

Climate change without extinction: Tasmania's small-mammal communities persisted through the Last Glacial Maximum–Holocene transition.

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Abstract

Global ecosystems underwent major changes through the Quaternary, as climates cycled from cool and dry glacial conditions to relatively warm and humid interglacial conditions. How these changes affected the diversity and composition of small-mammal communities is mostly unknown, especially for the southern-temperate regions of Australia. We used fossil assemblages from owl regurgitates to investigate changes in small mammals from Tasmania's forest environments over the last 20,000 years, encompassing the transition from cold glacial conditions of the Last Glacial Maximum (LGM) into the warmer Holocene. During the early part of this period, Tasmania was connected to mainland Australia via a low-elevation land bridge, but was transformed into a large island by rising sea levels during the Late Pleistocene – Holocene transition. Despite these changes, the regional small-mammal fauna appears to have been persistent over this entire period, with no loss of species. However, the relative abundance of most species changed dramatically, apparently in response to habitat changes, which also provoked substantial shifts in community composition and diversity. A strong indicator of the magnitude of change is *Mastacomys fuscus*, a graminivorous specialist murid, which dominated the assemblage prior to and during the LGM, but declined as temperature and sea level rose during the Late Pleistocene – Holocene. In contrast, the generalist rodent *Pseudomys higginsii*, along with the small forest-dependent marsupials *Cercartetus* spp. and *Antechinus* spp., became more common during the Holocene. The continued survival of these species to the present, despite divergent environmental needs, implies that Tasmania's complex

geomorphology provided multiple refugia that conferred resilience in the face of environmental change.

1. Introduction

The Quaternary is characterised by multiple climate transitions between cool-dry glacial conditions and relatively warm-humid interglacial conditions (Barrows et al. 2002; Byrne et al. 2008). The most recent of these transitions occurred within the last 30 thousand years, starting with the last glacial maximum (LGM), a cold and dry period that reached an extreme 20,000 –17,000 years ago (ka), followed by rapidly rising global temperatures during the transition to the early Holocene (11.7 ka), and then a period of relative stability during the mid (6 ka) to late Holocene. In many places, Pleistocene – Holocene vegetation change occurred especially rapidly during relatively short warming events concentrated in the period between 14 and 10 ka (Mottl et al. 2021), which was also a period of rapid sea-level rise (Lambeck & Chappell 2001). Here we investigate owl-roost assemblages found in the now-forested areas of Tasmania, to build a composite record of how small mammals (<200 g) responded to these climate and environmental changes in the southern-temperate region of Australia.

In addition to the direct effects of temperature and precipitation change, the shifts in plant community composition and structure that characterised the period from the LGM to the Holocene presumably had large effects on the small-mammal communities that depend on specific habitats. Small-mammal communities are likely to have been especially strongly affected by vegetation change because different species of small mammals have strong preferences for vegetation structures related to their needs for food, shelter, nest sites, and refuge from predators.

Numerous pollen records have been compiled from lake and cave sediments across Tasmania and the Bass Strait islands (e.g., G. Hope 1978; Colhoun & Shimeld 2012 and papers therein; Fletcher et al. 2018; Adeleye et al. 2020; 2021). Colhoun & Shimeld (2012) reviewed pollen records from across Tasmania to compile a Late-Quaternary vegetation history. Palynological evidence from Tasmanian cores indicate that the colder, drier conditions of the Last Glacial Maximum (~20 ka BP; Barrows et al. 2002) were associated with a major expansion of heath and grassland, at the expense of forest cover (Macphail 1979). In particular, pollen of Poaceae and Asteraceae (grasses, herbs and daisies) dominates the terrestrial record, with *Eucalyptus* (sclerophyllous trees and shrubs) usually also contributing >10%, but pollen of rainforest species was rare. Offshore, Marine Core SO 36-7SL indicates the widespread presence of alpine grassland and herb fields, with very high quantities of Poaceae, Asteraceae and Chenopodiaceae pollen (Colhoun & Shimeld 2012). During the LGM the air temperature in Tasmania is estimated to have been an average of 6.5°C lower than present. This depressed the orographic snowline by ~1000

metres (Colhoun 1991) and allowed ice caps to form on the Central Plateau and West Coast Ranges of Tasmania (Barrows et al. 2002).

These conditions indicate vegetation across most of the island was probably similar to that classified as highland-treeless vegetation, and which is now largely found above 700 m in south-west Tasmania (Harris and Kitchener 2005). Highland treeless vegetation includes a variety of heathland, sedgeland, moorland, grassland, and herb field communities. Although these vegetation types are generally treeless, small eucalypts, conifers and shrubs may be present on sheltered aspects.

When temperatures began to rise substantially starting at ~15 ka (Rees and Cwynar 2010), glaciers began to melt and Poaceae declined (Colhoun et al. 2010). At the same time, wet eucalypt forest started to expand, reaching its present range by ~9 ka BP (Colhoun & Shimeld 2012). We infer that the Tasmanian caves we sampled have yielded fossil assemblages that reflect wet eucalypt forest for the duration of the Holocene, and possibly from as early as 15 ka. We examined small-mammal fossil assemblages from caves of the now-forested regions of Tasmania to document faunal change from across the last 20 ka, a period during which global warming drove major climate, vegetation and sea level change and isolated Tasmania from mainland Australia.

2. Study area

Tasmania, Australia's largest land-bridge island (64,519 km²), is situated in south-eastern Australia (Figure 1). Under current interglacial conditions Tasmania is isolated from mainland Australia by the ~200 km-wide Bass Strait. However, during glacial periods sea level fell by up to 125 m, exposing the continental shelf and transforming the Bass Strait into the Bassian Plain, which bridged the gap between Tasmania and the adjacent Mainland (Figure 1). We excavated five owl-roost accumulations located on and near the high-elevation central region of Tasmania (Figure 1). Excavation sites were chosen based on: (i) the presence of fossil bones on and in surface sediments of karst caves, (ii) the likelihood of stratigraphic integrity, and (iii) minimal disturbance. We sought a broad geographic spread of sites, identified during earlier reconnaissance surveys and communications with speleological groups. The selection was constrained by the limited number of recognised owl-roost deposits. Four of these are within a few tens of kilometres of each other in south-central Tasmania while the fifth is located ~120 km to the north, on the edge of the Central Plateau.

2.1. Caves and excavation sites

Five caves found to preserve animal remains were selected for excavation, and are described below.

Arrakis Cave (MW-1) is located near Mt Weld (-42.99°S 146.62°E), approximately 440 m above sea level (Figure 1). Three samples of bone-rich sediment were collected from ~10 cm deep sandy material covering limestone boulders on the floor of the dry upper-level chamber.

Owl Pot (JF-221) is located in the Florentine Valley (-42.72°S , 146.55°E), approximately 640 m above sea level (Figure 1). Bone-rich, silty fine sands were found in the entrance chamber, overlying the entrance boulder cone and on ledges above. Sediments were collected from a 0.5×0.5 m pits to a maximum depth of 30 cm.

Bone Pit (JF-203) is located in the Tyenna Valley (-42.67°S , 146.50°E), approximately 670 m above sea level (Figure 1). Several pockets of bone-rich sediments were found lodged between boulders. Some had clearly been reworked by flowing water, but others appeared undisturbed. Six apparently undisturbed pockets were collected.

Briggs Squeeze (JF-339) is located on the floor of the Florentine Valley (-42.55°S , 146.46°E), approximately 380 m above sea level (Figure 1). A small unstratified sediment cone consisting of red-brown loamy clay was found in a small chamber approximately 30 m from the entrance. Sediments were excavated in 5 cm excavation units (XUs) to a depth of 45 cm where rocks halted further excavation.

Devils Earhole (MC-9) is located on the Great Western Tiers (-41.58°S , 146.29°E), approximately 600 m above sea level (Figure 1). Bone-rich sediment were deposited on a boulder floor near the Cave entrance. Bone and bone-bearing sediments were collected from two sedimentary layers. Layer 1 was 5 cm thick and consisted of brown loam. Layer 2 was 10cm thick and consisted of light silty sand, draped over limestone boulders.

The present-day dominant vegetation across all study sites (Figure 1) is classified as wet eucalypt forest and woodland on the TASVEG 4.0 vegetation map of Tasmania (DPIPWE 2020). Forest of this type may contain trees up to 100 m tall, often in dense stands over closed understoreys of rainforest species or broad-leafed trees and shrubs. At Arrakis and Devils Earhole, wet forest is interspersed with patches of dry eucalypt forest and woodland on rocky ridges and rainforest in gullies. At Owl Pot and Bone Pit the forest is regenerating from timber harvesting in the c.1970s, and at Briggs Squeeze natural wet eucalypt forest has been converted to pine plantation. Arrakis, Devils Earhole, Owl Pot and Bone Pit are now protected within the Tasmanian Wilderness World Heritage Area and were excavated under authority from the Tasmanian Parks and Wildlife Service. Briggs Squeeze is located on private land and was excavated with the landowner permission.

3. Methods

3.1. Accelerator Mass Spectrometry (AMS) Radiocarbon dating

Twenty-eight bones were selected from the five fossil assemblages for radiocarbon dating, based on bone completeness, weight and stratigraphic depth. Twenty-two bones were submitted to the Australian National University Radiocarbon Dating Laboratory (ANU) and six were submitted to the Waikato Radiocarbon Dating Laboratory (Wk) for AMS Radiocarbon dating. Both Laboratories use standard ultrafiltration AMS radiocarbon techniques (see Beaumont et al., 2010; Nejman et al. 2017), graphitisation and AMS methods (see Fallon et al. 2010). Dates have been calculated according to Stuiver and Polach (1977) using an AMS derived $\delta^{13}\text{C}$, and a bone specific background has been subtracted. Ages were calibrated to the SHCal20 Southern Hemisphere calibration curve (Hogg et al. 2020) using OxCal v4.4 (Ramsey 2009).

3.2. Excavation and processing

Cave sediments were excavated within stratigraphic layers. However, in the absence of stratigraphic layering, or where a stratigraphic layer exceeded a depth of 5 cm, sediments were collected in 5 cm excavation units (XUs) to avoid excessive time averaging (*sensu* McDowell et al. 2013). Excavated sediments were placed in labelled bags for transport out of the cave and to the University of Tasmania.

Samples were wet-sieved using 1 mm mesh to clean and concentrate bones. Samples were air dried then sorted to extract all bones. Diagnostic bones (whole and part skulls, maxillae, dentaries and/or teeth, reptile vertebrae, frog ilia, and bird bones) were sorted from non-diagnostic bones then identified using published descriptions and comparative material held by the Tasmanian Museum and Art Gallery. All specimens were identified to the lowest taxonomic level possible (usually species for mammals, but rarely below order for reptiles and birds). Species richness was determined by calculating the number of species present in each XU. Specimens that could not be identified to species were excluded from the calculation of richness except where they represented the lowest level of identification. As the smallest collection was as rich as the largest collection sample size standardisation was deemed unnecessary. The number of identified specimens (NISP) was used instead of minimum number of individuals (MNI) because MNI is a function of NISP and can generally be relatively accurately predicted from NISP values, “NISP is to be preferred over MNI as the quantitative unit used to measure taxonomic abundance” (Lyman 2008 p. 81). NISP was calculated for each species in each stratigraphic layer or XU, then converted to an index of relative abundance ($R_i\%$), calculated as the % of all specimens contributed by that species. For some analyses and ecological interpretation, species-level data were pooled into habitat guilds that reflect preferred vegetation (Grassland, Heathland or Forest-woodland see Appendix A). Fossils collected

during this research have been registered in the palaeontology collection of the Tasmanian Museum and Art Gallery (Z10702–Z10715).

3.3. Taphonomy

Every fossil assemblage is inherently biased by the process or agent responsible for its accumulation. However, if fossil assemblages share characteristics that suggest they have been accumulated by the same predator or process, then they can be directly compared. On the other hand, if fossil assemblages have been subjected to different taphonomic processes, direct comparison will be misleading at best (McDowell et al. 2012).

Unlike the other assemblages reported here, bones collected from Bone Pit were not excavated from clastic sediments. Instead, they were found in small pockets trapped among rocks below the pitch at the cave entrance. This suggests the fossil assemblage has been hydraulically transported. Flowing water is expected to transport sediment and light bones first, leaving heavy bones as a lag deposit. In addition, a bone's shape can help or hinder the flow rate required to transport it (Kos 2003a Kos 2003b). Compared to larger mammals, all small mammal bones weigh very little and are easily transported, even by low water flows. This process also allows bones to be trapped at random over long periods of time, thereby averaging the environmental signal that is preserved in the other assemblages.

Because bones from Bone Pit have been subjected to intermittent water flows strong enough that bones only remain where they have been trapped by rocks, the Bone Pit assemblage has probably been subject to different accumulation biases compared to the other assemblages and therefore should be compared with them only with caution.

3.4. Interpreting species relative abundance

Because palaeontological samples are rarely of equal size, they cannot be directly compared. To overcome this problem, the NISP of a species from a sample must be converted to relative abundance. This is achieved by dividing the NISP of each species in a sample by the total NISP from that sample, multiplied by 100 to make it a percentage.

If we understand the environmental requirements of each species recovered from an excavation, and we can determine that the bones of a species from a given environment represent the occurrence of that environment at the time the bones were deposited, then changes in species relative abundance should reflect changes in the environment in which the accumulating agent operated. If we also have a strong chronological framework for each fossil assemblage, then we can estimate when faunal changes occurred in past environments and how they have changed through time (Fordham et al. 2020). This is easily done in a single continuous fossil assemblage but can also

be done using several small assemblages as long as they have been taphonomically biased in the same way.

We investigate the influence of habitat change over time on mammal-species richness from each assemblage. Specimens of each species were aggregated then assigned to habitat guilds according to vegetation preferences, based on known habitat preference of the living animals (see Appendix A). These data were then plotted as 100% column stacks against the median age of each calibrated radiocarbon date and undated XUs were positioned according to their relationship to dated XUs. These analyses were conducted in Microsoft Excel.

4. Results

4.1. AMS Radiocarbon Dating

All samples submitted to the ANU radiocarbon facility demonstrated excellent preservation and high to very high collagen yields well above 1% (Appendix B). In addition, C:N ratios and %C values were as expected for collagen (see Van Klinken 1999). In contrast, bone samples AMS radiocarbon dated by Waikato tended to have lower collagen yields. Of those bones that could be dated, only one sample was large enough to obtain stable isotope values by Isotope Ratio Mass Spectrometry (IRMS), although all had collagen yields above 0.5%. It is difficult to assess reasons for differential success in collagen extraction between the two laboratories as different bones were analysed.

AMS Radiocarbon Dating (see Table 1 for a summary and Appendix B for the full dataset) indicates that each fossil assemblage accumulated rapidly during the Late Quaternary. The Arrakis Cave assemblage accumulated near the beginning of the LGM, some 20 ka (Appendix B). Despite being buried in very shallow alkaline sediments, bones from Arrakis Cave demonstrated excellent collagen preservation. Dated specimens were collected from different areas of the cave but yielded similar ages, suggesting they are representative of the assemblage as a whole.

The next youngest assemblage was collected from Bone Pit. One radiocarbon age was obtained from each of the three pockets of bones. Two of the ages were very similar but the third was somewhat younger (Appendix B) suggesting bones may represent several thousand years of accumulation.

Fossils collected from Briggs Squeeze were excavated from a 45 cm tall clay-rich sediment cone in 5 cm intervals. Radiocarbon ages obtained from Briggs Squeeze (Appendix C) suggest the sediment cone accumulated extremely quickly (<780 years), then sedimentation apparently stopped.

Fossils collected from Owl Pot were excavated from 35 cm deep unstratified sediments that accumulated over the entrance boulder pile. Radiocarbon ages obtained from 15 bones (5 each from

0-5, 10-15 and 25-30 cm excavation units) indicate the assemblage accumulated very quickly and records fauna from the end of the Late Pleistocene into the early Holocene.

The youngest radiocarbon ages obtained in the study were sampled from Devils Earhole, Mole Creek (Appendix B). Two specimens were dated, one from the upper and one from the lower stratigraphic layers. The oldest originates from the late Holocene, while the youngest age postdates European arrival in Tasmania (Appendix B).

4.2. Taphonomy

The taphonomic signature of each assemblage investigated was very similar. Each fossil assemblage consisted predominately of nocturnal mammals with a maximum adult mass of 200 g (Appendix C; 94.6 – 99.7% of specimens). Species weighing > 200 g were poorly represented and almost always by juvenile specimens; mammals with a maximum adult mass of more than 1000 g were very rare. Bone preservation in each assemblage was excellent and bone breakage negligible. As small raptors (e.g., Boobook owls) have to compress the indigestible component of their diet into a smaller pellet compared with larger raptors (Andrews and Cook 1990) they tend to cause more damage to prey bones than larger raptors. The very low rate of bone breakage in each assemblage investigated, and the very high proportion of nocturnal species, suggests the assemblages were probably accumulated by a large Tytonidae owl (Kavanagh 2002).

4.3. Species composition

The NISP for each owl roost fossil assemblage investigated is reported in Appendix C. Combined, the fossil assemblages yielded 12,571 identified specimens representing at least 24 species. We recovered five carnivorous marsupial species, one bandicoot, two pygmy possums, one ringtail possum, one potoroo, one bettong, one kangaroo, five rodents (including the recently introduced *Mus musculus*), at least three insectivorous bats, at least two frogs, at least one lizard and several birds (including *Tyto novaehollandiae castanops*, the Australian masked owl). Small-mammal remains were abundant in every collection, but reptiles and frogs were rare and may not have been derived from owl prey. Bird bones were well represented in every assemblage but could rarely be identified below Family. Therefore, reptiles, amphibians and birds are reported in the faunal tables but excluded from further analysis.

4.4. Fossil assemblages

4.4.1. Arrakis

The Arrakis fossil assemblage was the oldest we collected, being dated to 20,425 – 19,721 cal. BP. It is dominated by *Mastacomys fuscus* (the broad-toothed rat, see Appendix A, Table 1) and even though it was a small sample, species richness was comparable with the other assemblages (Appendix B).

4.4.2. Briggs Squeeze

The Briggs Squeeze fossil assemblage was the second oldest we collected. The three ages acquired from this site were very tightly grouped, with just 770 years between the youngest and oldest calibrated ages (Appendix B). The oldest XUs were dominated by *M. fuscus* (see Appendix C; Table 3) but the relative abundance of this grass-eating species decreased almost by half from the oldest to youngest XUs.

4.4.3. Owl Pot

The Owl Pot fossil assemblage (Appendix B, Table 4) was aged between 15,926 cal. BP and 8,542 cal. BP. The relative abundance of *M. fuscus* continued to decline throughout the measured span of this assemblage. In the deepest XU it makes up 36.29 Ri%, but declines to just 3.83 Ri% in the uppermost XU.

4.4.4. Devils Earhole

Aged between 1,994 and 15 cal. BP, the Devils Earhole fossil assemblage (Appendix B; Table 5) was the youngest of the sites excavated. This assemblage is young enough that its upper layers should be representative of the present-day mammal community of the area. *Mastacomys fuscus* makes up very little of the Devils Earhole fossil assemblage (<0.5 Ri% of the uppermost XU), being largely replaced by the Forest dwelling rodent *P. higginsii*, the two pygmy possums *C. nanus*, *C. lepidus*, and the small dasyurids *A. swainsonii* and *A. minimus* (see Appendix C). This is also the only assemblage in which *Pseudomys novaehollandiae* was found, a species no longer present in the area. The remains of *Mus musculus* were also recovered from the cave floor surface, indicating that predators are still using the cave today.

4.4.5. Change in community composition over time

As illustrated in Figure 2, near the peak of the LGM (~20 ka), the temperature was approximately 6.5°C cooler than today and owl prey consisted of around 80% Grassland species, 15% heath species and just 5% forest woodland species (See Appendix C) However, as global temperature began to increase, forest/woodland taxa became more common at the expense of Grassland taxa. Near the end of the Pleistocene, when global temperature was about 4°C cooler than

today, owl prey consisted of around 80% forest woodland species, 15% heath species and just 5% Grassland species.

Figure 2 shows that while the relative proportions of Tasmania's mammal fauna in these assemblages has changed dramatically since the peak of the LGM, the species composition (i.e., the identity of the species in the community) of these sites has remained remarkably stable (Figure 3). Over the last 20 ka, none of the species recorded have gone extinct in Tasmania and only one mammal species (of sufficiently small mass to be hunted by owls) has invaded (the house mouse; see Appendix C). The only exception is *Pseudomys novaehollandiae*, which was found in every layer of the Devils Earhole assemblage, dated at 1994–15 cal. BP but was absent from all or the more southern sites. Devils Earhole is much further north than other sites we examined (Figure 1) and though *P. novaehollandiae* was recently recorded on Flinders Island (<https://www.abc.net.au/news/2021-10-20/native-new-holland-mouse-found-on-flinders/100553568>) when last seen alive on the Tasmanian mainland in 2004, *P. novaehollandiae* was restricted to small pockets in the north east, where it inhabited floristically diverse heathlands and associated vegetation communities that typically arise from mosaic burns (Lazenby et al. 2018). As *P. novaehollandiae* is rarely found in tall forests, its absence from the other assemblages is understandable. Its presence in wet forest at Devils Earhole suggests that it may have been taken there by an owl foraging on Grassland at lower elevation. Devils Earhole extends the historic range of the species further west and deeper inland than previously appreciated.

Mastacomys fuscus occurred in almost every XU from every fossil assemblage we investigated. However, while it dominated the older sites, its relative abundance steadily decreased with time until it was almost absent near the present day, contributing >1% of the uppermost XU of Devils Earhole aged 287–15 cal. BP (Appendix B). As the relative abundance of *M. fuscus* decreased. The relative abundance of *P. higginsii*, *C. nanus*, *C. lepidus*, and to a lesser extent *R. lutreolus*, increased (Appendix C). The decline of *M. fuscus* correlates strongly with increasing palaeo-temperature and the expansion of forest/woodlands at the expense of grasslands.

5. Discussion

In this study we investigated the effect of environmental change on Tasmania's mammal fauna over the last 20 thousand years. Between 20–11.7 ka the Earth experienced the cool dry conditions and lower sea level characteristic of Late Pleistocene ice ages. In contrast, between 11.7–0 ka the Holocene was typically warmer and more humid. The cave assemblages we investigated record the cool, dry period of the last ice age followed by a period of rapid warming that caused sea level to rise up to 125 m, inundating the continental shelf and transforming its hills and promontories (including Tasmania) into islands. Such substantial environmental change was

expected to result in species turnover, particularly amongst Tasmania's small-mammal fauna, but our results indicate that Tasmania's mammals were extremely resilient to environmental change. Indeed, over a third (37.5%) of native mammal species now in Tasmania were present in every fossil assemblage (Appendix B), although *Potorous tridactylus* and *Pseudomys novaehollandiae* were both found only in the Devils Earhole assemblage. *Potorous tridactylus* is probably rare in our samples due to its comparatively large body mass (660–1640 g). However, *P. novaehollandiae* has a body weight range of just 12–26 g and is commonly found in owl-roost assemblages across south-eastern Australia (e.g., Wakefield 1960 a & b; Menkhorst 1995; Bilney et al. 2010). The two radiocarbon ages indicate that this particular assemblage accumulated very recently (2000–15 cal. BP). Its absence from the other assemblages probably relates to its preference for dry-heathland vegetation (Lazenby et al. 2018). Except for the occurrence of *P. novaehollandiae* and *P. tridactylus* in the youngest and northern-most assemblage investigated, the species composition of each fossil assemblage did not change over the last 20 ka, but species proportions change dramatically. Grassland species declined and were replaced by forest species that increased in synchrony with Holocene global warming, and is consistent with a wetting trend.

The Broad-toothed mouse *Mastacomys fuscus* is a native graminivorous rodent that today occurs in New South Wales, Victoria and Tasmania (Driessen 2001; Happold 2008). Historically, *M. fuscus* was more widespread than today. The species has been found in numerous fossil assemblages across South Australia, Victoria and south-eastern New South Wales, and several fossil sites occur outside the species' current recognised distribution and habitat, e.g., McEacherns Cave and McEacherns Deathtrap Cave (Kos 2003 a, b) Mount Gambier (Thomas 1922), Kangaroo Island (McDowell 2013; McDowell et al. 2015; Adams et al. 2016), Naracoorte Caves (Reed & Bourne 2000), Rapid Bay (Fusco et al., 2015) and the Southern Flinders Ranges (Liddle et al. 2018) in South Australia, and the Wellington Caves (Lydekker 1885; Dawson & Augee 1997; Green & Odborne 2003), Jenolan Caves (Morris et al. 1997) and Wombeyan Caves (Ride 1960; Calaby & Wimbush 1964), Yarrangobilly Caves (Bilney 2020) and Wee Jasper (Theden-Ringl et al., 2020) in New South Wales. The fossil record suggests *M. fuscus* once occupied a wider range of drier habitat types (<700 mm rainfall) at lower elevations (<100 m) compared with its current distribution (Bilney et al., 2010; Fusco et al., 2015; Menkhorst 1995). Several researchers (e.g., Ride 1956; Watts and Aslin 1981; Happold 2008; Schulz et al 2019; Menkhorst 1995; Green & Osborne 2003; Menkhorst et al. 2008) attribute this to the cooler, wetter conditions of the late Pleistocene, suggesting the modern distribution of *M. fuscus* had been limited by climate change. However, recent radiometric dating has shown many of these fossil deposits actually accumulated during the Holocene, suggesting the species may have suffered a rapid range contraction in response to anthropogenic ecosystem modifications consequent to European settlement (Fusco et al. 2015;

Tammone et al. in press). As threatening processes are still in effect, *M. fuscus* will probably continue to decline unless conservation management actions are enacted (Seebeck & Menkhorst 2000; Green & Osborne 2003; Green et al., 2008; Menkhorst et al., 2008; Happold 2008; Seebeck 1971; McDowell 2013; Menkhorst 1995; Hocking & Driessen 2000; Bilney et al., 2010).

Each of the caves we investigated occur in forested environs today. Therefore, the pattern of faunal change we observed may not be representative of Tasmania as a whole. However, this pattern of faunal rearrangements but not replacements has also been observed in the fossil record of Badger Island, Bass Strait (Sim 1998; McDowell et al. in review.), suggesting it is representative of environmental change in the greater geographic region.

The arrival of Europeans and the suite of introduced mammals that typically accompany them appears to have had a devastating effect on Tasmania's native small mammals, but only in areas where native vegetation has been heavily modified or removed. Species recovered from the uppermost 5 cm of sediment excavated from Devils Earhole date to the last few centuries, and therefore should be representative of the surrounding fauna which, with the exception of *Mus musculus*, consists entirely of native mammals. All of the owl-roost assemblages we report here except Briggs Squeeze are largely natural areas within the Tasmanian Wilderness World Heritage Area, whereas owl assemblages reported by Mooney (1993) and Todd (2012) come from highly modified environments and are dominated by introduced species (Mooney 1993; Todd 2012). Juvenile rabbits and black rats have largely replaced native rodents, and the introduced (from mainland Australia) sugar glider *Petaurus brevipes* has reduced the importance of the Common Ringtail Possum. Mainland studies have also found lagomorphs and introduced rodents to be common in the diet of the Masked Owl (Mooney 1992, 1993; Kavanagh 1996; Kavanagh & Murray 1996; Kavanagh 2002). This implies that native mammals still occur where native vegetation persists but introduced mammals dominate disturbed habitat.

6. Conclusion

Our study shows that Tasmania's mammal fauna has been remarkably resilient to climatic and environmental change over the last 20 ka. While species composition remained constant during a period of unprecedented climate change, the relative abundance of species within these communities changed dramatically. Tasmania's apparently low mammal diversity may allow some mammals to occupy a broader niche width compared to more speciose habitats on the mainland, or potentially even multiple niches. This may have provided refuge for multiple species, making them more resilient to climate or environmental change.

Cold-tolerant grassland species were dominant during the LGM, but as global temperature increased they became increasingly rare. In contrast, forest and woodland species were quite uncommon during the LGM but increased quickly and became dominant as global temperature increased through the end Pleistocene and into the Holocene. We found no evidence of elevated extinctions following Tasmania's isolation from the mainland, suggesting the main island of Tasmania is big enough to play the role of a biogeographic 'mainland', buffering the impact of isolation. However, unlike most of mainland continental Australia, Tasmania has retained 74–76% of its native vegetation coverage (Michaels et al. 2010), and the European red fox (*Vulpes vulpes*) has not established, suggesting that its native-mammal communities may be largely intact in terms of the mix of species present since the LGM. Tasmania appears to have provided refugia for multiple species, both before and after Pleistocene–Holocene transition, supporting the view that it has potential as a translocation destination for south-eastern Australia's threatened species (Morris et al. 2020). Equally, geographic isolation has clearly been critical to the survival of species already present in Tasmania, despite profound shifts in climate and vegetation since the LGM.

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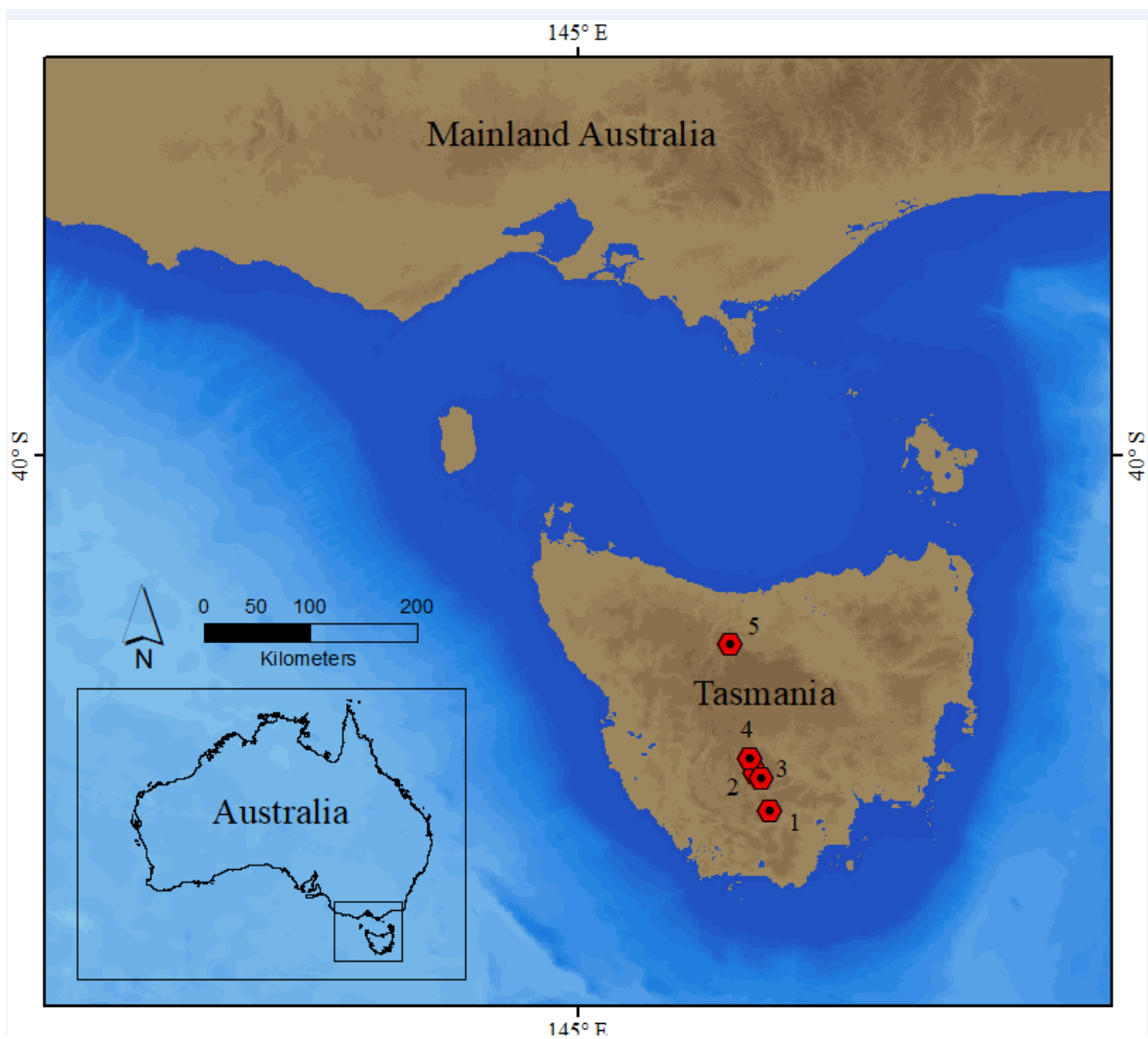


Figure 1: Location of 1, Arrakis Cave; 2, Owl Pot; 3, Bone Pit; 4 Briggs Squeeze, and 5, Devils Earhole.

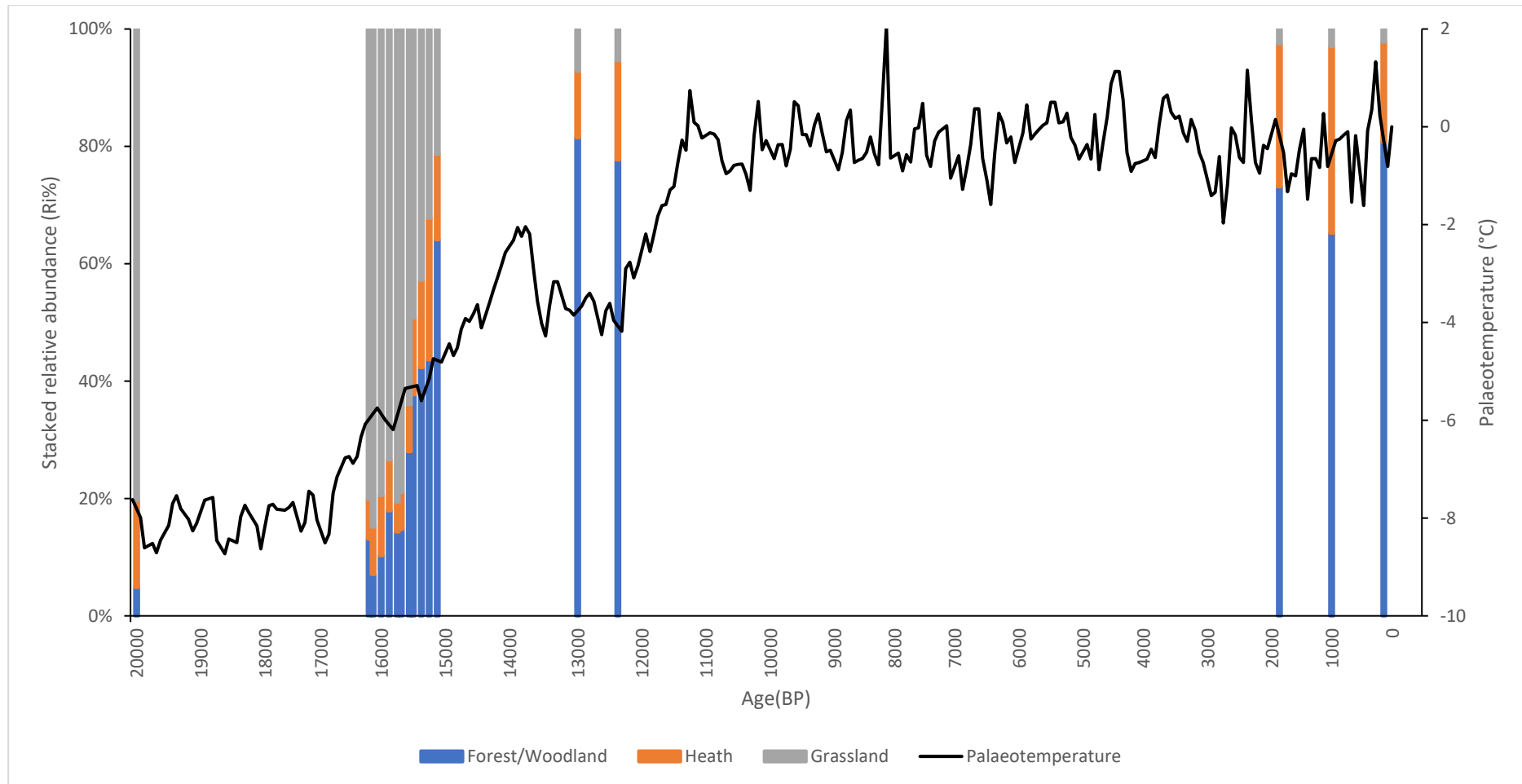


Figure 2: Relative abundance of mammal species (combined into habitat guilds) recovered from fossil-assemblage excavation units. Stacked columns show how proportional representation of habitat guilds changes in relation to palaeotemperature (°C Black line) derived from the Vostok ice cores (Jouzel et al. 1993; Jouzel et al. 1996; Petit et al. 1999).

Figure 3: Species relative abundance trends show that over the last 20,000 years forest-woodland taxa increase while grassland dwelling taxa decrease.

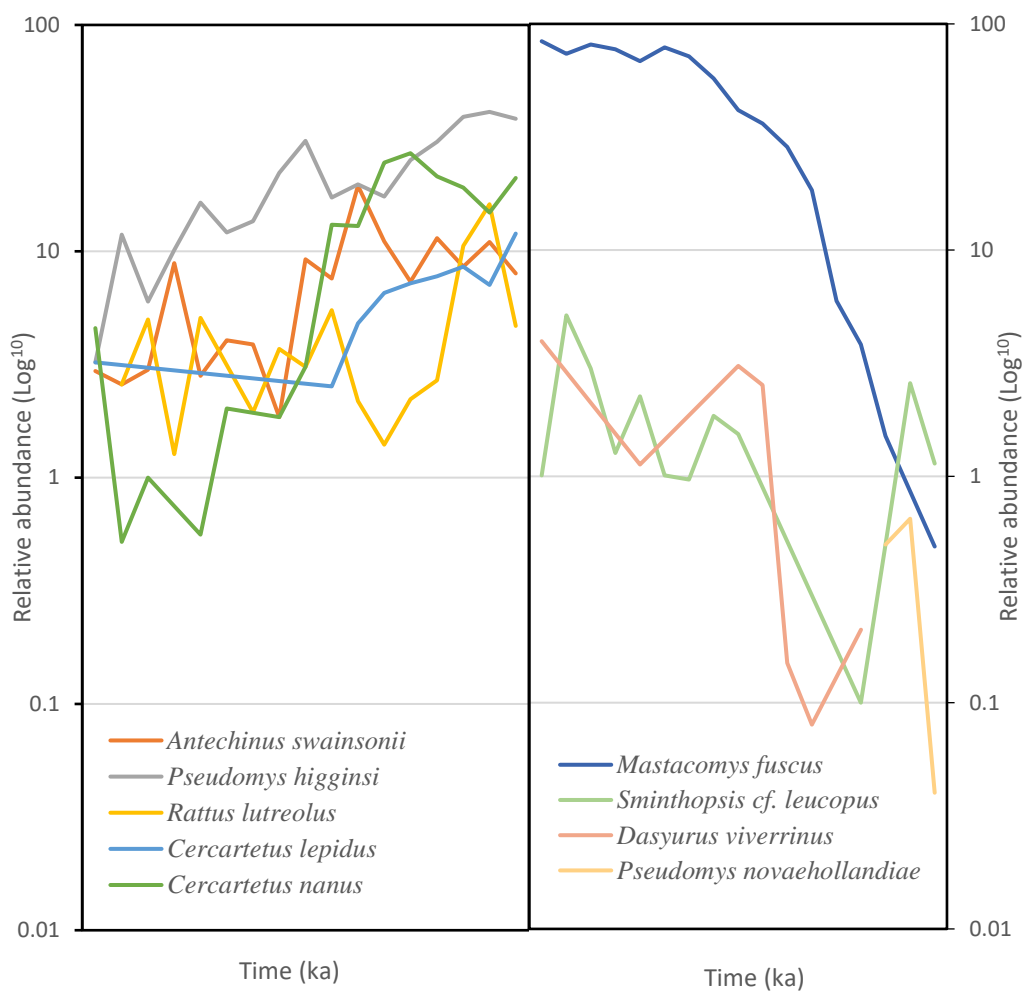


Table 1: A summary of radiocarbon dates showing the maximum age range of each fossil assemblage. For detailed radiocarbon dating results see Appendix B.

Site Name	Maximum depth range (cm)	Maximum age range (cal. BP)
Devils Earhole	0–15	1994–15
Owl Pot	0–30	15251–8542
Briggs Squeeze	0–45	16315–15545
Bone Pit	0–10	16335–12680
Arrakis Cave	0–10	20425–19721