

Papers in Honour of Ken Aplin

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Characterizing Environmental Change and Species' Histories from Stratified Faunal Records in Southeastern Australia: A Regional Review and a Case Study for the Early to Middle Holocene

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ABSTRACT. We explore the potential contribution of faunal assemblages from the Australian Alps and surrounding regions towards the characterization of climate and landscape change, and for geo-chronological species distribution mapping. The limitations of existing faunal sites and collections—their rarity, their stratigraphic integrity and resolution, and accurate dating of their histories—are discussed in a regional review of known and potential assemblages and locations. We also revisit a faunal sequence from a stratified cave deposit at Wee Jasper, focusing on a Holocene “climatic optimum” phase. A suite of species fluctuations between 8000 and 6000 cal. BP suggests responses to local changes such as a warmer and possibly moister environment, with probable associated vegetation shifts. For example, eucalypt forests had replaced more open communities across the region by 8600 cal. BP, and were generally dominant until after 6000 cal. BP. Several faunal species are examined in a regional context using available chronologically defined species histories. Emerging robust multi-proxy investigations demonstrate the potential of faunal assemblages for the development of geographically detailed histories of species that can provide indications of palaeoenvironments. This approach can be strengthened by increasing resolution and developing improved age models in presently known fauna-bearing sites.

Introduction

Many natural archives in south-eastern (SE) Australia, including fluvial, alluvial, peat, and lake records, have for decades contributed stratified layers with inclusions such as dust, charcoal, pollen, and other environmental

components to act as proxy records for the reconstruction of palaeoenvironmental conditions since the Last Glacial Maximum (LGM) (e.g., Costin, 1972; Dodson *et al.*, 1994; Eriksson *et al.*, 2006; Kemp & Hope, 2014; Marx *et al.*, 2009, 2011; Stanley & DeDeckker, 2002). In contrast, the contribution of faunal assemblages to inform our

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understanding of the environmental history of this region has typically been minor. In fact, faunal assemblages have usually been placed into a known environmental context based on other proxies, rather than informing environmental change in their own right. There are several reasons for this.

First, relatively old and well-preserved faunal deposits are rare in the Australian montane country and surrounds, and still absent from the subalpine and alpine areas above 1100 m altitude. This is despite the promising existence of numerous limestone karst areas, which are known to preserve organic materials including bone, and the unique “rain shadow” feature of much of the high Monaro plain to the east of the main ranges, which has resulted in several fauna-rich alluvial basalt-derived terraces. Second, known faunal deposits are very rarely continuous, often preserving only “snapshots” for certain periods of time, disrupted by erosion events, absence of deposition, breccia formation, etc. And third, even where relative chronological continuity may have existed in an in-situ deposit, the long history of faunal investigation in SE Australia since the 1830s, with a strong resurgence during the 1960s and 1970s, has resulted in the majority of assemblages being associated with little accurate chronological information due to the unavailability (and/or expense) of accurate dating techniques at the time. This problem is compounded by the fact that pre-treatment chemistry associated with radiocarbon and other dating techniques prior to the 1990s was inadequate, significantly failing to account for contaminants in ancient deposits. Undated, poorly dated, dated at coarse resolution, or with chronologies inferred through comparison to other sequences, these assemblages simply lack the fine-scale resolution required for use as environmental proxies.

The purpose of this paper is to explore the current and emerging potential of faunal assemblages as proxies for environmental change from the Late Pleistocene and through the Holocene. We summarize and assess some of the known faunal assemblages and their contexts from the Australian Alps region, with selected geographical extensions northwards to the Southern Tablelands and southern Blue Mountains, eastwards along the steep coastal ranges of the New South Wales South Coast, and southwards into the lower Gippsland region of Victoria. Our focus here is on faunal assemblages known or thought to date from after the height of Last Glacial Maximum (LGM) to the present; we ignore the deeper time question of environmental change coinciding with Late Pleistocene megafauna extinctions.

In a case study towards examining faunal shifts for a phase of environmental fluctuation—an early to middle Holocene “Climatic Optimum”—we discuss the faunal assemblage from a deep, stratified cave deposit near Wee Jasper, site Wee Jasper 99 (hereafter “WJ99”). The faunal assemblage from WJ99 was analysed by one of the authors (KPH) under the careful supervision of Ken Aplin in 2016 (see Theden-Ringl *et al.*, 2018), and it is in Ken’s honour that we re-visit the collection here. The faunal changes associated with the Holocene Climatic Optimum at this site are compared

to other regional faunal assemblages coinciding with this time period, and also to other proxies for environmental change, in order to assess (and attempt to define) the capacity and limitations of faunal assemblages, as well as several individual species, as environmental proxies.

Regional context and review

The Australian Alps have a complex geological history, consisting of a series of undulating plateaux and ridges, surrounded and dissected by steep slopes, gorges, river valleys, and escarpments. They are formed from a large range of rock types including sedimentary sandstone and mudstone, volcanic basalts, metamorphic slate, schist, and gneiss. The Monaro Plain (Fig. 1), for example, is a large area of Cenozoic basalt lava flows. Large bodies of Palaeozoic granite, resistant to erosion, form many of the distinct plateaux and ridges visible throughout the Alps landscape today. Former coral reefs formed pockets of limestone, which over time dissolved to form caves and gorges in the limestone karst areas.

The underlying conditions lending themselves to the preservation of faunal materials are relatively sparse in the Australian Alps and wider region, where many of the surface sediments are derived from the regions’ granodiorite geology. Archaeological excavations of granitic rock shelter sites in the Namadgi Ranges in the northern Alps region, for example, have in many cases yielded only highly fragmented and heavily calcined bone material, typically only from late Holocene units (<2000 years cal. BP), and in most cases unsuited to species-level identification (e.g., at Birrigai, Flood *et al.*, 1987; at Nursery Swamp 2, Rosenfeld *et al.*, 1983; and at Middle Creek and surrounding sites, Flood, 1980 and Theden-Ringl, 2016). Similar issues with older bone preservation were encountered by Josephine Flood (1973) and Phil Boot (2002) in rock shelter excavations within sandstone and granite areas along the NSW South Coast escarpment. Boot ascribed the poor preservation conditions to geology, drainage patterns and soil acidity.

Sites with well-preserved faunal remains are thus typically limited to certain geologic regions. One such area is found on the high Monaro Plain, where alluvial terraces form favourable preservation conditions for fossil beds due to a combination of arid conditions (a rain shadow in the lee of the Alps affects the Monaro) and of weathering and calcium richness from the Monaro’s basalt geology (Ride & Davis, 1997). Of the Monaro fossil beds, several have faunal assemblages dating to the Late Pleistocene and Holocene. The gully walls of Pilot Creek, for example, revealed stratigraphically distinct faunas dated by radiocarbon analysis (Davis, 1996; Ride *et al.*, 1989). The oldest unit dates to 30,800–27,900 cal. BP (SUA-2088 and Beta-18297).¹

Holocene units (unit PCB and PCLB), dated to 7660–6720 cal. BP (SUA-2087) and 5580–4870 cal. BP (Beta-18300) respectively, are interpreted by the authors to have been

1 To allow for consistent comparison of regional dated sites, most radiocarbon ages noted here have been calibrated by the authors against SHCal13 (Hogg *et al.*, 2013) using Oxcal v4.2 at 95.4% probability (Bronk Ramsay, 2009). Calibrated age ranges are expressed as years “cal. BP”. Where calibration by the authors was not possible (due to insufficient data, or because published age ranges were inferred from age-depth models), uncalibrated dates and age ranges are specifically expressed as years “BP (uncal.)” or “ka (uncal.)” depending on the authors’ original terminology. In several instances, published age ranges are based on calibrated age-depth models. Here, we defer to the already published age ranges (years “cal. BP”).



Figure 1. Map of SE Australian Alps and region, indicating locations of sites with faunal material mentioned in text.

deposited during a dry interval dated between 6 and 2 ka (uncal.) (Ride *et al.*, 1989: 95). The base of a nearby road cutting also containing mammal fossils, Cooma Creek, was radiocarbon dated to 27,200–25,300 cal. BP (Beta-18298). At both sites, the older Pleistocene units include megafauna species and the sites are interpreted by the authors as having been deposited during a phase of widespread erosional instability of slopes, and active alluviation of valley floors (Ride *et al.*, 1989). The differences in species representation between the older and younger faunal assemblages are significant. In all samples, however, the number of species represented is relatively small. Teapot Creek, on the Monaro Plain, also contains a younger terrace dated by two radiocarbon dates to around 6280–5320 cal. BP (Beta-50156 and Beta-50157), and an older, undated, terrace (Armand *et al.*, 2000; Dansie, 1992). Armand *et al.* (2000: 113) speculated that the Holocene terrace was formed during a wet period between 8 and 5 ka (uncal.) that saw increased transport capacity of the creek and consequent erosion of the plains. The fact that only three bone fragments were found in the Holocene deposit limits the site's interpretive potential for this period of time.

These examples of open sites come with their own significant sets of interpretative issues. They include not only selective preservation of faunal materials due to their exposed and reworked contexts, episodic clay expansion and contraction, and calcrete impregnation, but also the limitation of coarse stratigraphic and rudimentary chronological frameworks. Accurate dating, particularly of older deposits, has also presented issues at the open sites in the region, with problematic materials such as soils and organic rich silts frequently used for radiocarbon dating. This was demonstrated, for example, at the Mugga Lane site in South Canberra, where a radiocarbon date of c. 19,700 years (uncal.) from organic-rich silty clays, on which the dating of nearly fossil kangaroo bone layers was interpreted, was later demonstrated to post-date those bone layers (Macphail & Hope, 2002, revised 2012). Thus, the region's open sites generally are able to characterize subsets of species for broad windows in time, and to infer prevailing environmental conditions and environmental changes that occurred between units. But they lack the fine chronological resolution and fauna preservation capacities necessary for bone assemblages to inform on environmental change for any contiguous sequence of time.

Pockets of limestone karst occur scattered throughout the SE Australian mountain regions; it is these geological formations that have proven the most promising for the stratified deposition and accumulation of sediments and for the preservation of organic materials. The regions' limestone karst areas are well documented (e.g., Lishmund *et al.*, 1986; Matthews, 1985; Nicoll & Brush, 1976; Spate, 2018). Faunal studies of limestone cave deposits have a long history in SE Australia, dating back to the 1830s when one of the earliest studies of Australian palaeontology was carried out in the Wellington Caves complex near Dubbo, to the north of the immediate region investigated here (Dawson & Augee, 1997; Ride & Davis, 1997). Another fossil site that received early palaeontological attention occurs as part of the Wombeyan Caves complex in the Blue Mountains (Broom, 1896). Faunal investigations pre-dating the onset of scientific dating techniques typically focused on anatomical descriptions and taxonomic classifications of new species,

including Australia's unique megafauna, rather than on the ages of the assemblages. In the case of the Broom Breccia from Wombeyan, this led to the first descriptions of several small marsupials, notably the previously unknown *Burramys parvus*, the mountain pygmy possum. Over half a century later, W. D. L. Ride's re-investigation of the Broom breccia from Wombeyan added to the list of newly described species (Ride, 1960). At the same time, *B. parvus* was also discovered within the faunal remains found in Pyramids Cave in the Buchan limestone region of Victoria by Norman Wakefield (Wakefield, 1960a, 1960b).

Wakefield's work at Pyramids Cave led to one of the first regional attempts to place a faunal assemblage into a chronological context from which to assess palaeoecological interpretations (Wakefield, 1972a, 1972b). Initially basing his age classification of the (apparently mechanically mixed) faunal remains on a two-fraction analysis relying primarily on colour and texture, Wakefield's interpretation of two discrete assemblages (Holocene and Pleistocene) separated in time by a discontinuity in accumulation, was called into question by a series of six radiocarbon dates on the bone material. Including six Pleistocene dates ranging from > 33,000 to 15,450 years BP (uncal.), and two late Holocene dates (calibrated here to 3850–1890 cal. BP and 2740–2360 cal. BP [GaK-1103]), the dates did not correlate with the estimated ages based on colour. Given our modern understanding of difficulties in directly radiocarbon dating bone and tooth material (e.g., issues of diagenesis, contamination, and "legacy data" from pre-standardized laboratory practices prior to the 1990s), the chronological interpretations from Pyramids Cave based on both physical appearance and on radiocarbon dates of bulk bone material must be viewed cautiously. The additional issues of coarse-grained excavation, and consequent dismissal of stratigraphy as an analytical factor (Wakefield, 1972b: 7), further highlight significant problems for chronostratigraphic interpretations.

Nevertheless, at the time, Wakefield's colour fractionation and radiocarbon dates formed an important chronological context upon which Flood and Jeannette Hope based their comparative faunal analyses from the newly excavated site of Cloggs Cave only several kilometres from Pyramids Cave (Flood, 1973, 1974). With several Late Pleistocene and one early Holocene radiocarbon dates from the main cave excavation, Flood and Hope found "an excellent fit" (Flood, 1973: 260) between the faunal assemblages of the two sites. Other cave studies in the Buchan region (Mabel Cave, M27 and M28, in Wakefield, 1972b) remain undated.

Similarly forced to rely on the few available dates known for regional faunal sequences, Hope (1982) based her chronological interpretations of species fluctuations from the Wombeyan Broom breccia and the later salvaged Wombeyan Quarry assemblage on the inferred chronological sequence of the Cloggs Cave faunal assemblage. In a study that will undoubtedly have far-reaching consequences, partnership research currently being undertaken at Cloggs Cave by researchers from Monash University and the region's Gunaikurnai Traditional Owners through the Gunaikurnai Land and Waters Aboriginal Corporation (GLaWAC), indicates that the original dates obtained by Flood for the main sequence of human occupation (post-dating the lower, Pleistocene, megafauna-associated layers) are inaccurate (R. Mullett, B. David, and J. Freslov, pers. comm.). Rather than primarily representing a sequence transitioning from

the terminal Pleistocene to the early Holocene, all material associated with Aboriginal use of the eastern, excavated parts of the main excavation pit can now be shown to have been deposited during the Holocene (e.g., David *et al.*, in press). The new chronology from Cloggs Cave will have implications not only for the cultural and faunal assemblages from this particular site, but also for many studies that have relied on the Cloggs Cave sequence to extrapolate patterns of timing and events for other undated site sequences.

Surprisingly, despite the introduction of radiocarbon dating and other dating techniques decades ago, very few robust faunal sequences of relative temporal continuity and depth are known from in and around the Australian Alps, even within limestone contexts. To the west of the Blue Mountains, a number of radiocarbon dates from the Late Pleistocene to the late Holocene were obtained from several caves at Abercrombie during the 1980s, although their stratigraphic associations and relationships are unclear (Willis, 1993). An earlier archaeological excavation at Abercrombie Arch Shelter by Johnson (1977) recovered some faunal material, analysed and reported to family level by Ken Aplin. But deposit concretion, lack of dating, and unclear stratigraphic relationships due to heavy roof fall means the site was unable to be used in the reconstruction of archaeological or environmental histories through time.

During the 1990s, several further studies attempted to define the chronologies of cave deposits and the associated faunal (and cultural in some cases) assemblages. One date of 8.2 ka (uncal.) was obtained from Coronation Cave in the Wombeyan complex (Ride & Davis, 1997: 212), but the authors, without explanation, considered the date to be unreliable for the associated fauna. At Nettle Cave in the nearby Jenolan karst area, where faunal remains are typically uncommon, Deborah Morris and colleagues (Morris *et al.*, 1997) obtained two conventional radiocarbon dates from dark charcoal lenses in a 68 cm deep deposit which consisted primarily of owl pellet remains. The upper deposit (overlying the lower radiocarbon date) was excavated in four arbitrary spits. Thus, as calibrations of the two dates give ages of 8450–7435 cal. BP (ANU-7897, at 28/29 cm depth) and 10,490–9030 cal. BP (ANU-7898, at 35/36 cm depth), the entire Holocene sequence above these dates, even if dated retrospectively, would be at a very coarse resolution. Interestingly, however, a cemented, calcareous layer between the two dates suggests an external change, which Morris and colleagues attributed to an early to middle Holocene humid period. Below 35 cm, excavation proceeded in spits of 2 to 5 cm depth. All inferences made from the faunal assemblages assumed constant rates of accumulation, despite the observation of several changes in deposition and an unconformity. Nevertheless, Nettle Cave remains a site with significant potential for further detailed study: the cave retains deposits with good chronostratigraphic resolution, appears well stratified, and a wide range of species are represented. Improvements in radiocarbon and other dating methods increase the likelihood of being able to date the deposit at fine resolution.

Other cave studies conducted in the 1980s and 1990s ran into excavation and stratigraphic issues: the archaeological excavations at New Guinea II in Gippsland (Ossa *et al.*, 1995) and at Douglas Cave near London Bridge in the Canberra region (Boot & Cooke, 1990; earlier excavation

work undertaken by J. Hope) both contained deep deposits rich with cultural and faunal remains. Radiocarbon dates from both sites included Holocene and Late Pleistocene ages: ten radiocarbon dates from charcoal ranging (non-sequentially) from 21,000 +900/–800 to 1080 ± 70 BP (uncal.) at New Guinea II, and three Pleistocene/Holocene transition dates from bulk bone material in Douglas Cave (16,120–14,350 cal. BP [ANU-7464], 13,170–11,810 cal. BP [ANU-7463], and 12,000–10,410 cal. BP [ANU-7462]). But stratigraphic and excavation inconsistencies exacerbated by masses of rock fall, and possible deposit reworking through burrowing, respectively, impacted on the reliability and the resolution of the chronologies from both sites (for example, evidence of *Sarcophilus harrisii* and *Oryctolagus cuniculus* in the same excavation unit at New Guinea II). No detailed quantification is available for the thousands of fragmented vertebrate remains from New Guinea II, although a general species list including several *Pseudomys* species, *B. parvus* and *Mastacomys fuscus*, is provided (Ossa *et al.*, 1995). Of the Douglas Cave material, faunal material of only five spits was analysed (with the authors also noting difficulties in identifying small mammals species such as *Pseudomys*), an estimated additional metre of deposit remains underneath the 1.57 m excavation depth, several other complementary analyses were undertaken on the sediments themselves, and the question of whether or not the deposit almost wholly represents a very brief accumulation period at the Pleistocene/Holocene transition was not resolved. The Douglas Cave material is a potential resource for further investigation, particularly if undertaken with dating work to resolve and clarify the site's chronology.

A more recent excavation by Aplin and colleagues (Aplin *et al.*, 2010) of the deposit from cave Y259 in the Yarrangobilly karst region (cave previously investigated by Drummond, 1963) was archaeologically most notable for its discovery of the earliest dated layers containing cultural stone artefacts from the high-altitude region of the Australian Alps (>1000 m). Despite sparse but reliable AMS radiocarbon dating of the cultural unit (indicating at least two visits by people dated to 9695–9525 cal. BP [Wk-18839] and 9440–9135 cal. BP [Wk-18838]) and good site integrity, the shallow (around 30 cm deep) and discontinuous nature of the deposit, including two flowstone horizons, means that while the study represents a valuable record of several environmental and human “snapshots” in time, it is unable to contribute a contiguous, high-resolution sequence through time.

There are other known localities for bone assemblages where the data they contain are yet to be explored and/or analysed. The Cooleman karst region, for example, has received some archaeological attention including a late Holocene radiocarbon date (1350–990 cal. BP, ANU-6191) on collagen from an Aboriginal skull found on the surface of rock shelter CP75, and several faunal species identified in associated sediments by J. Calaby and J. Wombey (Cooke, 1988). But no below-surface investigation has been undertaken at Cooleman.

Fossil faunas of Quaternary age are known from cave fills and bone breccia in the Wee Jasper karst area, notably in Punchbowl and Dip Caves (Dunkley *et al.*, 2010; Rich *et al.*, 1993), from a now-submerged floor deposit at Cave Flat (now Cave Island) excavated in 1881 by Charles Jenkins (Hope ms) and from surface collection by Hope

at Narrangullen (Hope, ms). Willis (1993: 107) cited a personal comment by Gillieson and Spate providing a radiocarbon date from cave earth at Cave Island (21,840–17,970 cal. BP).

A faunal assemblage from the Mt Fairy limestone caves near Weereewaa (Lake George) was recently excavated as part of an ARC Linkage project, but the excavation and analysis are yet to be reported. Previously, megafauna remains were found at a disused dolomite quarry near Mt Fairy (Flannery & Hope, 1983). Other sites for faunal remains, of unknown chronological potential, include Nargun Cave, Marble Arch, and Wyanbene in the Deua limestone region (Calaby & Wimbush, 1964; Hall, 1975), Jerrara Cave and others near Bungonia (Osborne, 1993; Willis, 1993), Kybean Caves southeast of Cooma (Willis, 1993), the Lake George region (Sanson *et al.*, 1980), and various caves near Jenolan (Hope, ms; Willis, 1993).

Combined, the known faunal sites of the Australian Alps and surrounding regions are generally plagued by issues that limit and compromise their value for reconstructing and understanding environmental sequences from the Late Pleistocene to the present. Despite their limitations, both the undated and the poorly dated collections of the region may still be useful for broad geographical mapping of pre-European versus modern species distributions, but they do lack demonstrated chronological depth. An early attempt at forming a geographical transect through SE Australia, for example, was made by Aplin in the 1970s (unpublished) in collaboration with Hope. Nonetheless, the largest past and ongoing barrier to the understanding of faunal assemblages in SE Australia (and elsewhere) is the ability to chronologically characterize the observed changes in species. Even today, Ride & Davis' (1997: 206) comment that “dating (together with a lack of stratigraphic understanding) remains the single most pressing impediment to the interpretation of the cave faunas”, remains apt.

Case study:

WJ99 and the Holocene Climatic Optimum

The cave WJ99 lies in the northern foothills of the northern Australian Alps region (Fig. 1). As part of the Taemas Limestone formation of the Wee Jasper valley, the site (entrance at 400 m above sea level) overlooks the Goodradigbee River to the east. The valley sits at the interface between the mountainous high country of New South Wales and the milder tablelands to the north, providing a geographically and ecologically sensitive location likely to have been locally influenced by climatic shifts through time. In addition to archaeological evidence for Aboriginal use of the cave since at least 14,260–13,860 cal. BP shortly after sediment began accumulating, a 2 m × 1 m exploratory test pit excavated to 3.6 m in 10 cm vertical units in 2013 revealed a well-stratified and superbly preserved faunal record (accumulated predominantly from the pellets of roosting owls and from prey remains of smaller predators) that dates from the terminal Pleistocene to just after 1990–1750 cal. BP (Fig. 2). The upper sediment (below a layer of modern dung) was dry sieved through 3 mm mesh; due to increasing moisture, sediment below c. 70 cm was wet sieved through a 1.5 mm mesh. The deposit contains no discernible evidence of significant sedimentation breaks or

gaps. The chronological, sedimentary, archaeological, and faunal contexts have been published separately (Theden-Ringl & Gadd, 2017; Theden-Ringl & Langley, 2018; Theden-Ringl *et al.*, 2018) and a taphonomic assessment is also available (Hislop, 2017).

With the exception of material from one anomalous stratigraphic unit interpreted as a filled-in burrow, SU7, faunal analysis included all recovered faunal material from Square 10B. All tooth-bearing elements and isolated teeth were collected, as were cranial and selected postcranial elements (further details in Theden-Ringl *et al.*, 2018). Number of Individual Specimens (NISP) are presented in Table 1 and show a wide variety of taxa present in the pre-European landscape. Two specimens of Rabbit (*Oryctolagus cuniculus*) are preserved in the upper analysed excavation unit; the remainder of the assemblage comprises native fauna.

The chronology of WJ99 is based primarily on ten AMS radiocarbon dates on sedimentary charcoal from throughout the deposit (Fig. 2). The value of this site is in its relatively stable and rapid sedimentation record, allowing for a contiguous account of faunal species fluctuations, almost to century-scale for some units, which can improve and more narrowly define the chronological histories for many species. For example, the Pleistocene-Holocene transition around 11,700 cal. BP corresponds closely to a series of species fluctuations at this time. They include the significant reduction of *Mastacomys fuscus*, *Pseudomys fumeus*, *Pseudomys higginsi*, *Isoodon obesulus*, *Cercartetus lepidus*, and *Perameles nasuta*, and corresponding increases in numbers of *Rattus* spp. and *Conilurus albipes*. The faunal patterns suggest a developing local landscape including establishing forest and wetland habitats, and a reduction of heath, scrubland, and grassland at this time.

Of particular interest to this case study are the changes to the faunal assemblage, and their implications, for the early to middle Holocene. The Holocene Climatic Optimum is identified in most parts of the world as a complex and prolonged period of warm conditions occurring sometime between 10,000 and 4000 years ago (e.g., Marcott *et al.*, 2013; Zhou *et al.*, 2004), exhibiting significant temporal and spatial variation globally. Its local timing and landscape effects for the SE Australian mountain ranges are still being refined. Figure 3 summarizes some of the environmental shifts and their timing identified from various proxy records, including dust, pollen, elements, etc., for the SE Australian high country during the early to middle Holocene. The figure highlights the significant challenge of determining the timing—the commencement, height, and conclusion—of this phase. When viewed together, information from even just the handful of regional studies summarized here demonstrates that the timing is broad and that changes may have occurred gradually and cumulatively. The commencement of wetter and warmer conditions is dated to anywhere from shortly after 10,000 to 7000 years ago, while the end of the phase, generally thought to have been triggered by the onset of ENSO conditions, is dated to sometime after 6000 years ago.

In part, the broad chronological resolution for the Holocene Climatic Optimum may be due to dating resolution affecting studies. Another problem is that many early to middle Holocene records—particularly fluvial, peat, and

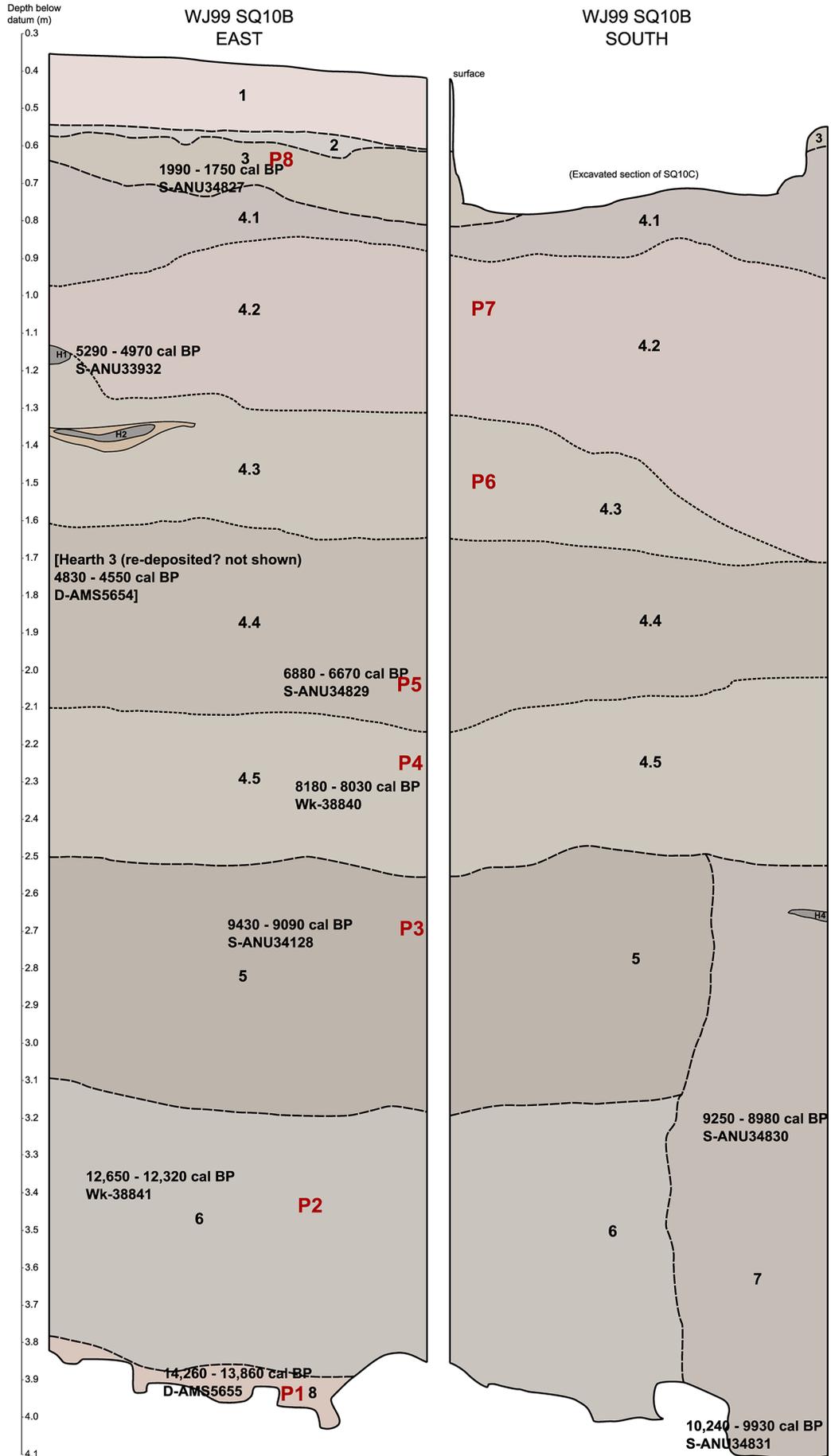


Figure 2. Representative (east and south) sections of WJ99 Square 10B, showing locations of AMS radio-carbon dates and of sediment samples (Px) from which pollen was extracted.

Table 1. Taxonomic composition of the WJ99 vertebrate fauna recovered from all excavation units (XU36–XU2) in Square 10B, excluding SU7, as identified from crania and mandibles. Taxa listed as “indet.” are identified only to the indicated taxonomic level. [EX] = extinct; [ex] = extinct in SE Australia. The two megafauna species were demonstrated to be chronologically anomalous to the faunal assemblage (Theden-Ringl *et al.*, 2018).

taxon	common name	NISP	%
<i>Rattus fuscipes/tunneyi</i>	Bush Rat/Pale Field Rat	604	
<i>Rattus lutreolus</i>	Australian Swamp Rat	192	
<i>Rattus</i> sp. indet.		1	
<i>Conilurus albipes</i>	White-footed Rabbit Rat [EX]	172	
<i>Hydromys chrysogaster</i>	Rakali/Water Rat	1	
<i>Mastacomys fuscus</i>	Broad-toothed Rat	248	
<i>Pseudomys australis</i>	Plains Mouse [ex]	17	
<i>Pseudomys fumeus</i>	Smoky Mouse	650	
<i>Pseudomys gracilicaudatus</i>	Eastern Chestnut Mouse	133	
<i>Pseudomys higginsii</i>	Long-tailed Mouse [ex]	409	
<i>Pseudomys novaehollandiae</i>	New Holland Mouse	388	
<i>Pseudomys oralis</i>	Hastings River Mouse	240	
total murids		3055	51.8
<i>Acrobates</i> spp.	Feathertail Gliders	48	
<i>Burrhamys parvus</i>	Mountain Pygmy Possum	1	
<i>Cercartetus lepidus</i>	Tasmanian Pygmy Possum	36	
<i>Cercartetus nanus</i>	Eastern Pygmy Possum	160	
<i>Petaurus breviceps</i>	Sugar Glider	19	
total small possums		264	4.5
<i>Petaurus norfolcensis</i>	Squirrel Glider	6	
<i>Pseudocheirus peregrinus</i>	Common Ringtail Possum	40	
<i>Trichosurus vulpecula</i>	Common Brushtail Possum	31	
total medium to large possums		77	1.3
<i>Phascolarctos cinereus</i>	Koala	7	
<i>Vombatus ursinus</i>	Common Wombat	21	
total koalas and wombats		28	0.5
<i>Aepyprymnus rufescens</i>	Rufous Bettong	23	
<i>Bettongia lesueur</i>	Boodie/Burrowing Bettong [ex]	2	
<i>Bettongia penicillata</i>	Woylie/Brush-tailed Bettong [ex]	2	
<i>Bettongia</i> spp.		24	
<i>Potorous tridactylus</i>	Long-nosed Potoroo	9	
<i>Potorous/Bettongia</i> sp. indet.		117	
total potoroids		177	3.0
<i>Petrogale penicillata</i>	Brush-tailed Rock Wallaby	229	
<i>Wallabia bicolor</i>	Swamp Wallaby	6	
<i>Notamacropus rufogriseus</i>	Red-necked Wallaby	6	
<i>Macropus giganteus</i>	Eastern Grey Kangaroo	2	
<i>Osphranter robustus</i>	Common Wallaroo	17	
<i>M. giganteus/O. robustus</i>		7	
<i>Lagorchestes leporides</i>	Eastern Hare-wallaby [EX]	4	
<i>Lagostrophus fasciatus?</i>	Banded Hare-wallaby [ex]	1	
<i>Procoptodon gilli</i>	Short-faced Kangaroo [EX]	2	
<i>Procoptodon brownneorum</i>	Short-faced Kangaroo [EX]	1	
total macropodids		275	4.7
<i>Isoodon obesulus</i>	Southern Brown Bandicoot	189	
<i>Perameles nasuta</i>	Long-nosed Bandicoot	126	
<i>Perameles</i> sp. 2		1	
bandicoot gen. et sp. indet.		2	
total peramelids		318	5.4

continued ...

Table 1 (continued).

taxon	common name	NISP	%
<i>Thylacinus cynocephalus</i>	Thylacine/Tasmanian Tiger [EX]	3	
<i>Sarcophilus harrisii</i>	Tasmanian Devil [ex]	8	
<i>Dasyurus viverrinus</i>	Eastern Quoll [ex]	29	
<i>Phascogale tapoatafa</i>	Brush-tailed Phascogale	7	
Dasyuridae sp. indet. (small)		975	
total dasyurids & thylacinids		1022	17.3
Microchiroptera spp.	Insectivorous bats	61	
total microchiropterans		61	1.0
Aves (small)	Small birds	180	
Aves (large)	Large birds	57	
total birds		237	4.0
<i>Egernia</i> spp.	Large skinks	35	
Scincidae small spp.	Small skinks	253	
<i>Tiliqua</i> spp.	Blue-tongued Skinks	1	
Agamidae spp.	Lizards	80	
total reptiles		369	6.3
Anura	Frogs	9	0.15
Anguilliformes	Eel	1	0.02
<i>Oryctolagus cuniculus</i>	European Rabbit	2	0.03
total all vertebrates		5895	100

alluvial—are frequently “missing” due to what is thought to be a combination of increased rainfall and river flows resulting in enhanced flushing of sediments, and less supply available for sediment re-accumulation due to well-vegetated catchments (Cohen & Nanson, 2007; Eriksson *et al.*, 2006; Johnston & Brierly, 2006; Kershaw & Strickland, 1989).

In contrast, the sedimentation rates at WJ99 appears to have increased just prior to 8000 cal. BP, resulting in enhanced vertical resolution available to map faunal changes from this time (estimated to between 400 years to less than 200 years per 10 cm excavation unit). The phase begins with a distinct sedimentary transition from compact and dry sandy clayey silt, to weak and moist silt (transition between SU5 and SU4.5). The transition marks not only the onset of more rapid sediment deposition (the cave floor of WJ99 acts as a sediment trap), but also the beginning of significant changes in local species composition that would last until around 6000 cal. BP. Given that many species, particularly Australian native murids, have highly specialized features suited to clearly defined habitat preferences and do not adapt well to habitat disturbance (Breed & Ford, 2007), changes in their histories at WJ99 can indicate local environmental fluctuations.

Figure 4 shows representations of selected species from WJ99 through time. A summary of taxon change from 10,000 to 4000 cal. BP is also included in Fig. 3. Three particular trends are noted. First, the peak of the Holocene Climatic Optimum, placed here from 8000 cal. BP to just before 6000 cal. BP, was different enough to earlier and later conditions to have affected the ability of species to reside locally. Very little significant taxon fluctuation is seen in the two millennia preceding 8000 cal. BP, or in the three millennia after 6000 cal. BP (Theden-Ringl *et al.*, 2018). Broadly, the timing corresponds to the peak of Holocene

Climatic Optimum conditions indicated by other proxies for the high country, and the date of 8000 cal. BP gives a definitive “tipping point” for the start of local species shifts.

A second observation is that the final disappearance of “cold-adapted” species (whose populations had declined from the Pleistocene/Holocene transition, but which had locally remained nonetheless) was not simultaneous, but possibly spaced over a period of 1500 years. An isolated final occurrence of the pygmy possum, *Cercartetus lepidus*, is recorded at 8000 cal. BP, the Broad-toothed Rat *Mastacomys fuscus* is last recorded around 7250 cal. BP, and the Long-tailed Mouse *Pseudomys higginsii* persisted until 6500 cal. BP. Both *M. fuscus* and *P. higginsii* persisted in SE Australia at relatively low elevations until a few hundred years ago (Aplin *et al.*, 2010) so the timing of their decline at WJ99 is useful to contribute to a more precise timing of distributional changes of the species. As in many other SE Australian records, the Hastings River Mouse, *Pseudomys oralis*, appears to have “replaced” other murid species, with numbers at WJ99 increased substantially from 8000 cal. BP. The spaced disappearance and appearance of species within the 8000 to 6000 cal. BP window of time may indicate two factors: (a) that each species had different tolerances/tipping-points to environmental change; and/or (b) that ecosystem changes occurred gradually over centuries rather than as abrupt shifts.

Third, and related to the previous point, the relatively large number of species experiencing distinct fluctuations during the period from 8000 to 6000 cal. BP allows for a more holistic approach to interpreting landscape change, extending not only to temperatures, but also to moisture, vegetation, and other habitat shifts. The decline of *C. lepidus*, for example, may signal a further decrease in shrub availability around

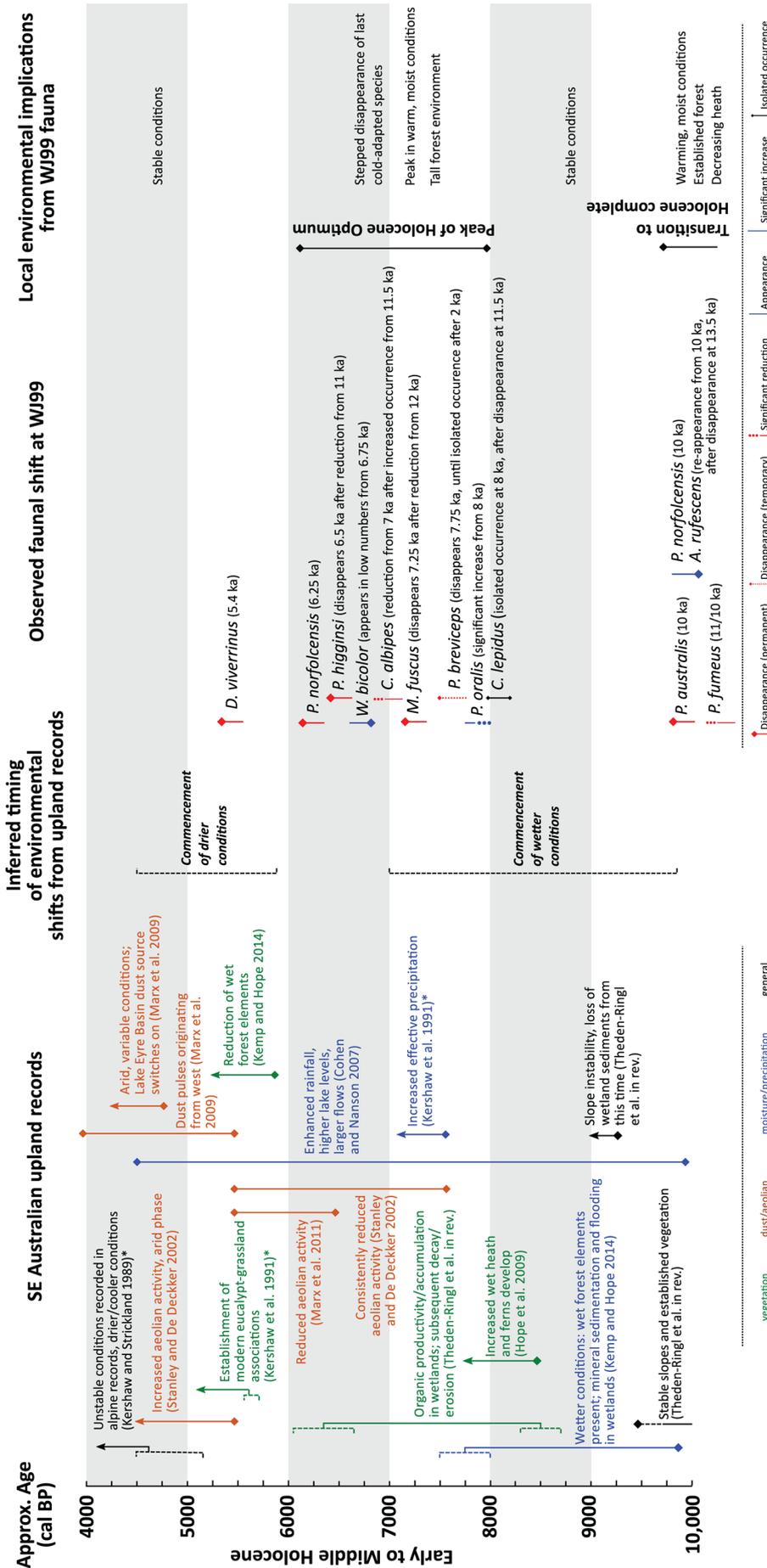


Figure 3. Summary of known environmental shifts during the early to middle Holocene from SE Australia, chronologically related to notable temporal changes within (and environmental inferences from) the faunal composition of WJ99. * Approximate calibrated date ranges inferred from original uncalibrated dates.

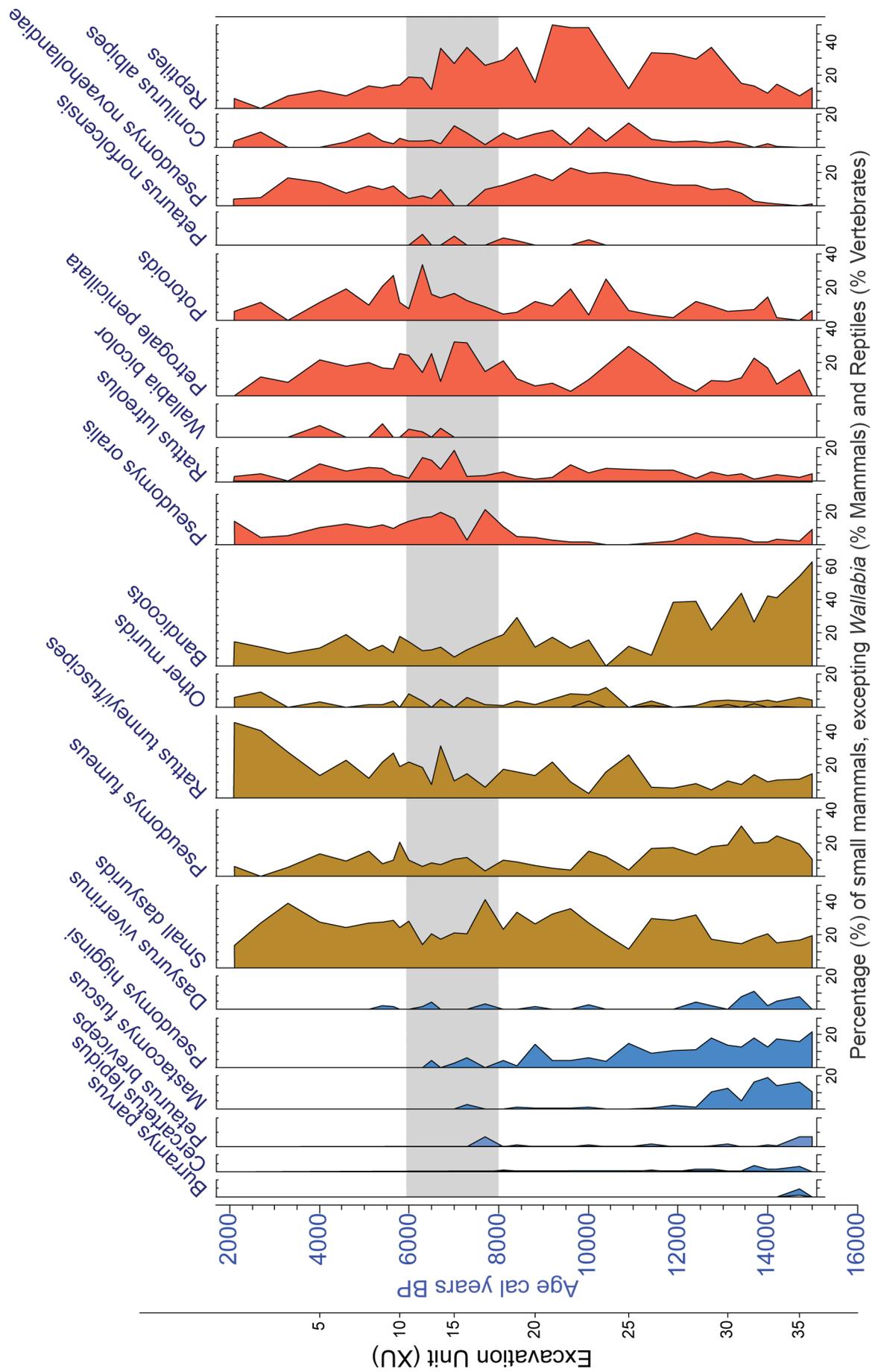


Figure 4. Selected species representations at WJ99. Species are sorted by those that show decline into the Holocene (blue), those whose values generally do not show particular decline or increase during the Holocene Climatic Optimum (gold), and those whose numbers appear to be affected—decline or increase—during the Holocene Climatic Optimum (red). Grey shading indicates approximate timing of peak Holocene Climatic Optimum conditions.

8000 cal. BP (already reduced from the early Holocene) as more open forest displaced heath. The simultaneous specimen increase in *P. oralis*, an open forest dweller (Breed & Ford, 2007), substantiates the suggestion. The swamp wallaby, *Wallabia bicolor*, appears in low numbers from 6750 cal. BP, and together with a small increase in the swamp rat, *Rattus lutreolus*, at 7000 cal. BP, may suggest increased moisture in the landscape.

Contradicting the suggestion of open forest replacing shrub is the slight reduction of the White-footed Rabbit Rat, *Conilurus albipes*, from 7000 cal. BP. This rat was widespread prior to European colonization and preferred tall open eucalypt forest, relying on tree hollows and logs for shelter (Dyck *et al.*, 2013: 162). At WJ99, a specimen increase occurs around 10,000 cal. BP as forest appears to have established locally, but favoured conditions were apparently not maintained.

The sugar glider, *Petaurus breviceps*, disappears by 7750 cal. BP (it reappears in isolated cases after 2000 cal. BP), as does the squirrel glider *Petaurus norfolcensis* by 6250 cal. BP, but the overall low numbers of both species means any interpretations must be made with caution.

The WJ99 faunal trends noted here for the Holocene Climatic Optimum—and their inferences—are preliminary only, intended to demonstrate the potential for more detailed patterns that can emerge from increased chronological resolution of stratified deposits. There are, of course, more complex considerations that may require assessment for individual sites and species. For example, the estimation of potential time lags between environmental change and species extinction/appearance/fluctuation requires knowledge of species-specific behaviours, habitat constraints and tipping-points, and the potential for short-term population fluctuations and/or responses to extreme events such as fires or drought.

Another site-specific consideration is the accumulation agent(s) for faunal remains at that locality. Arboreal predators such as owls, non-arboreal small to large predators, the activities of people, natural death components, faunal traps, or combinations of these agents, would result in different species representations between sites and possibly also within single deposits, with indirect relationships to local environmental changes. At WJ99, for example, owls were considered the primary accumulation agent, with carnivorous marsupials a secondary agent (Theden-Ringl *et al.*, 2018). People, *Thylacinus*, and *Sarcophilus* were also present during phases including the early to middle Holocene. So although no direct evidence of predation or butchery was identified from the bone material, the presence of burnt bone and a shift towards larger prey species corresponding to units with increased evidence for human activity and with units corresponding to evidence of large predators, suggests a portion of the assemblage may well derive from such agents.

Preliminary pollen, diatom, and microcharcoal analysis of eight selected sediment samples from WJ99, largely coinciding with dated sections (Fig. 2), offers local vegetation proxies with which to compare and validate the inferences made from the faunal shifts. Fine fractions (< 125 µm) of the samples were processed with heavy liquid to collect the organic fraction; percentages (or presence) for pollen and spores, and for diatoms, are shown in Fig. 5.

Pollen was only abundant within the upper 120 cm of the

deposit, where a eucalypt woodland with abundant ferns is indicated. Below this only scattered pollen from resistant pollen types such as Asteraceae occurs showing that most pollen has decayed. It is not possible to reconstruct the source vegetation in these lower levels although it is clear that grass (indicated by phytoliths) is abundant around 14,000 cal. BP and again around 7000 cal. BP, when there is also an indicator of daisy yam (Asteraceae-Liguliflorae) being a component in the ground cover. Diatoms are present in very low frequencies and may indicate moist surfaces and drips. Microcharcoal is present from the deepest levels of the deposit but reaches its highest concentrations in the early to middle Holocene. It probably reflects hearth debris but possibly also particulates from fires outside the cave that arrived with the sediment.

Interpreting the likely vegetation setting of WJ99 can be assisted by a pollen record from a montane fen 28 km to the south of WJ99. Micalong Swamp, at 980 m altitude, provides a 16,000-year record of transition from the Late Pleistocene (Kemp & Hope, 2014). Open grasslands were replaced by subalpine woodland by 16,000 to 15,000 cal. BP. Well-developed eucalypt forest was present after 10,000 cal. BP and indicators of wet forest, such as tree ferns, persisted until around 6000 cal. BP. This record supports the view that WJ99 was surrounded by open forest or woodland and that conditions may have been wetter during the early Holocene. The local information suggests that the woodland was grassy at that time.

Despite the limited information to be obtained from the pollen and microcharcoal samples from this particular site, the tests do contribute to the multi-proxy nature of the site's analyses and interpretations. In combination with archaeological and faunal investigations, dating at regular intervals, and information from sedimentary analyses including geochemical and particle tests, a comprehensive site history can be compiled.

Regional comparisons and discussion

The stratified deposit from WJ99 is not unique in providing a record for the early to middle Holocene: a small number of other sequences from the SE Australian mountain ranges also represent this period. Interestingly, the open fossil terraces of the Monaro appear to contradict the trend of eroded and/or scoured deposits characterizing landscapes of the Holocene Climatic Optimum. But although sites such as Teapot Creek and Pilot Creek contain early to middle Holocene deposits, their scarcity of faunal remains, selective preservation and coarse chronological resolution means the open Monaro sites' value lies in assessing faunal and environmental change over vast periods of time rather than along continuous timelines. More detailed chronological resolution and higher future research potential lies with the region's cave deposits. Several murid species from these sites are compared and discussed here, revealing their potential for addressing questions of species and landscape change.

At Y259 on the Yarrangobilly Plateau, Aplin *et al.* (2010) suggested that the bulk of the taxa represented the relatively warm and moist conditions of the Holocene Climatic Optimum. The two early Holocene dates were derived from the lowest unit, III; in terms of improving Holocene resolution, a date from Unit II (distinctly underlain and

overlain by flowstones) would be ideal to distinguish its antiquity from that of the uppermost Unit I. Two murids from Y259, *Pseudomys higginsi* and *Mastacomys fuscus*, are worth noting here for the purpose of geographical mapping of species through time, particularly for altitudinal comparison: Y259 representing a high elevation site (1100 m), and WJ99 representing a lower elevation site (400 m) 70 km to the north. Unlike at WJ99, *Pseudomys higginsi* is represented in all units at Y259, indicating its persistence in the SE high country until recent times. Direct AMS dating of *P. higginsi* bones to less than 500 years old at other Yarrangobilly sites confirms its late local presence (Breed & Ford, 2007); Aplin *et al.* (2010) noted the mainland populations' history of post-glacial range reduction and apparent retreat to higher elevation regions. The contrast to WJ99 at a lower altitude, where *P. higginsi* is the last of the murids to disappear during the later Holocene Climatic Optimum phase (around 6500 cal. BP), provides the beginnings for mapping the species' chronological and geographical retreat to relatively cooler habitats.

Given the present work being undertaken at Cloggs Cave (including recovery and analysis of new faunal material), only a brief mention is made here of the original faunal analysis. Flood (1973) placed the extinction of *P. higginsi*, abundant in the lower levels but disappearing by level 12, at around 14,000 BP (uncal.). She also observed the appearance of *Pseudomys oralis* in level 20 (inferred to date to the Late Pleistocene), with early low numbers increasing towards the deposit surface. Ignoring the precise chronology of the Cloggs Cave sequence for the moment, the two general patterns are reflected in the WJ99 sequence. At WJ99, the disappearance of *P. higginsi* is timed at around 6500 cal. BP, and although *P. oralis* is present in low numbers from the earliest units, the species experiences a significant population increase around 8000 cal. BP. The apparent "replacement" of several *Pseudomys* species by *P. oralis* is noted from sequences across SE Australia (Breed & Ford, 2007) so a better understanding of the nature and timing of this transition may be widely applicable. It is yet to be seen whether new data from Cloggs Cave, including in a part of the cave where a Holocene sequence was previously interpreted as a Late Pleistocene to early Holocene sequence, correlates with the chronologies for these two species at WJ99.

The presence/absence of *Mastacomys fuscus* presents a similar case study to *P. higginsi*, again highlighting how little is known about a species' past geographical and chronological distributions. At Y259, *M. fuscus* is present throughout all units. Today, the species persists in the higher altitudes of the Australian Alps, with a broader and lower altitude range in Victoria (Wallis, 1992). It is thought to have disappeared from lower altitude sites throughout the Southern Tablelands only in the past 200 years (Ford *et al.*, unpublished, cited in Aplin *et al.*, 2010). A study of the morphologies and $\delta^{13}\text{C}$ isotopes of modern and ancient specimens found that increased aridity is unlikely to have reduced the range of *M. fuscus* (May, 1990). Rather, May concludes that higher temperatures which favoured forest environments and increased diversity at the expense of grassland availability, sometime between 10,000

and 5000 BP (uncal.), may have led to the establishment of the species' modern range at that time. It is worth noting that *M. fuscus* was recorded in high numbers in the uppermost levels at Cloggs Cave (Flood, 1973), indicating that even with the anticipated revision of the chronology of this site's deposit, *M. fuscus* persisted well into the middle to late Holocene in the low-lying East Gippsland region of Victoria. Its remains were also recovered from London Bridge, both within the upper layers of the Douglas Cave excavation (of unknown antiquity, probably Holocene) and from an associated open site excavation (Burra Shelter) dated to within the past 1000 years (Boot & Cooke, 1990). In Nettle Cave at Jenolan, *M. fuscus* is also recorded throughout the deposit including the upper units (Morris *et al.*, 1997). Relative abundance trends, however, indicate it decreasing through the Nettle Cave sequence, with a corresponding increase of *Pseudomys oralis*. As noted above, *P. oralis* increased at WJ99 and at Cloggs Cave during the early to middle Holocene, mirroring that species' trend from Nettle Cave. For *M. fuscus*, however, its complete disappearance from the Wee Jasper valley after 7250 cal. BP, following a reduction in numbers from 12,000 cal. BP, is perhaps then an anomaly. A suite of questions, including whether the absence of *M. fuscus* from the middle Holocene in WJ99 is a local or a broader trend for the lower elevations surrounding the northern Australian Alps, requires more chronologically robust stratified faunal sequences, of both known sites that have potential for finer chronological assessments, and of new sites.

The species comparisons highlighted above, and the questions and themes they raise, are not new. Attempts to trace and map species' geochronological distributions relative to changing environments, for both the understanding of pre-European climates and landscapes and of post-European losses, have been made for many decades. But until now, the few known stratified sites, combined with poor dating resolution for most of these sites, has rendered most observed patterns both chronologically vague and thematically distanced from the landscapes and climates in which the records were formed. Shifts towards both fine-resolution recovery techniques and the increased use of multi-proxy analyses have the potential to fundamentally change the way in which faunal information can be interpreted and incorporated into wider palaeoecological themes. For example, emerging analytical techniques include the use of X-ray fluorescence for high-resolution geochemical characterization of stratified sediments through the use of portable hand-held units and laboratory-based scanners. The combination of several dating methods on various materials to strengthen and validate the chronological sequence of a site is also now commonplace. As briefly touched upon in this study, the analysis of micro fossils such as diatoms and pollen, or of macro fossils such as charcoal and seeds, can add further dimensions to the environmental and cultural histories of sites. Fine-resolution, multi-proxy studies are the ideal platform from which to start developing, through cross-referencing with other proxies, solid reference material to reconstruct species histories within their environmental contexts.

Conclusion

Faunal fluctuation patterns have typically been used to strengthen and validate signals of local environmental change as determined from other proxies, rather than viewed as primary environmental proxies in their own right. In the past, the main reason for this has been the inability to obtain site chronologies at anywhere near the resolution necessary for such analyses. Even today, the known number of stratified faunal-bearing sites with reasonable chronological resolution and integrity remains small for the Australian Alps and surrounds, insufficient to chronologically cross-reference stratigraphic sequences and associated faunal patterns with any certainty.

Yet as this review and study demonstrates, the information that can be extracted from stratified faunal assemblages—given a solid chronological and environmental framework—is significant. Robust multi-proxy approaches can provide the beginnings from which detailed species' histories linked to local environmental shifts can be mapped. Combined and interpreted regionally, such studies have significant potential to characterize how certain faunal species reacted to environmental shifts, to map their geographic distributions through time, and ultimately, to be able to utilize this information to confidently infer environmental change from faunal assemblages in their own right.

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