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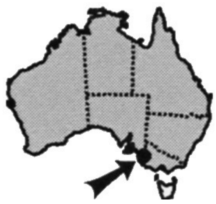
Palaeoenvironmental proxies used to reconstruct the Quaternary of Australia: a case study from Naracoorte Caves, South Australia



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Abstract

Understanding environmental changes through time gives insight into past faunal community change and possible explanations for extinctions. Australia has a rich climate history that has been studied using multiple proxies including both marine and terrestrial records. The Naracoorte Caves World Heritage Area contains sedimentary and fossil records within well stratified sequences, which span the last 500,000 years. Stable isotope analysis of biogenic material, such as mammalian tooth material, has become a globally recognised proxy for the purpose of palaeoenvironmental reconstructions. With refined chronology and dating techniques, stable isotope analysis at the Naracoorte Caves has the potential to provide a palaeoenvironmental record through the Quaternary. Comparing this record with changes in biodiversity through time allows for improved reconstruction of the palaeoecology of local vertebrate faunas. This in turn allows for the elucidation of extinction events that have occurred and their possible links to changes in the environment.

Key words: Naracoorte Caves, Quaternary, Palaeoenvironmental proxies, stable isotopes, palaeoecology, caves

Introduction

The study of Quaternary palaeoenvironments is important for understanding long-term patterns of climate change and drivers of faunal responses to change. Importantly, palaeoenvironmental reconstructions provide a comparative context for modern climate change and its influence on fauna (Fordham and others, 2020). Australia is the driest inhabited continent in the world and its Quaternary deposits have yielded a dynamic record of past climate change (Bird and others, 2016). Shifts in environment over time have driven evolutionary changes in native fauna and flora which have led to the specialisation seen today (Tedford and others, 2006).

The Quaternary spans the last 2.6 million years and is divided into two epochs, the Pleistocene (approximately 2.6 Ma to 11.7 ka) and the Holocene (approx. 11.7 ka to present day). Reconstruction of the environments of the Pleistocene and the Holocene not only improves understanding of past climatic and evolutionary events, but also modern changes in the environment (Forbes and others, 2007). Such study requires data from fossil sites with fine-scale chrono-stratigraphic resolution, and preservation of materials that serve as proxies for palaeoenvironmental variables. Caves act as natural collectors of organic and inorganic material and preserve deep sedimentary records representing long periods of time (Reed, 2012). Cave deposits, such as those preserved at the Naracoorte Caves World Heritage Area (NCWHA) in south-eastern South Australia (Figure 1), provide ‘time capsules’ of information on the diversity and distribution of mammal communities over the past 500,000 years (Macken and others, 2011; Macken & Reed, 2013). When paired with climate and geochronological analysis, these faunal records have the potential to resolve the palaeoecology of these communities, including the causation and timing of both past and historical extinctions and their drivers (Reed & Bourne, 2000; Macken & Reed, 2013).

During the Pleistocene, around 46 ka, Australia and New Guinea lost approximately 60 species of mammals, birds and reptiles, mostly of body masses greater than 40 kg (Johnson, 2005). The cause of these extinctions has created great debate amongst scientists for over a century (Johnson, 2005; Wroe & Field, 2006; Saltré and others, 2016). There are three main hypotheses for the cause of these extinctions: overhunting by humans, modification of habitat due to changes in fire regime (argued by some to have been driven by humans) and changes in climate (Roberts and others, 2001; Trueman and others, 2005). More recently, another major extinction event occurred, following European settlement. Today, approximately one third of

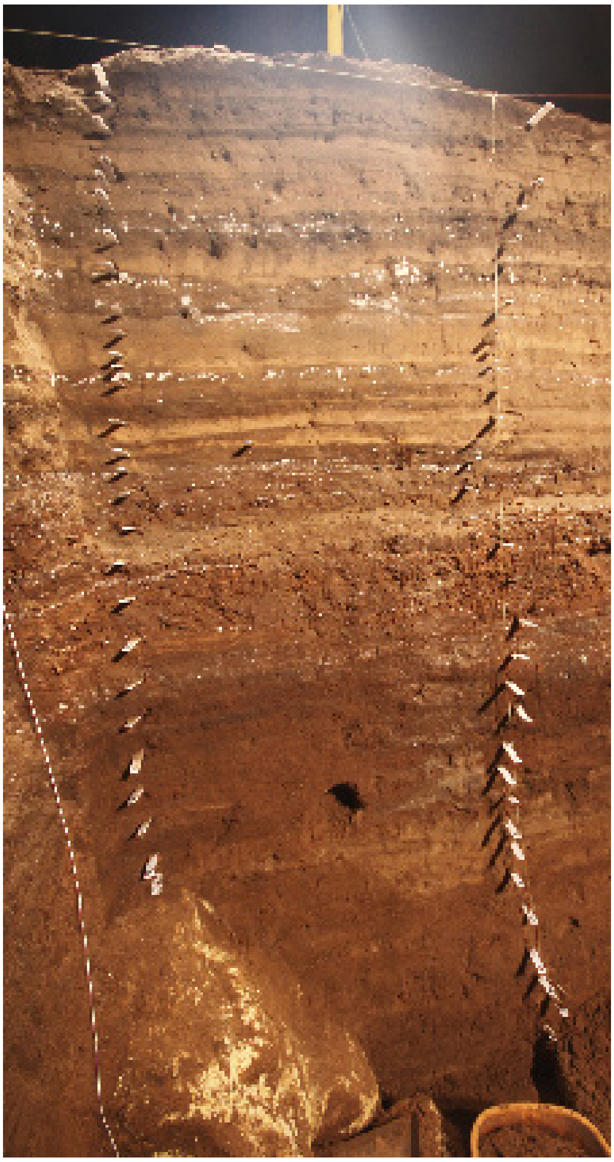

Figure 1. Finely bedded sediment section of the Blanche Cave excavation site, Naracoorte Caves World Heritage Area. Photo Steve Bourne

the pre-European native mammalian biodiversity of Australia has become extinct or is at risk of extinction (Fusco and others, 2016).

This paper provides a broad overview of key approaches to using proxies for interpreting Quaternary palaeoenvironments. The Naracoorte Caves World Heritage Area is used as a case study to illustrate the application of some of these proxies and to highlight gaps in knowledge for this important locality.

Palaeoecology

Palaeoecological research has given insight into the taxonomy and biodiversity of both living and extinct species, as well as changes in the climate of south-eastern Australia during the Quaternary (Macken and others, 2013; Grealy and others, 2016). However, there is a lack of high resolution data on the palaeoecology of vertebrate faunas through time in relation to changes in climate and habitat (Hocknull and others, 2007; Fraser & Wells, 2010). Palaeoecology is the study of fossilised remains of organisms and the interactions they have with other organisms and/or the environment in which they live (Brenchley, 1998). This type of study relies on the involvement of a number of scientific disciplines including but not limited to; palaeontology, taxonomy, geochemistry, geology, palaeobiology and palaeoclimatology (Brenchley, 1998; Twitchett, 2006). Combining these disciplines enables a reconstruction to be made of past ecosystems and the communities within them, and the influences of climate on the environment. This is an important tool in the study of life habits of now extinct fauna. Many aspects of mass extinction events, including the extinction of Australia's megafauna, remain little understood and have been under-represented in the study of mass extinctions (Twitchett, 2006). Palaeoecology studies of the Quaternary can aid in the understanding of decline in taxa through time and provide critical information for ecosystem restoration and recovery in the present day biodiversity crisis (Birks, 1996; Huntley, 1996). This allows for better understanding of natural variability within communities in response to changes over long time periods (Macken & Reed, 2014).

Overview of palaeoenvironmental proxies used in Quaternary research

Palaeoenvironmental studies have helped determine how Australia's ecosystems have been shaped and the driving forces that have shaped them. Australia contains a wide range of environments, including the constantly wet equatorial tropics, the seasonally wet monsoonal tropics, the arid interior, the semi-arid northwest, and the temperate south (Williams and others, 2009). These have remained largely unchanged throughout the Holocene (Anderson, 2007). Reconstructions of past climatic and environmental changes have traditionally been based on physical geological evidence that is stratigraphic in nature (Anderson, 2007). In recent decades, with the advances in technology and refinement of analytical techniques, more ways have been devised in which environmental changes can be reconstructed. These methods, outlined in the following sections, are all indirect measures of environmental and climatic change and are referred to as *proxies*. The use of a single proxy at a specific location only provides a limited range of information; therefore, the use of multiple proxies is recommended to obtain a comprehensive reconstruction of broader environmental changes (Mann, 2002; Anderson, 2007). To create a reliable reconstruction, the proxy needs to be chronologically authenticated with well-established dating techniques (Bowler and others, 1976; Steinman & Abbott, 2013; De Deckker and others, 2019).

Marine cores

Marine cores provide a record of deep sea sediment that is generally less disrupted than are terrestrial sediment records. This allows for a more complete history of climatic change to be reconstructed (Anderson, 2007). These records provide information on past sea surface temperature, ocean currents, sea level change and atmospheric concentrations related to climate variability. Deep sea sediment cores contain multiple proxies which can be analysed using a variety of techniques including analytical studies of both benthic and planktonic foraminifera, stable isotope ratios, aeolian dust content, fluvial sediments, pollen and charcoal (Harle, 1997; Cordova and others, 2009; De Deckker and others, 2019). Changes in marine records can be used to determine large scale change in global climate. Although marine cores remain less disrupted than those of terrestrial sediment records, the occurrence of reworked sediments, plant and microfossil materials may not be representative of past climate and vegetation. This, paired with the large amount of sample that is needed from the core, limits the validity of the reconstruction (Groot & Groot, 1966).

Lake records

Lake sediments are commonly used for the reconstruction of past environments and are analysed for their chemical and physical characteristics, as well as the biological remains that they contain. When compared with other terrestrial proxies, lake sediments provide a continuous record of sedimentation and environments through time (Anderson, 2007). Environmental changes are reflected in the biological, chemical and physical profile of the lake sediments, with data obtained via the use of sediment cores obtained from the lakebed. Sediment cores are typically analysed for changes in bulk density, organic content, isotopic signature and moisture content, which give insight into changes in past hydroclimatic conditions (Steinman and others, 2010). Limiting factors on this proxy are those related to the environment surrounding the lake and characteristics of the lake itself, which may influence the composition and the nature of the sediments that are collected (Anderson, 2007).

Sediment analysis

The analysis of sediments can be used in a wide range of sampling environments, including but not limited to: lakes, marine environments and caves. Modern sediment analyses incorporate a variety of approaches including stratigraphy, sedimentology, geochemistry, mineralogy, isotopic analysis and micro-morphology. Sedimentary analysis is a fundamental technique for identifying changes in environments and characterising the broader climate, from which a palaeoenvironmental reconstruction can be built (De Deckker and others, 2019). Understanding the origin of sediments via geochemical analysis, for example dust transport, can help elucidate factors such as palaeocirculation patterns and associated climate (Petherick and others, 2008). Analysis of minerals within the deposit can be used as indicators of depositional conditions. An example of this is gypsum, which can be indicative of the presence of water or bat guano in cave settings (Audra and others, 2019). There are other morphological analyses that can be conducted on individual sediment grains to estimate transport distance, via grain roundness, grain size and surface alterations, such as etching (Darrénougué and others, 2009). When pairing these characteristics with geochemical analysis of the sediments and the deposit, an interpretation of the origin and the depositional environment in which these materials were deposited can be made (Forbes & Bestland, 2007; Darrénougué and others, 2009). The rate of sediment accumulation varies according to depositional setting. For example, the low rate at which sediments are accumulated in deep ocean environments or differences in accumulation rate with change in cave entrance shape and size (Groot & Groot, 1966; Reed, 2008). Reworking of sedimentary sequences has implications for stratigraphic and chronological integrity and can limit the resolution for applications of this proxy (Hunt and others, 2015).

Palynology

As pollen has an outer wall (exine) composed of sporopollenin, it is relatively resistant to decay, creating the potential for fossil pollen embedded in sediment deposited in a variety of depositional environments including caves, lakes, and marine deposits (Groot & Groot, 1966; Cordova and others, 2009; Darrénougué and others, 2009). Due to the, at times, abundance of both pollen and spores in sedimentary records, they are valuable for quantitative and statistical analysis for palaeoenvironmental reconstructions. This allows for elucidation of evolution and change in the distribution of vegetation communities throughout the Quaternary (Kershaw and others, 1991). The percentage of plant types represented in a core can be used to estimate the vegetation coverage and hydrology through time. An example of this is the ratio of tree and shrub species to herbaceous species (Kershaw and others, 2007; De Deckker and others, 2019). Some species of spores present in the deposits can be used as a proxy for herbivore biomass present at that time (Van Der Kaars and others, 2017), such as *Sporormiella*, which can be used to determine the presence of megafauna in the Pleistocene (De Deckker and others, 2019; Perrotti & Asperen, 2019). Even where it is abundant, pollen offers a relatively low taxonomic resolution, making it difficult to identify pollen to species level, limiting the accuracy of vegetation reconstructions (Cordova and others, 2009). Other useful vegetation proxies include phytoliths, leaf waxes and macro plant remains.

Charcoal

Burnt macroscopic remains of plants, namely charcoal, can be used as an indicator of past vegetation diversity and occurrences of fire events through time (Cordova and others, 2009). Charcoal can be found in terrestrial, lacustrine and marine deposits. Like pollen, microscopic analysis of this material can be used to identify dominant plant types which can be indicative not only of vegetation presence, but sometimes also distribution (Kershaw and others, 2007). The identification of fire events can be combined with other proxies, to help determine how vegetation communities have changed over time (Harle, 1997; Kershaw and others, 2007). Such information has been used to investigate the peopling of Australia (Harle, 1997; Kershaw and others, 2007), and might also yield information regarding the late Pleistocene megafaunal extinctions. Increased biomass burning due to human influence is one of the proposed hypotheses for the cause of this extinction event (Trueman and others, 2005; Roberts and others, 2019). However, the transportation of charcoal is usually over short distances, which limits its use to a local proxy of vegetation change rather than change on a larger scale (Cordova and others, 2009).

Speleothems

Speleothems provide high temporal resolution from which a reconstruction of terrestrial palaeoclimate, mainly precipitation, can be built (Bestland & Rennie, 2006). Secondary cave calcite deposits, such as speleothems (Figure 2), are the

Figure 2. Speleothem structures in Victoria Fossil Cave, Naracoorte Caves World Heritage Area. Photo Steve Bourne

result of chemical interactions between rainwater, carbon dioxide and limestone bedrock. Combined with uranium series dating, speleothems have been used to determine environmental change through Quaternary glacial cycles (Ayliffe & Veeh, 1988; Hellstrom & McCulloch, 2000; Bestland & Rennie, 2006). Other properties such as stable isotopes of oxygen and carbon, trace elements and humic substances, that cause colour differences and pronounced luminescent bands, can be used to explore aspects of environmental change (Desmarchelier and others, 2000; Bestland & Rennie, 2006; Smailer & White, 2013; Blyth and others, 2016). Speleothems provide important information on palaeoenvironments as they are not affected by post-depositional alteration, unlike some other climate proxies (Desmarchelier and others, 2000). However, speleothem growth is dependent on correlated environmental variables such as the quantity of infiltrated rainwater, presence of a carbon dioxide source and regional temperature (Ayliffe & Veeh, 1988; Ayliffe and others, 1998). Speleothem growth is favoured by wet, warm environments rather than dry, cold environments, in which there is little growth, which can cause hiatuses in the record (Ayliffe & Veeh, 1988).

Palaeontological Records

Studies into the habitats of extant fauna provide insight into the environmental niches they fill within modern communities (Moriarty and others, 2000; Hocknull and others, 2007; Fusco and others, 2016). The presence or absence of particular fauna within fossil deposits can be reflective of the environment and habitat at that particular time (Grün and others, 2001). A common outcome of the analysis of fossil material is an attempt at reconstruction of palaeoenvironments by analysing the dietary niche of preserved species, for example, the proportion of browsing fauna relative to grazing fauna (Price & Sobbe, 2005). As grazing fauna tend to inhabit open, grassy environments and browsing fauna, woodland to forest environments, the ratio of these two distinct classes of fauna can be indicative of the past landscape (Prideaux and others, 2009; Fraser & Wells, 2010; DeSantis and others, 2017). Features of mammalian dentition can also be used to indicate the diet of now-extinct species, providing an indicator of palaeo-habitat (Prideaux and others, 2009). This relies on the assumption that faunal communities fluctuate due to dietary preferences and food availability. Micro-abrasions or microwear on the enamel surface of teeth can be used to determine the likely dominant plant type eaten by a herbivore. Combining various types of analyses provides a sound basis for reconstruction of past habitats from mammal fossils. The reconstruction of the ecologies and dietary preferences of extinct fauna have traditionally been determined by taxonomic similarities to extant relatives, with the assumption of uniformitarianism of dietary preferences and ecologies, and dental morphology (Hopley and others, 2006). However, it has been established that extant species of close relation to extinct fauna do not always have similar dietary preferences or ecologies, and that dental morphologies can be a result of generalist adaptions rather than dietary behaviours (Hopley and others, 2006).

Stable isotope analysis of fossil vertebrate faunas

Stable isotope analysis of biogenic materials, such as bioapatite derived from tooth material, is a commonly used proxy for the reconstruction of environments and faunal ecologies of the past (Gehler and others, 2012; Barham and others, 2017). Stable isotopes have the potential for not only providing information on the diet and behavioural characteristics of animals, but also the environment in which these animals lived (Crawford and others, 2008). This type of analysis has been used to better understand individuals, populations and the broader ecosystems of present faunal communities (Crawford and others, 2008), and is also becoming an increasingly important tool in understanding the ecology of now-extinct species (Clementz, 2012). Different environmental and climatic settings, such as glacial and interglacial periods, provide a range of isotopic signatures. These signals are obtained and recorded in faunal materials through physiology, behaviour, dietary preferences and resource partitioning (Kohn & Cerling, 2002; Gehler and others, 2012). Stable isotope analysis of this material, such as bioapatite, is then used to infer drinking behaviour and dietary preferences, which in turn can be used to reconstruct environmental settings (Gehler and others, 2012). Stable isotopes, in contrast to other proxies, offer semi-quantitative palaeoecological and dietary preferences of extinct fauna, independent of morphological assumptions (Hopley and others, 2006; Clementz, 2012). In the past, the use of stable isotopes has predominantly focused on large mammalian material (Barham and others, 2017). A disadvantage of this is the wide range of environments that these animals migrate over, thus representing the environments they have moved through rather than the environment in which they died (Grimes and others, 2008). Large mammals are also relatively less abundant in fossil deposits, in comparison with small mammals

(Grimes and others, 2008; Gehler and others, 2012). Recent research addresses this limitation by focusing on abundant small mammal faunas which often provide a more representative record of past communities (Grimes and others, 2008; Gehler and others, 2012).

Applications of palaeoenvironmental proxies at Naracoorte Caves World Heritage Area

The vertebrate fossil deposits of the NCWHA span the last 500,000 years and provide insight into the climate and fauna of the south-eastern region of South Australia during the late Quaternary (Darrénougué and others, 2009). The study of fossil deposits, such as those found at the NCWHA, yield information about past faunal communities; including both living and extinct groups, taphonomic processes within caves and environmental changes through time (Reed, 2012; Macken & Reed, 2013; Grealy and others, 2016). This site is well known for its fossil record of megafauna. With refined chronology and investigation of palaeoenvironmental proxies, it has also contributed to research in vegetation and climate changes through time, as well as faunal community responses to these changes (Macken and others, 2011; Macken and others, 2012; Macken and others, 2013).

Sediment sequences in caves typically have a complex depositional history (Osborne, 1984; White, 2007; Hunt and others, 2015). Material such as fossils, pollen, charcoal and sediments are subject to erosional and depositional events that can cause unconformities, stratigraphic reversals, biases and changes in the lateral facies making reconstructions of past climate and faunal records difficult (Osborne, 1984; Forbes and others, 2007). The processes and accumulation mechanisms within cave environments can be further elucidated when studied across multiple sites within a locality (Osborne, 1984; Reed, 2008). The NCWHA contains multiple sites that contain finely resolved stratigraphy and chronology, whilst lying within close proximity to each other, collectively spanning 500,000 years (Reed, 2012; Reed, 2019). This provides the opportunity to study contemporaneous sites within a confined time frame and with different collection mechanisms. These factors improve understanding of inter-site variability and allow for the past climate and faunal communities to be verified and correlated through time (Macken and others, 2013; Macken & Reed, 2014; Reed, 2019). The abundance and high-level preservation of the fossils at Naracoorte, along with the presence of multiple palaeoenvironment proxies, gives the opportunity to explore the faunal community responses to change.

Climate record

Palaeoclimate studies conducted in the sites within the NCWHA, have applied a wide range of climate proxies. Records of middle to late Pleistocene glacial and interglacial climate cycles have been captured by proxies such as speleothem records (Ayliffe & Veeh, 1988; Ayliffe and others, 1998; Desmarchelier and others, 2000; Moriarty and others, 2000; Grün and others, 2001; Bestland & Rennie, 2006). There have also been investigations into the faunal assemblages in relation to climate (Brown & Wells, 2000; Prideaux and others, 2007; Fraser & Wells, 2010; Macken and others, 2012; Macken & Reed, 2014), as well as sedimentary and pollen analysis (Ayliffe and others, 1998; Desmarchelier and others, 2000; Forbes and others, 2007; Darrénougué and others, 2009; Macken and others, 2011; Macken and others, 2013).

Palaeoenvironment records from speleothems have revealed cycles of wet and dry phases over the Naracoorte record (Ayliffe and others, 1998; Desmarchelier and others, 2000; Prideaux and others, 2007). Ayliffe and others 1998 identified four major growth periods of speleothems during the last 500,000 years. The first occurred from 420 to 340 ka. Periods of active speleothem growth are commonly associated with an increase of effective precipitation, while hiatuses in growth are associated with a decrease in effective precipitation (Ayliffe and others, 1998).

The second growth period occurred between 300 and 270 ka. Vertebrate fauna records show a high diversity of large fauna, including megafauna species, during this time (Prideaux and others, 2007). Within this major growth period, at approximately 280 ka, there was a relatively high abundance of browsing fauna that supports the interpretation of a wetter climatic phase at this time (Prideaux and others, 2007). The second speleothem growth period was succeeded by a relatively dry period; evidenced by a hiatus in speleothem growth (Ayliffe and others, 1998). This relatively dry period lasted from approximately 270 ka to 220 ka, with peak interglacial conditions occurring around 240 ka. This dry period also saw a vegetation shift to grassland and open woodland environments at 230 ka (Prideaux and others, 2007), though it has been generally characterised as a heath dominated environment, based on species habitat preferences found in Cathedral Cave spanning this time-frame (Prideaux and others, 2007).

The third speleothem growth period, which lasted from 220 to 155 ka, contained the Penultimate Glaciation (195 to 128 ka) (Ayliffe & Veeh, 1988; Desmarchelier and others, 2000). This glacial period had both cold and dry conditions and local speleothem growth occurred at NCWHA. This growth was initiated in cold conditions with the dominance of herbaceous vegetation at 185 ka (Desmarchelier and others, 2000) and continued from 179 to 162 ka, where there was a period of active vegetation coverage dominated by woody taxa and temperatures similar to those of today (Desmarchelier and others, 2000; Bestland & Rennie, 2006). At approximately 157 ka there was a return to cooler conditions with herbaceous taxa dominance (Desmarchelier and others, 2000). The time preceding the Penultimate Glaciation saw a period of high temperature and low effective moisture availability, with no speleothem growth (Macken and others, 2011). At 125 ka there was a temperature peak between 1 and 3 °C warmer than today (Fraser & Wells, 2010; Macken and others, 2011). The co-existence of browsing and grazing herbivores, arboreal and heath dwelling mammals around 120 ka indicates the presence of open forest/woodland environments leading up to the next speleothem growth phase (Brown & Wells, 2000).

Within the fourth speleothem growth phase, which occurred from 115 to 20 ka, there was some local change in climate at Naracoorte. From approximately 115 to 70 ka there was local speleothem growth (Ayliffe and others, 1998; Grün and others, 2001; Bestland & Rennie, 2006), indicating an increase in effective precipitation (Macken and others, 2011). This is supported by the increase in the relative abundance of a species (*Potorous tridactylus*) which is found in a high rainfall environment and the decrease of a species (*Perameles gunnii*) found today in grasslands around 80 to 70 ka from a fossil assemblage in Victoria Fossil Cave (VFC) (Macken and others, 2012). However also at this time, there is an increase of species that inhabit open heath vegetated environments that would indicate drying climatic conditions (Macken and others, 2012). There was a recorded hiatus in speleothem growth found in two chambers within VFC, that spans approximately 70 to 50 ka (Moriarty and others, 2000). From 50 to 20 ka there is a period of wetter conditions, with peaks in speleothem growth at 50 to 40, 31 and 23 ka (Ayliffe & Veeh, 1988; Ayliffe and others, 1998; Grün and others, 2001). This wetter event is supported by the presence of gypsum in the sedimentary sequence within Blanche Cave (Darrénougué and others, 2009). The pollen record also shows a wetter condition with the presence of woodland taxa at the expense of herbaceous and woody-herbaceous plants (Darrénougué and others, 2009; Macken and others, 2013; Macken & Reed, 2014). However, during this period there was a hiatus in the speleothem record, from 40 to 35 ka, showing a low effective moisture availability at this time (Ayliffe and others, 1998; Macken and others, 2013). The Last Glacial Maximum (LGM), 22 to 17 ka, showed a period of time where there was little to no speleothem growth, with the influx of rounded and polished quartz grains entering the caves (Ayliffe and others, 1998; Macken and others, 2013). The vegetation at the time was predominantly herbaceous (Darrénougué and others, 2009; Macken and others, 2013) with the exception of 20 ka when the percentage of woody taxa reached 90% (Darrénougué and others, 2009). After the LGM there was a return to wetter conditions with the increase of woody-herbaceous taxa, and the increase of effective moisture (Forbes and others, 2007; Darrénougué and others, 2009; Macken and others, 2013; Macken & Reed, 2014).

Palaeoecology

Due to the preservation of material within multiple, well-stratified sequences, the NCWHA deposits provide an opportunity to improve the relationship between faunal and palaeoenvironmental records. This can be used to determine the relationship between community changes and climate and understand the palaeoecology and possible cause of extinctions (Macken and others, 2011). Previous palaeocommunity studies at NCWHA have revealed fluctuations in the composition and relative abundances of species in response to changes in climate and environment in the Pleistocene (Prideaux and others, 2007; Fraser & Wells, 2010; Macken and others, 2012). However, the diversity at NCWHA was largely maintained prior to the megafaunal extinction (Prideaux and others, 2007; Macken & Reed, 2013). In the Cathedral Cave fossil assemblage there was a decline in large species during the 270 to 220 ka dry interval; however, they recovered later in the record prior to the megafaunal extinction (Prideaux and others, 2007). The Grant Hall fossil site (VFC) shows that there was no change in the total species richness with some variation in the relative abundance between species of differing ecologies, from 93 to 70 ka (Macken and others, 2012). Unlike the Cathedral Cave deposit, Grant Hall shows no decline in species richness of large mammals. However, there were species absent from Grant Hall that were present in Cathedral Cave, suggesting not all taxa are resilient at the same time or to the same extent across climatic and environmental change (Macken and others, 2012). The palaeoecology of small mammals of Wet and Blanche Caves showed that the palaeocommunity was stable through the early glaciation and LGM (Macken & Reed, 2014). However, there was variation in the species abundance during early glaciation and post-LGM deglaciation. There was also significant variation in species richness, leading to community reorganisation, during the early stages of post-LGM deglaciation due to reaching a threshold of climate change (Macken & Reed, 2014).

Palaeoecological analyses of now-extinct fauna and their responses to past climate are limited if only the inferred habitats and dietary niches of the species themselves are used as the primary palaeoenvironmental proxy (Hocknull and others, 2007). This is due in part to the taphonomic biases and the incomplete representation of communities in the fossil record (Grimes and others, 2008; DeSantis and others, 2017). There are also uncertainties regarding assumptions that extant fauna and their environmental tolerances have remained unchanged over time (Macken and others, 2012). Interpretation of dietary niche and habitat through stable isotope analysis provides a direct quantitative approach to understanding the relationship between fossil faunas and their environment.

Stable isotope analysis of fossil vertebrates at NCWHA

Studies of the stable isotopic composition of biological materials conducted in Australia include seasonal variations in present day kangaroo teeth of southern Australia (Brookman & Ambrose, 2012; Brookman & Ambrose, 2013), modern and fossil macropod tooth material from the northwest coast (Skippington and others, 2018), marsupial tooth enamel from Pliocene fauna deposits of south-eastern Queensland (Montanari and others, 2013), present day fauna and pre-contact human bone collagen studies of Roonka Flat archaeological site in South Australia (Pate, 1998), isotopic variation in Bare-nosed Wombat teeth from Tasmania (Roberts and others, 2019), fossilised fauna tooth enamel from Cuddie Springs in south-eastern Australia (DeSantis and others, 2017), isotopic and microwear analysis of macropod species tooth material in south-eastern Australia (Prideaux and others, 2009) and isotopic composition of land snails from Tight Entrance Cave in south-western Australia (Faith & O'Connell, 2011). As the NCWHA contains well stratified deposits that span a wide range of time (Figure 1), including glacial cycles, that are in association with multiple proxies and fossil material (Reed, 2019), the site has the potential of providing a near-continuous record of climate. However, the use of stable isotope analysis is yet to be fully explored in these deposits, despite it being a globally recognised proxy (Gehler and others, 2012). This field is the subject of current research by the author. Recent research using stable isotope analysis of rodent teeth from Blanche Cave revealed a shift in climate and vegetation during the LGM from drier to wetter conditions, with concurrent changes in the relative abundance of three species of *Pseudomys* (Bampton, 2018).

Utilising proxies such as isotope analysis of mammalian teeth has the potential of not only providing information on the environmental and vegetation changes through time, but to also elucidate the life habits and preferences made by the fauna present in those environments (Clementz, 2012; Gehler and others, 2012). Using traditional palaeontological techniques, such as morphological similarities to extant relatives or the association of the fossil in the sedimentary environment, to reconstruct the life habits and climates in which these animals lived can be problematic (Clementz, 2012). Fossils provide information on now-extinct animals through their palaeoecologies which can shed light on the cause of extinction (Reed & Gillieson, 2003). This information, paired with modern palaeontological, geological and ecological studies, gives opportunity to understand faunal response to climate and the life habits of now-extinct fauna. One of the species (*Pseudomys auritus*) in the current research by the author, became extinct soon after European arrival; consequently, little is known of its ecology (Prideaux and others, 2007). The use of stable isotopes indicated the dietary and habitat preference of this species during the last glacial cycle (Bampton, 2018). Understanding extinction events and their links to climate change and evolution is critical for the conservation of present day species that are currently under threat from human-driven extinction and changes in climate (Hocknull and others, 2007).

Conclusion

Palaeoenvironmental studies are important for understanding the climatic history of Australia and the corresponding biodiversity response. The NCWHA has an extensive faunal record that lies within well-stratified deposits that contain many palaeoenvironmental proxies. With refined chronology and dating techniques, this site holds the potential for improving understanding of changes in climate and fauna in south-eastern Australia during the Quaternary. Understanding fine scale changes in vegetation and water availability through glacial cycles can aid our understanding of changes in faunal communities, including megafauna, through time. Stable isotope analysis of biological materials, such as bioapatite derived from mammalian tooth material, has become a globally recognised proxy for reconstruction of palaeoenvironments and palaeoecology. This technique provides an opportunity to expand our knowledge of environmental change in south-eastern Australia during the Quaternary, and how fauna has been directly affected by these changes. Pairing this analysis with other established proxies, such as microwear, has the potential to provide insights into now-extinct species and their behaviour, dietary preferences and the habitats in which they lived. The stable isotopic composition of extinct megafaunal remains has the potential to improve understanding of the cause of these extinctions, by elucidating the palaeoecology of these animals. This information also provides a critical baseline for understanding recent extinctions and the impacts of present and future climate changes on faunal communities in their environments and how these communities may be conserved for the future.

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