i>	Forest scrub
cf.		
<i>Lepidosperma</i>	<i>Lepidosperma concavum</i> , <i>L. filiforme</i> , <i>L. longitudinale</i> , <i>L. laterale</i>	Forest, scrub, heathland, wetland
cf. <i>Gahnia</i>	<i>Gahnia radula</i> , <i>G. grandis</i> , <i>G. filum</i>	Scrub, sedgeland
cf. <i>Sprengelia</i>	<i>Sprengelia incarnata</i>	Heathland
<i>Monotoca</i>	<i>Monotoca elliptica</i>	Heathland
<i>Epacris</i>	<i>Epacris obtusifolia</i> , <i>E. impressa</i> , <i>E. paludosa</i> , <i>E. lanuginosa</i>	Heathland
<i>Restionaceae</i>	<i>Leptocarpus tenax</i> , <i>Centrolepis facicularis</i> , <i>C. strigosa</i> , <i>Empodisma minus</i>	Heathland
<i>Xanthorrhoea</i>	<i>Xanthorrhoea australis</i>	Heathland

Table S2: AMS radiocarbon dates for Big Reedy (BRL), Yakka (YL), truwana East Coast (tECL), and Green Lagoon (GL), measured at 'DirectAMS', Washington.

Sites	Lab ID	¹⁴ C yr BP	Error (1σ)	Depth (cm)	Cal yr BP
BRL	D-AMS 035025	1090	24	1	1008 ± 36
BRL	D-AMS 035026	2663	26	5	2776 ± 14
BRL	D-AMS 033241	3973	34	9	4463 ± 42
BRL	D-AMS 026684	5587	31	18	6365 ± 35
BRL	D-AMS 035027	7836	32	48	8618 ± 25
BRL	D-AMS 026685	8191	36	65	9150 ± 79
BRL	D-AMS 026686	9323	38	118	10536 ± 44
BRL	D-AMS 026687	10527	45	168	12475 ± 162
BRL	D-AMS 026688	11688	45	194	13575 ± 136
YL	D-AMS 036732	603	40	41	603 ± 39
tECL	D-AMS 026689	2017	28	18	1969 ± 30
tECL	D-AMS 026690	3474	30	38	3763 ± 51
tECL	D-AMS 032459	4299	30	55	4866 ± 17
tECL	D-AMS 026691	5659	32	68	6447 ± 30
GL	D-AMS 036721	890	22	11	829 ± 58
GL	D-AMS 036722	1414	26	11	1318 ± 9
GL	D-AMS 036723	3951	28	57	4425 ± 64
GL	D-AMS 036724	4501	31	81	5174 ± 88
GL	D-AMS 036725	5392	30	115	6230 ± 36
GL	D-AMS 036726	6226	33	129	7141 ± 84
YL	<i>Pinus</i> pollen	-	-	22	100
tECL	<i>Pinus</i> pollen	-	-	6	100

10.3. Appendix S3 (for Chapter 4)

Summary key to aid identification of fossil Myrtaceae pollen from the Bass Strait islands

1a. Pollen parasyncolpate...

2a. Pollen with large to medium apocolpial field (angular parasyncolpateness) ...

3a length 15 – 30 μm , wall thickness 0.6 – 2.6 μm , pore height 1.0 – 6.5 μm ...

4a. Pollen length $>25 \mu\text{m}$, colpi length $>8 \mu\text{m}$, pore height $>3.6 \mu\text{m}$...

Eucalyptus (Symphomyrtus type)

4b. Pollen length $<19 \mu\text{m}$, colpi length $<8 \mu\text{m}$, pore length $<3.6 \mu\text{m}$... *Eucalyptus* (Peppermint type)

3b. Pollen length 13 -19 μm , wall thickness 0.5 – 1.2 μm , colpi length 3.0 – 6 μm , pore height 1.0 – 2.0 μm ... *Melaleuca pallida*

2b. Pollen with small apocolpial field, pollen length 12 – 24 μm , wall thickness 0.5 – 1.7 μm , pore height 0.7 – 3.5 μm ... *Melaleuca* (if sides are concave and $<21 \mu\text{m}$ it is likely *M. armillaris*)

5a. Pollen $>16 \mu\text{m}$... *Melaleuca squarrosa* type

5b. Pollen $<16 \mu\text{m}$... *M. ericifolia*

1b. Pollen syncolpate...

6a. Pollen straight sided or slightly concave, pollen length 11 – 21 μm , wall thickness 0.1 – 1.6 μm , wall verrucate or scabbrate (can be psilate) ...

7a. Pollen with rounded pore area/amb... *M. gibbosa* or *Kunzea ambigua* (if with bumpy walls in the equatorial view it is *M. gibbosa*)

7b. Pollen (like a perfect triangle) with pointed or notched pore area...

Leptospermum laevigatum type (if pollen is $<12 \mu\text{m}$ it is likely *L. glaucescens*).

6b. Pollen with deeply concave sides, pollen length 12 – 18 μm , wall 0.6 – 1.3 μm , pore wideness $>2 \mu\text{m}$ and psilate... *Calytrix tetragona*

10.4. Appendix S4 (for Chapter 5)

Table S1: AMS radiocarbon dates for Bumpy Lagoon (BL), measured at 'DirectAMS', Washington.

Lab ID	^{14}C yr BP	Error (1σ)	Depth (cm)
D-AMS 026692	486	25	18
D-AMS 032457	2702	29	28
D-AMS 032458	3396	25	36
D-AMS 026693	3584	40	44

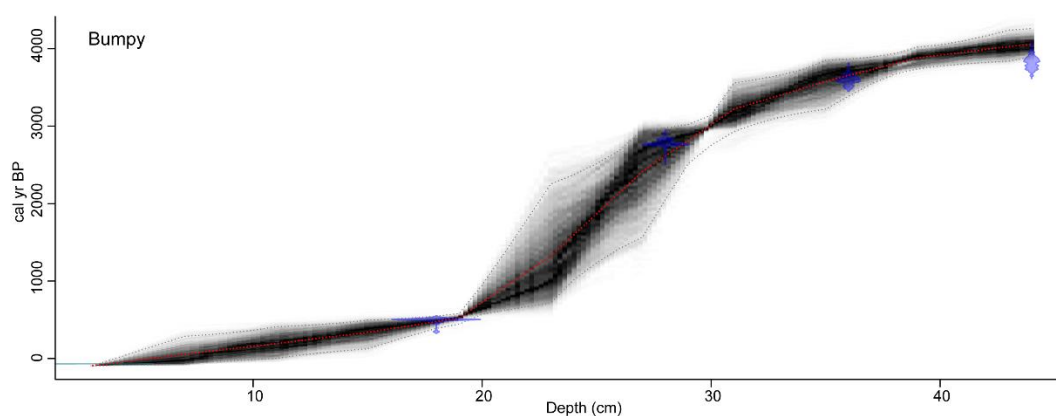


Fig. S1: Age-depth model (Bacon) for Bumpy Lagoon, showing calibrated ^{14}C dates (purple), age-depth model (dark shaded grey), 95% confidence intervals of calibrated range (light shaded grey), and single 'best' model based on the weighted mean age for each depth

Table S2: Summary table of NPP types on truwana/Cape Barren Island, Bass Strait, southeast Australia, and their ecological interpretations based on previous ecological and palaeoecological studies

NPP types	Category	Ecological significance
<i>Botryococcus</i> (HdV-766)	Algae	Depending on the species, <i>Botryococcus</i> can occupy freshwater lakes, ponds, swamps, and bogs in different environmental conditions. Some species can also occupy brackish/saline habitats (Batten and Grenfell 1996; Jankovská and Komárek 2000; van Geel 2001). However, <i>Botryococcus</i> generally proliferate in shallow waters in areas of low rainfall, with varying environmental conditions (Guy-Ohlson 1992). In palaeoecological records, it is used alongside other alga types especially <i>Pediastrum</i> to infer open waters in some cases, but mostly used to infer waters with a shallow–variable depth if aquatic macrophytes are present (e.g., Davis 1999; Cook et al. 2011).
<i>Pediastrum</i> (HdV-760 types)	Algae	Although different species can reflect different water depths and physicochemical conditions, <i>Pediastrum</i> in fossil records is generally used to infer open, oligotrophic waters (e.g., Singh et al. 1981; Dodson 1974; Davis et al. 1977). <i>Pediastrum integrum</i> is the main type recorded in BRL and tECL records, and mostly occurs in clear, cold, small, shallow lakes or ponds (Komárek and Jankovská 2001; Jankovská and Komárek 2000; Wolowski et al. 2002).
Zygnemataceae	Algae	Members of the Zygnemataceae mostly produce their spores in shallow, stagnant, clear, oxygen-rich warm waters and their presence in fossil records is mostly used to infer shallow or temporary standing waters. The types recorded on truwana/CBI include <i>Zygnema</i> , <i>Spirogyra</i> and <i>Debarya</i> . <i>Zygnema</i> (HdV-141) presence mostly indicates shallow (~0.5 m deep), stagnant, warm waters, while <i>Spirogyra</i> (HdV-130) and <i>Debarya</i> (HdV-214) are often used to infer seasonal

		fluctuation in freshwater, seasonal soil inundation, or temporary shallow waters (Hoshaw 1968; van Geel 2001).
<i>Gloeotrichia</i> (HdV-146)	Algae	<i>Gloeotrichia</i> is a nitrogen-fixing cyanobacterium, and often inhabits shallow, warm waters with low nitrates due to its ability to convert atmospheric nitrogen to nitrate (Graham and Wilcox 2000). The presence in fossil records is mostly used to infer shallow nitrogen-poor waters (Cook et al. 2011; van Geel et al. 1989).
Type A2	Algae	Type A2 has only been previously recorded in fossil records from Australia and is thought to be associated with waters with variable depths (Cook et al. 2011).
HdV- 233	Algae	An indicator of oligotrophic conditions (van Geel et al. 1989).
HdV- 229	Algae	An indicator of sandy pools (van Geel et al. 1989).
HdV- 333	Algae	This type is thought to be associated with <i>Sphagnum</i> peat formation (van Geel et al. 1981).
Type 66/209	Algae	An indicator of mesotrophic conditions (van Geel 1978).
<i>Operculonidium</i> <i>centrocarpum</i> (HdV-230, Type 704A)	Algae	A marine dinoflagellate cyst, indicative of marine influence and changes in sea surface temperature (van Geel et al. 1989; Baker and van Smeerdijk 1982; Verleye et al. 2012; Koike et al. 2006; Santos et al. 2017).
<i>Protoperidinium</i>	Algae	Heterotrophic marine dinoflagellate cyst.
Diatoms	Algae	Both pennate and centric types were recorded on truwana/CBI. Pennate species mostly recorded are <i>Pinnularia</i> and <i>Diploneis</i> cf. <i>elliptica</i> , which are mostly found

		in shallow waters, pond and sediment/mud. The most commonly recorded centric diatom is cf. <i>Actinocyclus octonarius</i> (Jovanovska et al. 2015; Sonneman et al. 1999).
Chironomid remains (HdV-88, 219)	Chironomidae	Chironomid larvae mentum, mandibles and head capsules are usually used in palaeoclimatic reconstructions and their abundance in fossil records can be used to infer warmer or cooler climates and wetter conditions (van Geel et al. 1989; Cook et al. 2011).
Copepod spermatophore (HdV-28)	Copepoda	An indicator of standing or temporary open water (Anderson 1998; Huntley et al. 2013; van Geel 1978; Rull et al. 2008).
<i>Assulina muscorum</i> (HdV-32A)	Rhizopoda	<i>Sphagnum</i> peat testate amoebae (van Geel 1989; Lacourse et al. 2019; Warner and Charman 1994).
<i>Centropyxis</i>	Rhizopoda	Mostly present in wetland sediment, peat moss and fen (Siemensma 2020; Lanscac-Toha et al. 2000; Booth et al. 2008; Warner and Charman 1994).
Animal hair (HdV-52)	Invertebrate	Limited information available about the origin of this NPP type and the recovery in fossil records. It is suggested to be a bog-dwelling invertebrate hair (van Geel 1978).
Sponge spicules	Porifera	This is a freshwater sponge and has been used to infer transitions from aquatic to fen systems (van Geel et al. 1989). It is also thought to be related to erosion associated with European activities in Australia (Cook et al. 2011).
Coprophilous fungi	Fungi	These are dung fungi and the types recorded on truwana/CBI include, <i>Podospora</i> (HdV-368), <i>Sporomiella</i>

		(Hdv-113) and <i>Sordaria</i> (Hdv-55). They are used to infer presence of megafauna or large herbivores, as well as past human occupation (e.g., Davis and Shafer 2006; Raper and Bush 2009; van Geel et al. 1981, 1983; Buurman et al. 1995).
<i>Glomus</i> (HdV-207)	Fungi	An endomycorrhizal fungus, which occurs on different host plants and their chlamydospores are usually securely buried in soils. Hence, their abundance in fossil records is used to infer increased soil erosion or sediment input in water bodies. The fungal type is also used to infer open landscapes with active sediment transport, especially during periods of anthropogenic land use (Anderson et al. 1984; van Geel et al. 1989).
<i>Helicoon</i> (HdV-30)	Fungi	<i>Helicoon</i> is an aeroaquatic fungus and the spores have been recovered from decaying leaves of birch, pine, oak and grass in peat fens and marsh (van Beverwijk 1954; Abdullah et al. 1998). There is a limited information about the recovery in fossil records except that the spores were absent in minerotrophic peats (van Geel 1978).
Gaeumannomyces (HdV-126)	Fungi	The abundance of hyphopodia of the members of Gaeumannomyces in fossil records is thought to be associated with <i>Carex</i> species (Cyperaceae) during phases of low lake levels (van Geel et al. 1989).
<i>Gelasinospora</i> (HdV-1)	Fungi	Mostly occur in highly decomposed peat and sediments containing charcoal and used to infer dry conditions and period high fire activity (van Geel et al. 1989).
<i>Lycoperdon</i>	Fungi	Mostly found in shallow waters (Jarzen and Elsick 1986).

<i>Byssothecium circinans</i> (HdV-16)	Fungi	An indicator of dry conditions and grassy vegetation (van Geel et al. 1981; van Geel 1978; Montoya et al. 2010).
HdV-18	Fungi	This fungal type is thought to be related to <i>Eriophorum vaginatum</i> (Cyperaceae) abundance in fossil records and has been used to infer the presence of standing water with sedgeland (van Geel et al. 1981; van Geel 1978; Huntley et al. 2013).

Notes and comments on sparsely-recorded and indeterminate NPPs in sedimentary records (Plate III)

Neorhabdocoela (HdV-353), HdV-3, *Nebela* and *Arcella* were sparsely recorded in BRL, but *Nebela* was only present in the basal lateglacial sample, dated to ~14,000 cal yr BP. HdV-299 was sparsely recorded in top samples of YL. HdV-179, *Tilletia* (HdV-27) and HdV-20 were sparsely recorded in GL, but HdV-179 was only recorded in one sample, dated to ~5800 cal yr BP (Plate III).

ANH-1 (Plate III_{14–15}): This NPP type has a serrated-circle shape and is about 14 µm. It consists of 14 appendages arranged like fruit mesocarps, which are invisible in most cases as in Plate III₁₅. Considering the shape and near-transparent colour of this type, we suspect it is of an alga origin. It was consistently recorded in BRL from ~14,000 to 9000 cal yr BP, intervals dominated by aquatic macrophytes and chironomid remains. It is also present in tECL in the last ~1000 years, which is dominated by aquatic macrophyte *Myriophyllum muelleri* and alga type *Gloeotrichia*. This may suggest an ecological overlap exists between ANH-1 and aquatic/wetland plants, especially *Myriophyllum* species.

ANH-2 (Plate III_{16–17}): This type is a large echinate cell (about 92 µm) and may be a non-vascular plant spore (e.g., bryophyte). It is sparsely recorded in BRL lateglacial samples (~14,000–13,000 cal yr BP) and abundant in tECL in the last ~1000 years, which are characterized by shallow wetland and herbland assemblages, including *Myriophyllum* species. This suggests ANH-2 may be affiliated with shallow wetlands or/and aquatic herbland and dry conditions.

ANH-3 (Plate III₁₈): This NPP type (~35 µm) may be a dinoflagellate cyst and looks like the cysts of *Ataxiodum chaoane* and *Scippsiella trifida* (Mudie et al., 2017).

ANH-4 (Plate III₉): This NPP type is about 49 µm in size and may be of algal origin. It was sparsely recorded in BRL between ~8000 and 6000 cal yr BP, a transitional phase from a high (lake system) to low hydrology (wetland system) regime, and dominated by Restionaceae, copepod spermatophore and HdV-18.

ANH-5 (Plate III₂₀): This NPP type (~30 µm) is likely a fungal spore and may be related to HdV-20 (Plate III₄). ANH-7 was sparsely recorded in YL.

ANH-6 (Plate III₂₁): This NPP type is large (~120 µm) and may be of fungal or invertebrate origin. It was sparsely recorded in BRL.

ANH-7 (Plate III₂₂₋₂₃): This NPP type is a fungal cell (possibly spore) in cluster and is about 33 µm. It is consistently present in tECL record in the last ~4000 years, an interval generally dominated by *Myriophyllum* species, Restionaceae, sponge spicules and *Glomus*, suggesting ANH-7 is related to shallow wetlands.

ANH-8 and ANH-9 (Plate III₂₄₋₂₅): These NPP types are likely of fungal origin. ANH-10 is about 141 µm long and ANH-11 is about 215 µm long. They are consistently present in BRL between ~12,000 and 8000 cal yr BP, an interval dominated by *Isoetes* and chironomid remains. The long and narrow shape of these NPPs suggests they may be ascospore/conidia of freshwater fungi (Shearer and Raja, 2010). Specifically, ANH-10 looks like *Isthmosporella* sp, which mostly inhabits submerged woody remains in lakes (Raja et al., 2020; Shearer and Crane, 1999), and inferred lake system and woodland development (Adeleye et al., 2021a) in BRL during the early Holocene may have contributed to the presence of ANH-10 at the site.

ANH-10 (Plate III₂₆₋₂₈): A large (~82 µm) globose NPP type, with wall like an amoeba test; however, the aperture is unclear or not visible. It may also be an aquatic invertebrate egg. The NPP was recorded in BRL and most abundant around 11,000 cal yr BP when *Isoetes* was most abundant. ANH-12 may share ecological preference with *Isoetes* species growing at BRL at this time. ~11,000 cal yr BP falls within the period interpreted as the development of a lake system or increasing hydrology at BRL.

Note and comment on Big Reedy Lagoon surface NPPs (Plate IV)

Big Reedy Lagoon (BRL) is presently a peaty swamp, with pockets of standing water. The swamp surface is walkable, especially during summer, and supports thickets of tall and medium-sized shrubs (e.g., *Melaleuca*, *Leptospermum* and *Kunzea*), as well as sedgeland (see Fig. 1b in main text). This suggests the water table at BRL is low in most parts of the year in recent times, hence, NPPs recorded on the surface of the lagoon (Plate IV) likely reflect the present low water level at the site.

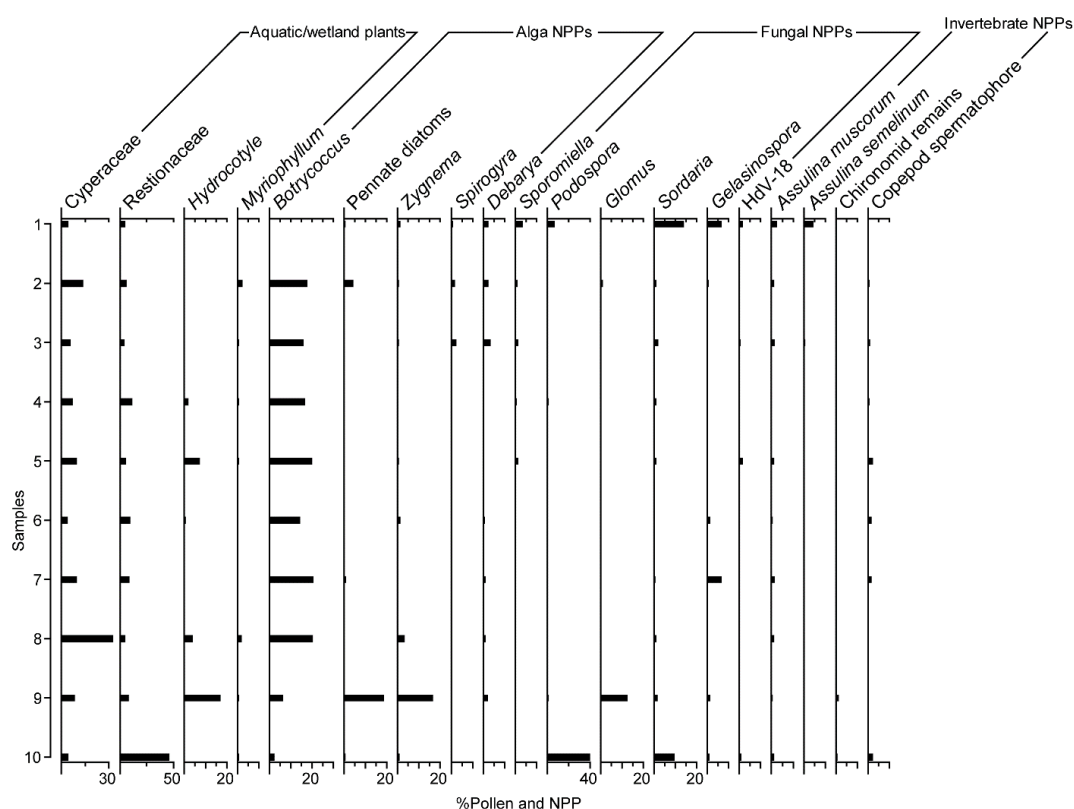


Fig. S2: Percentage diagram for major palynomorphs recorded in Big Reedy Lagoon (BRL) surface samples (10 sampling points on a transect across the centre of the wetland surface). Note: sponge spicules were abundant in all samples.

10.5. Appendix S5 (for Chapter 6)

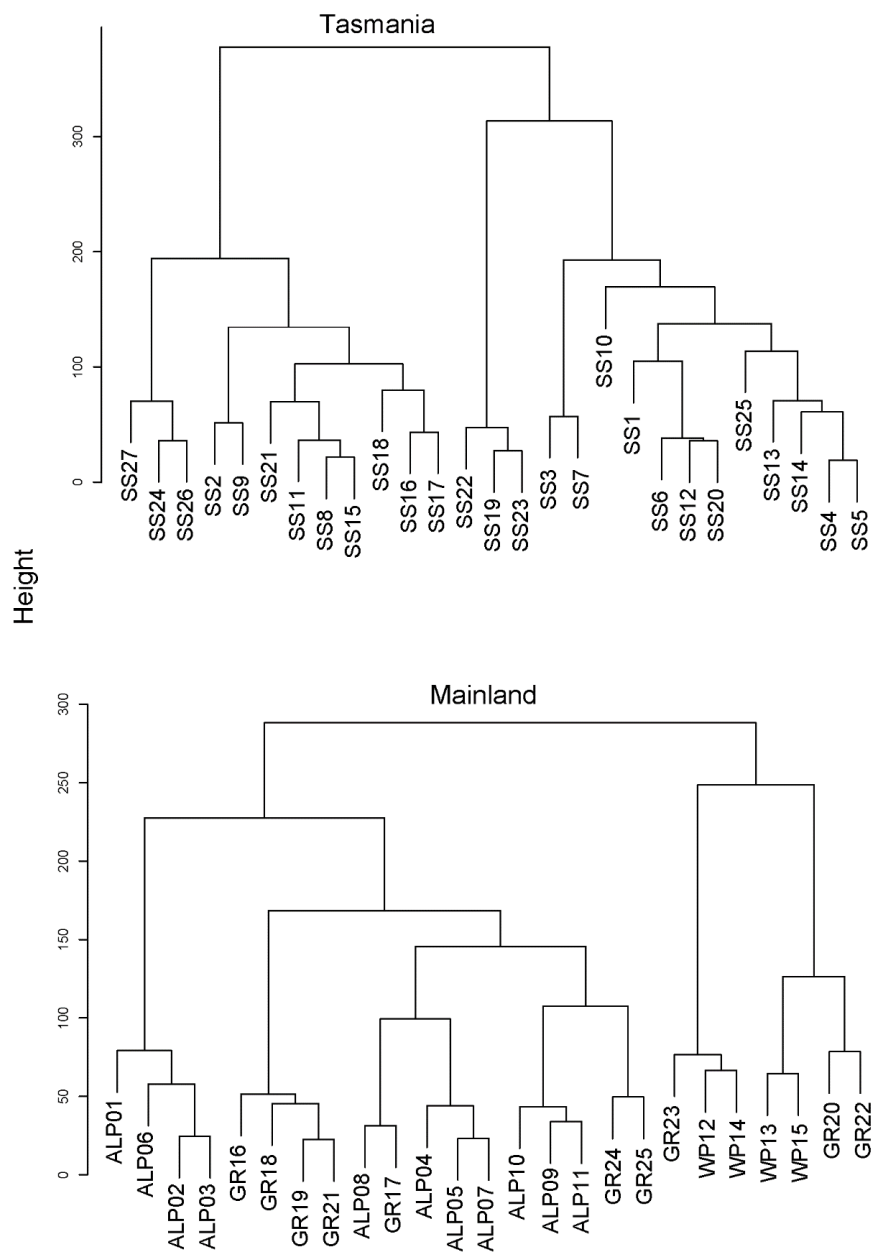


Figure S1: Results of the Ward's cluster analysis of modern vegetation in Tasmania and southeast Australian mainland (Victoria). See Table S3 for corresponding vegetation type(s) for each site code.

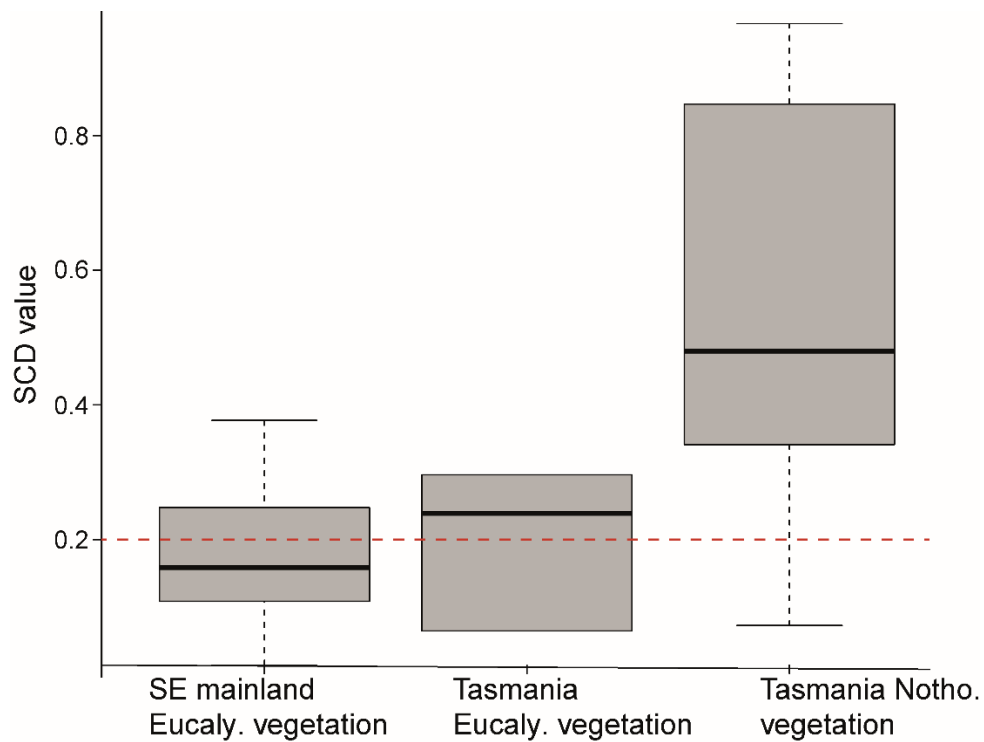


Figure S2: Box plot showing SCD distribution in SE mainland *Eucalyptus* dominated vegetation, as well as Tasmania's *Nothofagus* and *Eucalyptus*-dominated vegetation. Red dash line represents the empirical threshold (SCD > 0.2) for significant vegetation turnover.

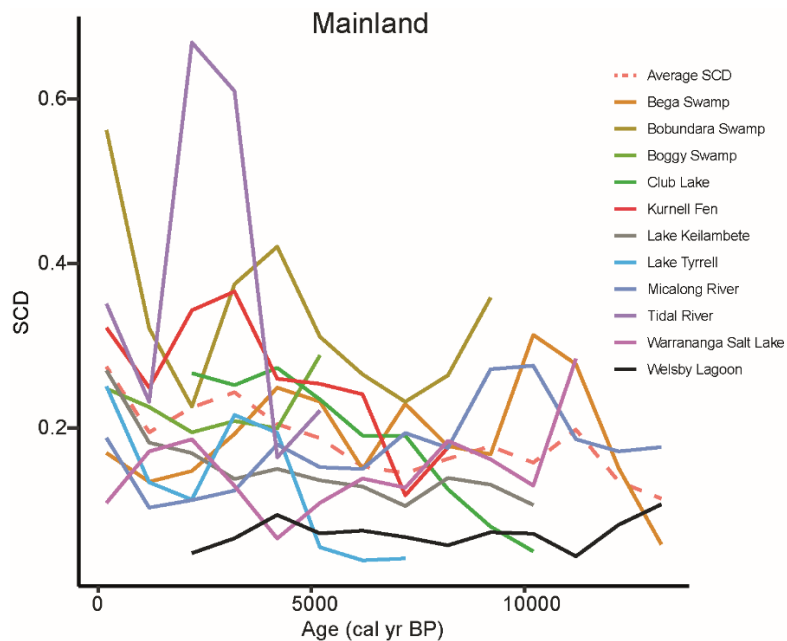


Figure S3a: Average (dashed line) and individual sites' turnover (SCD) through time on the southeast Mainland of Australia.

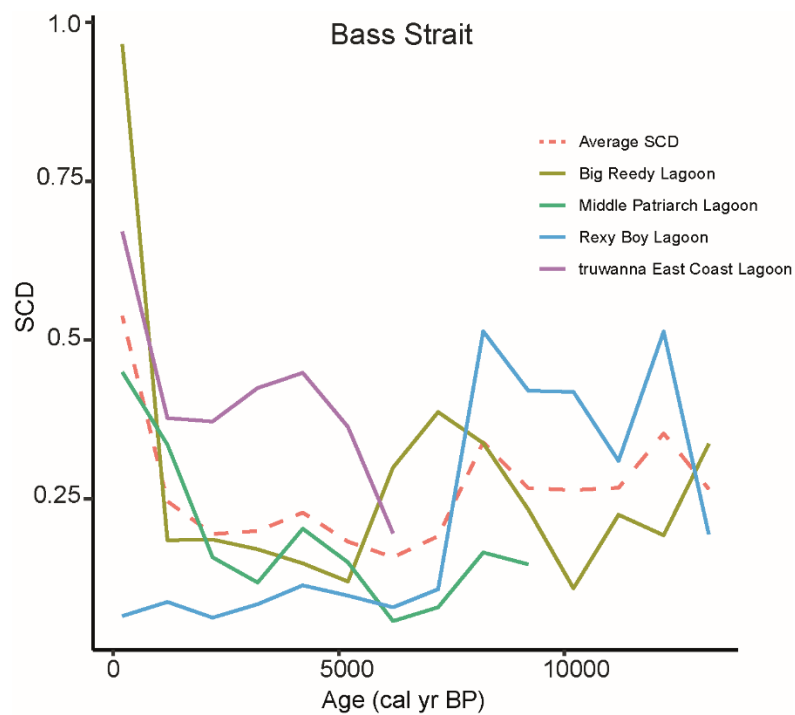


Figure S3b: Average (dashed line) and individual site turnover (SCD) through time on the Bass Strait islands.

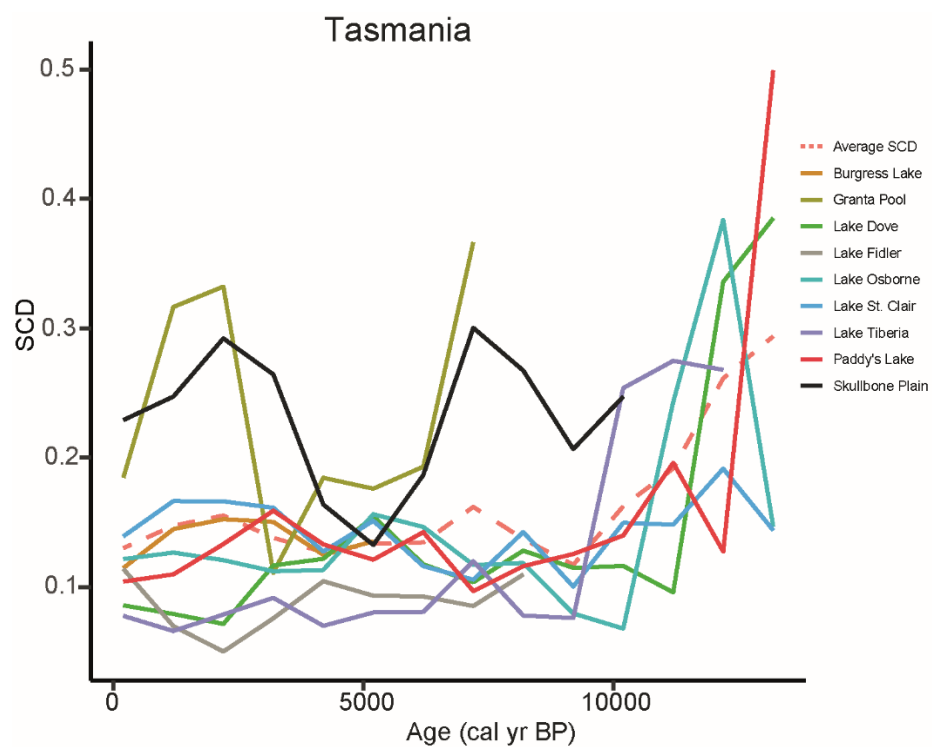


Figure S3c: Average (dashed line) and individual site turnover (SCD) through time in Tasmania.

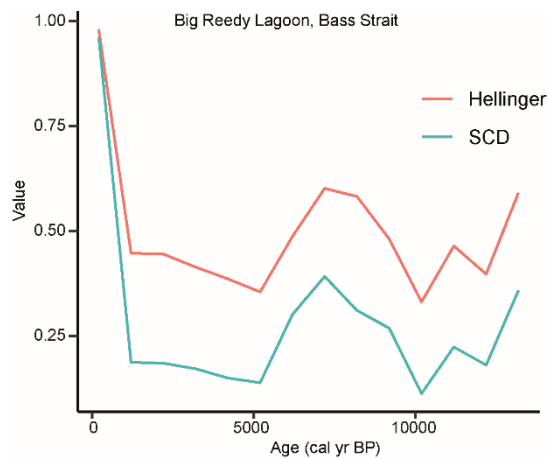


Figure S4a: Similar patterns of turnover in a Bass Strait record (Big Reedy Lagoon) using Squared Chord Distance (SCD) versus Hellinger transformation.

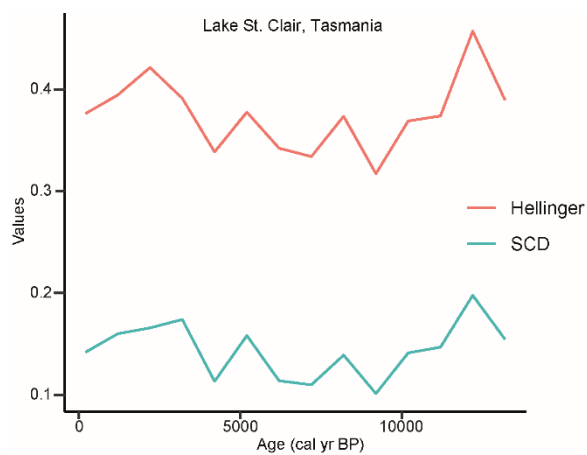


Figure S4b: Similar patterns of turnover in a Tasmanian record (Lake St. Clair) using Squared Chord Distance (SCD) versus Hellinger transformation.

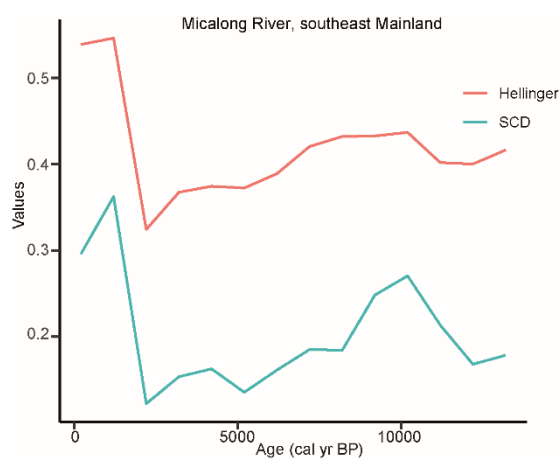


Figure S4c: Similar patterns of turnover in a southeast Australian mainland record (Micalong River) using Squared Chord Distance (SCD) versus Hellinger transformation.

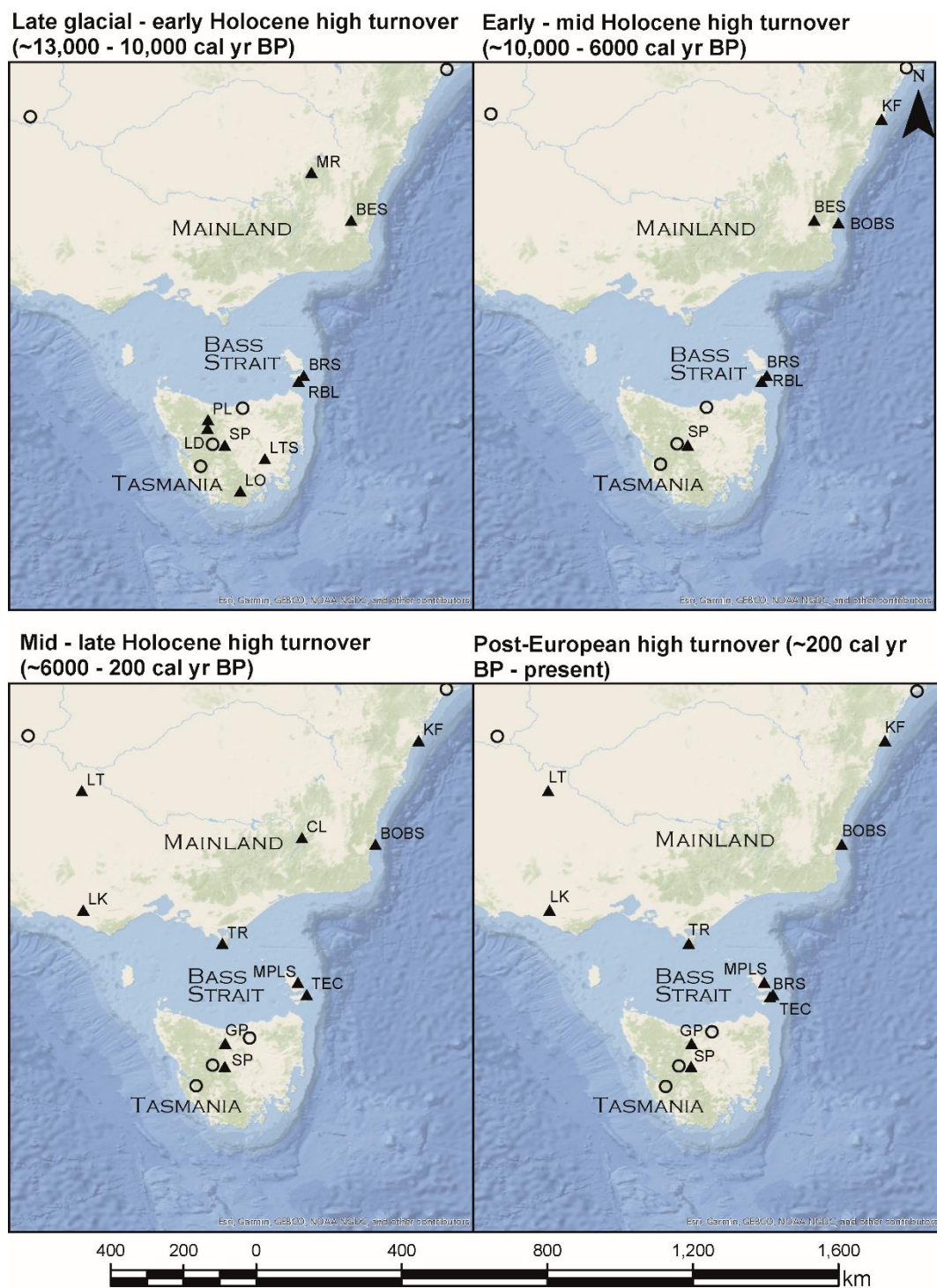


Figure S5: Study sites with periods of significant turnover ($SCD > 0.2$). Black triangles represent sites with significant turnover during the respective periods and black hollow circles represent other sites without significant turnover ($SCD < 0.2$) in that period. Key to site codes is included in Table 1. Turnover mainly occurred in Tasmania and the Bass Strait in the lateglacial-early Holocene, and the Bass Strait sites between early and mid- Holocene, and both the SE mainland and the Bass Strait islands from mid- to late Holocene (including the European period).

Table S1: Pollen records used in this study including site locations, elevations, regions and references. Site selection is based on strict sampling and dating criteria, which include pollen sample and radiocarbon date resolution of at least 500 and 3000 years, respectively.

Sites and codes	Region	Longitude	Latitude	Elevation (m asl)	References
Welsby Lagoon (WL)	mainland	153.45	-27.44	29	Colhoun (1986)
Boggy Swamp (BOGS)	mainland	151.5167	-31.8667	1160	Dodson et al. (1986)
Warrananga Salt Lake (WSL)	mainland	141.5517	-33.9672	85	Cupper (2005)
Kurnell Fen (KF)	mainland	151.1667	-34.0167	2	Martin (1994)
Lake Tyrrell (LT)	mainland	142.842	-35.255	42	Luly (1993)
Micalong River (MR)	mainland	148.5167	-35.3333	1100	Kemp and Hope (2014)
Club Lake (CL)	mainland	148.283	-36.417	1955	Martin (1986)
Bega Swamp (BES)	mainland	149.5	-36.5167	1080	Green et al. (1988)
Bobundara Swamp (BOBS)	mainland	150.1	-36.5833	1	Hope et al. (2006)
Lake Keilambete (LK)	mainland	142.8779	-38.2094	132	Dodson (1974a)
Tidal River (TR)	mainland	146.3167	-39.0333	2	Hope (1974)
Middle Patriarch Lagoon (MPL)	Bass Strait	148.1833	-39.9963	15	McWethy et al (2017)
Truwana East Coast Lagoon (TECL)	Bass Strait	148.3611	-40.3311	1	Adeleye et al. (2021a)
Big Reedy Lagoon (BRL)	Bass Strait	148.2381	-40.3589	26	Adeleye et al. (2021a)
Rexy Boy Lake (RBL)	Bass Strait	148.2178	-40.5422	8	Hopf et al. (in prep)
Paddy's Lake (PL)	Tasmania	145.9615	-41.451	1065	Beck et al. (2017)
Granta Pool (GP)	Tasmania	146.3853	-41.5081	685	Fletcher et al. (2014)
Lake Dove (LD)	Tasmania	145.95	-41.6667	954	Dyson, W. D. (1995)
Skullbone Plain (SP)	Tasmania	146.3753	-42.0789	965	Hope et al. (2017)
Lake St. Clair (LSC)	Tasmania	146.1833	-42.103	737	Hopf (2018)
Lake Tiberias (LTS)	Tasmania	147.3667	-42.4167	442	Macphail (1979)
Lake Fidler (LF)	Tasmania	145.6771	-42.5087	1	Harle et al. (1999)
Lake Osborne (LO)	Tasmania	146.7589	-43.2159	924	Mariani et al. (2019)
Burgess Lake (BL)	Tasmania	146.5971	-43.2213	721	Fletcher, unpublished

Table S2: New Bacon-generated calibrated age for Middle Patriarch Lagoon, Bass Strait Island, using *Pinus* as a marker for ~200 cal yr BP.

Depth (cm)	Age	27	3769	55	6329
0	-67	28	3888	56	6418
1	-38	29	4008	57	6507
2	-9	30	4127	58	6596
3	20	31	4218	59	6685
4	48	32	4309	60	6774
5	77	33	4399	61	6857
6	125	34	4490	62	6940
7	172	35	4581	63	7023
8	219	36	4670	64	7106
9	266	37	4760	65	7188
10	314	38	4850	66	7276
11	660	39	4939	67	7363
12	1007	40	5029	68	7450
13	1353	41	5116	69	7537
14	1700	42	5203	70	7625
15	2046	43	5290	71	7711
16	2232	44	5377	72	7797
17	2418	45	5464	73	7883
18	2604	46	5551	74	7969
19	2790	47	5638	75	8055
20	2976	48	5725	76	8125
21	3087	49	5812	77	8194
22	3198	50	5899	78	8264
23	3308	51	5985	79	8333
24	3419	52	6071	80	8403
25	3530	53	6157	81	8469
26	3649	54	6243	82	8535

83	8601	113	10331	143	11331
84	8667	114	10364	144	11364
85	8733	115	10398	145	11397
86	8798	116	10431	146	11430
87	8863	117	10465	147	11464
88	8928	118	10499	148	11497
89	8993	119	10532	149	11530
90	9058	120	10566	150	11563
91	9125	121	10600	151	11634
92	9192	122	10634		
93	9259	123	10667		
94	9326	124	10701		
95	9392	125	10735		
96	9456	126	10769		
97	9519	127	10803		
98	9582	128	10837		
99	9646	129	10870		
100	9709	130	10904		
101	9776	131	10938		
102	9842	132	10971		
103	9909	133	11004		
104	9975	134	11038		
105	10042	135	11071		
106	10080	136	11103		
107	10118	137	11135		
108	10156	138	11167		
109	10193	139	11200		
110	10231	140	11232		
111	10264	141	11265		
112	10298	142	11298		

Table S3: Sampling sites of modern vegetation (shown in Fig. 1) and corresponding vegetation classification (Mariani, Connor, et al., 2016).

Tasmania		Mainland	
Site code	Vegetation classification	Site code	Vegetation classification
SS1	(WDU) <i>Eucalyptus delegatensis</i> wet forest	ALP01	Alpine Grassland
SS2	(undifferentiated); (WDA) <i>Eucalyptus dalrympleana</i> forest	ALP02	Alpine Grassy Heathland
SS3	(SMM) <i>Melaleuca squamea</i> heathland	ALP03	Alpine Grassland
SS4	(RKF) <i>Athrotaxis selaginoides</i> - <i>Nothofagus gunnii</i> short rainforest; (MBE) Eastern buttongrass moorland; (RKP) <i>Athrotaxis selaginoides</i> rainforest	ALP04	Herb-rich Foothill Forest
SS5	(RMU) <i>Nothofagus rainforest</i> (undifferentiated)	ALP05	Montane Dry Woodland
SS6	(GPH) Highland <i>Poa</i> grassland; (SHS) Subalpine heathland; (DCO) <i>Eucalyptus coccoifera</i> forest and woodland; (GPH) Highland <i>Poa</i> grassland	ALP06	Montane Wet Forest
SS7	(HSE) Eastern alpine sedgeland; (RSH) Highland low rainforest and scrub; (DCO) <i>Eucalyptus coccoifera</i> forest and woodland; (MBE) Eastern buttongrass moorland	ALP07	Sub-alpine Woodland
SS8	(RKF) <i>Athrotaxis selaginoides</i> - <i>Nothofagus gunnii</i> short rainforest	ALP08	Montane Damp Forest
SS9	(MBE) Eastern buttongrass moorland	ALP09	Shrubby Dry Forest
SS10	(HSE) Eastern alpine sedgeland; (MBE) Eastern buttongrass moorland; (RMU) <i>Nothofagus rainforest</i> (undifferentiated); (MGH) Highland grassy sedgeland	ALP10	Wet Forest
SS11	(RPW) <i>Athrotaxis cupressoides</i> open woodland	ALP11	Damp Forest
SS12	(MBE) Eastern buttongrass moorland; (WSU) <i>Eucalyptus subcrenulata</i> forest and woodland	WP12	Warm Temperate Rainforest
SS13	(RSH) Highland low rainforest and scrub; (SMM) <i>Melaleuca squamea</i> heathland	WP13	Heathy Woodland
SS14	(DCO) <i>Eucalyptus coccoifera</i> forest and woodland; (SHS) Subalpine heathland; (SMM) <i>Melaleuca squamea</i> heathland	WP14	Estuarine wetland
SS15	(MBE) Eastern buttongrass moorland; (DCO) <i>Eucalyptus coccoifera</i> forest and woodland; (RPP) <i>Athrotaxis cupressoides</i> rainforest	WP15	Coastal Alkaline Scrub
SS16	(MBW) Western buttongrass moorland; (WNL) <i>Eucalyptus nitida</i> forest over <i>Leptospermum</i>	GR16	Granitic Hills Woodland
SS17	(MBU) Buttongrass moorland (undifferentiated); (RKP) <i>Athrotaxis selaginoides</i> rainforest	GR17	Lowland Forest
SS18	(MRR) Restionaceae rushland; (RKS) <i>Athrotaxis selaginoides</i> subalpine scrub	GR18	Valley Grassy Forest
SS19	(MBS) Buttongrass moorland with emergent shrubs; (WNL) <i>Eucalyptus nitida</i> forest over <i>Leptospermum</i>	GR19	Shallow Sands Woodland
SS20	(WDR) <i>Eucalyptus delegatensis</i> forest over rainforest; (RMU) <i>Nothofagus rainforest</i> (undifferentiated)	GR20	Plains Grassy Woodland
SS21	(WDR) <i>Eucalyptus delegatensis</i> forest over rainforest	GR21	Grassy Woodland
	(MBE) Eastern buttongrass moorland; (WDR) <i>Eucalyptus delegatensis</i> forest over rainforest; (WSU) <i>Eucalyptus subcrenulata</i> forest and woodland		

SS22	(RMU) <i>Nothofagus rainforest</i> (undifferentiated)	GR22	Lowan Sands Mallee
SS23	(RMU) <i>Nothofagus rainforest</i> (undifferentiated)	GR23	Rocky Outcrop Herbland
SS24	(GPH) Highland <i>Poa</i> grassland; (DAD) <i>Eucalyptus amygdalina</i> forest and woodland on dolerite	GR24	Hills Herb-rich Woodland
SS25	(RMU) <i>Nothofagus</i> rainforest (undifferentiated); (DPD) <i>Eucalyptus pauciflora</i> forest and woodland on dolerite; (WDR) <i>Eucalyptus delegatensis</i> forest over rainforest	GR25	Heathy Woodland
SS26	(DAD) <i>Eucalyptus amygdalina</i> forest and woodland on dolerite		
SS27	(DAD) <i>Eucalyptus amygdalina</i> forest and woodland on dolerite; (SLL) <i>Leptospermum lanigerum</i> scrub		

10.6. Appendix S6 (for Chapter 7)

Details of sites of charcoal records from the mainland and Tasmania

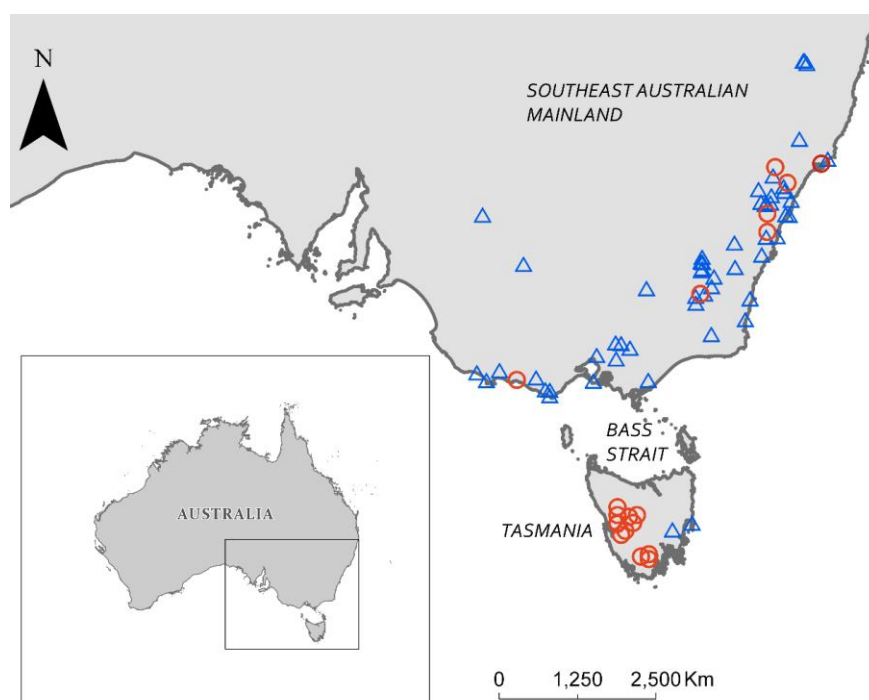


Figure S1: Sites with macroscopic (red circles) and microscopic (blue triangles) charcoal records from the mainland (55 sites) and Tasmania (16 sites). Fourteen of out of the 16 records from Tasmania are macroscopic charcoal records, while the remaining two sites from eastern Tasmania are microscopic charcoal records ($<125\ \mu\text{m}$). For the southeast mainland, all charcoal records were extracted from the Global Paleofire Database, and records selected had at least one radiocarbon dates every 2500 years. Seven out of the 55 records from the southeast mainland are macroscopic charcoal records, while the remaining 48 are microscopic charcoal records (see Table S1 for details). Microscopic charcoal records were considered due to the limited availability of macroscopic charcoal records in eastern Tasmania and the southeast mainland. Although macroscopic and microscopic charcoal records are usually used to infer local and regional fire signals, respectively (Whitlock and Larsen, 2001), composite analysis of multiple macroscopic and/or microscopic charcoal has proven to be effective in past regional biomass burned reconstructions [Mooney et al., 2011]. Only macroscopic charcoal records were used for recurrence-rate-of-fire-episodes reconstruction.

Table S1: Site information for charcoal records (mostly >125 µm) from western Tasmania (W.Tas), eastern Tasmania (E.Tas), and southeast mainland (SEM). Numbers in bracket in SEM sites are site identification numbers in the Global Paleofire Database. Other 47 sites included for SEM are microscopic charcoal (<125 µm) and can be assessed in the Global Paleofire Database (<https://www.paleofire.org/>) using the setting 'lat>-39, lat<(-28), long>140, long<154, date_int<=2500' in the 'paleofire' package in 'R'.

Site name	Latitude	Longitude	Elevation	Region	Source
Basin	-41.98082°	145.5483°	577	W.Tas	Mariani and Fletcher (2017)
Gaye	-41.82642°	145.6033°	892	W.Tas	Mariani and Fletcher (2017)
Gwendolyn	-42.26238°	145.8231°	923	W.Tas	Mariani and Fletcher (2017)
Nancy	-42.25877°	145.8271°	1037	W.Tas	Mariani and Fletcher (2017)
Vera	-42.27459°	145.8799°	571	W.Tas	Mariani and Fletcher (2017)
Osborne	-43.21621°	146.7593°	920	W.Tas	Mariani and Fletcher (2017)
Julia	-41.88923°	145.5761°	616	W.Tas	Mariani and Fletcher (2017)
Square tarn	-43.21431°	146.5942°	865	W.Tas	Mariani and Fletcher (2017)
Hartz	-43.23809°	146.7566°	952	W.Tas	Mariani and Fletcher (2017)
Selina	-41.87772°	145.6094°	516	W.Tas	Mariani and Fletcher (2017)
Owen tarn	-42.09961°	145.6094°	969	W.Tas	Mariani and Fletcher (2017)
Isla	-41.97053°	145.6654°	720	W.Tas	Mariani and Fletcher (2017)
Rolleston	-41.92149°	145.6248°	650	W.Tas	Mariani and Fletcher (2017)
St. Clair	-42.1°	146.1667°	825	W.Tas	Hopf et al. (2000)
Stoney*	-42.35°	147.6°	394	E.Tas	Jones et al. (2017)
Hazard*	-42.17222°	148.2892°	1.8	E.Tas	Mackenzie and Moss (2017)
Nwctw (215)	-38.31°	142.36°	20	SEM	D'Costa et al. (1989)
Blue (631)	-36.14°	148.43°	1950	SEM	Raine (1974)
Grey pole (632)	-32.61°	152.31°	9	SEM	Horn (2005)
Griffith (633)	-33.28°	151°	20	SEM	Mooney et al. (2007)
Howes (635)	-33.01°	150.66°	280	SEM	Mason (2004)
Baraba (216)	-34.23°	150.53°	305	SEM	Black et al. (2006)
Kings (637)	-33.01°	150.66°	280	SEM	Black (2001)
Wingecarribee (729)	-34.56°	150.51°	685	SEM	de Montford (2008)

AMS dates and age-depth model of unpublished sites on the Furneaux Group islands, Bass Strait.

Table S2.: AMS radiocarbon dates for Apple Orchard Lagoon, Bumpy Lagoon, Tobacco Lagoon, and Piano Point Lagoon, measured at 'DirectAMS', Washington.

Site	Lab ID	¹⁴ C yr BP	Error (1σ)	Depth cm
Apple Orchard Lagoon	D-AMS 036727	2207	35	21
Apple Orchard Lagoon	D-AMS 036728	5819	33	43
Apple Orchard Lagoon	D-AMS 036729	6292	30	65
Apple Orchard Lagoon	D-AMS 036730	6991	32	85
Bumpy Lagoon	D-AMS 026692	486	25	18
Bumpy Lagoon	D-AMS 032457	2702	29	28
Bumpy Lagoon	D-AMS 032458	3396	25	36
Bumpy Lagoon	D-AMS 026693	3584	40	44
Tobacco Lagoon	D-AMS 036733	576	37	15
Tobacco Lagoon	D-AMS 036734	3004	37	41
Piano Point Lagoon	D-AMS 036735	982	25	15

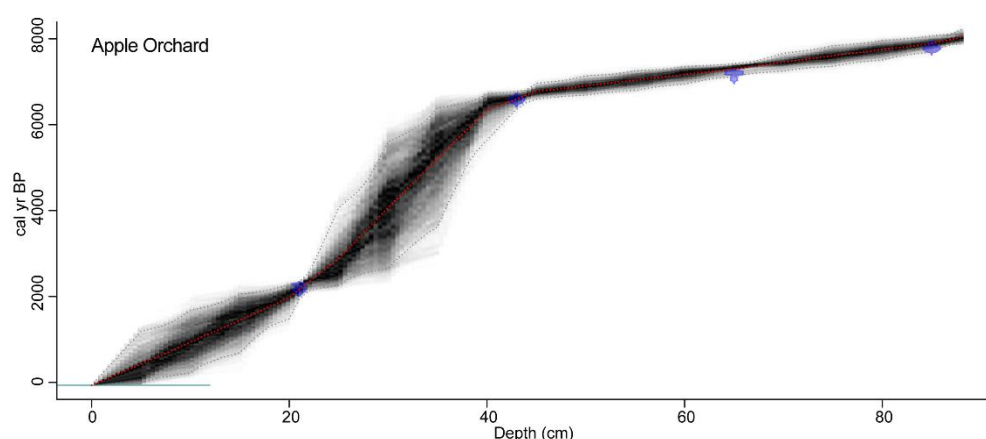


Figure S2: Age-depth model (Bacon) for Apple Orchard Lagoon, showing calibrated ¹⁴C dates (purple), age-depth model (dark shaded grey), 95% confidence intervals of calibrated range (light shaded grey), and single 'best' model based on the weighted mean age for each depth (red curve). Cal yr BP is calendar year before present (where 'present' is 1950 AD by convention).

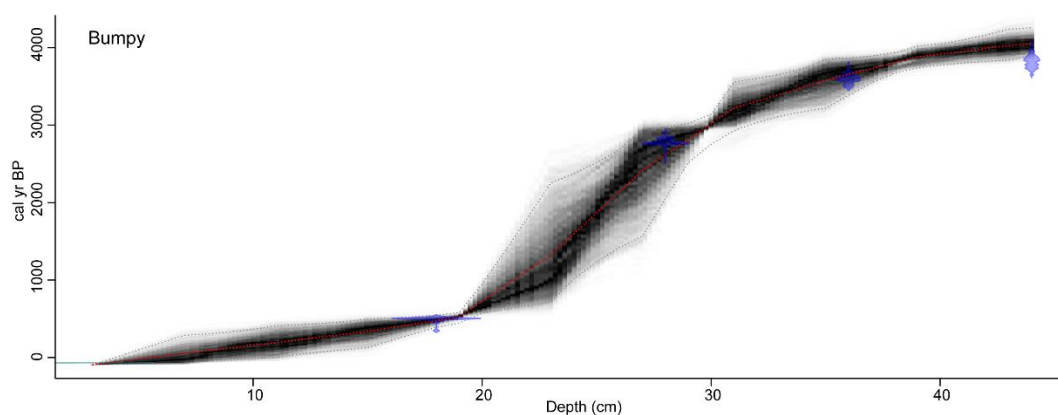


Figure S3. Age-depth model (Bacon) for Bumpy Lagoon, showing calibrated ^{14}C dates (purple), age-depth model (dark shaded grey), 95% confidence intervals of calibrated range (light shaded grey), and single 'best' model based on the weighted mean age for each depth (red curve).

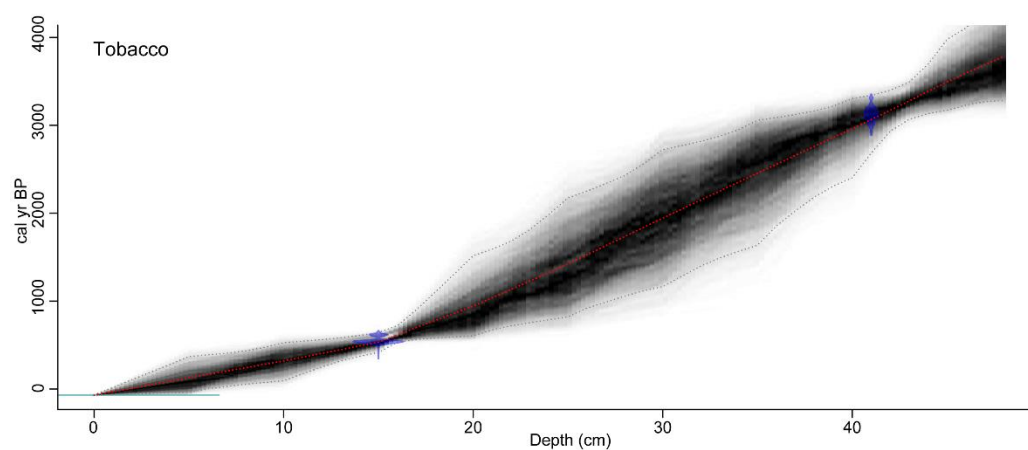


Figure S4: Age-depth model (Bacon) for Tobacco Lagoon, showing calibrated ^{14}C dates (purple), age-depth model (dark shaded grey), 95% confidence intervals of calibrated range (light shaded grey), and single 'best' model based on the weighted mean age for each depth (red curve).

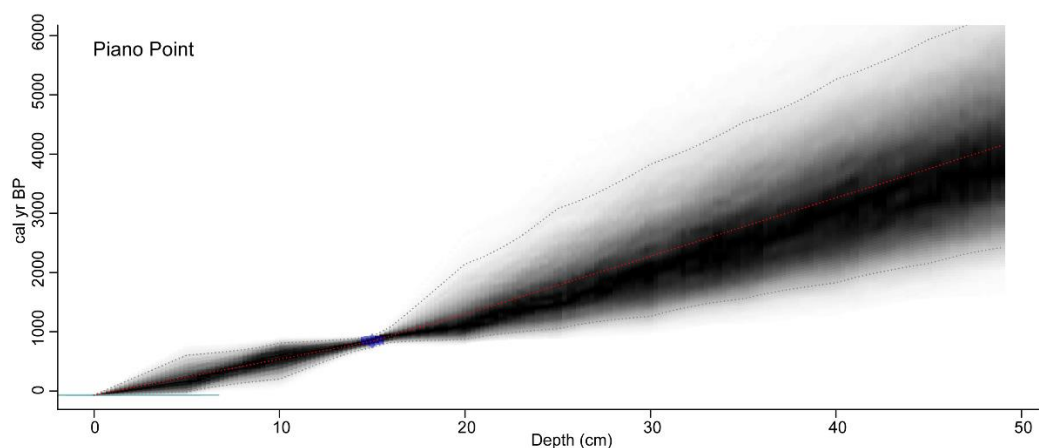


Figure S5: Age-depth model (Bacon) for Piano Point Lagoon, showing calibrated ^{14}C dates (purple), age-depth model (dark shaded grey), 95% confidence intervals of calibrated range (light shaded grey), and single 'best' model based on the weighted mean age for each depth (red curve).

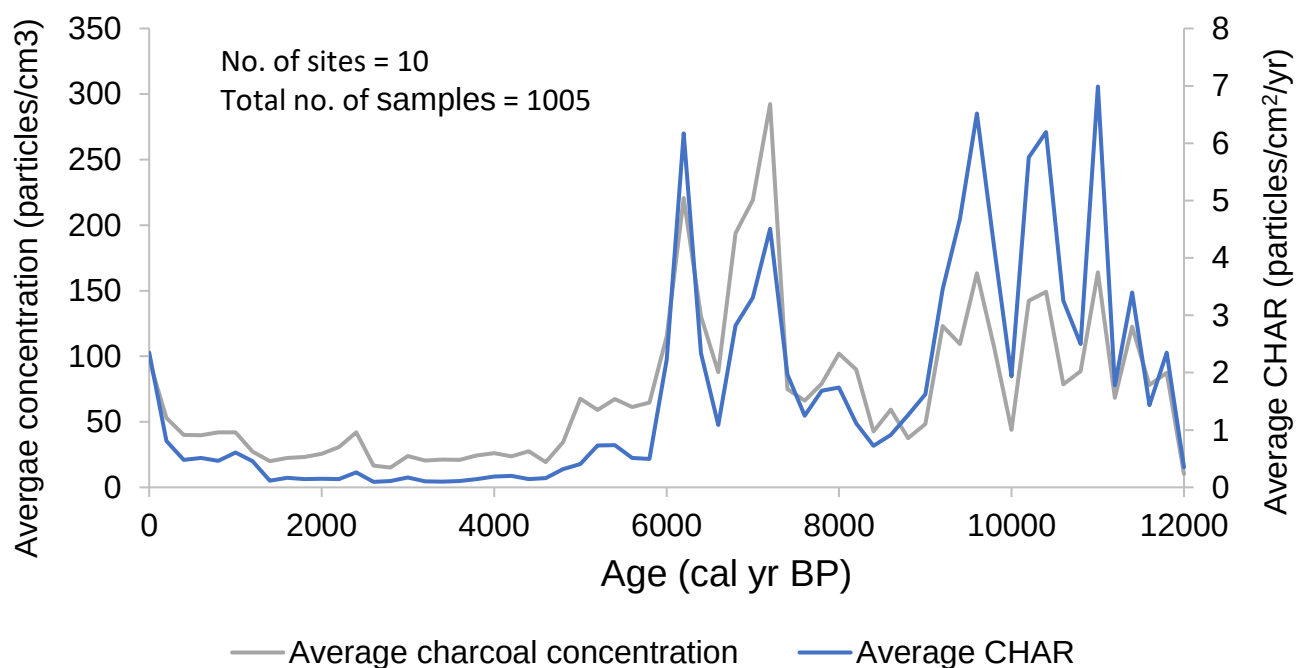


Figure S6: Average charcoal concentration and charcoal accumulation rates (CHAR) for the Furneaux Group Islands during the Holocene.

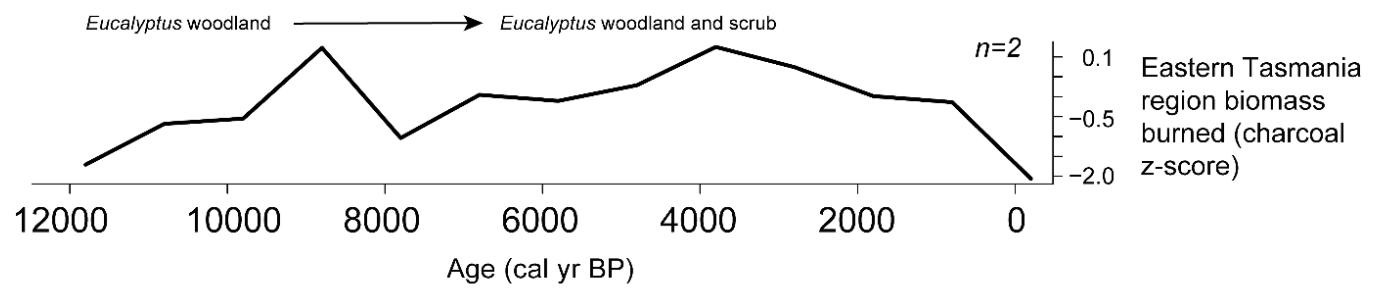


Figure S7: Regional biomass burned (charcoal z-score) for western Tasmania, using the 'pfCompositeLF' function with two-way smoothing.

10.7. Appendix S7 (for Chapter 8)

Table S1: Sites of charcoal records drawn from the Global Paleofire Database. For more information on data and data accessibility, the following code can be used in 'R' after loading the 'paleofire' package:

ID=pfSiteSel(lat>-39, lat<(-28), long>140, long<154,date_int<=3000).

Sites	Latitude	Longitude
Black Swamp	-30.02	151.48
Boggy Swamp	-29.96	151.49
Butchers Swamp	-29.97	151.45
Tadpole Swamp	-38.13	145.27
Buxton	-37.44	145.69
Oaks Creek	-37.58	146.16
Powelltown	-37.86	145.7
Lake Mountain	-37.46	145.87
Tiger Snake Swamp	-38.13	145.27
Gooches Swamp	-33.45	150.26
Sapphire Swamp	-30.03	151.56
Burruga Swamp	-32.02	151.43
Killalea Lagoon	-34.6	150.86
Bondi Lake Centre Core	-36.8	149.93
Warrananga	-33.97	141.56
Bobundara Swamp	-36.25	150.06
Kurnell Fen	-34.01	151.1
Ryans Swamp	-35.09	150.39
Cotter Source Bog center	-35.96	148.81
Rennix Gap	-36.22	148.3
Ginini Flats	-35.31	148.46
Griffith Swamp	-33.28	151
Kings Tableland Swamp_short core study	-33.73	150.48
Kings Waterhole	-33.01	150.66
Aire Crossing	-38.64	143.47
Bondi Lake South Core	-36.8	149.93
Lake Condah	-38.06	141.83
Tea Tree Swamp Core DRA	-37.21	148.83
Tea Tree Swamp Core DRE	-37.21	148.83
Tea Tree Swamp Core DRN-A	-37.21	148.83
Wildes Meadow Swamp	-34.62	150.51
South Salvation Creek Swamp	-33.63	151.25
Bridgewater Lake Core B	-38.3	141.38
Greens Bush	-38.43	144.93
Ingar Swamp	-33.76	150.45
Katoomba Swamp	-33.71	150.31
Long Swamp	-38.08	141.08
Breadalbane	-34.8	149.51
Brooks Ridge Fen	-36.15	148.59

Burralow Creek Swamp	-33.53	150.63
Chapple Vale Swamp	-38.62	143.32
Club Lake	-36.4	148.31
Notts Swamp	-33.8	150.4
Newnes Swamp	-33.38	150.22
Kurnell Swamp	-34.03	151.21
Worimi Swamp	-32.51	152.33
Blundells Flat	-35.19	148.49
Warrimoo Swamp	-33.72	150.61
Cobrico Swamp	-38.3	143.03
Mill Creek	-33.4	151.03
Rotten Swamp Core 4	-35.7	148.88
McKenzie Road Bog	-38.43	146.76
Micalong Swamp	-35.33	148.51
Mulloon	-35.44	149.55
Snowy Flats	-35.54	148.47
Yaouk Swamp	-35.49	148.5
Bolin Billabong combined core	-37.76	145.06
Hogan's Billabong	-36.02	146.71
Lake Hordern	-38.78	143.46
Lake Surprise	-38.06	141.92
Lake Tyrrell2	-35.31	142.78

Table S2: Sites of pollen records and references

Sites	Latitude	Longitude	Elevation (m asl)	References
Bega Swamp	-36.5167	149.5000	1080	Green et al., 1988
Blue Lake	-36.4167	148.3167	1890	Raine, 1982
Boggy Swamp	-31.8667	151.5167	1160	Dodson et al., 1986
Burruga Swamp	-32.0833	151.4500	1100	Dodson et al., 1994
Giandarra Bog	-35.8500	148.4900	1400	Thomas, 1991
Killalea Lagoon	-34.6000	150.8700	3	Dodson et al., 1993
Killer Bog	-32.0667	151.5500	1320	Dodson et al., 1986
Lake Colac	-38.3000	143.5900	152	Mills et al., 2013
Lake Keilambete	-38.2094	142.8779	132	Dodson, 1974b

Part B

10.8. Appendix S8: Holocene sea-level change in Bass Strait, southeast Australia

This appendix presents a ~7500-year record study of macrofossil assemblages on truwana/Cape Barren Island, and it provides some insight into the mid- and late Holocene sea-level change in Bass Strait and southeast Australia at large.

Background

The termination of the Last Glacial Maximum (LGM) was accompanied by a major rise in global sea level as a result of eustatic and isostatic processes related to the melting of ice sheets (Lambeck and Chappell, 2001). The Australian continent is generally tectonically stable due to its intra-plate setting and distance from heavy ice sheets that covered a large part of the Northern Hemisphere continents during the LGM (Lambeck and Nakada, 1990). This tectonic stability in Australia provides a natural experiment for investigating past sea-level changes, especially during the Holocene.

Postglacial sea-level changes in Australia remain contentious, especially regarding the timing of high stand, and sustained late Holocene high stand vs terminated high stand (Lewis et al., 2013). Existing studies suggests sea level attained a high stand between 8000 and 5000 years ago (e.g., Sloss et al., 2007, 2018; Woodroffe et al., 1995; Dougherty et al., 2019; Leonard, 2016; Nakada and Lambeck, 1989). However, some studies suggest sea-level high stand was reduced to the present level in the late Holocene (Sloss et al., 2007, 2018), while others suggest a sustained high stand (Donner and Junger, 1981; Lambeck and Nakada, 1990). In order to gain some insights into this pattern, a mid- to late Holocene record of macrofossils in a coastal lagoon (Apple Orchard Lagoon) on truwana/Cape Barren Island, Bass Strait, is explored to better understand the timing of past sea-level changes in the region and southeast Australia at large.

Apple Orchard Lagoon

Apple Orchard Lagoon (AOL; -40.325°, 148.2161°, 3 m asl) sits on the north coast of truwana/Cape Barren Island in Bass Strait, southeast Australia (Fig. 1). The lagoon is one of a chain of lagoons underlain by Devonian granitic rocks at the rare of the beach (Cocker,

1980; McClenaghan et al., 2011), and is an infilled catchment, with shallow depressions in some parts, which is frequently inundated. This is typical of coastal lagoons on truwana/Cape Barren Island. A herbfield characterized the surface of the lagoon and is dominated by salt-tolerant plants such as *Samolus repens*, *Mimulus repens* and *Sarcocornia*, with surrounding sedgeland and scrub (Fig. 1a–c).

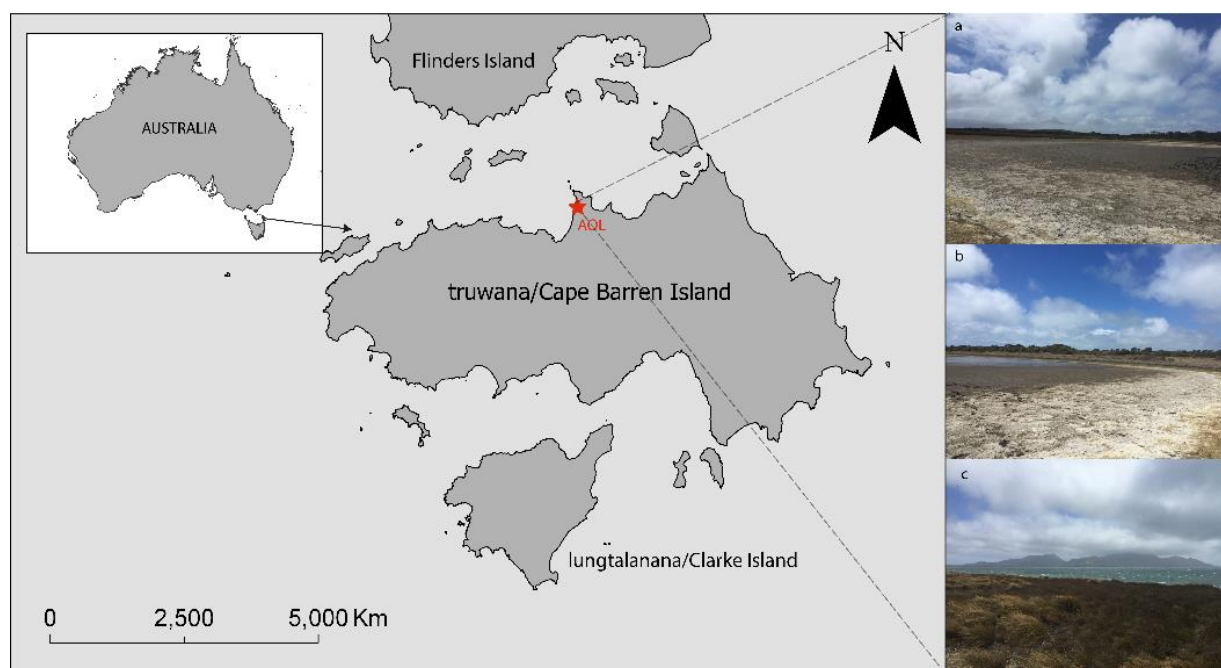


Figure 1: Coring site (red start) Apple Orchard Lagoon (AOL) on truwana/Cape Barren Island, Bass Strait, southeast Australia. The right panels show Apple Orchard Lagoon site (a and b) at a close proximity to the ocean (c). On the horizon in panel 'c' is Flinders Island, north of truwana/Cape Barren Island.

Methods

Core collection, chronology, and macrofossil analysis

A 0.9-m sediment core was collected from Apple Orchard Lagoon (Fig. 1) and radiometrically dated by Accelerator Mass Spectrometry (AMS). The Resulting radiocarbon dates were used to create an age-depth model (SHCal20) using the 'rbacon' package (Blaauw et al., 2020) in 'R' (R Core Team, 2020; Hogg et al., 2020).

1.25 cm³ samples were taken from sediment cores at 1cm interval for macrofossil analysis and samples were processed following macrocharcoal processing method of Whitlock &

Larsen (2001). Macrofossil were identified using texts and online Atlas (Grove, 2020; Lei et al., 2017; Soulié-Märsche et al., 2018; Williams and Mellor, 1991). Macrofossils were expressed as concentrations (macrofossils/cm³). Diagrams were produced using Tilia 2.1.1 and CONISS was used to identify macrofossil assemblage zones (<https://www.tiliait.com/>).

Results

Chronology and lithology

Apple Orchard Lagoon (AOL) core age-depth model produced an estimated calibrated basal age ~8000 cal yr BP (calendar years before present), with an average sediment accumulation rate of 0.2 mm/yr, but macrofossils were only recovered from ~7500 cal yr BP to present (Table 1, Fig. 2 and 3). The core is mostly characterized by woody plant materials, mixed with silty clay from ~70–40 cm (~7500–6300 cal yr BP), silty clay from 40–20 cm (~6300–2000 cal yr BP) and coarse sand dunes from 20–0 cm (~2000 cal yr BP–present) (Fig. 2).

Table 1: AMS radiocarbon dates for Apple Orchard Lagoon measured at 'DirectAMS', Washington.

Depth cm	Lab ID	¹⁴ C yr BP	Error (1σ)
21	D-AMS 036727	2207	35
43	D-AMS 036728	5819	33
65	D-AMS 036729	6292	30
85	D-AMS 036730	6991	32

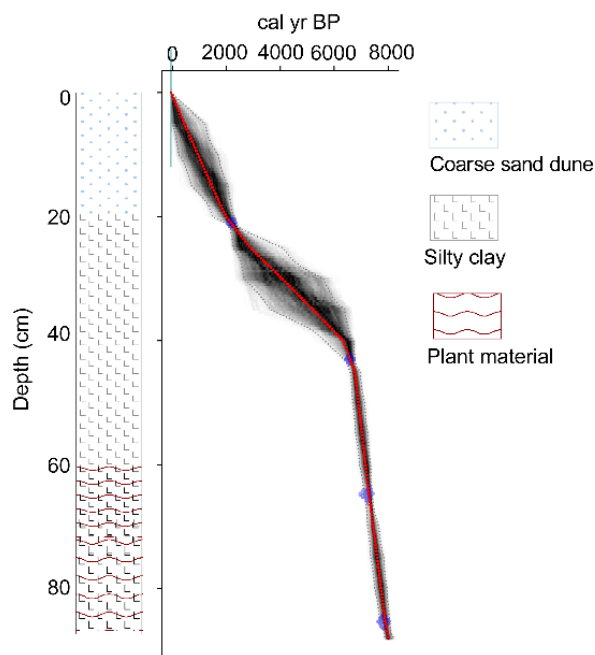


Figure 2: Age-depth model (Bacon) for Apple Orchard Lagoon, showing calibrated ^{14}C dates (purple), age-depth model (dark shaded grey), 95% confidence intervals of calibrated range (light shaded grey), and single 'best' model based on the weighted mean age for each depth (red curve). Cal yr BP is calendar age before present.

Macrofossil assemblage and zones

Five macrofossil types were documented in AOL record and they include woody plant materials, gastropods (*Coxiella strata*), bivalves (*Arthritica semen*), foraminifera (*Elphidium*), and green algae (charophyte gyrogonite). The macrofossil assemblage is divided into four major zones, AOL1–4 (Fig. 3)

Woody plant materials dominate zone AOL1 (~7500–6300 cal yr BP) at the base of the record, with low occurrence of *C. strata*. *Coxiella strata* and *Elphidium* increased in zone AOL2 (~6300–2900 cal yr BP), with a decline in woody plant materials, and charophyte gyrogonite started to increase towards the end of the zone (Fig. 3). Zone AOL3 (~2900–1800 cal yr BP) sees a further increase in *Elphidium* and charophyte gyrogonite, with a minor decline in *C. striata*. *Arthritica semen* also increased in this zone. Zone AOL4 (~1800 cal yr BP–present) at the top of the record sees a major decrease in all macrofossil abundance, and only *C. striata* continued to be present in low abundance (Fig. 3).

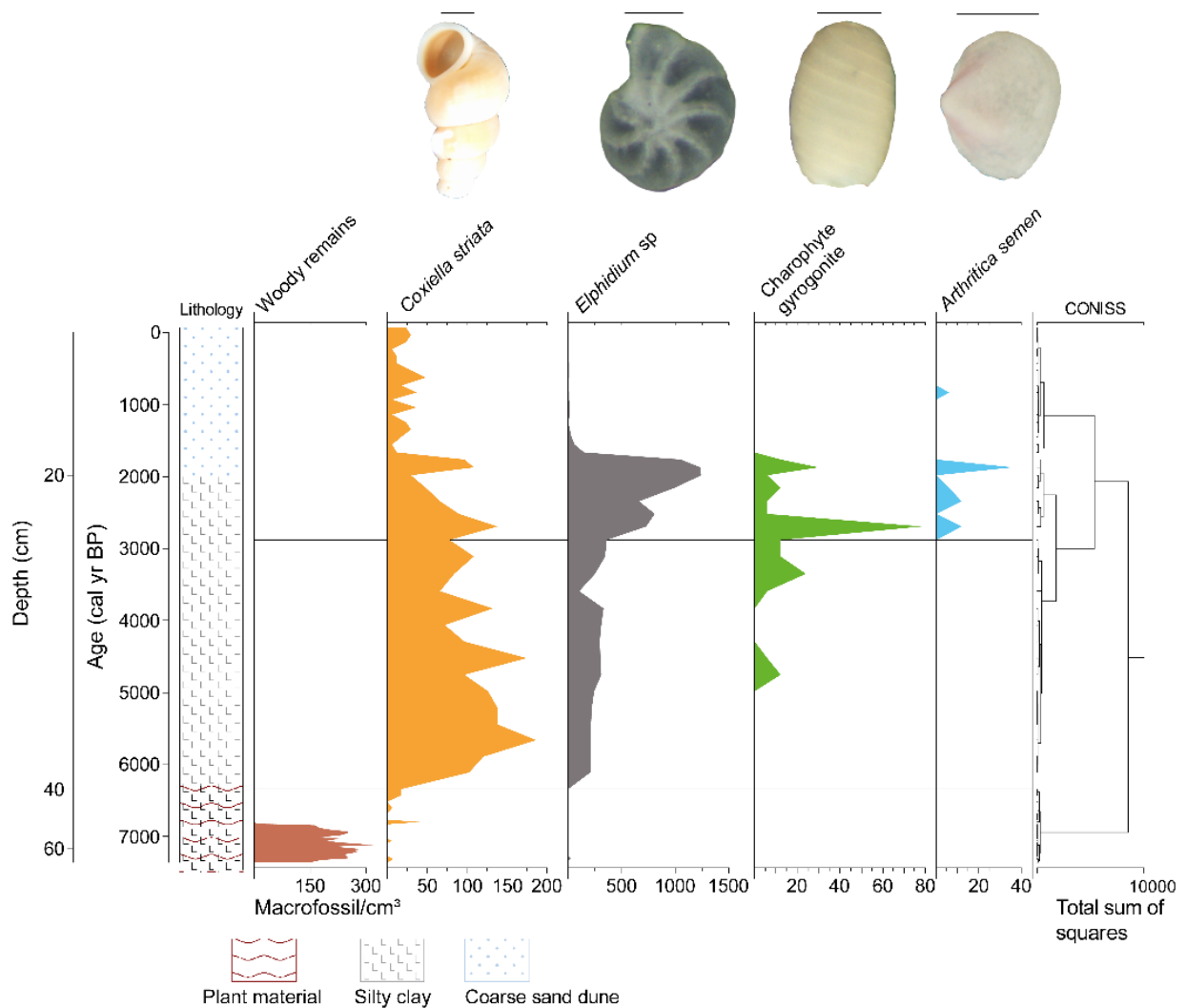


Figure 3: Macrofossil diagram (including CONISS zones) for Apple Orchard Lagoon, truwana/Cape Barren Island, Bass Strait. Macrofossil image scale is 100 μ m.

Discussion

Mid- to late Holocene sea-level change in Bass Strait

Earlier studies of Bass Strait environment suggest the Furneaux Group (as a single island) was formed between about 8500 and 8000 years ago, and the individual islands (including truwana/Cape Barren Island) that make up the Furneaux Group today were formed shortly before 6000 years ago when sea level attained a high stand (Orchiston, 1979). Later studies of sea-level reconstructions for southeast Australia proposed a major rise in sea level started around 9000 years ago and a high stand was attained between about 7700 and 7400 cal yr BP (Sloss et al., 2007; Williams et al., 2018). Meanwhile a later mid-Holocene high stand date of ~6800 cal yr BP is now proposed in a recent study, which

redated earlier evidence of mid-Holocene sea-level high stand in southeast Australia (Dougherty et al., 2019). This high stand is thought to be sustained until about 2000 years, followed by the decrease to present level (Sloss et al., 2007). Although, some earlier studies argued a sustained high stand till present (Donner and Junger, 1981). The insufficient localized sea level-related proxies in southeast Australia limits our understanding of past changes in sea level in the region. The recovered macrofossil assemblages from Apple Orchard Lagoon (AOL) in Bass Strait may reflect sea-level change signals at the site, providing some insights into regional sea-level changes in the region during the Holocene (Fig. 3 and 4).

Mid-Holocene sea-level high stand in Bass Strait

Although sea-level high stand is thought to have been reached between about 7700 and 6800 years ago, this is not reflected in AOL macrofossil assemblages, as shown by the low presence of macrofossils, except woody plant remains in this interval (Fig. 3 and 4). The abundance of woody plant materials may indicate woody vegetation at least around AOL, which may have served as a barrier against wind-blown dune and salt from the ocean into the lagoon during this period. The minor presence of salt-tolerant gastropod *Coxiella striata* may be related to a low lagoon salinity (Williams and Mellor, 1991), and the absence of marine foraminifera *Elphidium* maybe related a reduced oceanic input at the site (Lei et al., 2017). It could also be that sea level had not reached its maximum at least around the northern part of truwana/Cape Barren Island during this period, and the minor presence of *C. striata* was as a result of changes in lagoon salinity as ENSO started to intensify, with a gradual increase in dry conditions (Moy et al., 2002).

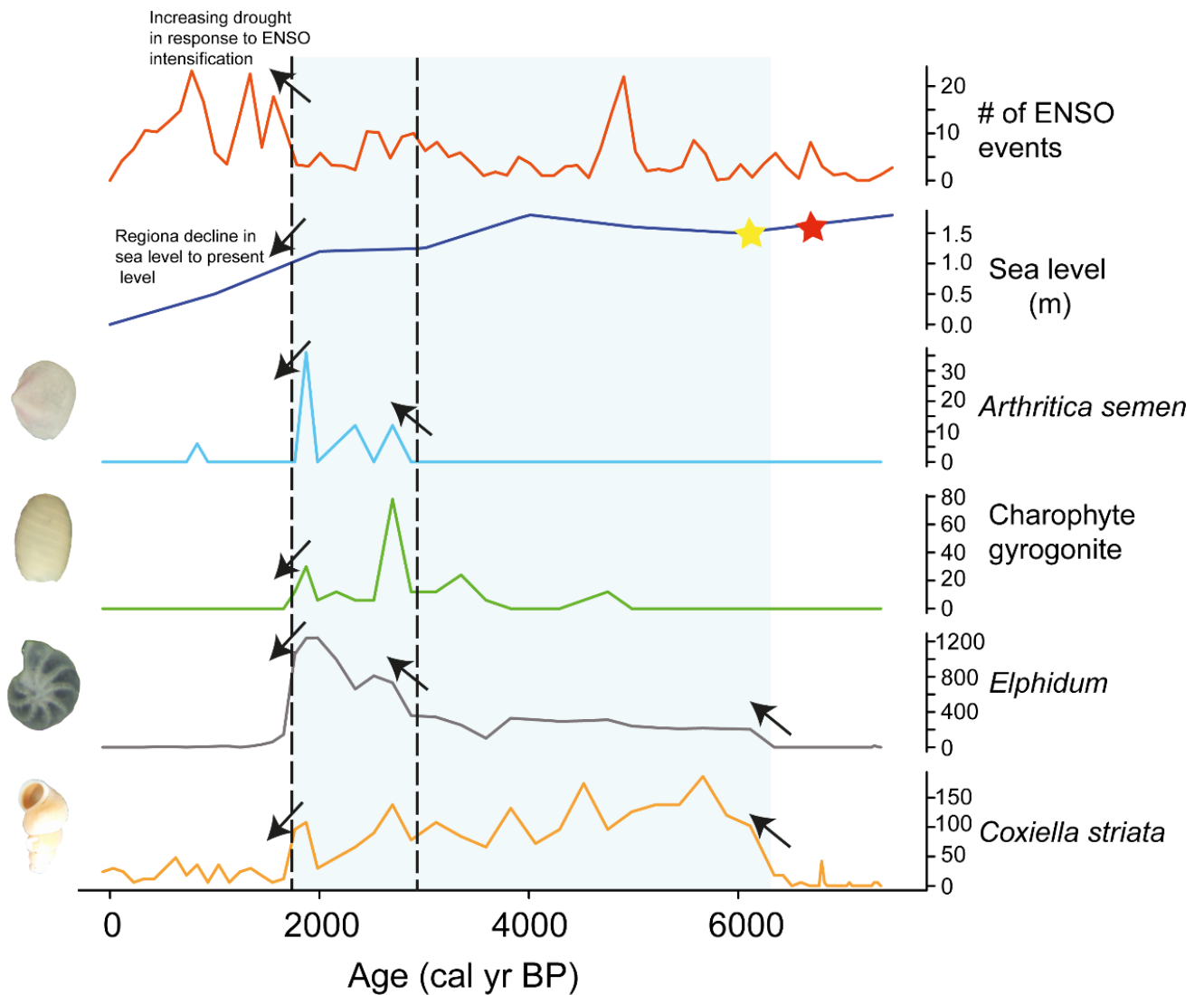


Figure 4: Major macrofossils recorded in Apple Orchard Lagoon, truwana/Cape Barren Island, Bass Strait, compared to Holocene record of ENSO events (Moy et al., 2002) and the major existing record of Holocene sea-level change for southeast Australia (Sloss et al., 2007). Also shown is the estimate of sea-level high stand (red star: ~6800 cal yr BP) for southeast Australia by Dougherty et al. (2019) and sea-level high stand (yellow star: ~6000 cal yr BP) for Bass Strait by Orchiston (1979). Blue-shaded area reflects period of maximum marine and salt-lake macrofossil abundance (~6400–1800 cal yr BP), a reflection of a generally sustained sea-level high stand in Bass Strait or at least in the north coast of truwana/Cape Barren Island during the Holocene. Marine species include *Elphidium* and *Arthritica semen*, while *Cociella striata* is salt-lake species. Black dashed lines reflect potential increase in sea level between ~2800 and 1800 cal yr BP, at least in the north coast of truwana/Cape Barren Island before the decline to present level after ~1800 cal yr BP.

The abundance of *C. striata* and *Elphidium* from about 6400 cal yr BP suggests increased oceanic input and salinity in AOL (Fig. 4; Nagy, 1984; Williams and Mellor, 1991; Lei et al., 2017; Horton et al., 2003). Woody plant remains were absent in the record at this time, and

indicate opening of vegetation around AOL, which allowed frequent oceanic input into the lagoon. Perhaps frequent salt blasting of vegetation before ~6400 cal yr BP, possibly from about 6800 cal yr BP when sea level reached high stand, as suggested by Dougherty et al. (2019), later led to the exclusion of trees and other salt intolerant plants (Adeleye et al., 2021a), with the exposure of AOL to direct oceanic input from ~6400 cal yr BP. Alternatively, it could be that sea-level high stand was just attained in Bass Strait or at least around the northern part of truwana/Cape Barren Island around 6400 cal yr BP, which is consistent with when the Furneaux Group islands were formed (Orchiston, 1979). This timing also agrees with the timing of sea-level high stand in north-eastern Australia (Leonard, 2016: 6500–5500 cal yr BP) and in most Australian continental margins at large (Nakada and Lambeck, 1989: 6500–6000 cal yr BP).

Late Holocene sea-level high stand termination to present level

The expansion of intertidal marine species *Elphidium* and *Arthritica semen* (Lei et al., 2017; Grove, 2020; Horton et al., 2003) between ~2800 and 1800 cal yr BP may reflect inundation of AOL by sea level, or the coastline was at least closest to AOL, with regular oceanic input during this period. Could it then be that sea level increased further in Bass Strait or at least in the north coast of truwana/Cape Barren Island during this period? Or better still, increases in *Elphidium* and *Arthritica semen* may reflect strong wind activities in the area, transporting the marine species to AOL. Further proxy-based studies of Holocene sea-level changes are required in Bass Strait, especially on the eastern Bass Strait islands (Furneaux Group) to better understand this pattern.

Although *C. striata* is salt tolerant, excessive salinity can also drive its decline in salt lakes (Williams and Mellor, 1991; Timms, 1983), and minor decline in the gastropod between ~2800 and 1800 cal yr BP may be related to excessive salinity in AOL (Williams and Mellor, 1991; Timms, 1983). While charophytes mainly reflect freshwater conditions (Coops, 2002; Soulié-Märsche et al., 2018), the low presence of the aquatic macrophyte's gyrogonite and overall abundance of other saltwater-related species during this period suggest the gyrogonite is likely of allochthonous origin, possibly from adjacent fresher lagoons.

A major decline in all macrofossils in the last ~1800 years may be related to sea-level decline at this time (Fig. 3 and 4). The decline in *Elphidium* and *Arthritica semen* suggests a

reduction in oceanic input at AOL, possibly related to shoreline advancements, with lowering of sea levels during this period (Sloss et al., 2007). The decline in oceanic input in AOL may have also led to the major decline of *C. striata*. However, increased lake salinity associated with prolonged periods of drought is also capable of marginalizing the gastropod in lakes (Williams and Mellor, 1991). Further increase in lagoon salinity associated with increasing drought driven by ENSO intensification following the episode (~2800–1800 cal yr BP) of major marine input at the site, may have at least partly driven the major decrease in *C. striata* abundance in the last ~1800 years.

Similarly, the disappearance of freshwater charophyte gyrogonite in the last ~1800 years is likely linked to shallowing of lagoons on truwana/Cape Barren Island (Adeleye et al., 2021a) and increasing salinity associated with increasing drought driven by ENSO intensification (Soulié-Märsche et al., 2018; Moy et al., 2002). The presence of coarse sand in AOL during this period may reflect dune deposition in the lagoon, which is associated with beach progradation and sea-level decrease. This may have contributed to a major decrease in lagoon depths and increased salinization as it is in the area today, with abundant salt-tolerant plants (e.g., *Samolus repens*, *Mimulus repens* and *Sarcocornia*) growing on the surface of AOL and adjacent lagoons. Charophytes have also been found to be absent in the interval containing coarse sand dunes in sediment cores from the Mediterranean (Soulié-Märsche et al., 2018). However, the link between coarse sand dune and charophyte absence was not clarified in this study, and charophyte absence was also mainly attributed to high lake salinity at the interval.

Conclusion

The mid- to late Holocene macrofossil record from Apple Orchard Lagoon on truwana/Cape Barren Island provides some insights into past sea-level changes in the Bass Strait area and southeast Australia at large. Results suggest sea-level high stand was attained in Bass Strait around or shortly before ~6400 cal yr BP, which generally agrees with previous estimates. Results also supports existing views of sea-level high stand termination to present level around 2000 years ago in southeast Australia. A high stand is also suspected at least locally around the north coast of truwana/Cape Barren Island between ~3000 and 2000 cal yr BP before the decline to present level. Further proxy-based studies of Holocene

sea-level changes in Bass Strait is recommended to confirm and better understand these patterns.

Local proxy-based records of past sea-level change are currently limited in Australia, particularly in southeast Australia. Results from Apple Orchard Lagoon shows the usefulness of coastal wetland macrofossil records in palaeoenvironmental reconstructions, including past sea-level changes. Of particular interest is *Coxiella striata*, a salt-lake gastropod endemic to Australia, and one of the major macrofossils recorded in Apple Orchard Lagoon. The gastropod is widespread in southern Australia, and future studies of their occurrence in coastal sediment cores is recommended, as the species may hold one of the keys to fully understanding past climatic and sea-level changes in southeast Australia.

Part C

10.9. Appendix S9: A snapshot of the educational material being developed from thesis.

The preview of the booklet draft below is aimed to summarize my thesis in plain language for high school students in Tasmania. The booklet is currently being put together in collaboration with truwana Indigenous community and the wider Tasmanian Indigenous communities and Centre of Excellence for Australian Biodiversity and Heritage.

