

Large mammal species richness and late Quaternary precipitation change in south-western Australia

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ABSTRACT: The precipitation history of south-west Australia since the Last Glacial Maximum (LGM) has important implications for understanding southern hemisphere climate dynamics. Previously reported environmental records indicating more open vegetation during the LGM have been interpreted in terms of aridity, but such changes can be explained by alternative mechanisms. To provide new evidence concerning the region's Quaternary precipitation history, we examine temporal changes in large mammal richness at four south-west Australian fossil sites: Devil's Lair, Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave. Large mammal richness is correlated strongly with mean annual precipitation across 53 modern Australian communities. Extending this relationship to the fossil record, a steady increase in richness from the LGM to the onset of the Holocene at both Devil's Lair and Tunnel Cave is consistent with increased precipitation through time. This supports previous interpretations of a more arid LGM and implies regional heterogeneity in the position of the southern hemisphere westerlies. A reduction in richness during the last ~1000 years is unlikely to be the result of precipitation change and may be related to more frequent burning of the landscape by hunter-gatherers in an effort to increase availability of large prey.

KEYWORDS: Devil's Lair; paleoecology; species richness; Tunnel Cave; westerlies.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/jqs.2888

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Introduction

The late Quaternary climate history of south-west Australia has important implications for understanding the diversity and distribution of its endemic flora (Cowling *et al.*, 1996; Hopper and Gioia, 2004; Yates *et al.*, 2010), its rich archaeological and palaeontological records (Archer *et al.*, 1980; Dortch and Smith, 2001; Prideaux *et al.*, 2010; Dortch *et al.*, 2012), and the mechanisms underlying a substantial decline in precipitation over the last several decades (Treble *et al.*, 2005; Hope *et al.*, 2010). Despite this importance, the nature and drivers of precipitation change in the region since the Last Glacial Maximum (LGM, ~26–20 ka) remain unresolved.

Today, precipitation in south-west Australia is strongly seasonal, with most rainfall occurring in the winter when the southern hemisphere westerlies migrate northward and embedded fronts transport moisture inland. Displacement of the southern hemisphere westerlies during the LGM probably played a central role in determining regional precipitation regimes at this time (Wyrwoll *et al.*, 2000; Shulmeister *et al.*, 2004; Fletcher and Moreno, 2012), but consensus concerning their position is lacking. Hubbard (1995a,b) suggests that the expansion of Antarctic sea ice during glacial conditions would have contributed to an equatorward displacement of the westerlies, bringing more winter rainfall to south-west Australia (see also Van Zinderen Bakker, 1976). This is consistent with dust records from the Tasman Sea, which indicate a ~350-km equatorward migration of the westerlies during the LGM and previous glacial phases (Hesse, 1994; Kawahata, 2002; Hesse *et al.*, 2004). In contrast, drawing on lake level records across the continent, Harrison (1993) argues that reduced LGM lake levels reflect aridity caused by a poleward shift of the westerlies (see also Harrison and Dodson, 1993), which is also suggested by the general circulation model presented by Wyrwoll *et al.* (2000; but see Shulmeister *et al.*, 2004). More recently, it has been argued that there was little change in the winter westerly track in south-east Australia at the LGM (McGowan *et al.*, 2008; Shulmeister *et al.*, 2016). Conflicting interpretation of LGM palaeoclimate records and their implications for the position of the westerlies is not unique to Australia, but is typical of all southern hemisphere landmasses (Markgraf, 1987; Heusser, 1989; Lamy *et al.*, 1999; Stuetz *et al.*, 2004; Chase and Meadows, 2007; Fletcher and Moreno, 2012; Faith, 2013).

Faunal and vegetation records from south-west Australia have generally been interpreted as indicative of arid conditions during the LGM (Balme *et al.*, 1978; Pickett, 1997; Dortch and Smith, 2001; Dortch, 2004b; Dortch and Wright, 2010; but see O'Connor *et al.*, 1993). These interpretations are based primarily on evidence suggesting more open forest cover in the LGM, giving way to closed forest during the Holocene. However, these vegetation shifts can be explained by alternative mechanisms. Reduced atmospheric CO₂ concentrations during the LGM (Monnin *et al.*, 2001) may contribute to an opening of vegetation structure irrespective of precipitation change, especially in the fire-prone ecosystems of south-west Australia (Gill and Catling, 2002). Under conditions of low CO₂, the growth rate of trees is reduced, potentially preventing them from reaching a fire-proof size between burn intervals and allowing fast-growing grasses and shrubs to expand at the expense of trees (Bond and Midgley, 2000; Bond *et al.*, 2003). This may be compounded by the competitive advantage of C₄ plants (grasses), which are otherwise rare in the region today (Hattersley, 1983), at lower CO₂ concentrations (Ehleringer *et al.*, 1997; Prentice *et al.*, 2011). In other contexts, including parts of southern Africa with a similar Mediterranean climate, the confounding effect of atmospheric CO₂ has complicated attempts to infer LGM precipitation regimes based on environmental proxies that, as is the case of south-west Australia, indicate an expansion of open habitats (Avery, 1982; Klein, 1983; Deacon and Lancaster, 1988; Chase and Meadows, 2007; Faith, 2013). In addition, in the near-coastal settings of south-west Australia, a lower water table related to the LGM marine regression could potentially drive more open vegetation structure irrespective of precipitation change (see discussions in Pickett, 1997; Dortch, 2004b). These complicating factors imply that vegetation change alone is an imperfect proxy for LGM precipitation regimes. It follows that new data are needed to provide a more robust interpretation of the late Quaternary precipitation history of south-west Australia. Our aim here is to provide such evidence based on an analysis of temporal changes in large mammal species richness.

Methods

Species richness and precipitation

The relationship between species richness and precipitation is well documented by biogeographers, ecologists and palaeoecologists across a diverse range of taxa and ecosystems (e.g. Rosenzweig, 1995; Grayson, 1998; Andrews and O'Brien, 2000; Olff *et al.*, 2002; Lomolino *et al.*, 2010; Faith, 2013). Broadly, higher precipitation translates to greater primary productivity, in turn supporting more herbivore biomass and more species in a given area. In some cases, richness has been observed to decline at higher precipitation, in part due to a reduction in plant nutrient content (Olff *et al.*, 2002). For Australian mammals, Smith *et al.* (1994) document a moderate relationship ($r^2 = 0.348$) between richness and annual precipitation using coarse data from $5^\circ \times 5^\circ$ cells across the continent. We provide a more refined perspective here using species lists from 53 Australian National Parks and wildlife areas (Travouillon and Legendre, 2009) coupled with precipitation data [mean annual precipitation (MAP)] extracted from the 5 arc-minute WorldClim global climate layers (Hijmans *et al.*, 2005, Table 1). Large mammals (>500 g; mass data from Travouillon and Legendre, 2009) are emphasized here because microfauna (e.g. small-bodied dasyurids and murids) from fossil assemblages in south-west Australia and elsewhere are inconsistently reported in the literature. The 500-g size threshold for large mammals has no ecological basis and may differ from schemes devised elsewhere; it is used here solely to maximize comparability between the modern communities and the fossil assemblages we examine. Invasive large-bodied mammals introduced since European colonization are excluded from our counts of species richness. In addition to MAP, we also consider richness in relation to the geographical area of each wildlife reserve, given its probable effects on species richness (i.e. the species–area curve; Rosenzweig, 1995).

The fossil sample

We analyse temporal trends in large mammal richness across four sites in south-west Australia: Devil's Lair, Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave (Fig. 1). These sites are located within a limestone ridge (Tamala Limestone) in the Leeuwin-Naturaliste Region in the far south-west corner of Australia, which is today characterized by diverse plant communities including heath, scrub, woodland and forest. All sites lie within 1–2 km of all components of the modern forest mosaic (Beard, 1981) and receive between 1000 and 1100 mm annual rainfall (Hijmans *et al.*, 2005). A detailed account of the stratigraphy, chronology, archaeology and faunal remains for each site is provided by Dortch (2004a) and Dortch and Wright (2010); see also Dortch *et al.* (2012). The faunal data used here are derived from the species lists provided in Dortch and Wright (2010).

The stratigraphy and radiocarbon chronology of the faunal samples are reported in Table 2 (from Dortch, 2004b). Radiocarbon dates are calibrated using the IntCal13 calibration curve (Reimer *et al.*, 2013) in OxCal 4.2 (Bronk Ramsey, 1995). Devil's Lair preserves a Late Pleistocene faunal sequence dating to before, during and after the LGM. Tunnel Cave provides a faunal sequence dating from the onset of the LGM through the Holocene, with nearby (<10 km) Witchcliffe Rock Shelter and Rainbow Cave providing complementary records for the last ~1000 years. We exclude the basal Devil's Lair assemblages from our analysis (DL1–2), given the substantial amount of time-averaging indicated by the radiocarbon dates (Dortch, 2004b). Likewise, the uppermost assemblages (DL12–14) are excluded because of small sample sizes (DL14) and because associated age estimates suggest that they sample both Pleistocene and mid-Holocene faunas (DL12/13) (Dortch, 2004b). At the remaining sites, we include only those 15 assemblages providing number of identified specimens (NISP) counts of at least 50 to eliminate the potential effects of small samples.

Table 3 reports large mammal abundances, according to NISP (Tunnel Cave, Witchcliffe Rock Shelter, Rainbow Cave) or minimum number of individuals (MNI: Devil's Lair), and the number of taxa (NTAXA) for the faunal assemblages included in the analysis. Because variation in NTAXA is

strongly influenced by sample size (Grayson, 1984; Lyman, 2008), we control for sample size effects using rarefaction analysis, whereby larger faunal sample sizes are rarefied down to a smaller sample size, allowing a direct comparison of species richness at comparable effective sample sizes. Rarefaction analysis was conducted using the Paleontological Statistics (PAST) software package (Hammer *et al.*, 2001), which makes use of the algorithm outlined by Krebs (1989).

The Devil's Lair assemblages are unusual compared with many other fossil assemblages (Lyman, 2008) in that the observed NTAXA is identical across assemblages (Table 3) despite substantial variation in sample size (MNI: 44–265). This may suggest that relatively few individuals are needed to sample all species in the community, perhaps reflecting the impoverished local faunas following massive extinctions through the Pleistocene (Johnson, 2006). Rarefaction analysis remains a useful tool in this context, however, by providing an indication of how quickly species accumulate as sampling effort increases, with more diverse (heterogeneous) communities providing greater richness at smaller sample sizes.

To place temporal trends in species richness within a broader context of faunal change, we conduct a correspondence analysis (CA) on taxonomic abundance data for each of the sites (Greenacre and Vrba, 1984). This allows us to examine associations between different stratigraphic units and different taxa. We use the primary axis scores (CA Axis 1) for each stratum to broadly summarize its taxonomic composition and examine how these values change through time and in relation to NTAXA. Devil's Lair is considered separately because of the different abundance measure published for its fauna (MNI vs. NISP).

Taphonomic evidence implicates humans, carnivores and raptors in the accumulation of faunal remains from these sites (Dortch, 2004a). It is therefore important to evaluate whether changes in NTAXA are the result of taphonomic change. Bone modification data tracking the contributions of different accumulators (e.g. cut-marks, carnivore tooth-marks and gastric etching) are unavailable for the assemblages examined here, but we are able to examine the relationship between rarefied NTAXA and several relevant taphonomic variables (Table 4; data from Dortch, 2004a). For Tunnel Cave, these include the density of flaked-stone artefacts and percentage of burned bone, both of which provide proxies for human occupation intensity, and the density of coprolites, probably from Tasmanian devil (*Sarcophilus harrisii*), which provides a proxy for carnivore activity. Complementary data for Devil's Lair are available only for flaked-stone artefact densities. We assume that variation across these variables tracks bone accumulation by different taphonomic agents.

Results

Species richness and precipitation

Table 1 reports NTAXA, MAP (mm a^{-1}) and geographical area (ha) for each of the 53 modern communities. Consistent with observations in Australia and beyond, we observe a significant positive correlation between NTAXA and MAP ($r^2 = 0.543$, $P < 0.001$; Fig. 2). This relationship is not homoscedastic; the residuals of the reduced major axis regression between NTAXA and MAP increase significantly at higher values of MAP (Breusch–Pagan test for heteroscedasticity: $P = 0.005$). Log-transformation of both NTAXA and MAP provides a tight linear relationship ($r^2 = 0.706$, $P < 0.001$) that is also homoscedastic (Breusch–Pagan test: $P = 0.963$).

Surprisingly, we observe a weak *inverse* relationship between NTAXA and (log-transformed) geographical area ($r^2 = 0.091$, $P = 0.028$; Fig. 2). This relationship is probably spurious, however, as there is also a weak inverse relationship between MAP and geographical area ($r^2 = 0.104$, $P = 0.018$), indicating that larger wildlife reserves are also among the driest (e.g. Simpson Desert National Park). Multiple regression considering all variables (log-transformed) simultaneously indicates a significant effect of MAP ($P < 0.001$) but not of area ($P = 0.606$).

Late Quaternary changes in richness

Results of the CA are illustrated in Fig. 3. For the analysis of Devil's Lair and the combined analysis of Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave, species that prefer more open habitats (*Petrogale lateralis*, *Perameles bougainville*) versus closed habitats (*Setonix brachyurus*, *Macropus eugenii*) are at opposite ends of CA Axis 1, suggesting that this axis is primarily an indicator of habitat structure (see also Dortch and Wright, 2010). When CA Axis 1 scores for Devil's Lair are plotted through the sequence, there is a stronger open habitat signal from units DL6 to DL9, broadly corresponding to the LGM (Table 2), with closed conditions observed before and after. A complementary pattern is observed at Tunnel Cave, which documents a stronger open habitat signal during the LGM and Lateglacial compared with a closed habitat signal during the Holocene.

The Devil's Lair assemblages are rarefied down to an effective sample size of 44 individuals, corresponding to the smallest assemblage (DL11) considered here (Table 3). Rarefied richness increases slightly but steadily from the onset of the LGM (DL6) through the end of the Pleistocene (DL11) (Fig. 4; Spearman's rho: $r_s = 0.943$, $P = 0.003$). This broadly tracks the shift to increasingly closed habitats (Fig. 3), although the correlation between rarefied NTAXA and CA Axis 1 scores is only weakly significant ($r_s = 0.617$, $P = 0.076$). Rarefied NTAXA is not correlated with artefact densities ($r_s = -0.100$, $P = 0.776$).

For Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave, assemblages are rarefied down to an effective sample size of 69 specimens, corresponding to the sample size of the Rainbow Cave assemblage (Table 3). Tunnel Cave documents a similar increase in richness from the onset of the LGM at base of the sequence (TC9L/10) to terminal Pleistocene assemblage TC5L (Spearman's rho: $r_s = 0.810$, $P = 0.022$). Following the transition to closed habitats at the Pleistocene–Holocene transition (Fig. 3), richness remains high through the early Holocene (TC5U and TC2), but drops to levels below those observed during the LGM in assemblages dating to the last ~1300 years at Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave. There is no significant relationship between rarefied NTAXA and CA Axis 1 scores ($r_s = 0.382$, $P = 0.160$) at these sites. For the Tunnel Cave assemblages, rarefied NTAXA is unrelated to artefact densities ($r_s = 0.145$, $P = 0.670$), the percentage of burned bone ($r_s = 0.391$, $P = 0.235$) or coprolite densities ($r_s = 0.282$, $P = 0.401$).

Discussion

Consistent with observations from a broad range of ecosystems and spatial scales (e.g. Rosenzweig and Abramsky, 1993; Rosenzweig, 1995; Danell *et al.*, 1996; Grayson, 1998; Olff *et al.*, 2002; Faith, 2013), large mammal richness in Australia is strongly mediated by precipitation (Fig. 2). The observed heteroscedasticity (Fig. 2) probably reflects the fact that at low MAP, richness is consistently low because of limited primary productivity (i.e. richness cannot be high), but as MAP increases, the effects of other variables that can also influence richness, especially nutrient availability (Bell, 1982; Olff *et al.*, 2002), become important and allow for richness to take on a broader range of values. Variance may also be introduced by local extinctions in historical times, primarily due to landscape transformation and introduction of invasive species (Fusco *et al.*, 2016), resulting in lower richness in some modern communities than predicted by precipitation. The lack of a significant positive correlation between richness and geographical area may reflect habitat homogeneity within the National Parks, such that increasing area does not sample new habitats and new sets of species (Travouillon and Legendre, 2009).

Changes in NTAXA at Devil's Lair and Tunnel Cave (Fig. 4) are not readily explained by taphonomy (Table 4), in which case a palaeoenvironmental explanation is reasonable (see also Dortch and Wright, 2010). Based on the modern relationship between richness and MAP, the observed changes in NTAXA can be interpreted as reflecting a steady increase in precipitation from the LGM to the end of the Pleistocene. The extent to which this reflects changes in absolute precipitation versus effective precipitation is unclear, given the opposing effects of increasing temperatures (Petit *et al.*, 1999) and a potential decline in wind speeds on evaporation rates (Larsen, 2011). Richness through

the early to mid-Holocene at Tunnel Cave remains high, suggesting enhanced precipitation compared with during the LGM. The weak (Devil's Lair) or insignificant (Tunnel Cave) correlations between NTAXA and the principal axis of the CA (Fig. 3) indicates that these long-term trends in richness are not directly related to the shift from open to closed forests (CA Axis 1).

These trends are consistent with previous interpretations derived from faunal (Balme *et al.*, 1978; Dortch, 2004a; Dortch and Wright, 2010), pollen (Pickett, 1997) and charcoal assemblages (Dortch, 2004b), suggesting drier conditions during the LGM of south-western Australia, in contrast to the scenario whereby an equatorward shift of the westerlies during the LGM contributed to greater rainfall in the region (Hubbard, 1995a,b). Global climate modelling of the LGM in south-west Australia produces highly variable results because the region has few constraining data points. Nevertheless, the average model consensus is that westerly circulation did not change much and modelled precipitation is very similar to modern (Wyrwoll *et al.*, 2000). The key elements that would have controlled the position of the westerlies are the extent of winter sea-ice in the eastern Indian Ocean sector of the Southern Ocean and the persistence and location of a blocking winter high-pressure cell over temperate southern Australia that may have impeded the approach of westerly fronts. Estimates of winter sea-ice from this sector of the Indian Ocean are sparse, but it appears that there was a northward expansion of sea-ice by up to 10° of latitude at the LGM (Gersonde *et al.*, 2005). This would have displaced the westerly wind belt northward, but while high-latitude ocean fronts moved strongly equatorward, the frontal shifts probably became more compressed northwards. This would have generated a zone of increased storminess south of western Australia, but may not have resulted in substantially increased onshore flow. The pattern would have been reinforced by the intensification of winter high pressure over southern Australia as lower LGM winter temperatures enhanced downwelling. Evidence for little overall change in the LGM winter westerlies is now emerging from south-east Australia (McGowan *et al.*, 2008; Shulmeister *et al.*, 2016) and this work suggests either little change or even reduced winter westerly penetration in south-west Australia.

The rather ambiguous pattern of (little) change in the westerlies is similar to southern South America, where conflicting evidence suggests both significant shifts in track or no movement at the LGM (e.g. Lamy *et al.*, 1999; Rojas *et al.*, 2009), but differs from the western portion of southern Africa where the LGM was clearly wetter and the westerlies were displaced equatorward (e.g. Stuut *et al.*, 2004; Chase and Meadows, 2007; Faith, 2013). This suggests that changes in the Southern Hemisphere westerlies were not uniform. Instead it implies that the winter polar jet was deflected southwards during the LGM in the eastern Indian Ocean/western Australian region, resulting in reduced westerly flow in the southern portion of western Australia.

The youngest assemblage from Tunnel Cave, as well as the similar-aged records from Witchcliffe Rock Shelter and Rainbow Cave, are characterized by the lowest species richness observed over the last ~25 000 years. While this could reflect marked aridity during the last ~1300 years, there is no evidence of dry conditions in the charcoal assemblage from Tunnel Cave (Dortch, 2004b) or in regional pollen records (Newsome and Pickett, 1993; Pickett, 1997). It seems likely that this recent decline in richness is related to alternative mechanisms. One such mechanism is fire. Intensified fire regimes can contribute to a grassy or sparse forest understorey, in turn driving a reduction in herbivore richness (Gill and Catling, 2002). At Tunnel Cave, the abundance of macrocharcoal (g kg⁻¹ of excavated sediment), much of which probably washed into the site during winter storms, increases substantially through the Holocene (Dortch, 2004b). To the extent that observations linking fire frequencies to macrocharcoal abundances in lacustrine environments (e.g. Tinner *et al.*, 1998; Conedera *et al.*, 2009) can be applied to cave settings, this pattern is consistent with more frequent forest fires.

The increase in fire frequency documented at Tunnel Cave is not observed in charcoal records across temperate Australia (Mooney *et al.*, 2011), but it does track a possible increase in human occupation of south-west Australia (Dortch, 2004a). Aboriginal hunter-gatherers may have deliberately increased burning regimes to enhance availability of large prey, as macropods are common in recently burned areas (Christensen and Kimber, 1975) and expansion of the grassy understorey may also attract large grazers (Cork and Catling, 1996). Both oral history (Kelly, 1999) and historical accounts (Hallam, 2002) indicate that fire was employed by south-west Australian hunter-gatherers to clear dense vegetation and drive macropod species into the open. A link between

fire and macropod hunting is also suggested at the Wonitji Janga rock shelter, 40–55 km north of the sites examined here. A preliminary report on the faunal remains documents a significant decline of macropods in the upper stratigraphic units post-dating European colonization (Dortch *et al.*, 2014), coincident with a reduction in fire frequency suggested by regional pollen cores (Pickett, 1997).

We propose that reduced richness in the last ~1300 years is the result of intensified fire regimes related to human subsistence strategies. Provisional support for this scenario is provided by an inverse relationship between rarefied NTAXA and the abundance of western grey kangaroo (*Macropus fuliginosus*), the largest extant mammal known from the region, across the Holocene assemblages at Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave ($r_s = -0.857$, $P = 0.012$). Thus, the reduction in richness in the latest Holocene, which tracks intensified burning at Tunnel Cave (Dortch, 2004a), is associated with increased representation of a preferred prey species (Dortch and Wright, 2010). Whether this increase is due to human prey choice or a decline in the availability of species that require a more dense forest understorey remains to be determined.

Conclusions

Understanding the drivers of LGM–Holocene precipitation change in south-west Australia, and more broadly throughout the southern hemisphere, first requires consensus concerning the region's precipitation history. In particular, establishing whether the LGM was wet or dry has important implications for debates concerning the position of the southern hemisphere westerlies (Wyrwoll *et al.*, 2000; Shulmeister *et al.*, 2004; Fletcher and Moreno, 2012). Previous interpretations of environmental records from south-west Australia suggest an arid LGM, but the evidence for this – namely a more open vegetation structure – could be influenced by alternative mechanisms.

Here we contribute to an understanding of precipitation change in south-west Australia through an examination of species richness in the fossil record. We show that large mammal richness is strongly influenced by MAP in modern Australian ecosystems. Extending this relationship to the past, we observe significant increases in large mammal richness, suggesting increased precipitation, from the LGM to the end of the Pleistocene. This supports the hypothesis of an arid LGM, although it is incompatible with models predicting an equatorward expansion of the southern hemisphere westerlies into the region. In addition, the fossil records document a substantial decline in richness in the latest Holocene. This is unlikely to reflect precipitation change, but may instead be related to more frequent burning of the landscape by human populations in an effort to increase availability of large high-ranking prey.

Acknowledgments. J.T.F. was supported by an Australian Research Council (ARC) Discovery Early Career Researcher award (DE160100030). J.D. thanks the Australian Institute for Aboriginal and Torres Strait Islander Studies (AIATSIS) and the ARC (LP0669233) for supporting the laboratory analyses of the fossil assemblages, and the ARC (DP1201003725) for funding the excavation of Wonitji Janga rock shelter. We thank Lee Lyman (reviewer) and Matthew McDowell (reviewer) for their helpful comments and suggestions.

Abbreviations. CA, correspondence analysis; LGM, Last Glacial Maximum; MAP, mean annual precipitation; MNI, minimum number of individuals; NISP, number of identified specimens.

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Figure 1. Location of south-west Australian fossil sites (inset) and the 53 modern large mammal communities compiled by Travouillon and Legendre (2009). See Table 1 for key to sites. Mean annual precipitation (MAP) data from Hijmans *et al.* (2005).

Figure 2. (Top) The relationship between large mammal richness and mean annual precipitation in Australia (mm). (Bottom) The relationship between large mammal richness and geographical area in Australia [$\log(\text{ha})$]. Solid lines represent the reduced major axis (RMA) regression.

Figure 3. Correspondence analysis of large mammals across stratigraphic units at (top) Devil's Lair and (bottom) Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave. Axis 1 values are reversed for Devil's Lair so that assemblages with greater abundances of open habitat species (e.g. *Petrogale lateralis*, *Perameles bougainville*) plot to the right. LGM assemblages are consistently associated with open habitat species (positive Axis 1 scores for Tunnel Cave and negative Axis 1 scores for Devil's Lair).

Figure 4. Results of rarefaction analysis for (top) Devil's Lair and (bottom) Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave. The Devil's Lair assemblages are rarefied to a sample size of 44 individuals (sample size of DL 11), while those from the remaining sites are rarefied to a sample size of 69 specimens (sample size of RC1).

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Table 1. Large mammal richness (NTAXA), mean annual precipitation (MAP) and geographical area (ha) of the 53 modern communities. Site numbers used in Fig. 1 are in parentheses.

Modern community	Latitude	Longitude	NTAXA	MAP (mm)	Area (ha)
Abercrombie NP (1)	-34.1	149.7	9	855	19 000
Ben Lomond NP (2)	-41.6	147.7	13	1312	16 456
Blue Mountains NP (3)	-33.6	150.5	19	1264	267 297
Boodjamulla NP (4)	-18.7	138.3	10	538	282 000
Bookmark Biosphere Reserve (5)	-33.6	140.7	6	240	603 342
Bundjalung NP (6)	-29.2	153.3	17	1434	20 119
Carnarvon NP (7)	-25.1	148.2	22	714	298 000
Croajingolong NP (8)	37.7	149.4	19	1000	101 000
Currawinya NP (9)	-28.8	144.5	9	320	151 300
Deua NP (10)	-35.9	149.7	13	987	117 826
Diamantina NP (11)	-23.8	141.3	7	256	500 000
Douglas-Apsley NP (12)	-41.8	148.2	13	936	16 080
Fitzgerald River NP (13)	-33.9	119.9	9	479	242 727
Flinders Ranges NP (14)	-31.4	138.6	7	349	95 000
Gawler Ranges NP (15)	-32.5	135.4	4	299	166 000
Grampians NP (16)	-37.1	142.5	13	695	167 200
Gregory NP (17)	-15.6	131.3	8	838	1 300 000
Gundabooka NP (18)	-30.5	145.7	8	358	63 903
Iron Range NP (19)	-12.7	143.3	17	1722	47 090
Kakadu NP (20)	-13.1	132.4	16	1383	1 980 400
Kalbarri NP (21)	-27.8	114.2	7	415	183 004
Karijini NP (22)	-22.2	118.0	9	401	627 400
Kinchega NP (23)	-32.5	142.3	8	259	44 262
Kosciuszko NP (24)	-36.5	148.3	19	1708	625 525
Ku-ring-gai Chase NP (25)	-33.6	151.2	15	1261	14 928
Lamington NP (26)	-28.2	153.2	22	1648	20 500
Little Desert NP (27)	-36.5	142.0	7	445	132 000
Main Range NP (28)	-28.1	152.4	24	1103	18 400
Millstream-Chichester NP (29)	-21.4	117.9	5	330	200 000
Mount Barney NP (30)	-28.3	152.7	20	1377	13 000
Mount Buffalo NP (31)	-36.7	146.8	10	1385	31 000
Mount Field NP (32)	-42.7	146.7	15	1041	15 881
Mount Remarkable NP (33)	-32.8	138.1	10	511	16 000
Mungkan Kandju NP (34)	-13.4	142.3	14	1529	456 000
Mungo NP (35)	-33.5	143.1	4	299	88 637
Mutawintji NP (36)	-31.2	142.4	7	267	68 912
Nitmiluk NP (37)	-14.1	132.5	14	1154	292 800
Prince Regent River NP (38)	-15.4	125.4	11	1341	633 825
Purnululu NP (39)	-17.5	128.4	11	590	200 000
Savage River NP (40)	-41.3	145.4	14	1853	35 660
Shoalwater Bay Conservation Park (41)	-22.3	150.2	21	1002	239 100
Simpson Desert NP (42)	-25.4	138.2	2	166	1 000 000
Snowy River NP (43)	-37.2	148.4	21	889	98 700
South-East Forest NP (44)	-37.0	140.7	21	950	115 534
Stirling Range NP (45)	-34.4	117.9	12	501	115 920
Uluru-Kata Tjuta NP (46)	-25.4	131.0	4	320	132 550
Vulkathunha-Gammon Ranges NP (47)	-30.4	139.1	5	305	122 900
Wadbilliga NP (48)	-36.4	149.6	14	898	98 530
Wilson's Promontory NP (49)	-38.9	146.3	9	992	49 000
Witjira NP (50)	-26.4	135.6	4	133	777 000
Wyperfeld NP (51)	35.5	142.0	7	356	356 800

Yumbarra Conservation Park (52)	-31.7	133.6	4	263	327 000
Yuraygir NP (53)	-29.8	153.2	15	1444	30 955

Table 2. The stratigraphy and radiocarbon chronology of the faunal samples from Devil's Lair, Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave. AMS radiocarbon dates for Devil's Lair are in bold type.

Assemblage	Age (^{14}C a BP)	Age (cal a BP)	Assemblage	Age (^{14}C a BP)	Age (cal a BP)
Tunnel Cave			Devil's Lair		
Layer 1 (TC1)	1370 ± 40	1291 ± 34	Phase 11 (DL11)	11 870 ± 150	13 724 ± 175
Layer 2 (TC2)				12 050 ± 140	13 935 ± 201
Layer 3 (TC3)	4280 ± 60	4845 ± 98		13 050 ± 80	15 621 ± 153
Layer 5U (TC5U)	6900 ± 60	7742 ± 64	Phase 10 (DL10)	11 960 ± 140	13 823 ± 177
	8270 ± 80	9254 ± 114		12 000 ± 180	13 907 ± 262
	9940 ± 110	11 473 ± 187		12 950 ± 110	15 493 ± 175
Layer 5L (TC5L)	12 890 ± 250	15 354 ± 429		13 300 ± 120	15 989 ± 177
	12 400 ± 240	14 564 ± 406	Phase 9 (DL9)	13 975 ± 450	16 925 ± 206
Layer 6 (TC6)	–		Phase 8 (DL8)	17 560 ± 460	21 264 ± 569
Layer 7U (TC7U)	16 080 ± 90	19 398 ± 130		16 970 ± 620	20 596 ± 772
Layer 7L (TC8L)	17 380 ± 105	20 983 ± 166	Phase 7 (DL7)	19 160 ± 380	23 135 ± 437
	17 110 ± 250	20 669 ± 329		17 370 ± 290	21 015 ± 383
	16 850 ± 110	20 323 ± 148		19 835 ± 75	23 872 ± 124
	17 010 ± 260	20 544 ± 335		21 270 ± 620	25 541 ± 700
Layer 8 (TC8)				21 820 ± 480	26 187 ± 509
Layer 9U (TC9U)	19 300 ± 650	23 377 ± 772	Phase 6 (DL6)	17 100 ± 810	20 809 ± 992
	19 735 ± 130	23 764 ± 171		19 000 ± 250	22 929 ± 297
Layer 9M (TC9M)	21 110 ± 220	25 420 ± 251	Phase 5 (DL5)	19 250 ± 900	23 395 ± 1078
Layers 9L–10 (TC9L/10)	21 100 ± 360	25 342 ± 407		23 050 ± 250	27 323 ± 232
	21 215 ± 165	25 543 ± 174		24 930 ± 335	29 031 ± 383
	19 110 ± 460	23 103 ± 529		24 200 ± 1400	28 794 ± 1502
	22 410 ± 850	26 751 ± 829	Phase 4 (DL4)	25 500 ± 275	29 679 ± 383
				20 400 ± 1000	24 678 ± 1126
				21 850 ± 210	26 127 ± 218
			Phase 3 (DL3)	26 590 ± 360	30 727 ± 318
				25 900 ± 300	30 116 ± 368
Witchcliffe Rock Shelter			Rainbow Cave		
Layers 1–3L (WRS1–3L)	400 ± 50	430 ± 63	Spits 1–5 (RC1)	340 ± 45	397 ± 56
Layers 4U–	680 ± 90	640 ± 69			

M
(WRS4U/M)
Layers 4L-5 Undated
(WRS4L/5)

Table 3. Sample size (MNI for Devil's Lair; NISP for Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave), species richness (NTAXA) and rarefied NTAXA (MNI = 44 for Devil's Lair; NISP = 69 for Tunnel Cave, Witchcliffe Rock Shelter and Rainbow Cave) across the 24 large mammal assemblages included in the analysis. See Table 1 for chronology.

Assemblage	Sample size	NTAXA	Rarefied NTAXA
Devil's Lair			
DL11	44	12	12.0
DL10	229	12	11.3
DL9	116	12	11.2
DL8	90	12	11.0
DL7	126	12	11.1
DL6	265	12	10.7
DL5	74	12	11.5
DL4	86	12	10.9
DL3	167	12	11.3
Tunnel Cave			
TC1	94	9	8.9
TC2	83	11	10.8
TC5U	224	11	10.6
TC5L	317	12	11.4
TC6	442	12	10.9
TC7U	291	12	10.9
TC7L	477	12	10.8
TC8	155	11	10.3
TC9U	205	11	10.4
TC9M	118	10	9.5
TC9L/10	413	11	10.5
Witchcliffe Rock Shelter			
WRS1-3L	120	8	7.8
WRS4U/M	163	9	8.9
WRS4L/5	97	9	8.9
Rainbow Cave			
RC1	69	8	8.0

Table 4. Artefact density (number L⁻¹ sediment at Devil's Lair and number kg⁻¹ sediment at Tunnel Cave), abundance of burned bone (%), and coprolite density (number kg⁻¹ sediment) at Devil's Lair and Tunnel Cave.

Assemblage	Artifact density	% Burned bone	Coprolite density
Devil's Lair			
DL11	0.400	–	–
DL10	0.895	–	–
DL9	0.151	–	–
DL8	0.330	–	–
DL7	3.312	–	–
DL6	2.331	–	–
DL5	0.180	–	–
DL4	0.059	–	–
DL3	0.041	–	–
Tunnel Cave			
TC1	0.010	0.46	0
TC2	0.003	0.14	0.033
TC5U	0.006	0.03	0.018
TC5L	0.025	9.29	0.029
TC6	0.128	2.53	0.156
TC7U	1.095	13.90	0.585
TC7L	2.108	34.07	0.116
TC8	0.089	3.60	0.068
TC9U	0.148	7.51	0.040
TC9M	0.135	5.91	0.140
TC9L/10	0.026	2.01	0.051

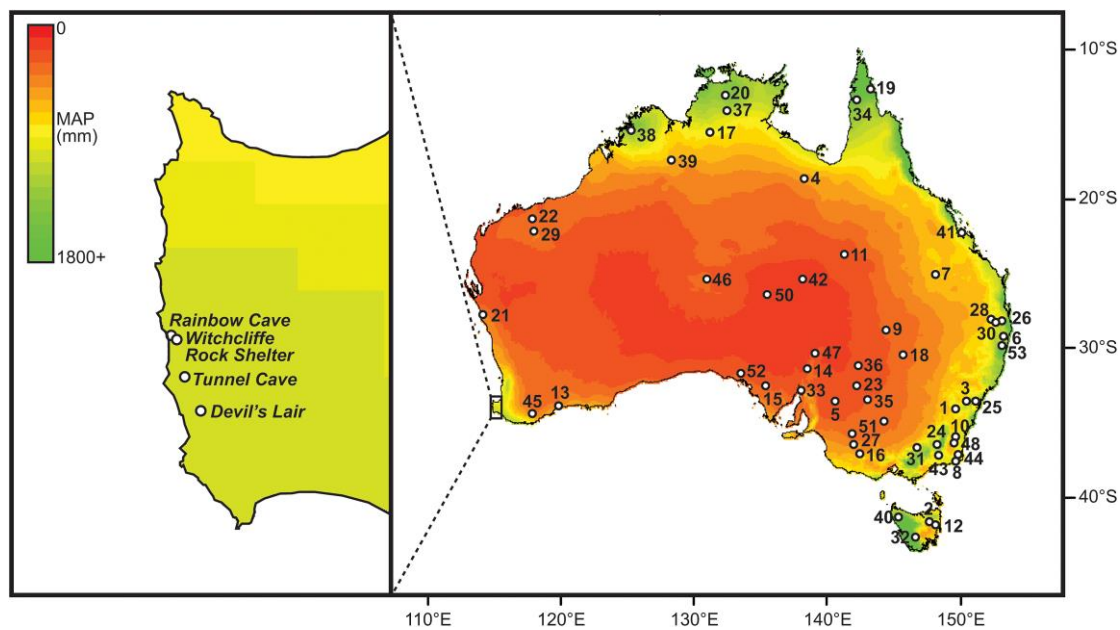


Figure 1

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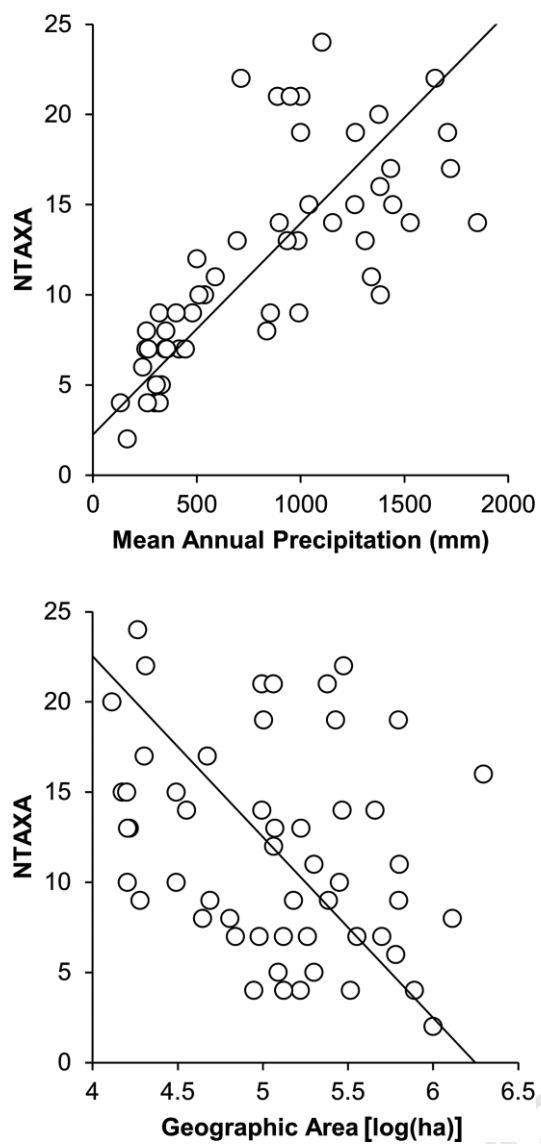


Figure 2

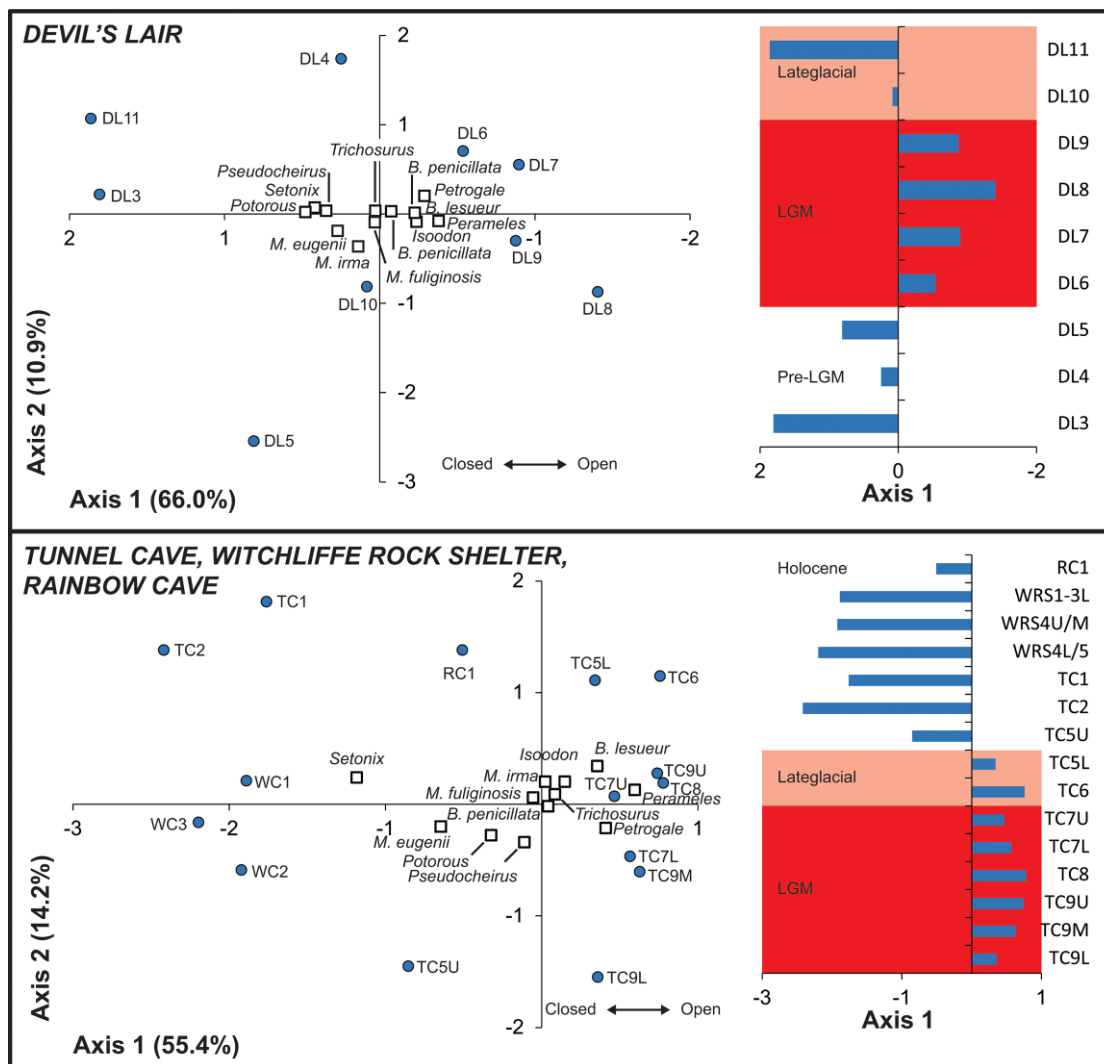


Figure 3

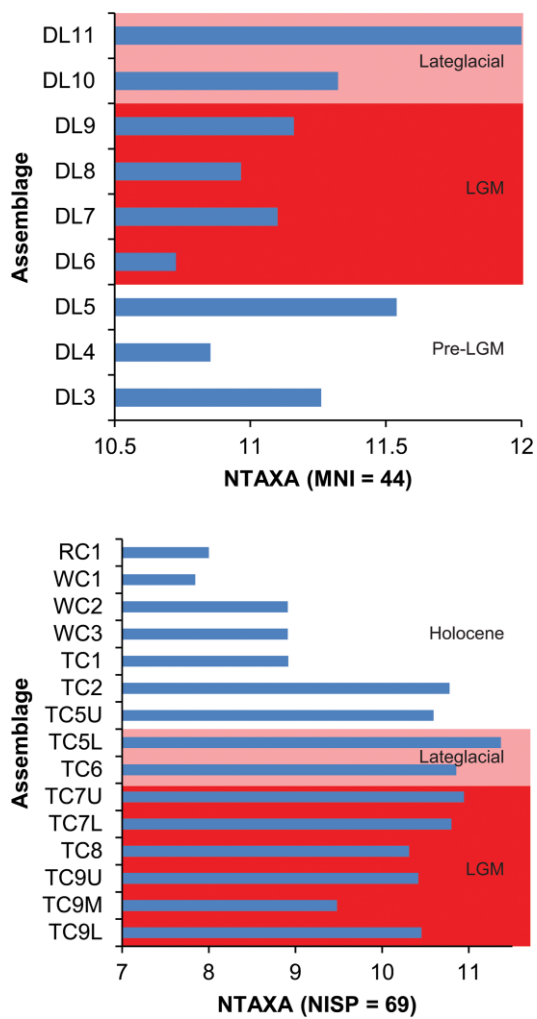


Figure 4