Short Paper

Revisiting the late Pleistocene mammal extinction record at Tight Entrance Cave, southwestern Australia

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ABSTRACT

Tight Entrance Cave (TEC) in southwestern Australia provides a Pleistocene sequence documenting the extinction of 14 large mammal species. This record has been interpreted as indicating that extinctions did not occur during or before the penultimate glacial maximum (PGM) and that humans played a primary role in the extinctions. However, it remains possible that the majority of extinct megafauna persisted no later than the PGM. The TEC extinctions correspond with vegetation change, a cooling/drying trend, increased biomass burning, and increasingly unstable small mammal communities. The initiation of these trends predates human arrival on the continent and implies environmentally mediated extinctions.

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Introduction

The late Quaternary is characterized by massive extinctions of megafauna (animals >44 kg) across the continents (Barnosky et al., 2004; Koch and Barnosky, 2006). The losses in Sahul (Pleistocene Australia–New Guinea) were exceptionally severe, with ~90% of its megafaunal genera disappearing before the end of the Pleistocene (Roberts et al., 2001; Field et al., 2008; Grün et al., 2010). What caused these extinctions is the subject of intense debate, with prevailing hypotheses including global climate change (Trueman et al., 2005; Wroe and Field, 2006; Price et al., 2011) and direct (e.g., hunting) or indirect (e.g., landscape burning) human impacts (Martin, 1984; Miller et al., 1999; Johnson, 2005; Miller et al., 2005; Brook et al., 2007).

Resolving the contribution of environmental and/or anthropogenic extinction mechanisms is hindered by a poorly resolved fossil record and a lack of reliable extinction chronologies (Price et al., 2011). Although the extinctions are often characterized as falling within a 40–50 ka window (Roberts et al., 2001; Miller et al., 2005), encompassing the 45 ka date for human arrival on the continent (O'Connell and Allen, 2004), the majority of extinct megafaunal species are not known to have survived the middle Pleistocene (Wroe and Field, 2006; Field et al., 2008). At the same time, numerous species lack associated radiometric dates altogether (Price et al., 2011) and relatively few are known to have been present when humans first colonized the continent (Field et al., 2008).

Located in the Tamala Limestone Formation of extreme southwestern Australia, Tight Entrance Cave (TEC) (34°04 S, 115°01 E) offers a unique opportunity to evaluate the mechanisms responsible for Sahul's megafaunal extinctions (Ayliffe et al., 2008; Prideaux et al., 2010). Previous excavations at TEC uncovered a stratified paleontological sequence dating from ~143 ka to 31 ka (Ayliffe et al., 2008; Prideaux et al., 2010), encompassing the middle-to-late Pleistocene transition (~130 ka), including the arid penultimate glacial maximum (PGM), and the arrival of humans on the continent. The diverse faunal assemblage is important as there is an absence of sequences spanning this time frame, leaving open the possibility that environmental change contributed to the majority of Sahul's extinctions long before human arrival (Wroe and Field, 2006). Taphonomic evidence suggests that the fauna were incorporated into the TEC deposits as pitfall victims through now-blocked solution pipes (Ayliffe et al., 2008).

Prideaux et al. (2010) provide a recent examination of the TEC faunal sequence. Their assessment of the paleontological and paleoecological evidence leads them to conclude the following: (1) the arid PGM did not trigger extinctions; (2) the extinctions are not solely/primarily the result of climate change; (3) human impacts were the primary driver in the extinctions. In this study, we critically examine the extent to which the TEC data support these conclusions, providing new analyses and an alternative reading of the evidence.

Does the TEC record rule out earlier extinctions?

The TEC faunal record includes 14 species of extinct large mammals (>5 kg), which disappear from the sequence between ~104 ka and ~48 ka (Prideaux et al., 2010). There are no extinctions

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Table 1
Extinct mammals documented at TEC. Last appearance date (LAD) from Wroe and Field (2006). Inferred dietary habits from Johnson (2006). Species names follow Prideaux et al. (2010), after the taxonomic revisions in Prideaux (2004).

Taxon	Dietary Niche	LAD (ka)	LAD (ka) at TEC
Borungaboodie hatcheri	Omnivore	NA	104
Congruus kitcheneri	Browser	55[a]	104
Macropus sp. nov.	Unknown	NA	70
Megalibgwilia ramsayi	Insectivore	55	104
Metasthenurus newtonae	Browser	164[b]	104
"Procoptodon" browneorum	Browser/Mixed Feeder	46[c]	48
Protemnodon cf. P. roechus	Browser	46.5	48
Simosthenurus occidentalis	Browser	46	48
"Simosthenurus" pales	Browser	164	48
Sthenurus andersoni	Browser	52	104
Thylacoleo carnifex	Carnivore	46.5	48
Vombatidae sp. indet.	Unknown	NA	70
Vombatus hacketti	Grazer	46	48
Zygomaturus trilobus	Browser	55	48

[a] = as *Wallabia kitcheneri*.
[b] = as *Simosthenurus newtoni*.
[c] = as *Simosthenurus brownei*.

documented in the transition from the PGM, represented by the lowermost fossiliferous horizon (Unit B) at ~143 ka, to the late Pleistocene. Because the arid PGM had no apparent impact on the fauna recovered from TEC, Prideaux et al. (2010) conclude that it could not have triggered the extinction of Sahul's large mammals. We note, however, that of the 14 extinct species known from TEC, nine were previously known to have survived to the late Pleistocene (~130 to 12 ka) (Roberts et al., 2001; Wroe and Field, 2006) (Table 1). The remaining species include a large wombat (Vombatidae sp. indet), a new species of *Macropus*, an oversized rat-kangaroo (*Borungaboodie hatcheri*), and two megafaunal kangaroos previously unknown from the late Pleistocene ("*Simosthenurus*" *pales* and *Metasthenurus newtonae*).

The TEC fauna is significant in demonstrating the survival of four to five new species to the late Pleistocene, two of which ("*S.*" *pales* and *M. newtonae*) broadly overlap with human arrival on the continent (O'Connell and Allen, 2004). However, the TEC record says relatively little that is new about the magnitude of extinctions during or before the PGM, since the majority of the large mammals at TEC were known to be late Pleistocene survivors and numerous taxa remain unknown from the late Pleistocene record (see also Field et al., 2011). Given that eight new species of middle Pleistocene kangaroos were recently reported from the Thylacoleo Caves in south-central Australia (Prideaux et al., 2007),

the addition of four to five late Pleistocene taxa at TEC still leaves at least 43 species (63%) absent from the late Pleistocene (Wroe and Field, 2006; Field et al., 2008). There is abundant potential for substantial extinctions during or prior to the PGM.

Of ~68 extinct Pleistocene species (Field et al., 2008), there are presently 25 known from the late Pleistocene and 15 known to broadly overlap the date of human arrival on the continent. Wroe and Field (2006) attribute this pattern to massive extinctions during or prior to the PGM, perhaps resulting from the long-term trend towards more arid and variable climates on the continent over the last 300–350 ka (e.g., Kershaw et al., 2003a, 2003b). On the other hand, Brook et al. (2007) attribute the missing megafauna to the Signor–Lipps effect (i.e., sampling error). Parallel arguments exist in the context of North American late Pleistocene extinctions, where the staggered extinction chronology has led some to characterize the losses as a potentially long-term process (Grayson and Meltzer, 2003; Grayson, 2007) and others as a synchronous event obscured by sampling error (Haynes, 2002; Martin, 2005; Fiedel, 2009). Quantitative analyses of the fossil record support the latter interpretation (Faith and Surovell, 2009). In the case of Sahul, similar quantitative analyses are lacking and both scenarios remain equally plausible; the circularity of assuming otherwise because of the inferred extinction mechanism is clearly problematic. We note that in the Darling Downs (eastern Australia), where the problem of sampling has been addressed, there is quantitative evidence for a long-term extinction process that predates human arrival and cannot be attributed to sampling error (Price and Webb, 2006; Price et al., 2011). This conflicts with Roberts et al.'s (2001) characterization of the extinctions as synchronous. Until more quantitative and empirical evidence is provided, it will remain unclear whether the chronology reflects long-term extinctions or a synchronous event.

Does the TEC record support human impacts or climate change?

Tests of extinction hypotheses require that the extinction chronology be arrayed against paleoenvironmental and archaeological data. At TEC, relevant paleoenvironmental data include the fauna, a charcoal record of bushfire history, and stable carbon and oxygen isotopes of land snails, which broadly indicate vegetation cover and temperature/humidity. The argument forwarded by Prideaux et al. (2010) in support of human contributions to the extinctions depends on their rejection of environmental extinction mechanisms rather than on direct evidence for human impacts. Here, we evaluate the extent to which this is justified.

Table 2
Abundance (MNI = minimum number of individuals; q = relative abundance over stratigraphic range) of extinct mammals at TEC and the probabilities of sampling them in stratigraphic units post-dating their last appearance (LAD, ka), following the methods outlined in the text. Significant values in bold. Data from Prideaux et al., 2010. Approximate dates (ka) for each stratigraphic unit in parentheses.

Taxon	MNI	q	Stratigraphic Units				
			D (104)	E* (70)	E–G (48)	H (35)	J (31)
Zygomaturus trilobus	7	0.031	–	–	LAD	0.802	0.533
Vombatidae sp. indet.	1	0.005	–	LAD	0.883	0.852	0.799
Protemnodon sp. cf. *P. roechus*	6	0.027	–	–	LAD	0.828	0.584
"Simosthenurus" pales	8	0.035	–	–	LAD	0.777	0.486
Simosthenurus occidentalis	25	0.111	–	–	LAD	0.440	0.096
Thylacoleo carnifex	5	0.022	–	–	LAD	0.855	0.639
Sthenurus andersoni	1	0.006	LAD	0.884	0.769	0.739	0.687
"Procoptodon" browneorum	70	0.310	–	–	LAD	0.075	**0.001**
Metasthenurus newtonae	2	0.011	LAD	0.781	0.590	0.545	0.471
Congruus kitcheneri	2	0.011	LAD	0.781	0.590	0.545	0.471
Vombatus hacketti	8	0.035	–	–	LAD	0.777	0.486
Macropus sp. nov	6	0.030	–	LAD	0.469	0.379	0.256
Megalibgwilia ramsayi	1	0.006	LAD	0.884	0.769	0.739	0.687
Borungaboodie hatcheri	1	0.006	LAD	0.884	0.769	0.739	0.687
Σ Large Mammal MNI			131	22	25	7	13

Extinctions at TEC take place between ~104 ka and ~48 ka (Table 1). Given potential sampling effects, this chronology cannot be taken at face value. Since the observed stratigraphic range of a taxon can underestimate its true temporal range, we establish confidence limits for the disappearance of extinct mammals. Following previous studies (Koch, 1987; Lyman, 1995; Barry et al., 2002), we estimate the probability of sampling an extinct taxon in stratigraphic levels post-dating its observed last appearance as $p_i = (1 - q_i)^n$, where p_i is the probability of sampling 0 individuals of taxon i, q_i is the relative abundance of taxon i over its stratigraphic range, and n is the number of individuals sampled in stratigraphic assemblages post-dating the last appearance of taxon i. We calculate q_i as the abundance of an extinct taxon relative to all large mammals (>5 kg) since large and small mammals can be accumulated by distinct taphonomic pathways (e.g., Marean et al., 2000; Thompson, 2010). A value of $p_i \leq 0.05$ indicates (with 95% confidence) that a taxon should have been sampled had it survived to that time.

Table 2 reports the probabilities of sampling extinct taxa across stratigraphic units at TEC. The 95% confidence limits on the last appearances of the majority of taxa include all stratigraphic units (Table 2). This is largely due to the rarity of most extinct mammals and the small sample sizes in late Pleistocene units E^* (~70 ka) to J (~31 ka) (Table 2). The sole exception is "*Procoptodon*" *browneorum*, whose last appearance likely occurred sometime between Units E–G (~48 ka) and Unit H (~35 ka). For the remaining taxa, it is difficult to reach any definitive conclusions about when extinctions took place.

Prideaux et al. (2010) argue that environmental change did not drive the extinctions because they predate the increase in aridity leading up to the Last Glacial Maximum (LGM = ~24–18 ka). As demonstrated above, however, the possibility that extinctions took place during the lead up to the LGM cannot be ruled out at TEC (Table 2). Even if it could, it remains the case that the extinctions window overlaps with a progressive transition from closed to open vegetation, a cooling/drying trend, and a marked increase in biomass burning at unit E^* (~70 ka) that coincides with an increase in fire frequency across the continent (Mooney et al., 2011) (Fig. 1). The isotopic evidence for increasingly open vegetation (Fig. 1), possibly promoted by the cooler/drier climate, is particularly significant since many of the extinct herbivores at TEC were likely browsers (Table 1) (Johnson, 2006) that required access to dense, shrubby vegetation. At the same time, the increase in burning could have accelerated vegetation change and further altered the availability of shrubland and woodland habitats (Miller et al., 1999, 2005). The onset of these trends predates the 45 ka human arrival date (O'Connell and Allen, 2004) by thousands of years (Fig. 1) and, given the current understanding of the human colonization of Sahul, cannot be attributed to human causation. These progressive environmental trends are precisely what one would expect in the case of environmentally mediated extinctions.

We also note that the small mammal community (<5 kg) becomes increasingly unstable through time, as reflect by chord distances calculated across successive pairs of stratigraphic assemblages (Fig. 1). Chord distance is a measure of faunal dissimilarity for relative abundance data (Ludwig and Reynolds, 1988), with values ranging from 0 for assemblages of identical taxonomic composition to $\sqrt{2}$ for assemblages with no taxa in common. Increasing chord distances for the small mammals across adjacent pairs of stratigraphic units (Fig. 1) indicate increasing turnover and community instability, likely reflecting rapid environmental perturbations. This long-term trend cannot be attributed to human impacts, as its onset predates human arrival. It also implies increasing variation in habitat structure through time, superimposed on other progressive environmental shifts (Fig. 1). We propose that this habitat variability, together with the transition from closed to open vegetation, the long-term cooling/drying trend, and the peak in biomass burning, played a central role in the TEC extinctions. That the small mammals
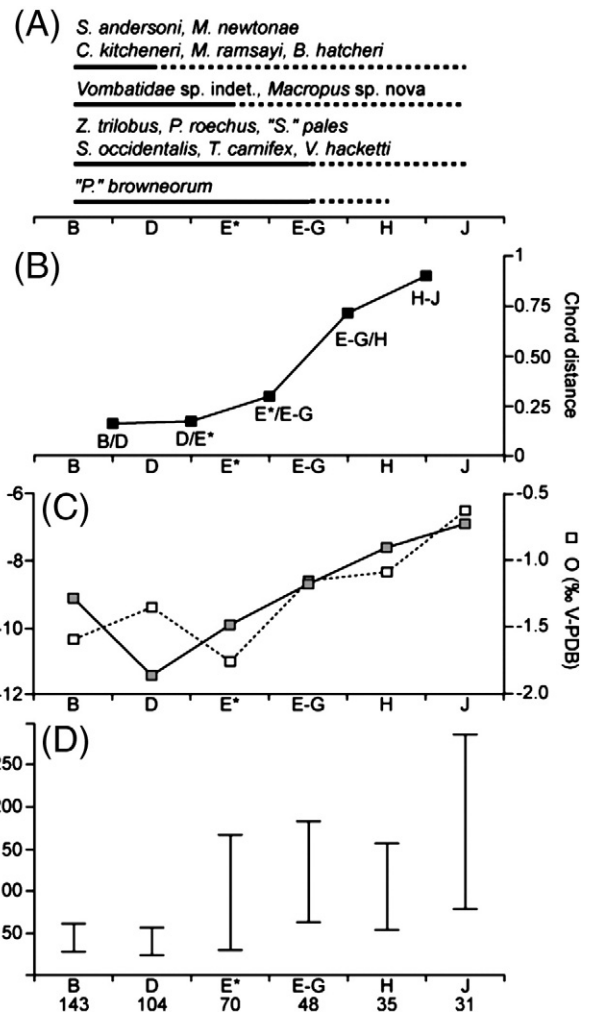

Figure 1. (A) The stratigraphic range of extinct mammals at TEC; solid lines indicate observed range; dashed lines indicate confidence limits for potential range from Table 2. (B) Chord distances of small mammal (< 5 kg) abundances across adjacent pairs of stratigraphic units. (C) Stable carbon and oxygen isotopes across stratigraphic units. (D) Range of microcharcoal values across stratigraphic units. Data from Prideaux et al. (2010).

endured these environmental stresses is explained by the fact that they can persist in smaller patches of their required habitats. Due to their greater range and forage requirements, however, large mammals would be especially sensitive to rapid habitat change. This is further compounded by their lower reproductive rates (Johnson, 2002), which would also limit their ability to recover from population declines in the face of rapidly changing environments. On the whole, we contend that the evidence in favor of environmentally mediated extinctions at TEC far outweighs the evidence in favor of anthropogenic contributions.

Conclusions

We provide a new interpretation of the large mammal extinctions record from TEC in southwestern Australia. Although numerous extinct mammalian taxa are documented at TEC, it remains possible that environmental change during or before the PGM triggered substantial extinctions long before human arrival on the continent. For those large mammals documented at TEC, the extinctions coincide with a progressive transition from closed to open vegetation, a cooling/drying trend, and a spike in biomass burning. At the same time, the small mammal communities become increasingly variable through time, suggesting increased variability in habitat structure. We

propose that the combination of these environmental and vegetational shifts played a decisive role in the extinctions at TEC.

Whereas proponents of human mediated extinctions often assume that late Quaternary glacial/interglacial cycles were of comparable severity and that climate change during the lead up to the LGM was insignificant, a growing body of evidence suggests otherwise (e.g., Kershaw et al., 2003a, 2003b; Wroe and Field, 2006; Cohen et al., 2011; Mooney et al., 2011; Murphy et al., 2011). It is becoming increasingly clear that beginning ~300–350 ka, the continent experienced a progressive trend toward increased aridity and climate variability superimposed on glacial/interglacial cycling (reviewed in Wroe and Field, 2006). Although a refined chronology is needed, such climate change could very well have contributed to extinctions during or before the PGM, a possibility allowed for by the TEC record. In addition, the evidence from TEC and elsewhere (e.g., Murphy et al., 2011; Price et al., 2011) shows that the late Pleistocene extinctions coincide with environmental changes initiated well before human arrival on Sahul. Together with evidence that the extinctions preferentially affected browsers (Bowman et al., 2010), an environmental explanation for the loss of Sahul's Pleistocene mammals becomes increasingly likely.

Acknowledgments

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