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## Interim report on the vertebrate deposits recovered from the Capricorn Caves, Rockhampton, Queensland

Julien Louys , Jonathan Cramb , Kyle Ferguson, Justine Kemp , Rachel Wood , Justyna J. Miskiewicz , Nathalia R. Dias Guimarães, Pennilyn Higgins , Kenny J. Travouillon , Scott A. Hocknull , Gregory E. Webb  and Gilbert J. Price 

### ABSTRACT

Late Pleistocene to Holocene-aged microfaunal assemblages are rarely reported in Australia despite their critical importance for palaeoecological studies, as well as their bearing on the megafaunal extinction debate. Capricorn Caves, central-eastern Queensland, hosts three Late Pleistocene to Holocene deposits containing significant faunal records. Excavations were conducted on these deposits over several seasons, with analyses of recovered material ongoing. Here, we report interim results and explore their implications for our understanding of the microfaunal record of central eastern Queensland. Fern Chamber was previously dated using U-series to the Holocene ( $>7.6 \pm 0.2$  ka). Honeymoon Suite was dated to  $>6.4 \pm 0.2$  ka using U-series. However, new charcoal dates from the deposit span approximately 7.5–15.5 ka, although the association between charcoal and fauna is unresolved. The fauna is likely Holocene. Colosseum Chamber is the oldest of the deposits, and new single-grain luminescence ages and age-depth modelling suggest that the deposit likely spans MIS 1–4. We use abundant fragmentary rodent remains to examine palaeoenvironmental change over this period. Carbon and oxygen isotope analyses of rodent incisor fragments reveal broad diets within the rodent community, and significant differences in precipitation between glacial and interglacial conditions. Rodent long bone histological analyses indicate significant differences in bone metabolism at the family level between the MIS 3 and 2 samples, but not MIS 1. We suggest that these data support evidence for a mid-Holocene arid anomaly in the region, and increased aridity through the Holocene relative to the terminal Pleistocene. The sites contain at least 10 small mammal species either globally extinct or locally extirpated, including the Capricorn rabbit-rat (*Conilurus capricornensis*), the white-footed rabbit-rat (*Conilurus albipes*), the plains mouse (*Pseudomys australis*), Gould's mouse (*Pseudomys gouldii*), Forrest's mouse (*Leggadina forresti*), the long-tailed hopping mouse (*Notomys longicaudatus*), swamp rat (*Rattus lutreolus*), the white-tailed rat (*Uromys caudimaculatus*), the narrow-nosed planigale (*Planigale tenuirostris*), the Liverpool Plains striped bandicoot (*Perameles fasciata*), the Cape York brown bandicoot (*Isoodon peninsulae*), and the southern brown bandicoot (*Isoodon obesulus*). We also record significant range contractions for frogs (*Phyllorhina* sp., *Neobatrachus* sp.) and earless dragons (*Tympanocryptis* sp.). This study demonstrates that significant changes in the microfaunal community of tropical Queensland occurred between the Late Pleistocene and the late Holocene. It also reinforces how poorly recorded native faunas are from the late Holocene through the historical period, to today. Such records underpin and are thus vital for modern biodiversity conservation efforts.

### ARTICLE HISTORY

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THE QUATERNARY is characterised by extreme cyclical changes in global climatic conditions that had profound impacts on ecosystems and the organisms that depend on

them (Allen *et al.* 1999, Kershaw *et al.* 2003, Wroe *et al.* 2013). During glacial maxima, Australia became cooler and more arid, causing contractions in mesic plant communities and available standing water (Kershaw *et al.* 2003). Most research into the effects of these changes on fauna have been at the community or whole-organism level. They

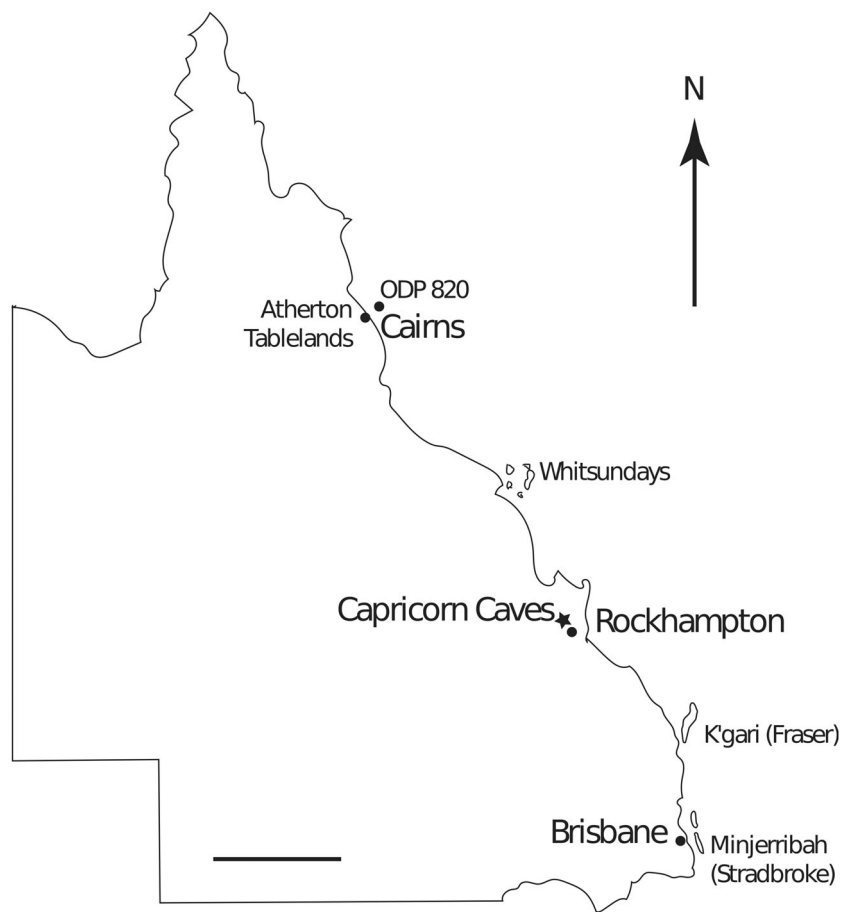
indicate geographic range reductions, as well as extinctions, of many species in response to increasingly arid conditions (Wroe *et al.* 2013, Hocknull *et al.* 2007, 2020, Price *et al.* 2019). Small-bodied vertebrates (here, informally termed ‘microfauna’ for species <5 kg in body weight) provide highly informative data for reconstructing local palaeoenvironmental conditions and for understanding ecological processes through time (Hadly 1996, Price *et al.* 2005, Price 2012, Blois *et al.* 2010). Because many microfauna are primary consumers and inhabit narrow ecological niches, they are good indicators of ecosystem health. Specifically, microfauna are more likely to be adversely affected by bottom-up ecological processes than are larger species, which typically have broader ecological requirements and a greater ability to disperse to more hospitable conditions (Sandel *et al.* 2011, Schloss *et al.* 2012). In particular, the distribution, diversity, and richness of vertebrate microfauna within any ecosystem is likely to be affected directly by changes in vegetation brought about by climate change or other extrinsic factors that affect primary productivity (e.g., anthropogenic habitat change). Such bottom-up processes have been recorded in numerous Quaternary microfaunal communities (e.g., Hadly 1996, Blois *et al.* 2010, Terry *et al.* 2011, Schap *et al.* 2021), and provide important information on ecosystem functioning in the geologically recent past. The conservation implications of these studies have been well noted (Bilney *et al.* 2010, Terry *et al.* 2011), but they also have important consequences for the debate on driver(s) of late Quaternary extinctions, including those of the large-bodied ‘megafauna’. Integrated palaeoenvironmental and extinction studies that incorporate microfaunal communities have the potential to indicate whether taxonomic losses were driven by bottom-up (climate) or top-down (human hunting) processes (Lyman 2012).

In Australia, the dominant hypotheses developed to explain megafauna extinctions are centred on human activities, climate change, or a combination of the two (e.g., Brook *et al.* 2007, Price *et al.* 2011, Field *et al.* 2013, Field & Wroe 2012, Wroe *et al.* 2013, Bird *et al.* 2013, Hocknull *et al.* 2020). Although late Pleistocene to Holocene-aged microfaunal deposits are relatively abundant, they are rarely reported to the same level of detail or subjected to the same level of scrutiny and analysis as are megafaunal deposits, through (for example) the use of multiple dating methods, detailed stratigraphic recording, and multiproxy palaeoecological analysis. This lack of testing is surprising, as adverse changes to late Quaternary small mammal faunas is a specific prediction of the hypothesis that climate change was the driver of megafaunal extinctions. For example, Brook *et al.* (2007, p. 562) stated: ‘We should, therefore, predict that small mammals would have been much more likely to have been confined to restricted refugia and, thus, more vulnerable to extinction during periods of climatic stress than would the megafauna.’ In north-eastern Australia, increasing aridity over the last 300,000 years impacted small mammals severely, with extinctions and extirpations linked directly to loss of preferred habitats (Price & Sobbe 2005, Hocknull *et al.* 2007, Cramb *et al.* 2018; Price *et al.* 2020). Habitat loss and fragmentation affects biodiversity through, amongst several factors, a reduction in resource availability (Kupfer

*et al.* 2006, Zanette *et al.* 2000). At the individual level, mammals can respond to resource and food scarcity by reducing their resting metabolism (Merkt & Taylor 1994, Gutman *et al.* 2006, Choshniak *et al.* 1995), a response that may be common across all mammal taxa (Merkt & Taylor 1994). At a population or species level, mammals can become locally extirpated, or, in cases where species range is already highly restricted, globally extinct (Murray & Hose 2005, Waller *et al.* 2017).

Caves remain one of the best sources of Quaternary microfaunal deposits (Lundelius 2006). On the east coast of Australia, cave deposits have produced abundant late Quaternary microfaunal remains. Fossil assemblages from caves in New South Wales (Jenolan Caves (Morris *et al.* 1997), Wombeyan Caves (Schram & Turnbull 1970), Wellington Caves (Dawson & Auger 1997), Manning River Caves (Price *et al.* 2019)), Victoria (Pyramids Cave; Wakefield 1972), North Queensland (Broken River; Price *et al.* 2020) and Southeast Queensland (Texas Caves; Archer 1978; Price *et al.* 2009) demonstrate that micromammal turnover occurred during the late Quaternary as a result of climate change. Morris *et al.* (1997) showed that extirpation of as much as 26% of the microfaunal assemblage from the terminal Pleistocene to the Holocene could be tied to environmental changes occurring over this time. Of the losses, two species—*Burramys parvus* Broom, 1896 and *Conilurus albipes* (Lichtenstein, 1829)—were not recovered in deposits younger than the Pleistocene. Conversely, McDowell *et al.* (2022) recorded no extinctions between the Last Glacial Maximum and the Holocene in Tasmanian assemblages, although changes in rodent abundances were observed. In western Victoria, Ramm *et al.* (2022) demonstrated that changes in reptile subfamily abundances correlated with known shifts to aridity over the late Pleistocene and Holocene.

In the Queensland tropics, Hocknull *et al.* (2007, 2020) demonstrated that, concomitant with Pleistocene changes in climate, considerable extinctions of both micro- and megafauna occurred over the last 500 ka. In the central eastern Queensland area, these records were recovered from a large complex of caves formed in an isolated Devonian limestone massif situated approximately 23 km north of Rockhampton (Fig. 1) in Darumbal Country. The caves, which include Capricorn Caves, Mount Etna, and Marmor, formed in allochthonous limestone blocks within what is thought to be the Devonian Mount Alma Formation (Yarrol Project Team 1997). Such blocks extend from the Marmor-Raglan area 50 km south of Rockhampton, to Princhester approximately 50 km north (Hocknull 2005). The Capricorn Caves are a system of 16 interconnected caverns situated within the Capricorn Caves Tourist Park (Fig. 2), with modern local vegetation including semi-evergreen vine thicket, shrubby woodland and grassy woodland (Hamilton-Smith & Champion 1975). The fauna of the area has received relatively little attention, and surveys have been few and sporadic; a list of modern fauna found around the caves is provided by Sprent (1970) and Hamilton-Smith & Champion (1975). Fossils have been known from the Rockhampton area for more than 100 years (Hocknull 2005)



**Figure 1.** Map of Queensland showing the location of Capricorn Caves (star) as well as major palaeoecological sites discussed in the text. Scale bar = 300 km.

but were not scientifically evaluated until 1924 (Longman 1924, 1925a, b); systematic collection and excavation of the Capricorn Cave deposits commenced only in 2004.

Hocknull *et al.* (2007) classified site faunas from the Rockhampton cave deposits into discrete temporal clusters, with faunas from individual caverns within the Capricorn Caves grouped together to make a composite Holocene faunal cluster. This was based on the geochronological analysis of two of the deposits from the Capricorn Caves: 'Icicle' Chamber (actually Fern Chamber, see below), and Honeymoon Suite, with sampled material from these caverns dated to the Holocene (Hocknull *et al.* 2007). 'Icicle' Chamber was assigned a minimum age of  $7.6 \pm 0.2$  ka based on U/Th dating of calcite cement, and Honeymoon Suite a minimum age of  $6.4 \pm 0.2$  ka based on direct U/Th dating of a kangaroo incisor (Hocknull *et al.* 2007). The Capricorn Caves Holocene faunal cluster had an essentially modern character (Hocknull 2005; Hocknull *et al.* 2007), particularly in comparison to the Middle Pleistocene deposits of Mount Etna, and clustered most closely with those of modern faunas (Hocknull *et al.* 2007, fig. 2). Nevertheless, Cramb *et al.* (2009) and Cramb and Hocknull (2010a, b) indicated that fossil species assemblages recovered from the Capricorn Caves show some differences to the micromammal community present in the region today, and since then, Honeymoon Suite and Colosseum Chamber have been cited independently when examining individual species

occurrences (Cramb *et al.* 2009, Cramb & Hocknull 2010a, b). Faunal accumulation is considered to have been primarily the result of owl predation due to the dominance of small, mostly unbroken, disarticulated bones, with a few larger bones fragmented and corroded, some with rounding; however, ghost bats (*Macroderma gigas* (Dobson, 1880)), pit falls, and terrestrial scavengers may have been minor contributors (Hocknull *et al.* 2007, Cramb 2012, Price *et al.* 2015).

Colosseum Chamber hosts a 2 m-thick unconsolidated owl roost deposit (Price *et al.* 2015). The fauna is, like 'Icicle' Chamber and Honeymoon Suite, dominated by small-sized taxa (e.g., rodents, frogs, bandicoots), with large-sized taxa (e.g., kangaroos) also present; it also includes one of the geologically youngest Australian continental records of giant varanids ( $\sim 50$  ka; Price *et al.* 2015). Initial dating indicates the deposit was formed relatively continuously over the last 40 ka, although the deposit likely extends to at least 60 ka (Price *et al.* 2015), thus extending the Holocene records from 'Icicle' Chamber and Honeymoon Suite. It represents a critical deposit to examine the effects of large-scale environmental changes on microfauna through time, and, because the owl roost deposit spans the relatively benign climatic conditions prior to the Last Glacial Maximum (LGM), the period of the LGM, and finally the current interglacial, it is an ideal assemblage for examining the effects of major climatic changes on micromammals.



**Figure 2.** Entrance to the Capricorn Caves Tourist Park, showing the layout and relationships of the 16 interconnected chambers.

It has been 10 years since the last major excavation of Colosseum Chamber was undertaken, and this seems like an appropriate milestone at which to provide an update on the work completed thus far (including new dates, updated species lists, and novel palaeoecological analyses). More appositely, it is an opportunity to better understand the extirpation and extinction of Australian fauna in celebration of the lifelong dedication of Mike Archer to palaeontology and biodiversity conservation, and his pioneering and continuing efforts in combining these fields (Archer *et al.* 1991, 2019). Archer and colleagues published some of the first research to explicitly use the fossil record to provide insights into conservation, research now often termed conservation palaeobiology (Louys 2012). His keen insights into the history and conservation of Australian mammals had, and continues to have, a great influence on the co-authors of this paper as well as the discipline as a whole.

## Materials and methods

### Nomenclature

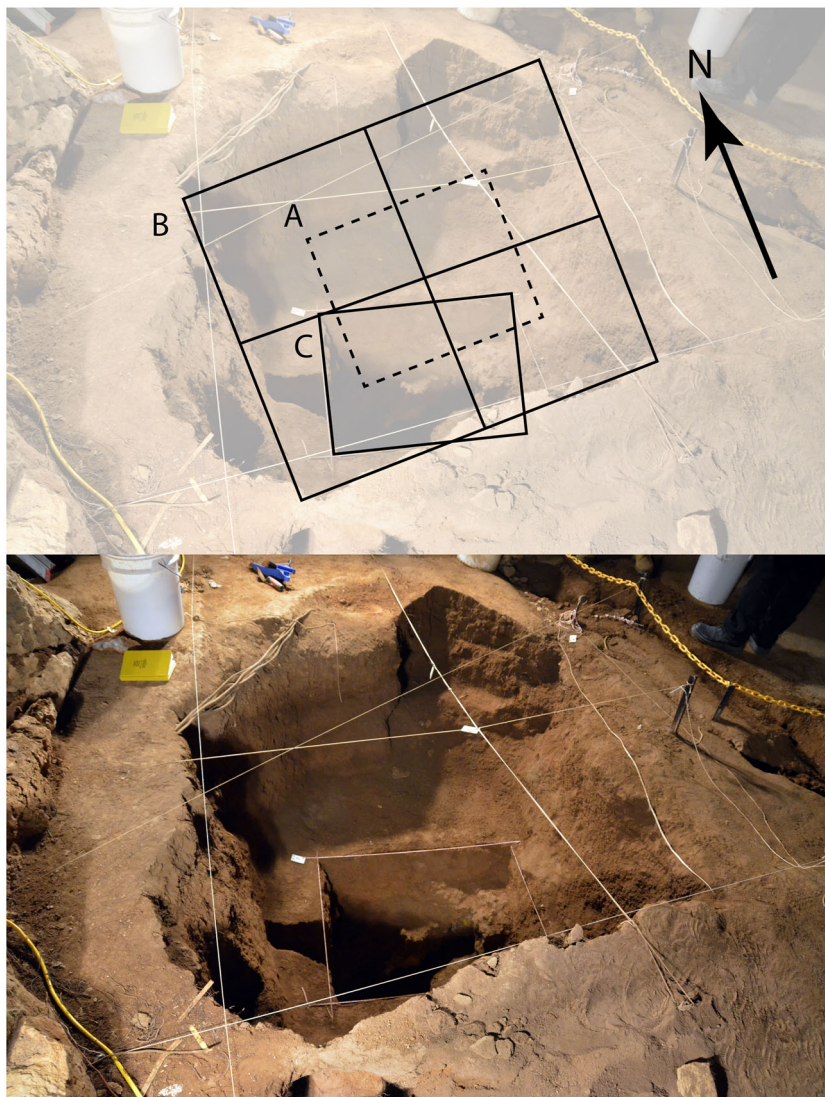
The Capricorn Caves were first documented in 1882 by John Olsen, who subsequently developed them for tourism. Since then, they have been known variously as Olsen's Capricorn Caves, Olsen's Caves or Capricorn Caves. Hocknull (2005, p. 16), Hocknull *et al.* (2007, p. 318) and Cramb & Hocknull (2010a, p. 127) used 'Olsen's Cave', while Cramb & Hocknull (2010b, p. 46) referred to them as 'Capricorn Caves'. Hereafter we refer to them as Capricorn Caves, as they are known locally today. Likewise, Colosseum Chamber (QML1456) has been spelled variously as 'Colluseum' (Cramb *et al.* 2009, p. 664, Cramb & Hocknull 2010b, p. 45) and 'Colosseum' (Butz 2004, p. 8, Cramb & Hocknull 2010a, p. 127). It has also been referred to as 'Horse head' (Butz 2004, p. 8). Here we refer to this site as

Colosseum Chamber, following local site usage. Honeymoon Suite (QML1457), a small side chamber of Cathedral Cave, has been spelt as either ‘Honey Moon Suite’ (Hocknull *et al.* 2007, p. 320) or ‘Honeymoon Suite’ (Cramb & Hocknull 2010b, p. 45). Here we use Honeymoon Suite, again following local site usage. Finally, all previously published reference to fauna and dates from ‘Icicle’ Chamber are incorrect: both dates and faunal sampling took place in Fern Chamber, the larger chamber adjacent to Icicle Chamber (Fig. 2), and so henceforth we refer only to Fern Chamber.

### Excavation and sampling

Excavations at Colosseum Chamber commenced in 2004–2005 by the Queensland Museum, with a  $1 \times 1$  m pit excavated at 10 cm intervals to a depth of 90 cm (Fig. 3). Excavations were resumed in 2005 in the same pit over a  $2 \times 2$  m area. The broader excavation again went down to 90 cm; however, in that instance, material was excavated in 5 cm spits. All material was wet sieved progressively in

10 mm, 5 mm, and 1 mm sieves. In 2012, a joint University of Queensland and Queensland Museum team returned to extend the excavation deeper to the floor of the cave. A datum point was established on the north wall of Colosseum Chamber, with a datum line extending over the pit. The western surface of the deposit is situated 7 cm below this line, and all spit depths from previous excavations have been converted to the distance below this line (for example, the 0–10 cm spit from the first excavation is referred herein as the 7–17 cm spit below datum). The 2012 excavation began at a depth of 105 cm below the datum in an  $80 \times 100$  cm pit centred at the base of the previous excavation (Fig. 3). This means that a gap exists between 97 cm (the base of the 80–90 cm spits of the original excavation) and 105 cm (the beginning of the 2012 excavation). This is likely due to a combination of sediment compaction and/or deflation and differences in how the spit distances were measured between seasons. The material between 105 and 112 cm was considered washed-in and/or disturbed material and was not collected. Undisturbed deposits were collected from 112 cm, and the 2012 work extended the depth of the



**Figure 3.** Plan view showing excavation squares of the Colosseum Chamber deposits. A, Original  $1 \times 1$  m 2004–2005 excavation. B,  $2 \times 2$  m 2005 excavation. C,  $0.8 \times 1$  m 2012 excavation.

excavation to 197 cm below the datum. At this point, the limestone cave floor was encountered over most of the pit floor. However, the deposit continues to an unknown depth in the southwestern corner of the pit. All additional excavated material was wet sieved on site as in previous seasons.

Bulk sampling of fauna in Honeymoon Suite and Fern Chamber occurred in 2004–2005. While both the Fern Chamber and Colosseum Chamber deposits are exposed on the modern cave floor, the Honeymoon Suite deposit is exposed in the wall of a low chamber adjacent to Cathedral Cave. The Honeymoon Suite fossil deposit was exposed during guano mining operations that had occurred in the caves almost a century prior to the excavations. These guano mining operations removed significant (approximately 2 m) of guano from above the silt-sediment floor within which faunal remains were recovered.

### Geochronology

Details of all the geochronological samples are provided in Table 1. Sampling procedures for charcoal and straw stalactites from Colosseum were described in detail in Price *et al.* (2015). Methodological considerations for U-series dating of the Fern Chamber and Honeymoon Suite are provided in Hocknull *et al.* (2007). In addition to these, soil samples and root intrusion were collected from Colosseum for additional radiocarbon dating, and four charcoal samples were collected from the wall of the cavern of Honeymoon Suite, approximately 50 cm below the contact between the limestone roof and the exposed fossil-bearing sediment. The scarcity of charcoal in any of the Capricorn Caves deposits suggests that they are unlikely to have been emplaced directly as a result of anthropogenic activity (Price *et al.* 2015). Sediment and root sampling and radiocarbon analysis from Colosseum followed the procedures described in Price *et al.* (2015). For Honeymoon Suite, four 10–20 mg samples of charcoal collected during excavation were dated at the Australian Nuclear Science and Technology Organisation (ANSTO) (Fink *et al.* 2004). Samples were pretreated using a hot acid base acid protocol, combusted and graphitised, before measurement by AMS. Ages were calculated following Stuiver & Polach (1977) using a  $\delta^{13}\text{C}$  measured by IRMS on graphite. Radiocarbon dates were calibrated against SHCal20 (Hogg *et al.* 2020) in OxCal v.4.4 (Bronk Ramsey 2009a).

Ten sediment cores were collected from Colosseum for luminescence dating: seven from the northern wall of the deposit from 40 cm to a maximum depth of 105 cm, and three from the western wall from 115 cm to 150.5 cm depth. Only the top (CC1) and bottom (CC10) cores have been dated. Luminescence dating was done at the Australian Research Centre for Human Evolution, Griffith University luminescence laboratories.

Sample preparation for single-grain optically stimulated luminescence dating was designed to isolate pure extracts of 180–212  $\mu\text{m}$  light-safe quartz grains following standard procedures (Aitken 1998). Treatments were applied to remove contaminant carbonates, feldspars, organics, heavy minerals, and acid soluble fluorides. The outer  $\sim 10 \mu\text{m}$  alpha-

irradiated rind of each grain was removed by double etching in 48% hydrofluoric acid for 40 min.

A burial dose ( $D_b$ ) was determined from measurement of the optically stimulated luminescence (OSL) signals emitted by single grains of quartz. Quartz grains were loaded onto custom-made aluminium discs drilled with a  $10 \times 10$  array of chambers, each of 300  $\mu\text{m}$  depth and 300  $\mu\text{m}$  diameter (Bøtter-Jensen *et al.* 2000). The OSL measurements were made on 1000–1300 grains on Risø TL/OSL DA-20 and Risø TL/OSL DA-15 readers using a green (532 nm) laser for optical stimulation, and the ultraviolet emissions were detected by an Electron Tubes Ltd 9235QA photomultiplier tube fitted with a 7.5 mm Hoya U-340 filter. Laboratory irradiations were conducted using a calibrated  $^{90}\text{Sr}/^{90}\text{Y}$  beta source mounted on the reader.

Equivalent doses ( $D_e$ ) were determined using a modified single-aliquot-regenerative dose (SAR) protocol (Olley *et al.* 2004). A dose-response curve was constructed for each grain. OSL signals were measured for 1 s at 125 °C (laser at 90% power) using a preheat of 240 °C (held for 10 s) for the ‘natural’ and regenerative doses, and a cut-heat of 160 °C (held for 10 s) for the test doses (50 s). The OSL signal was determined from the initial 0.1 s of data, using the final 0.2 s to estimate the background count rate. Each disc was exposed to infrared (IR) radiation for 40 s at 125 °C prior to measurement of the OSL signal to bleach any IR-sensitive signal.

Grains were selected based on criteria from Pietsch (2009) and Pietsch *et al.* (2013), i.e., grains were rejected if they did not produce a measurable OSL signal in response to the 50 s test dose, had OSL decay curves that did not reach background after 1 s of laser stimulation, produced natural OSL signals that did not intercept the regenerated dose-response curves, or had unacceptable sensitivity changes throughout the measurement cycle; i.e., they were rejected if either of the second or third Test Dose signals varied in sensitivity from the first Test Dose (associated with the Natural Dose) by more than 30%.

Lithogenic radionuclide activity concentrations of material extracted from sampling tubes were determined using high-resolution gamma spectrometry at Queensland Health (Murray *et al.* 1987). Dose rates were calculated using the conversion factors of Liritzis *et al.* (2013), with  $\beta$ -attenuation factors taken from Mejdahl (1979). Cosmic dose rates were calculated from Prescott and Hutton (1994). Burial doses were calculated using age modelling techniques of Galbraith *et al.* (Galbraith & Laslett 1993, Galbraith *et al.* 1999, Roberts *et al.* 2000).

### Age-depth modelling

Age depth models ( $P_{\text{Sequence}}$ ) for Colosseum Cave were constructed in OxCal v. 4.4 (Bronk Ramsey 2009a). In our favoured model, OSL dates were modelled using a General t-type Outlier Model, assuming each date had a 5% prior probability of being an outlier (Bronk Ramsey 2009b). U-Series ages on straw stalagmites were modelled in a similar way to charcoal (Bronk Ramsey 2009b), assuming that all dates had

Table 1. Dating samples from the Capricorn Caves analysed in this project.

Sample code	Site name	QML	Material/taxon	Colosseum spit(s) relative to datum (cm)	Depth relative to datum (m)	Measured C14 age	Uncertainty	Cal k.y. Bp $\pm 2s$ (14C k.y. Bp $\pm 2s$ )	U/Th age $\pm 2s$ ka	OSL age $\pm 1s$ ka	Age interpretation
AN11-27	CC127-132a	QML1456	Straw stalactite	127-132					46.6 $\pm$ 1.3		Maximum age for stratigraphic depth
AN11-28	CC127-132b	QML1456	Straw stalactite	127-132					40.6 $\pm$ 5.8		Maximum age for stratigraphic depth
AN11-29	CC132	QML1456	Straw stalactite	127-132	1.32				55.0 $\pm$ 4.2		Maximum age for stratigraphic depth
AN11-30	CC147-152	QML1456	Straw stalactite	147-152					50.7 $\pm$ 0.8		Maximum age for stratigraphic depth
Beta-324154	Colosseum Chamber	QML1456	Penetrating root	97-102	0.99	157.1	0.4 pMC	0.1 $\pm$ 0.1 (0.1571 $\pm$ 0.0008)	-		Minimum age for stratigraphic depth
Beta-324155	Colosseum Chamber	QML1456	Charcoal	57-62	0.615	24270	120	29.0 $\pm$ 0.5 (24.3 $\pm$ 0.24)	-		Deposition age (Model A only)
Beta-324156	Colosseum Chamber	QML1456	Soil organics	67-72	0.675	11890	50	14.0 $\pm$ 0.2 (12.0 $\pm$ 0.1)	-		Minimum age
Beta-324157	Colosseum Chamber	QML1456	Soil organics	52-57	0.55	15080	60	18.3 $\pm$ 0.3 (15.2 $\pm$ 0.12)	-		Minimum age
Beta-324158	Colosseum Chamber	QML1456	Soil organics	62-67	0.645	12910	50	15.9 $\pm$ 0.4 (13.0 $\pm$ 0.1)	-		Minimum age
Beta-324159	Colosseum Chamber	QML1456	Soil organics	37-42	0.4	15640	60	19.0 $\pm$ 0.2 (15.8 $\pm$ 0.12)	-		Minimum age
Beta-324160	Colosseum Chamber	QML1456	Soil organics	67-72	0.675	12470	60	14.9 $\pm$ 0.3 (12.6 $\pm$ 0.12)	-		Minimum age
Beta-324161	Colosseum Chamber	QML1456	Soil organics	37-42	0.41	12410	50	14.8 $\pm$ 0.3 (12.5 $\pm$ 0.1)	-		Minimum age
Beta-324162	Colosseum Chamber	QML1456	Charcoal	47-52	0.52	21120	80	25.3 $\pm$ 0.4 (21.1 $\pm$ 0.16)	-		Deposition age (Model A only)
Beta-324163	Colosseum Chamber	QML1456	Charcoal	67-72	0.69	25030	150	30.0 $\pm$ 0.4 (25.0 $\pm$ 0.3)	-		Deposition age (Model A only)
Beta-324164	Colosseum Chamber	QML1456	Charcoal	67-72	0.72	25650	140	30.7 $\pm$ 0.5 (25.6 $\pm$ 0.28)	-		Deposition age (Model A only)
Beta-324165	Colosseum Chamber	QML1456	Soil organics	52-57	0.57	18720	120	22.5 $\pm$ 0.5 (18.8 $\pm$ 0.24)	-		Minimum age
Beta-324166	Colosseum Chamber	QML1456	Soil organics	72-77	0.75	15260	60	18.4 $\pm$ 0.3 (15.4 $\pm$ 0.12)	-		Minimum age
Beta-324167	Colosseum Chamber	QML1456	Charcoal	72-77	0.74	25070	120	30.0 $\pm$ 0.3 (25.1 $\pm$ 0.24)	-		Deposition age (Model A only)
Beta-324168	Colosseum Chamber	QML1456	Soil organics	52-57	0.555	14600	70	18.0 $\pm$ 0.4 (14.7 $\pm$ 0.14)	-		Minimum age
Beta-324169	Colosseum Chamber	QML1456	Charcoal	67-72	0.72	20410	110	24.3 $\pm$ 0.4 (20.4 $\pm$ 0.22)	-		Deposition age (Model A only)
Beta-324170	Colosseum Chamber	QML1456	Soil organics	62-67	0.665	17030	70	20.5 $\pm$ 0.4 (17.1 $\pm$ 0.14)	-		Minimum age
Beta-324171	Colosseum Chamber	QML1456	Soil organics	102-107	1.07	NA	NA	15.8 $\pm$ 0.4 (13.0 $\pm$ 0.12)	-		Minimum age
Beta-324172	Colosseum Chamber	QML1456	Soil organics	102-107	1.07	15750	70	19.0 $\pm$ 0.2 (15.8 $\pm$ 0.14)	-		Minimum age
Beta-324173	Colosseum Chamber	QML1456	Soil organics	122-127	1.27	16330	70	19.7 $\pm$ 0.3 (16.4 $\pm$ 0.14)	-		Minimum age
Beta-324495	Colosseum Chamber	QML1456	Charcoal	67-72	0.68	25800	130	30.9 $\pm$ 0.4 (25.8 $\pm$ 0.26)	-		Deposition age (Model A only)

(continued)



Table 1. Continued.

Sample code	Site name	QML	Material/taxon	Colosseum spit(s)		Measured C14 age	Uncertainty	Cal k.y. Bp $\pm 2s$ (14C k.y. Bp $\pm 2s$ )	U/Th age $\pm 2s$ ka	OSL age $\pm 1s$ ka	Age interpretation
				Colosseum relative to datum (cm)	Depth relative to datum (m)						
Beta-324168	Colosseum Chamber	QML1456	Microfaunal fossil bone	52–57	0.555		Fail	–		Age of individual	
Coll-3	Colosseum Chamber	QML1456	Straw stalactite	67–77				37.8 $\pm$ 1.3		Maximum age for stratigraphic depth	
Coll80-85	Colosseum Chamber	QML1456	Straw stalactite	87–92				86.2 $\pm$ 13.2		Maximum age for stratigraphic depth	
OZL896	Colosseum Chamber	QML1456	Macropodid molar	7–17			Fail	–		Age of individual	
OZL897	Colosseum Chamber	QML1456	Macropodid molar	27–37			Fail	–		Age of individual	
OZL898	Colosseum Chamber	QML1456	Macropodid molar with associated jaw fragment	37–42			Fail	–		Age of individual	
OZL899	Colosseum Chamber	QML1456	Macropodid molar with associated jaw fragment	37–42			Fail	–		Age of individual	
OZL900	Colosseum Chamber	QML1456	Macropodid molar with associated jaw fragment	42–47			Fail	–		Age of individual	
OZL901	Colosseum Chamber	QML1456	Macropodid molar with associated jaw fragment	47–52			Fail	–		Age of individual	
OZL902	Colosseum Chamber	QML1456	Macropodid molar with associated jaw fragment	52–57			Fail	–		Age of individual	
OZL903	Colosseum Chamber	QML1456	Macropodid molar with associated jaw fragment	82–87			Fail	–		Age of individual	
OZN702	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones	12–17			Fail	–		Average mortality age of individuals	
OZN703	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones	27–32			Fail	–		Average mortality age of individuals	
OZN704	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones	37–42			Fail	–		Average mortality age of individuals	
OZN705	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones	52–57			Fail	–		Average mortality age of individuals	
OZN706	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones	57–62			Fail	–		Average mortality age of individuals	
OZN707	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones	62–67			Fail	–		Average mortality age of individuals	
OZN708	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones	72–77			Fail	–		Average mortality age of individuals	
OZN709	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones	87–92			Fail	–		Average mortality age of individuals	

(continued)

Table 1. Continued.

Sample code	Site name	QML	Material/taxon	Colosseum spit(s) relative to datum (cm)	Depth relative to datum (m)	Measured C14 age	Uncertainty	Cal k.y. Bp $\pm 2s$ (14C k.y. Bp $\pm 2s$ )	U/Th age $\pm 2s$ ka	OSL age $\pm 1s$ ka	Age interpretation
OZO815	Colosseum Chamber	QML1456	Bulk collected fossil mammal bones Charcoal	47–52	0.49	14350	70	17.5 $\pm$ 0.3 (14.4 $\pm$ 0.14)	–	–	Deposition age (Model A only)
ROK-H	Colosseum Chamber	QML1456	Snail shell	47–57				–	5 $\pm$ 1.9		Minimum age
ROK-I	Colosseum Chamber	QML1456	Macropodid tooth	47–57				–	12.4 $\pm$ 0.6		Minimum age
OZO816	Honeymoon Suite	QML1457	Charcoal			12870	60	15.5 $\pm$ 0.4 (12.9 $\pm$ 0.12)	–	–	Maximum age
OZO817	Honeymoon Suite	QML1457	Charcoal			12260	60	14.4 $\pm$ 0.4 (12.3 $\pm$ 0.12)	–	–	Maximum age
OZO818	Honeymoon Suite	QML1457	Charcoal			6585	40	7.5 $\pm$ 0.06 (6.6 $\pm$ 0.08)	–	–	Maximum age
OZO932	Honeymoon Suite	QML1457	Charcoal			12110	50	14.1 $\pm$ 0.3 (12.1 $\pm$ 0.1)	–	–	Maximum age
ROK 06	Colosseum Chamber	QML1456	Snail shell from Colosseum Cave	7–17					21.6 $\pm$ 8.4		Rejected – contamination?
ROK 07	Honeymoon Suite	QML1457	Kangaroo jaws & teeth, Honeymoon Cave Surface Collection						6.38 $\pm$ 0.17		Min Age based on late stage uptake
ROK 09	Colosseum Chamber	QML1456	Carbonate nodules within sediment Colosseum Cave - reworked cave wall 'coral'	7–17					164 $\pm$ 78		Rejected – reworked cave wall coral
OC-07	Icicle Chamber		Fern Chamber gastropods & calcite cement						7.6 $\pm$ 0.2		Deposition age
GU80.1	Colosseum Chamber	QML1456	OSL sample CC-1	37–47	0.4–0.46					16.7 $\pm$ 2.6	Bleaching age of sediment
GU80.2	Colosseum Chamber	QML1456	OSL sample CC-10	147–152	1.445–1.505					65 $\pm$ 8	Bleaching age of sediment

Note:  $\pm 2s$  means plus or minus 2 sigma.

a 100% prior probability of being too old in a t-type Outlier Model, where an exponential distribution is taken to run from  $-10$  to  $0$  with a time constant of  $1$ , and the shifts scaled between  $0$  and  $10,000$  years. All probability distributions converged at more than  $90\%$ , and probability ranges are presented.

Many of the radiocarbon dated samples are problematic and not included in the model (see the *Age-depth model section* in Results). Radiocarbon ages on sediment are a notoriously unreliable estimate of deposition date as multiple sources of carbon are present, all of which may have a different age (Fowler *et al.* 1986), and the charcoal dated has no functional relationship with the owl roost accumulation. U-series dates on bone and shell are also not included in the model. This type of date normally provides an estimate of when uranium diffused into the bone or shell, and is therefore a minimum estimate of deposition (Grün *et al.* 2014). Although the U-series dates for these specimens are likely minimum ages,  $^{230}\text{Th}$  age and U profiling (cf. Price *et al.* 2013) has not been undertaken to confirm this, hence we err on the side of caution by not including them in the age model. A U-series date on a carbonate nodule within the sediment and a radiocarbon age on a penetrating root were not included in the model, as both were extreme outliers given their context.

### Faunal analysis

Sorting of material and targeting taxonomically useful skeletal/dental elements was completed using a magnifying lamp, and binocular microscopes where necessary. Identifications were made through comparison with material in the Queensland Museum's fossil collection, the Natural History Museum (London, UK), Western Australian Museum, and modern faunal collections and published sources. Mammal identifications were made, wherever possible, to species level, using criteria described in the [Supplementary Information](#), Hocknull (2005), Cramb *et al.* (2009, 2018, 2020), Cramb & Hocknull (2010a, b), and Price *et al.* (2019, 2020), and where possible by direct comparison with type specimens. Range reductions, extirpations and extinctions were established based on comparisons to modern fauna, with modern species ranges determined at both the continental scale (after Breed & Ford, 2007; and Menkhorst & Knight, 2001), and the more local level through site-specific species lists from the Mount Etna Region (from Hocknull *et al.* 2007) and the Shoalwater and Corio Bays Area (Schodde *et al.* 1992, and Anonymous 1999; cited in Travouillon & Legendre 2009). For bandicoots, we used the distribution maps of Warburton & Travouillon (2016) and Travouillon & Phillips (2018). Bat presence/absence for Colosseum Chamber spits 7–97 were taken from Martinez (2010).

### Stable isotopes

To determine if fragmented rodent material could provide insights into changing environmental conditions through the

late Quaternary, we examined the carbon and oxygen stable isotope records from dental material recovered from our excavations. Isolated rodent incisors were randomly sampled from 11 spits from Colosseum Chamber spanning MIS1–4 (Spits 17–22 cm ( $n=8$ ), 27–32 cm ( $n=10$ ), 37–42 cm ( $n=10$ ), 47–52 cm ( $n=8$ ), 57–62 cm ( $n=8$ ), 87–92 cm ( $n=10$ ), 112–117 cm ( $n=6$ ), 122–127 cm ( $n=2$ ), 132–137 cm ( $n=10$ ), 142–147 cm ( $n=17$ ), 177–182 cm ( $n=5$ )), although efforts were made to select incisors that were roughly *Rattus*-sized, in order to minimize interspecific differences. Dentine-free incisor fragments were preferred; however, where these were not present, dentine was mechanically separated from the enamel with a dental pick under low-magnification microscopy. Incisor fragments were ultrasonically cleaned in Milli-Q water to remove any loose surface sediment and physical contaminants, and crushed into a fine powder using an agate mortar and pestle. The enamel samples were analysed at the University of Rochester's Stable Isotope Ratios in the Environment Analytical Laboratory (SIREAL). Organic impurities were removed through the addition of 1 ml of 30% hydrogen peroxide ( $\text{H}_2\text{O}_2$ ). Samples were rinsed in deionized water (DI). One ml of 95% methanol was added to rinsed samples, which were then sonicated, centrifuged, pipetted, and left overnight to dry. The  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values were calculated *via* the SIREAL's ThermoFinnigan Delta XP mass spectrometer, with a Gasbench inlet device. All data collected by the mass spectrometer were reported in the delta ( $\delta$ ) notation in per mill ( $\text{‰}$ ).

C and O isotope results are reported relative to VPDB (Vienna Pee-Dee Belemnite) and normalised (Coplen 1994) on scales such that NBS-19 carbon and oxygen isotopic values were  $1.95\text{‰}$  and  $-2.2\text{‰}$ , respectively, NBS-18 carbon and oxygen isotopic values were  $-5.01\text{‰}$  and  $-23\text{‰}$ , respectively, and the L-SVEC carbon isotopic value was  $-46.6\text{‰}$ . Enamel-diet enrichment factors for rodents suggest an average apatite enrichment of between  $+9.5\text{‰}$  and  $+11\text{‰}$  relative to dietary vegetation (DeNiro & Epstein 1978, Ambrose & Norr 1993, Tieszen & Fagre 1993, Jim *et al.* 2004, Crowley *et al.* 2010, Louys & Roberts 2020); here we applied a correction of  $+11\text{‰}$  following the most recent publications. Differences in C and O data between MIS samples were examined on the four groups using a non-parametric Kruskal–Wallis H test with significance evaluated at  $\alpha=0.05$ , and with post-hoc pairwise comparisons with both uncorrected and Bonferroni corrected values reported. Statistical analysis was undertaken using PAST 2.17c (Hammer *et al.* 2001).

### Histology

We tested whether environmental fluctuations influenced physiology at an organism level by measuring osteocyte lacunae densities (which are proxies for bone metabolic rates) from bone histology (see Miszkiewicz *et al.* 2019, 2020). Ten rodent femora of roughly *Rattus*-sized individuals were selected from each of the three excavated units from Colosseum Chamber, corresponding to MIS 3

(127–132 cm spit), the Last Glacial Maximum (MIS 2; 57–62 cm spit), and MIS1 (OSL-1 SED 15 CM ABOVE; this sample was recovered from a layer 15 cm above OSL sample CC-1, so 25 cm below the datum line). Using standard digital callipers, midshaft diameter was measured in each of the 30 femora. Femora were cleaned and processed for histology using standard methods (Chinsamy & Raath 1992; Miszkiewicz *et al.* 2019, 2020). Each femur was embedded in Buehler epoxy resin and cut at midshaft on a Kemet MICRACUT 151 low-speed saw equipped with a diamond wafering blade. Embedded portions with revealed midshaft femur cross-sections were glued to microscope glass slides, and then further trimmed on the same low-speed saw. Once trimmed down to  $\sim 0.5$  mm, the sections were ground and polished on a series of pads to an average thickness of  $100 \pm 15$   $\mu\text{m}$ . This was followed by cleaning in an ultrasonic bath, dehydrating in ethanol, and clearing in xylene, so that each ground section could be covered with a glass slip. Once cover-slipped, the thin sections were imaged under a high-powered Olympus BX53 microscope with a DP74 microscope camera. Using Olympus CellSens software, an entire cross-section of each femur histology was scanned at  $40\times$  magnification. Osteocyte lacunae counts were undertaken manually from raw images using ImageJ software with a grid plug in (Schindelin *et al.* 2012). A grid sub-divided into  $20,000 \mu\text{m}^2$  ( $0.02 \text{ mm}^2$ ) squares was applied to each cross-section. Preservation permitting, total counts from all four anatomical locations (lateral, medial, cranial, caudal) were converted into densities (osteocyte lacunae count divided by total area examined in  $\text{mm}^2$ , Miszkiewicz *et al.* 2019, 2020). Osteocyte lacunae density (Ot.Dn) was adjusted by midshaft diameter to account for possible scaling effects of body size on the number of bone cells (Miszkiewicz & Mahoney 2019, Miszkiewicz *et al.* 2020). Differences in Ot.Dn data between the three MIS groups were examined using a non-parametric Kruskal–Wallis H test, with post-hoc pairwise comparisons at  $\alpha = 0.05$  that were Bonferroni corrected for multiple testing. Statistical analysis was undertaken using PAST 4.06b (Hammer *et al.* 2001).

## Results

### Cave deposits

Sediment within the Colosseum Chamber deposit includes mostly un lithified sand and clay, with some scattered larger clasts of manganese oxide and calcium carbonate, and occasional inclusion of clasts of cave coral and fragmented cave straws. Vertebrate bones are abundant, with an estimated peak fossil density of  $\sim 20,000$  individual skeletal elements per  $20 \times 20 \times 20$  cm. The first two spits showed recent human-mediated disturbance, and electrical cables were discovered on the perimeter of the main pit. The majority of fossil remains are disarticulated microfaunal jaws and post-cranial elements, although some terrestrial gastropod shells and likely wasp nests were recovered during excavation. The microfaunal remains showed no preferred alignment; instead, they were preserved in random orientation throughout the excavation. No discernible significant changes in

sediment colour were observed between the spits. The deposit ranged in concentration of clasts and faunal remains, although for the upper part not predictably or systematically. However, spits 122–127 and 127–132 were particularly abundant with regards to microfaunal material, with more complete elements observable while excavating, including normally rare elements such as skull fragments. From the 132–137 spit, microfaunal remains became progressively rarer and larger manganese, carbonate, and limestone clasts became more common. A modern root was found in the 137–142 spit, demonstrating that root penetration occurred through much of the deposit excavated. Cave floor dominated the bottom of the excavation from the 147–152 spit, limiting the amount of excavated material recoverable. The excavation was ceased at the 192–197 spit, although some continuation of the deposit was visible in the southwest corner of the pit.

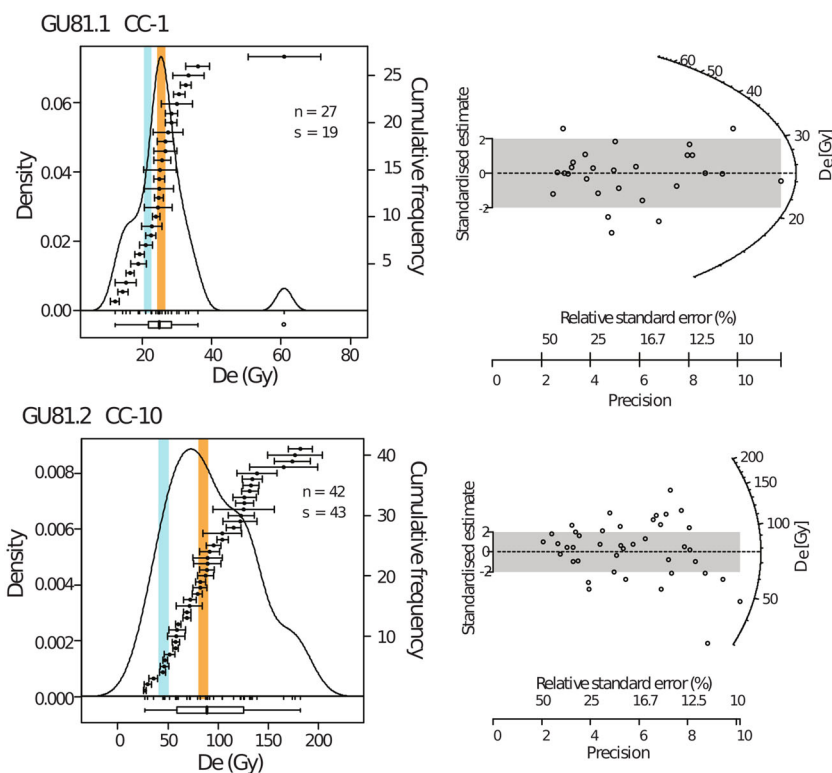
### Geochronological results

Table 2 provides the results of radionuclide analysis, the measured water content, and the calculated environmental dose rate, taking into account latitude, longitude, altitude, sample depths corrected for cave roof thickness, and the long-term water content for the new luminescence dates. Measured water content was  $<16$ – $27\%$  of dry weight (Table 2). Estimating long-term water content can be problematic owing to losses during collection and storage, the moderately seasonal climate, and longer-term changes in soil moisture that may have included periods of cooler temperatures in the Pleistocene. Relative humidity in the region is between 66% and 78% (Hamilton-Smith & Champion 1975); however, humidity variability would be even further attenuated inside the caves, and therefore measured water contents were used in the analysis.

The OSL results for all samples are shown on Fig. 4 as kernel density functions and radial plots. Recovery, i.e., the proportion of grains that yielded an acceptable luminescence signal according to criteria described above, was 3–4% (Table 3). Overdispersion ( $\sigma_d$ ), i.e., the degree of spread in the data beyond that which can be explained by measurement uncertainties, was excellent for the upper sample, CC-1, at 19% (GU81.1). A higher overdispersion parameter of 43% was calculated for GU81.2, which may reflect biological disturbance, beta dose rate heterogeneity, reworking by cave drip waters, or spalling or unbleached mineral sediments from the cave roof. Ages were modelled using both the Minimum Age Model (MAM) with an applied overdispersion parameter of 15%, and the Central Age Model (CAM) (Table 3). One contaminant (bleached) grain in 81.2 was removed from the modelled dataset. The quartz sand was

**Table 2.** Radionuclide activities, measured water contents, and calculated dose rates.

Lab code	$^{238}\text{U}$ Bq/kg	$^{232}\text{Th}$ Bq/kg	$^{40}\text{K}$ Bq/kg	Water % dry wt	Dose rate Gy/ka
GU81.1	$13 \pm 1$	$24 \pm 4$	$300 \pm 40$	15.6	$1.48 \pm 0.22$
GU81.2	$17 \pm 2$	$28 \pm 5$	$230 \pm 20$	27.3	$1.28 \pm 0.14$



**Figure 4.** OSL results shown as kernel density functions and radial plots. Values within the orange-shaded bands are within  $2\sigma$  of the dose components calculated using the Central Age Model (CAM) and, in blue, using the Minimum Age Model (MAM) with an applied overdispersion parameter of 15%.

**Table 3.** OSL results and ages.

Lab No.	Sample	$n$	Recovery (%)	$\sigma_d$ (%)	$D_e$ MAM (Gy)	$D_e$ CAM (Gy)	Age CAM (ka) <sup>a</sup>
GU81.1	CC-1	27	3	19	$22.3 \pm 2.6$	$24.6 \pm 1.3$	<b><math>16.7 \pm 2.6</math></b>
GU81.2	CC-10	41	4	43	$44 \pm 5$	$83 \pm 6$	<b><math>65 \pm 8</math></b>

<sup>a</sup>The preferred ages are shown in bold.

assumed to be aeolian, entering through the east-facing cave entrance. This interpretation is supported by the low overdispersion evident in GU81.1. Few saturated grains were observed that might indicate an older population eroded from the cave roof, and the site lies above the influence of flood waters. The Central Age Model accommodates the effects of biological mixing by fauna, as well as the effects of grain-scale variations in beta dose rate in this low dose rate environment, and therefore CAM ages are preferred for both samples. This yields an age of  $16.7 \pm 2.6$  ka for GU81.1 (CC-1) at 0.43 m and  $65 \pm 8$  ka for GU81.2 (CC-10) at 1.47 m.

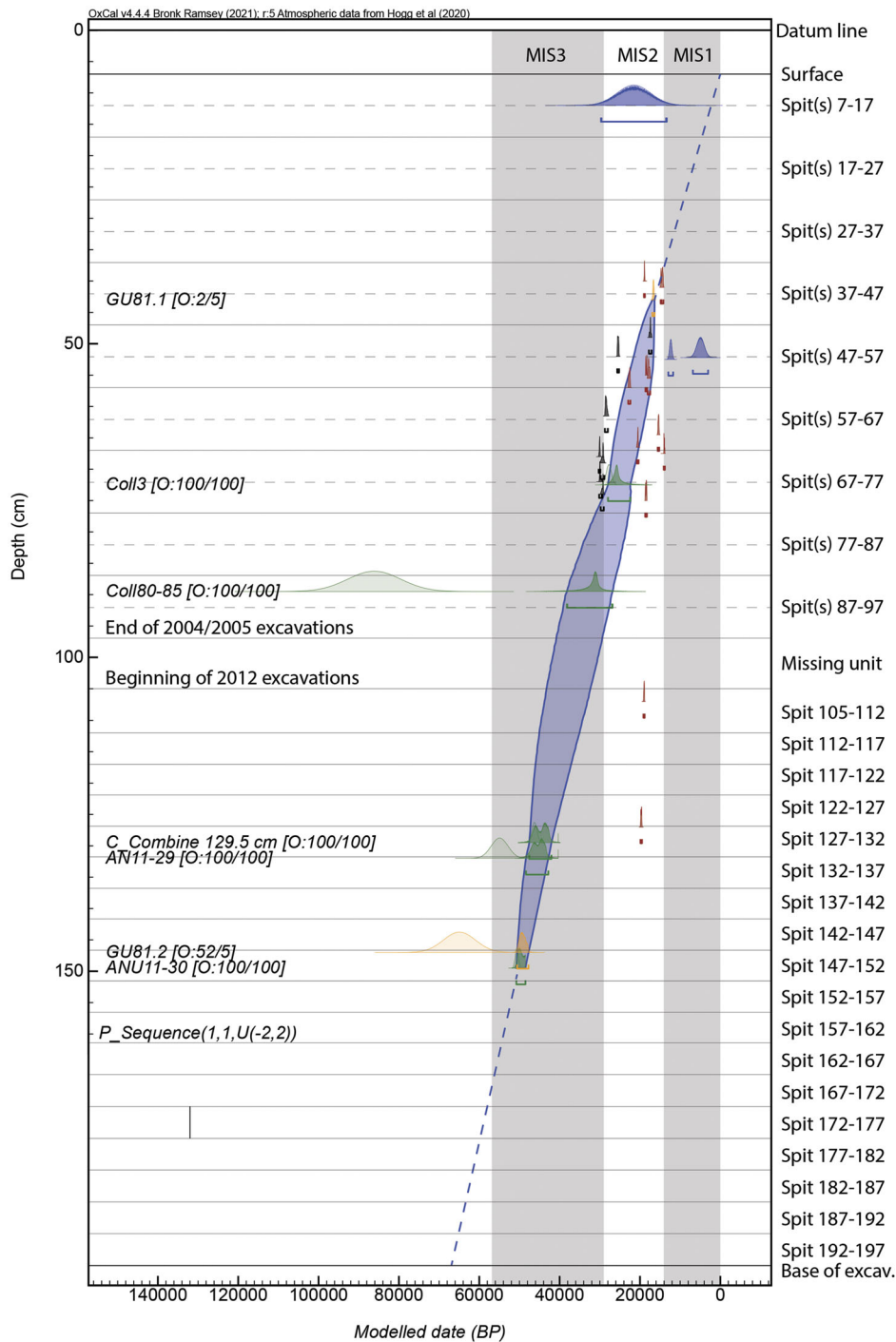
Four new AMS  $^{14}\text{C}$  dates from Honeymoon Suite were produced from *in situ* charcoal (Table 1). The ages range from approximately 7.5 to 15.5 ka.

### Age-depth model

Our favoured model (Fig. 5, supplemental Table S2) suggests a constant sedimentation rate between 150 cm and 43 cm, between 50.8–48.5 and 16.9–16.4 modelled k.y. BP. Unfortunately, the only age estimate between 0 cm and

40 cm is a U-series age on shell (ROK 06), and so this part of the sequence is less certain in terms of age. The upper OSL age GU81.1 is consistent with the U-series ages on speleothems. The deepest OSL age (GU81.2) has a 52% posterior probability of being too old. This sample had a high overdispersion factor, and the modelled age estimate (50.6–47.7 k.y. BP) falls between the MAM and CAM ages, and overlaps with the CAM age of  $65 \pm 8$  k.y. BP at  $2\sigma$ . U-series dates on straw stalagmites are all consistent with their Outlier Model, with three dates consistent with their context and two substantially older than their context.

Radiocarbon dates and U-series age estimates on bone and shell are shown in supplemental Fig. S1, but are not included in the favoured age model. Radiocarbon dates from the recovered charcoal fall between  $24.3 \pm 0.4$  cal k.y. BP ( $20.4 \pm 0.22$  k.y. BP (Beta-324169)) and  $30.9 \pm 0.4$  cal k.y. BP ( $25.8 \pm 0.26$  k.y. BP (Beta-324495)); both these dates are from the 67–72 cm spit. Soil organic dates fall between  $14.0 \pm 0.2$  cal k.y. BP ( $12.0 \pm 0.1$  k.y. BP (Beta-324156)) and  $22.5 \pm 0.5$  cal k.y. BP ( $18.8 \pm 0.24$  k.y. BP (Beta-324165)); these are stratigraphically inverted, with the youngest date from the 67–72 cm spit and the oldest from 52–57 cm. U-series analysis provided minimum ages of  $5 \pm 1.9$  ka and  $12.4 \pm 0.6$  ka for snail shell and macropodid teeth, respectively. Most of these dates fall outside the favoured model, and deviations are consistent with problems relating to sample types and methods. Radiocarbon dates on sediment are normally younger than the age model, and do not increase systematically with depth, suggesting a source of young carbon has migrated through the sediment. Radiocarbon dates on charcoal do increase



**Figure 5.** Preferred age model for the Colosseum Cave, constructed in OxCal v.4.4 (Bronk Ramsey 2009a) with radiocarbon dates calibrated against SHCal20 (Hogg *et al.* 2020). All age estimates are shown in the plot, but the model is only based on the labelled U-series age estimates on straw stalagmite and OSL age estimates. U-series ages on straw stalagmites are shown in green, OSL ages in orange, radiocarbon dates on charcoal are shown in grey, radiocarbon dates on sediment in brown, and U-series ages on bone/shell in blue. Outlier probabilities are shown in the form [O: posterior/prior], and the 95% probability window is shown in blue. Marine Isotope Stages (following Lisiecki and Raymo 2005) are shown in grey vertical bands. Datum line, spit depths, and other pertinent excavation markers are indicated on the figure.

with depth but appear consistently older than the model based on OSL and U-series. It is possible that these charcoal fragments are an inherited component in the sediment. When included in the model (Supplementary Information), they suggest a hiatus at 55 cm, which was not observed during excavation. As expected, the two U-series ages on bone/shell are younger than expected from the age model.

### Fauna

The faunal list from the Capricorn Caves deposits is presented in Table 4. Presence/absence data has been generated for Fern Chamber, Honeymoon Suite, and 17 of the spits from Colosseum. Of the latter, we have also generated Number of Identified Specimens (NISP) of rodents for seven spits. An additional three spits have presence/absence data







Table 4. Continued.

Mammalia	Eutheria	Rodentia	Muridae	Pseudomys	Site Spit (below datum)	Colosseum										71																				
						7-	17-	27*	37	47	57	67-	77-	87-	97-		105-	112-	117-	122-	127-	132-	137-	142-	147-	152-	157-	162-	167-	172-	177-	182-	187-	192-		
Mammalia	Eutheria	Rodentia	Muridae	<i>Pseudomys</i>	<i>Pseudomys</i>	7-	17-	27*	37	47	57	67-	77-	87-	97-	105-	112-	117-	122-	127-	132-	137-	142-	147-	152-	157-	162-	167-	172-	177-	182-	187-	192-			
Mammalia	Eutheria	Rodentia	Muridae	<i>Rattus</i>	<i>Rattus</i>	x	x	x	x	x	x	495	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			
Mammalia	Eutheria	Rodentia	Muridae	<i>Rattus</i>	<i>Rattus</i>	x	x	x	x	x	?	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			
Mammalia	Eutheria	Rodentia	Muridae	<i>Uromys</i>	<i>Uromys</i>																															
Mammalia	Eutheria	Rodentia	Muridae	<i>Zyomys</i>	<i>Zyomys</i>	x	x	1	x	x	x	6	x	x	x	x	x	x	x	x	1	1														
Mammalia	Eutheria	Rodentia	Muridae	<i>Zyomys</i>	<i>Zyomys</i>	x	x		x	x																										
Mammalia	Eutheria	Chiroptera	Emballonuridae	<i>Taphozous</i>	<i>Taphozous</i>																															
Mammalia	Eutheria	Chiroptera	Emballonuridae	<i>Taphozous</i>	<i>Taphozous</i>	x	x	x	x	x		?																								
Mammalia	Eutheria	Chiroptera	Megadermatidae	<i>Macrodarma</i>	<i>Macrodarma</i>	x	x	x	x	x																										
Mammalia	Eutheria	Chiroptera	Molossidae	<i>Mormopterus</i>	<i>Mormopterus</i>				x	x																										
Mammalia	Eutheria	Chiroptera	Rhinolophidae	<i>Rhinolophus</i>	<i>Rhinolophus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x															
Mammalia	Eutheria	Chiroptera	Miniopteridae	<i>Miniopterus</i>	<i>Miniopterus</i>	x	x	x	x	x	x																									
Mammalia	Eutheria	Chiroptera	Miniopteridae	<i>Miniopterus</i>	<i>Miniopterus</i>	x	x	x	x	x	x																									
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Chalinolobus</i>	<i>Chalinolobus</i>	x	x	x	x	x	x																									
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Chalinolobus</i>	<i>Chalinolobus</i>	x	x	x	x	x	x																									
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Chalinolobus</i>	<i>Chalinolobus</i>				x																											
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Chalinolobus</i>	<i>Chalinolobus</i>																															
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Nyctophilus</i>	<i>Nyctophilus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x															
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Scotorepens</i>	<i>Scotorepens</i>	x	x																													
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Vespadelus</i>	<i>Vespadelus</i>																															
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Vespadelus</i>	<i>Vespadelus</i>	x	x																													
Mammalia	Eutheria	Chiroptera	Vespertilionidae	<i>Vespadelus</i>	<i>Vespadelus</i>																															
Microchiropteran gen. et sp. indet.	x																																			

\*NISP from OSL-1 SED 15 CM ABOVE sample; †No material available for this spit.

x indicates presence, numbers indicate Number of Identified Specimens (NISP). Sorting and identification of remains are ongoing.

for select taxonomic groups. Taxa represented in the deposits include fish (Teleostei), ten species of amphibians (including Hylidae and *Limnodynastes*), 16 reptiles (including Agamidae, Gekkota, Scincidae, Elapidae, Varanidae and Pythonidae), and six birds (including Charadriiformes, Apodiformes, Passeriformes, Turnicidae, Colubridae and Strigiformes). Most mammals recovered were small-bodied, and included both marsupials (Dasyuridae, Peramelidae, Petauridae, Pseudocheiridae, Phalangeridae, Potoroidae, Macropodidae) and placentals (Muridae, Emballonuridae, Megadermatidae, Molossidae, Rhinolophidae, Miniopteridae, Vespertilionidae). Rodents are by far the most common elements in all spits, with small dasyurids being the next most abundant group. Larger marsupials (phalangerids, pseudocheirids, macropodoids) are generally rare. Birds, reptiles, and amphibians form a relatively small proportion of the specimens, but the high abundance of material in most spits means that they are still well represented in the deposit. Sorting and identification of the fauna is ongoing. No obvious differences were observed in the dominant size and/or diversity of the microfauna that could be related to differences in faunal accumulating agents between the sites. Confirmation of these observations will require future quantitative taphonomic analyses.

### Carbon and oxygen isotopes

Both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  signatures vary throughout the Colosseum Chamber assemblage (supplemental Table S4).  $\delta^{13}\text{C}$  values range from  $-13.5\text{‰}$  to  $+0.95\text{‰}$ , with a mean  $\delta^{13}\text{C}$  value of  $-5.0\text{‰}$ . Mean values across Stages ranged from  $-5.9\text{‰}$  (MIS 3),  $-4.6\text{‰}$  (MIS 2),  $-4.2\text{‰}$  (MIS 4), to  $-3.7\text{‰}$  (MIS 1). There were no significant differences between the Stages ( $n = 94$ ,  $H = 7.192$ ,  $p = 0.07$ ).

$\delta^{18}\text{O}$  values ranged from  $-10.9\text{‰}$  to  $+2.2\text{‰}$ , with a mean value of  $-2.3\text{‰}$ . Mean  $\delta^{18}\text{O}$  for MIS 1 was the lowest at  $-4.0\text{‰}$ , followed by MIS 3 at  $-3.1\text{‰}$ , MIS 2 at  $-2.1\text{‰}$ , and MIS 4 at  $-1.2\text{‰}$ . There were significant differences in oxygen isotope values between Stages ( $n = 94$ ,  $H = 10.62$ ,  $p = 0.01$ ); however, post-hoc tests only showed significant differences in the raw comparisons (Table 5). These raw comparisons indicate that the significant differences between Stages is linked to glacial/interglacial conditions, with MIS 1 and 3 (interglacial conditions) producing significantly lower  $\delta^{18}\text{O}$  values than MIS 2 and 4 (glacial conditions).

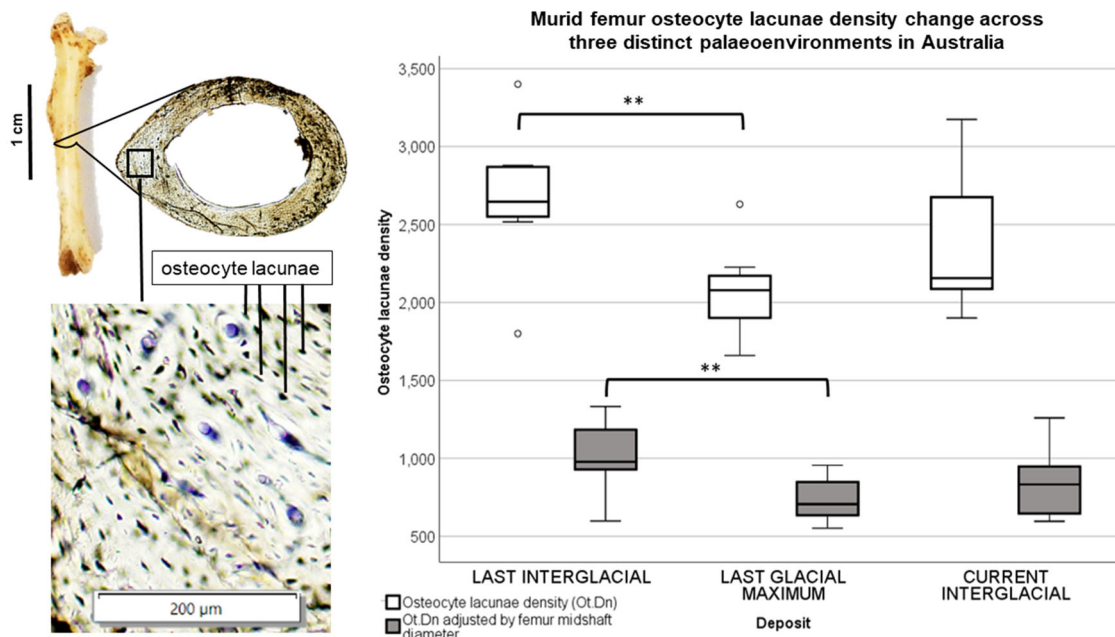
### Histology

Summary statistics are provided in supplemental Table S5, with raw values available at <https://doi.org/10.6084/m9.fig-share.21333792>. Statistically significant differences in Ot.Dn were observed on the entire sample, demonstrating that the distribution of bone histology changes with MIS ( $n = 30$ ,  $H = 8.613$ ,  $p = 0.013$ , bone size correction;  $n = 30$ ,  $H = 8.859$ ,  $p = 0.01$ ; Fig. 6; see supplemental Table S5 for descriptive data). Post-hoc analyses with Bonferroni correction revealed that rodents from the 127–132 cm spit (MIS 3) showed a statistically significant increase in Ot.Dn when compared to rodents from the 57–62 cm spit (MIS 2), where Ot.Dn was the lowest ( $n = 20$ ,  $U = 12.000$ ,  $p = 0.003$ ). Rodents from the OSL-1 SED 15 CM ABOVE deposit (MIS 1) had an

**Table 5.** Kruskal–Wallis test for  $\delta^{18}\text{O}$  across Marine Isotope Stages (MIS); upper diagonal uncorrected, lower diagonal Bonferroni corrected.

	MIS 1	MIS 2	MIS 3	MIS 4
MIS1		0.009224*	0.3008	0.01882*
MIS2	0.05535		0.0593	0.2949
MIS3	1	0.3558		0.04851*
MIS4	0.1129	1	0.291	

\*Significant values.



**Figure 6.** Summary of the histological findings. Top left is a representative murid femur before and after sectioning. Bottom left is a sample image showing osteocyte lacunae in the lateral region of cortical bone at midshaft femur. The box plots on the right show the distribution of the osteocyte lacunae for each stratigraphic sample (\*\* $p < 0.01$ ).

intermediate Ot.Dn value showing a relatively larger range of values compared to the other two MIS assemblages. These results are consistent when corrected for femur size as a proxy for body size ( $n = 20$ ,  $U = 11.000$ ,  $p = 0.02$ ).

## Discussion

### Geochronology

The geochronological results clearly demonstrate that the Colosseum Chamber deposit represents the longest period of deposition of the Late Pleistocene–Holocene sampled sites at the Capricorn Caves. It spans the Late Pleistocene and the Holocene, preserving records from MIS 4 to the present. Our preferred age model is consistent with sedimentological observations and suggests a relatively constant rate of deposition, at least for MIS 2–3. We have also observed modern owls roosting in the caves and dropping food scraps to the floor of Colosseum Chamber, consistent with ongoing faunal input into the deposit. In contrast, including the charcoal radiocarbon ages into the Bayesian model produces a depositional history with a marked hiatus at ~55 cm depth below the datum. We observed no such hiatus in the stratigraphic record, as would be indicated by an unconformity or a horizon indicating stabilisation of the cave floor (e.g., paedogenesis or speleothem formation), suggesting that this model should be rejected and the radiocarbon age contexts re-evaluated.

While the radiocarbon dates on sediment are all too young with reference to both our age-depth models, this is easy to explain as carbon in sediment can come from many different sources, some of which may also be mobile in the sediment. Discounting the radiocarbon dates on charcoal is not as straightforward. They provide older ages than our preferred model predicts but are mostly in stratigraphic order. The age offset is too large to be explained by an old wood effect. We suggest that these results are most likely a result of charcoal present in the sediment but outside the cave being washed in regularly from higher in the system, e.g., *via* Flower Pot Chamber, or potentially even blown in through the main entrance of Colosseum Chamber (see Fig. 3).

Our interpretation of the Colosseum Chamber ages has implications for Honeymoon Suite. It is likely that similar processes acted on the charcoal accumulation in both Colosseum Chamber and Honeymoon Suite, with the Late Pleistocene radiocarbon ages recorded in both sites overestimating the age of the corresponding faunal associations. We therefore suggest an early to mid-Holocene age for Honeymoon Suite is the most reasonable interpretation of the dates for this site.

### Palaeoecology

The Colosseum Chamber deposit spans major climatic periods, and preserves an important record of the environmental shifts associated with glacial/interglacial cycles in central eastern Queensland. Late Quaternary environments of

eastern Queensland have been reconstructed by palaeoecological records from offshore, lake, wetland, fen and marsh deposits from the tropical north and subtropical south of our study site, including the Atherton Tablelands, OPD820, and the Whitsundays to the north of Rockhampton, and K'gari (Fraser) and Minjerribah (Stradbroke) islands to the south (Fig. 1). They reveal distinct glacial-interglacial controls over climate and environmental variability, and a pronounced trend of increased aridity in the late Quaternary (Longmore 1997, Longmore & Heijnis 1999, Moss *et al.* 2017). Late MIS 4 is characterised by drier conditions than today, with both the tropics and subtropics dominated by grasslands and araucarian forests (Longmore 1997, Moss *et al.* 2017). Around the beginning of MIS 3, elements of the subtropical rainforests begin to decline in drier areas (Longmore 1997), but warm and moist conditions are also recorded (Donders *et al.* 2006), and the tropics see an increase in rainforests and decrease in grasses at this time (Longmore 1997, Moss *et al.* 2017). A cooling and drying trend associated with late MIS 3 is evident in the tropics and northern subtropics (Donders *et al.* 2006, Moss *et al.* 2017, Petherick *et al.* 2022), and by the early glacial period drier climates and open sclerophyll forest are recorded along the eastern coast (Donders *et al.* 2006, Moss *et al.* 2013, 2017).

Conditions during the LGM are very dry, as evidenced by a decrease in sclerophyll arboreal taxa in the OPD820 records (Moss *et al.* 2017) and a hiatus in the record for Lake Allom on K'gari (Fraser Island) (Donders *et al.* 2006). Continued dry conditions after the LGM are indicated in the palaeoecological records until about 13–14 ka (Moss *et al.* 2013, 2017, Hembrow *et al.* 2014), when increases in moisture and temperature are again observed (Longmore 1997, Barr *et al.* 2017, Moss *et al.* 2013, 2015, 2017).

The Late Pleistocene to early Holocene generally saw increases in aridity and climatic variability (Longmore 1997, Krull *et al.* 2004, Donders *et al.* 2006, Moss *et al.* 2013, 2017). In the subtropics, the early to mid-Holocene is associated with wetter conditions (Barr *et al.* 2017, Hembrow *et al.* 2014, Moss *et al.* 2013), although a reduction in overall precipitation compared to earlier interglacials prevented the re-establishment of rainforests to their previous levels (Longmore 1997), and open woodland sclerophyll forests dominated (Moss *et al.* 2013). The generally wetter conditions of the early Holocene gave way in the subtropics to a mid-Holocene dry period that peaked at ~5.5 ka (Longmore 1998). This period is anti-phase with moister conditions present in the rest of eastern Australia (Kershaw & Nix 1988, Genever *et al.* 2003, Moss *et al.* 2017). Meanwhile, the tropics saw a sharp increase in rainforest and wetter conditions from 9.5 ka, with rainforest stabilized by 8.5 ka (Moss *et al.* 2017), and with the highest rainforest components in the Whitsundays recorded in the mid-Holocene (Genever *et al.* 2003). Wetter conditions returned to the subtropics from about 4.5 ka (Longmore 1998, Krull *et al.* 2004, Moss *et al.* 2015); however, the overall drying trend of the Holocene is again evident in the youngest records (Krull *et al.* 2004, Moss *et al.* 2013, Genever *et al.* 2003, Hembrow

*et al.* 2018) and the effect of ENSO variability is evident in the subtropics after 3.2 ka (Barr *et al.* 2019). Offshore at Heron and One Tree reefs, at a latitude similar to that of the Capricorn Caves, water quality proxies recovered from reef cores suggest wet conditions with significant continental runoff in the early Holocene to around 7 ka (Salas-Saavedra *et al.* 2022). Drier conditions ensued as the Indonesian-Australian Summer Monsoon began to decrease, and then a trend towards much less runoff began from the mid-Holocene as ENSO reorganised from a more La Niña-dominated, wet climate phase to the current high amplitude El Niño-dominated system (Koutavas & Joanides 2012, Zhang *et al.* 2014, Salas-Saavedra *et al.* 2022).

Against this backdrop of climate change, we can compare our palaeoecological proxies and what they reveal about changes in the vicinity of the Capricorn Caves. Our rodent  $\delta^{13}\text{C}$  values range from  $-24.5\text{‰}$  to  $-10.05\text{‰}$  (after adjustment for enamel-diet enrichment) but showed no significant differentiation between Stages. Different plant species use different photosynthetic pathways (i.e.,  $\text{C}_3$ ,  $\text{C}_4$  and CAM) when assimilating  $\text{CO}_2$ , resulting in differences in their carbon isotopic signatures.  $\text{C}_3$  plants—largely represented by shrubs and trees—have an average  $\delta^{13}\text{C}$  value of  $-28\text{‰}$ , while  $\text{C}_4$  plants—largely tropical grasses—have an average  $\delta^{13}\text{C}$  value of  $-14\text{‰}$ . Most of the individuals we examined recorded  $\text{C}_4$  or mixed  $\text{C}_3/\text{C}_4$  diets, which is unsurprising given the random sampling of taxa, with potential diets ranging from either end of the  $\text{C}_3/\text{C}_4$  spectrum, *via* unidentified enamel fragments. Small rodents, which dominate our assemblages, are opportunistic feeders, with many species eating fungi, insects and fruit, although seeds play a large part in many species' diets (Breed & Ford 2007). Our  $\delta^{13}\text{C}$  results indicate that grasses were present in the vicinity of the caves throughout the late Quaternary, but the proportion of grasslands to more forested habitats in the landscape cannot be discerned from these data.

Enamel  $\delta^{18}\text{O}$  values were more informative. Mammals incorporate  $\delta^{18}\text{O}$  from a variety of sources, including water, respiration, food water content and metabolic breakdown of carbohydrates (Chew 1961, Johnson *et al.* 1997, 1998, Kohn 1999, Brookman & Ambrose 2012). The proportions of each dietary source from which  $\delta^{18}\text{O}$  signatures are derived are dependent on the biology of the organism (Fricke *et al.* 2008). Evaporation-insensitive fauna generally incorporate signatures largely derived from waterbodies, and thus their isotopic signatures generally reflect local meteoric conditions (Luz *et al.* 1984, Ayliffe & Chivas 1990, Levin *et al.* 2006). Evaporation-sensitive taxa typically incorporate a significant portion of  $\delta^{18}\text{O}$  from water content within consumed vegetation, and subsequent carbohydrate breakdown (Chew 1961, Ayliffe & Chivas 1988, Johnson *et al.* 1997, 1998). However, it is not clear that rodents select foods with higher water content even amongst arid-adapted species (Murray & Dickman 1997), and, although the LGM was significantly drier than previous or subsequent periods in our region, it never approached conditions found in the arid zone of Australia. Thus, we are confident that the  $\delta^{18}\text{O}$  values we obtained are indicative of meteoric conditions. Mean  $\delta^{18}\text{O}$

for MIS 1 was the lowest at  $-4.0\text{‰}$ , followed by MIS 3 at  $-3.1\text{‰}$ , both of which indicate wet conditions (Prideaux *et al.* 2007). Glacial periods were drier, at  $-2.1\text{‰}$  for MIS 2 and  $-1.2\text{‰}$  at MIS 4, but still consistent with tropical to subtropical climates and moderate to high rainfall (Prideaux *et al.* 2007, Montanari *et al.* 2013). While we cannot rule out that the significant differences observed are due to inter-specific physiological differences in the rodents sampled, it seems likely that they reflect changes in local environmental conditions because they closely track climatic conditions revealed through other proxies.

Our histology results indicate that bone physiology from murid communities was quite sensitive to regional environmental changes. The data demonstrate a statistically significant relationship between murid osteocyte lacunae densities and palaeoenvironmental change, adding support to ongoing efforts into using fossil bone histology to address palaeoenvironmental and palaeoecological questions (e.g., Köhler & Moyà-Solà 2009, Miskiewicz *et al.* 2020; Sanchez & Schoch 2013, Sanchez *et al.* 2010). While, like the enamel samples above, we cannot assign femora to species, our analyses show that femur size, and thus the body size distribution of these murids, were comparable across our samples (see Miskiewicz *et al.* 2019, 2020 for discussion on relationships between femur size, bone histology, and body mass in murids). They also show size differences that could be consistent with the presence of several different species (supplemental Table S5). The osteocyte densities of murids at the community level appear insensitive to taxonomic composition, at least for this site. The ranges of osteocyte densities remained similar within each MIS group, implying a lack of inter-individual variation in stimulation to bone growth, and thus the maintenance of stable bone physiology as a community. Generally, mammalian bone histology is also less influenced by phylogeny than it is by life history, behavioural and environmental signals (de Ricqlès 1993; but see Stein & Werner 2013). Therefore, the statistically significant difference in osteocyte densities between the MIS 3 and MIS 2 samples supports the hypothesis that different climatic regimes could be reflected in bone formation of murids at the family level. Despite femur size remaining consistent across these two MIS groups, proxies for bone maintenance cell densities were higher in MIS 3 than 2. Femur morphology (fused epiphyses) also indicated these were adult murids with fully formed bones, which means physiology responses to environmental stimuli would have occurred microscopically. A possible interpretation is that this difference reflects the change from wetter, more rainforest-like conditions to more arid, open sclerophyll forest and grassland environments, as recorded in regional palaeoecological records and consistent with our  $\delta^{18}\text{O}$  values discussed above, necessitating shifts in skeletal metabolic adaptation. Our findings match those of Miskiewicz *et al.* (2020), who also reported osteocyte density changes in fossil murid femora from forested conditions in late Quaternary samples from Timor.

The lack of statistically significant differences in osteocyte densities between samples from the LGM and the Holocene

was unexpected. However, this similarity may reflect regional environmental conditions that differ from those reconstructed elsewhere in Australia (e.g., Quigley *et al.* 2010, Moss *et al.* 2017). Our murid sample suggests that, although at the continental level environmental conditions were more benign during MIS 1 than the LGM, during MIS 1 the region around the Capricorn Caves was still drier than in MIS 3. This is consistent with an anti-phase mid-Holocene dry period, as recorded in the Old Lake Coomboo Depression, Fraser Island (Longmore 1997), as well as increased drying observed during the latest Holocene in several other subtropical records (Krull *et al.* 2004, Moss *et al.* 2013, Genever *et al.* 2003, Hembrow *et al.* 2018, Salas-Saavedra *et al.* 2022).

### Faunal change and extinction

Palaeontological assessment of the three excavated and dated sites from Capricorn Caves suggests that the microfaunal communities of central-eastern Queensland underwent significant changes through the late Quaternary, and that each of the deposits contain taxa that are now either globally or locally extinct. These took place at different times over the geological interval recorded in our deposits, and, like previous studies before ours (Archer 1978; Dawson & Augee 1997; Morris *et al.* 1997; Price *et al.* 2009, 2019, 2020; Schram & Turnbull 1970; Wakefield 1972), clearly demonstrate that late Quaternary extinctions were not restricted to large-bodied megafauna.

At least three amphibian and reptile species found in the deposits are today extirpated. The last recorded local occurrence of the mountain frog (*Philoria* Spencer, 1901) is from Honeymoon Suite, thus likely Holocene. The burrowing ground frog (*Neobatrachus* Peters, 1863) is recorded in each of the three Capricorn Caves deposits, with its youngest local record probably that from Fern Chamber, also Holocene. Australian frog faunas are particularly susceptible to landscape stress and reductions in geographic range (Hero *et al.* 2005, Murray & Hose 2005). While dating records from the Capricorn Caves cannot pinpoint exactly when in the Holocene these species disappeared, the local disappearance of both species may be a result of late Quaternary aridification (Cogger 2018). The mid-Holocene dry period, and increased aridification through the late Holocene discussed above, could conceivably have driven the local extinction records observed from the Honeymoon Suite and Fern Chamber records. However, *Neobatrachus* species are generally arid-adapted, and are unlikely to have been adversely affected by aridification alone (Tyler & Prideaux 2016). Changes in local hydrology and fragmentation of the landscape were probably necessary additional factors in driving frog extinctions (Hero *et al.* 2005, Murray & Hose 2005, Price *et al.* 2005, Tyler & Prideaux 2016). Local extirpation of the earless dragon (*Tympanocryptis* Peters, 1863) was probably around the middle Holocene, it being recovered from Honeymoon Suite and the 27–37 cm spits of Colosseum Chamber. Like the frogs, its extirpation could be linked to habitat fragmentation, as the modern decline of

this genus is driven by loss and fragmentation of native temperate grasslands (Dimond *et al.* 2012, Robertson & Evans 2009). Assigning a cause for these losses is complicated by dating difficulties and the paucity of modern and historical distribution data, issues that have been noted previously for the Australian tropics (Price *et al.* 2020). It is possible, even likely, that these losses occurred following European settlement, rather than earlier in the Holocene.

Faunal declines post-European arrival are particularly evident in Australian rodents (Smith & Quin 1996, Roycroft *et al.* 2021). Three rodent extinctions recorded in the Capricorn Caves are likely amongst those resulting proximally from habitat loss and fragmentation, introduced species, pathogens, changed fire regimes, continued aridification of the continent, or interactions among these factors; most of these can ultimately be traced to European arrival in Australia (Woinarski *et al.* 2015, Roycroft *et al.* 2021). The white-footed rabbit-rat (*Conilurus albipes*) and Gould's mouse (*Pseudomys gouldii* (Waterhouse, 1839)) were both recorded alive in mainland Australia in historical (post-European) times (Gould, 1863). The former is now globally extinct (Woinarski & Burbidge 2016); the latter was recently confirmed as surviving as an isolated offshore population in Western Australia (Roycroft *et al.* 2021). The Capricorn rabbit-rat (*Conilurus capricornensis* Cramb & Hocknull, 2010) was first documented from fossils at Capricorn Caves (Cramb & Hocknull 2010b), where it occurs in all three assemblages, including in the topmost spits in Colosseum Chamber. Cramb and Hocknull (2010b) suggested that, based on the preservation characteristics of specimens from other caves in tropical Queensland, this species may also have become extinct only very recently and after European settlement. Notably, both *Conilurus capricornensis* and *C. albipes* are found in sympatric association through most spits in Colosseum Chamber, suggesting some level of niche differentiation between species (*contra* Cramb & Hocknull's 2010b speculation that the two species were in competition). *Conilurus albipes*, however, does not appear in local records above the 47–57 cm spits, i.e., sometime after the Last Glacial Maximum, when presumably it became restricted to the southeast forests of Australia (Breed & Ford 2007, p. 17, fig. 3.2; Menkhurst & Knight 2001, pl. 70). Similarly, *P. gouldii* was last recovered from 57–67 spits, suggesting coincident extirpation of *P. gouldii* and *C. albipes* from the region. Like *C. albipes*, *P. gouldii* is thereafter restricted to a predominantly southern distribution (Roycroft *et al.* 2021), before final disappearance from the mainland in the nineteenth century.

At least two other rodents have recent extirpation records from the Capricorn Caves. The plains rat (*Pseudomys australis* Gray, 1832) and swamp rat (*Rattus lutreolus* (Gray, 1841)) are both found in the youngest deposits, but have not been recorded as living specimens in the region. Of the two, *P. australis* currently has a more central and arid Australian distribution. Its significant range reduction in the last 100 years has been previously noted (Breed & Ford 2007, Medlin 2008, Fusco *et al.* 2016, Leggett *et al.* 2018). Our records suggest an even greater range reduction,

certainly since the Holocene but also post-European settlement. The current range of *R. lutreolus* on the mainland is discrete, with *R. l. lutreolus* (Gray, 1841) mostly on the east coast extending as far north as K'gari (Fraser Island), but with a different subspecies *R. l. lacus* Tate, 1951 in the northern tropics between the Atherton Tablelands and Paluma (Menkhorst & Knight, 2001). The Capricorn Caves fossils may belong to either subspecies; in any case, its presence in the Rockhampton region also indicates significant range reductions in the Holocene.

Like *R. l. lacus*, the giant white-tailed rat (*Uromys caudimaculatus* (Krefft, 1867)) is today restricted to the tropical north of Queensland. However, unlike *R. lutreolus*, it was recovered only from the lower portion of Colosseum Chamber (spit 142–147), i.e., MIS 3. In a discussion of the significance of the Colosseum Chamber *Uromys* record, Cramb *et al.* (2020) suggested that the cave records point to a southern incursion by *Uromys caudimaculatus* into central-eastern Queensland during the Late Pleistocene, through the St Lawrence biogeographic barrier, and possibly following southern expansions of closed-canopy rainforests during more humid interglacial conditions. Local extirpation of this species after ~50 ka was ascribed to increasing aridity and loss of closed canopy rainforests from the region (Cramb *et al.* 2020).

Forrest's mouse (*Leggadina forresti* (Thomas, 1906)) fossils from the nearby Mount Etna deposits are the oldest record (ca 280 ka) for the species (Cramb *et al.* 2018). This species is also recorded in the Capricorn Caves deposits, which seems at odds with most field guides (e.g., Breed & Ford 2007; Menkhorst & Knight, 2001), which show the modern distribution of *L. forresti* restricted to central Australia. Conversely, *Leggadina lakedownensis* Watts, 1976 occupies a broad area of tropical Australia, including eastern central Queensland and the Mt Etna region, but has not been identified from the Capricorn Caves. It is possible that modern *L. lakedownensis* records from around the Mt Etna region represent *L. forresti*. Taxonomic re-evaluation of extant populations currently assigned to *L. lakedownensis* in eastern central Queensland is necessary to resolve this apparent discrepancy.

The long-tailed hopping mouse (*Notomys longicaudatus* (Gould, 1844)) is represented by two isolated upper first molars that are morphologically similar to both *N. longicaudatus* and *N. amplus* Brazenor, 1936. More material is required before a definitive identification can be made, but the former species is considered the more likely candidate as it is widespread in late Quaternary cave deposits in eastern Queensland. *Notomys longicaudatus* is present in a Chibanian-aged deposit (QML1312 Elephant Hole Cave) at Mount Etna, but had not previously been recorded from the Late Pleistocene in the region. It is an arid-adapted species with a historically broad distribution in central and western Australia (Menkhorst & Knight, 2001) prior to its likely extinction in the twentieth century.

The narrow-nosed planigale (*Planigale tenuirostris* Troughton, 1928) also likely has experienced range reduction in recent years (Medlin 2008), and its Holocene record

in Rockhampton represents a significant expansion of its current range. While found today in arid and semi-arid central Australia, ecological studies suggest that arid environments may not represent its optimal habitat (Haythornthwaite & Dickman 2006). A fossil potentially attributable to this species was also recovered from the Big Ho Cave deposits in Broken River, reconstructed as more open scrublands than exist in the region today (Price *et al.* 2020). It occurs in the most recent deposits in Capricorn Caves, namely Honeymoon Suite and the top spit of Colosseum Chamber, and, like several of the rodents, this likely represents a post-European extinction. As Cramb *et al.* (2018) observed, the most common small-bodied dasyurid found in Colosseum Chamber is the stripe-faced dunnart, *Sminthopsis macroura* (Gould, 1845), a species that was first recorded as extant in the area only in 2007. The apparent absence of *P. tenuirostris* in the region today may not be due to local extinction but rather insufficient surveys of modern fauna.

The southern brown bandicoot (*Isoodon obesulus* (Shaw, 1797)) occurs in the Colosseum and Honeymoon Suite deposits, but has not been recorded alive locally. Again, this suggests that *I. obesulus* suffered local extinction at least by the middle Holocene. It is important to note that modern populations of the species occur from Sydney in New South Wales, following the coast southward to Victoria and then South Australia, and Tasmania. Thus, our data on *I. obesulus* suggests that it experienced significant geographic range shifts prior to European colonization. It is not possible to temporally track the separation of the extant population due to a paucity of reliably dated fossil sites north and south of the modern populations (Price 2005).

Similarly, the Cape York brown bandicoot (*Isoodon peninsulae* Thomas, 1922) is found in Colosseum Cave. This is the first time this species has been recorded as a fossil, and it is found much further south than its current distribution, where it is restricted to two small patches of rainforest near Cairns and near the tip of Cape York (Warburton & Travouillon 2016). The Liverpool Plains striped bandicoot (*Perameles fasciata* Gray, 1841) was previously synonymised with *Perameles bougainville* Quoy & Gaimard, 1824 but is now recognised as a valid species (Travouillon & Phillips 2018). The Colosseum occurrences again represent the first time the species is recorded as a fossil. It seems to have been a common component of the local fauna and may have become locally extinct prior to European colonisation. Only a small population remained in New South Wales in historical times, before becoming globally extinct in association with the introduction of foxes and habitat loss from the rise of agriculture (Travouillon & Phillips 2018).

The extinct and extirpated taxa of Capricorn Caves present a seemingly unlikely mix of more arid or open-adapted species (*Neobatrachus*, *Pseudomys australis*, *Pseudomys gouldii*, *Planigale tenuirostris*, *Leggadina forresti*, *Notomys longicaudatus*) with more water or humid-adapted species (*Phloria*, *Uromys caudimaculatus*, *Rattus lutreolus*). Taken as a whole, these are reminiscent of Pleistocene non-analogue assemblages (past sympatric species with only modern

allopatric distributions; Lundelius 1983), and similar environmentally diverse, Pleistocene microfaunas have been found in other caves, e.g., in the Broken River area (Price *et al.* 2020). A small number of these extinctions and extirpations, perhaps only two or three, occurred early in the record of Colosseum Chamber and are likely attributable to environmental changes associated with the onset of LGM conditions. Thus, our study demonstrates that climatic stress did significantly impact some microfauna in the Late Pleistocene, most likely through bottom-up processes. That similar processes detrimentally impacted earlier microfauna and megafauna in the region seems likely.

Still, most extinct and extirpated microfauna are still present in the youngest deposits of the Capricorn Caves. Our current dates do not provide resolution of the last few thousand years of the Holocene. This was a period of generally increasing aridification that should not have had significant detrimental effects on the fauna, particularly those that survived the drier and more open LGM. We suggest that the disappearances of the arid and semi-arid species recorded in the youngest deposits of Capricorn Caves are historical. Moreover, we argue that the modern or historical distributions of these taxa, from which we infer their habitat preferences, are not wholly representative of their preferred ranges but are instead a result of confinement to sub-optimal habitats following European arrival. The presence of these species in the youngest Capricorn Caves deposits would thus be due to differences between (modern) realized niches and their fundamental niches, rather than late Holocene environmental change.

Late Quaternary non-analogue assemblages have been reported globally, and seem to be a feature of both animal and plant communities (Williams & Jackson 2007). Many non-analogue assemblages throughout southern Australia (Lundelius 1983) as well as northeast Australia (Price *et al.* 2020), have been interpreted as evidence of more heterogeneous habitats as well as more equable climatic regimes, with a Late Pleistocene shift from mesic conditions recorded at a continental level (Lundelius 1983). Mammals have responded to these changes in species-specific fashion, resulting in assemblages of species associations in the Quaternary unlike those found today (Graham 2005). Such interpretations are predicated on—indeed require—knowledge of modern geographic and habitat distributions of species which, in Australia, is much poorer compared to other continents such as North America (Lundelius 1983). The global distribution of non-analogue assemblages in the Pleistocene (Williams & Jackson 2007) suggests that the phenomenon is real; nevertheless, our results highlight that in Australia, shifts towards drier conditions may at least partly be the result of post-European restrictions of extant fauna to the arid interiors as much as changes in Pleistocene climates and habitat homogenisation. This again highlights the need for better distribution and ecological records for small-bodied species dating back to the past few hundred years, particularly for those regions where survey intensities have remained low.

Our shifting baselines hypothesis finds support through the presence of species in the Capricorn Caves deposits with modern and discrete northeast–southeast distributions largely outside central-eastern Queensland. These discrete ranges were likely a single broad range until the late Holocene, if not more recently. Species in this category include *Rattus lutreolus*, *Dasyurus maculatus* (Kerr, 1792), and smaller species of *Isoodon* (*I. obesulus/peninsulae*). This reinforces again how poorly recorded native faunas are from the late Holocene until widescale European settlement, and even today, with many small species suffering extirpations and extinctions shortly after European arrival but before being taxonomically evaluated or ecologically surveyed (see also Travouillon *et al.* 2019).

If our interpretation is correct, then optimal habitats for several micromammals currently restricted to arid and semi-arid environments may be wetter and more vegetated than previously appreciated. This has important implications for the ongoing conservation of micromammals. For example, if *Pseudomys gouldii* were to be reintroduced to the mainland, the national parks in central eastern Queensland might provide a highly suitable habitat for this species. Such translocation or ‘rewilding’ proposals are not new (Louys *et al.* 2014, Archer *et al.* 2019, Westaway *et al.* 2019), although reintroduction efforts in Australia tend to focus on marsupials such as potoroids, dasyurids and peramelids. We contend that rodents generally have relatively higher fecundity and faster reproductive cycles than these marsupials and should be ideal candidates for rewilding projects. More recent and better dated records of microfauna from the tropics are needed to test our hypotheses, particularly those spanning the last few hundred years.

## Conclusions

Based on radiocarbon, OSL and U/Th dating, the fossil deposits at Capricorn Caves, Fern Chamber, Honeymoon Suite, and Colosseum Chamber are clearly of late Quaternary age. Fern Chamber likely is the youngest of the deposits, dating to at least *ca* 7 ka or older (Hocknull *et al.* 2007). Honeymoon Suite was previously dated to the Holocene, and, despite new radiocarbon dates reported here, consideration of the source of the charcoal from which these dates are derived suggests a Holocene age for this fauna. The Colosseum Chamber deposit represents the longest period of deposition of the sampled sites, spanning the Late Pleistocene and much of the Holocene; our new age-depth model provides a rigorous framework in which to examine faunal and environmental change, particularly over MIS 2–3.

Our palaeoenvironmental analyses suggest that the anti-phase mid-Holocene dry period may have extended to the Rockhampton region, although further samples and additional proxies are required to confirm this. More broadly, we provide an important proof of concept for the use of taxonomically unidentified rodent remains for reliable environmental and climatic reconstructions based on their congruence with other palaeoecological proxies. Rodent long bone and incisor samples from owl roost deposits may

provide underused, but readily available and often exceptionally abundant, palaeoenvironmental indicators. For the isotopic analyses, increasing sample sizes across finer subdivisions of stratigraphic units may provide more highly resolved indications of past precipitation patterns at Colosseum Chamber. Further examination of relative osteocyte lacunae densities throughout the Colosseum Chamber sequence also has the potential to reveal greater insights into the impact of glacial–interglacial cycles in this region. In combination with more established techniques, such as palaeogenomics (Mitchell & Rawlence 2021, Peters *et al.* 2021), there is significant potential in examining otherwise fragmented and largely unidentifiable remains from owl roost deposits to reconstruct environmental histories through deep time.

This study demonstrates that significant changes in the microfaunal community of tropical Queensland occurred between the Late Pleistocene and the late Holocene, and that, while these changes did not occur simultaneously, most are recorded associated with the LGM or with the mid to late Holocene. It is likely that the latter regional and global extinctions were the result of extrinsic factors, most notably the arrival of Europeans. The deposits record the extinction of the Capricorn rabbit-rat (*Conilurus capricornensis*), the white-footed rabbit-rat (*C. albipes*), the long-tailed hopping mouse (*Notomys longicaudatus*), and the Liverpool Plains striped bandicoot (*Perameles fasciata*). Through the integration of palaeontological data and modern species record mapping, we also show that range contractions occurred for several small-bodied vertebrates including frogs (*Philoria* sp., *Neobatrachus* sp.), the earless dragon (*Tympanocryptis* sp.), the plains mouse (*Pseudomys australis*), Gould's mouse (*Pseudomys gouldii*), Forrest's mouse (*Leggadina forresti*), swamp rat (*Rattus lutreolus*), the white-tailed rat (*Uromys caudimaculatus*), the narrow-nosed planigale (*Planigale tenuirostris*), the southern brown bandicoot (*Isodon obesulus*), and the Cape York brown bandicoot (*Isodon peninsulae*). Many of these species could potentially be re-introduced in the area, although further assessment of causes of historical range reductions is necessary. Understanding the impacts of past climatic change on environments and biota is critical for planning effective conservation efforts and engaging in proactive strategies to safeguard future biodiversity.











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