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Responses of Quaternary rainforest vertebrates to climate change in Australia

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Abstract

A new middle Pleistocene vertebrate fossil record from eastern Australia, dated by U disequilibrium series, records the first Quaternary record of an Australian tropical rainforest fauna. This exceptionally rich fauna underwent extinction after a long period of relative faunal stability, spanning several glacial cycles, and persisted probably until 280 000 years ago. Some time between 280 000 and 205 000 years ago the rainforest fauna was replaced by a xeric-adapted fauna. Since that time, the xeric-adapted fauna was replaced by a mesic-adapted fauna which was established by the Holocene. This is the first vertebrate faunal evidence in Australia of the middle Pleistocene Mid-Brunhes Climatic Event (MBE), a major climatic reorganisation that led to increased aridity in northern Australia from around 300 000 years ago. Several independent palaeoclimate proxies suggest that the climatic shift to aridity was due to increased climatic variability and weakened northern monsoons, which may be manifested in the extinction of the aseasonal rainforest fauna and its replacement by an arid-adapted fauna. We extend the temporal ranges of several taxa from the Pliocene into the middle Pleistocene. We also reveal a longer palaeobiogeographic connection of rainforest taxa and lineages shared between New Guinea and Australia than was previously thought and show that their extinction on mainland Australia occurred sometime after 280 000 years ago.

Keywords: Quaternary rainforest; palaeoclimate; U–Th dating; megafauna; Australia

1. Introduction

Understanding the influence of climate change on the biogeography, evolution and extinction of faunas is critical for development of conservation strategies for modern habitats under threat from climate change and human disturbance (Archer et al., 1991; Moritz et al., 2005). This is of particular importance in Australia, where intensified aridity has shaped large portions of the continent and where habitats, such as tropical rainforests, are considered to be under threat of extinction from climate change and human impact (Thomas et al., 2004; Williams et al., 2003; Williams and Hilbert, 2006).

In spite of progressively more detailed Quaternary palaeoclimatic and palynological records in the Australian

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region, there remains a fundamental gap in our knowledge of faunal response to past climate change. This is primarily due to the scarcity of accurately dated, temporally extensive fossil faunas that sample a variety of palaeoecologies. Australia, in particular, has a paucity of chronometrically dated sites and a complete absence of a Quaternary rainforest vertebrate fossil record.

The post-middle Miocene rainforest vertebrate fossil record from the Australopapuan region is extremely poor, possibly reflecting the onset of progressive continent-wide aridity in the late Miocene (McGowran et al., 2000; Archer et al., 1999; Greenwood and Christophel, 2005). A single vertebrate locality (Hamilton Local Fauna) from south-eastern Australia indicates the only mainland rainforest record dated to the Pliocene (Turnbull and Lundelius, 1970). Restriction of the Quaternary rainforest vertebrate fossil record to sites in New Guinea, even though Quaternary vertebrate fossil sites are found across mainland Australia, has led to the proposition that Australian rainforest habitats were close to their present refugial status before the end of the Pliocene (Archer et al., 1995).

In the absence of a Quaternary fossil record, studies of modern Australian rainforest faunas have resorted to combine palaeoclimate records inferred from pollen and isotope records (Winter, 1997; Nix and Switzer, 1991) with phylogeographies and molecular clocks inferred from genetic studies (Moritz et al., 2005; Schneider and Williams, 2005) to interpret the affects of Quaternary climate cycles on faunal biogeography.

Without direct evidence from a fossil record, these interpretations and hypotheses cannot be adequately tested. Furthermore, it is impossible without a fossil record to accurately infer the presence of extinct taxa, their ecological roles, and the mitigating circumstances that led to their extinction, climate or otherwise. The purpose of this paper is to document a globally rare palaeofauna (e.g. tropical rainforest), via a suite of Quaternary fossil deposits from a single locality in central-eastern Queensland, Australia, which span an interval of intense climate change and fill a major temporal gap in our knowledge of vertebrate faunas from northern Australia.

2. Methods

2.1. Geologic settings

Caves formed within isolated Devonian limestone massifs north of Rockhampton, central-eastern Queensland, were systematically surveyed for bone-bearing sediments and breccias (Fig. 1). Vertical and horizontal joints, dictated by the gross orientation of limestone strata and structural features, have produced very deep cave systems with vertical shaft entrances and large chambers (Shannon, 1970). Limestone quarrying on the northwest face of Mt Etna has exposed in cross-section the deep sediment-filled chambers of at least two cave systems, exposing extensive and abundant fossil remains and associated speleothems. Additional cave deposits occur in nearby karst, including Limestone Ridge, Olsen's Caves and Karst Glen (Fig. 1). Systematic collections and site descriptions are reported elsewhere (Hocknull, 2005) with additional information and amendments presented herein. Site sedimentology and taphonomy is summarised in Appendix A.

2.2. Thermal ionization mass spectrometry (TIMS) uranium-series dating

TIMS uranium-series dating was undertaken using analytical procedures described elsewhere (Zhao et al., 2001), except the known $^{236}U/^{233}U$ ratio in a $^{229}Th–^{233}U–^{236}U$ mixed spike was used for mass fractionation correction for the unknown samples. $^{234}U/^{238}U$ and $^{230Th}/^{238}U$ activity ratios of the samples are normalised to the corresponding ratios measured for the secular-equilibrium HU-1 standard and their ages calculated using half-lives of 75,380 years (^{230}Th) and 244,600 years (^{234}U).

Sites chosen for dating include those with minimal transportation and reworking of sediments and with available speleothem, either basal to, within, or capping the fossil deposit. Capping or basal flowstones yielding ages within the dating window were used to bracket deposit ages, with basal flowstone dates representing maximum ages and capping flowstone dates representing the minimum ages of the enclosed deposit. Ages outside the dating window were assigned an age of >500 thousand years (ka). Broken flowstones and straws incorporated within the deposits are considered to be maximum ages; the youngest of these from a given deposit was used to establish maximum bracket ages of that deposit.

Where speleothem was not available, bone, teeth, shell, and calcite fillings of these, were analysed. Calcite fillings in bones and teeth yield minimum ages of the fossils because the calcite grows within the specimens post deposition. The bones, teeth and shell are considered to yield minimum ages because U is taken up subsequent to deposition, and the system is most likely to be closed in respect to U loss after uptake. This interpretation was tested and substantiated by the dating of both the bone and calcite fillings within the bone, where we show that calcite yielded an older age than the

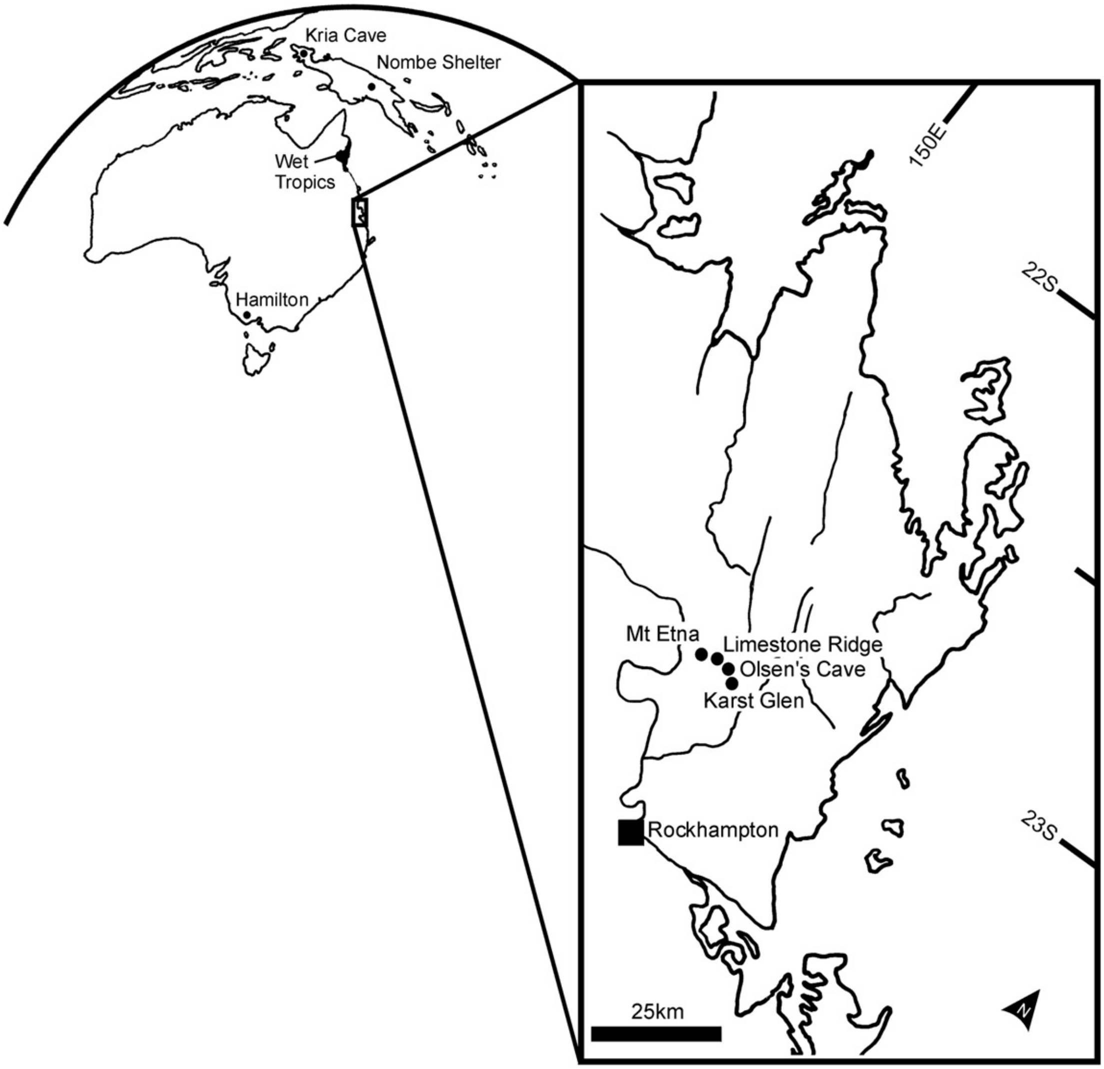

Fig. 1. Location of the post-Miocene Australopapuan rainforest vertebrate fossil record in relation to the present day Wet Tropics rainforests of north-eastern Australia, including the early Pliocene Hamilton fauna from south-eastern Australia, the Quaternary faunas from New Guinea and the eastern Australian Quaternary fauna presented herein.

bone (Table 1). Thus, U uptake in the bone occurred during or continued after calcite deposition. Therefore, the oldest age recovered using all of these materials was taken as the minimum age of the deposit.

2.3. Faunal analysis

Only non-volant vertebrate species of mammals, frogs and agamid lizards were used as proxies for habitat type. Fossils sharing generic and specific-level identity with living taxa were assumed to be representative of the habitat types and climates presently occupied by extant taxa and therefore are used as habitat proxies. All fossils used in the analyses are considered to represent species derived from proximal habitats to the fossil deposit; based primarily on the restricted foraging ranges of the two predator accumulators present in the deposits (Owl (*Tyto* sp.) and Ghost Bat (*Macroderma gigas*)) (Hocknull, 2005), and the pit-trap accumulation mode for non-volant, large-sized taxa. Cave entrances were all located high on exposed karst, with a single exception (Olsen's Cave), however, none of the sites possess fluvially transported sediments.

Analyses of faunal diversity and similarity include only mammalian taxa with body weight less than 3 kg (e.g. equal to, or smaller than, *Pseudochirops*), due to the body-size bias apparent in deposits derived predominantly from predator accumulators. Amounts of sediment sorted for vertebrate remains varied from site to site, ranging

Table 1
Representative U/Th dates for fossil sites at Mt Etna, central-eastern Queensland

QML	Locality	Sample name	Description	Age interpretation	(^{230}Th/^{232}Th)	Corr. ^{230}Th age (ka)	±2σ
Olsen's	Honey Moon Suite	ROK-07	*Petrogale* incisor	Min. age	33.7	6.3	0.2
Olsen's	Icicle Chamber	OC-07	Calcite cement	Close to real	19.3	7.6	0.2
1312	Elephant Hole Cave	ROK 10	Snail shell	Min. age	16.3	169	9
1312	Elephant Hole Cave	QML1312-6	Broken straw	Max. age	17.3	205	4
1313	Speaking Tube Cave	ROK02-4	Flowstone	Min. age	66.9	283	9
1313	Speaking Tube Cave	ROK02-5	Flowstone	Min. age	352	283	12
1383	Unit A	ROK F	Flowstone	Max. age of Unit A	31.0	419	28
1311	Deposit C/F contact	ROK04/04	Flowstone	Max. age of C	16.0	326	22
1311	Deposit C/F contact	ROK04/15	Flowstone	Mid flowstone	13.8	347	26
1311	Deposit C/F contact	ROK04/46	Flowstone	Min. age of F	24.6	432	54
1311	H deposit	ROK20-1 bone	Macropod bone	Min. age	5470	216	4
1311	H deposit	ROK20-4 cal	Calcite filling in bone	Min. age	749	454	48
1384	Lower Unit	ROK27 bone	Macropod bone	Min. age	1278	267	5
1384	Lower Unit	ROK27 cal	Calcite filling in bone	Min. age	38.6	332	14
1284	Mini Cave Layer A	MC/01	Capping flowstone	Min. age	92.6	284	9
1284	Layer B	MC-02 mid	Oldest flowstone	Max. age	22.3	484	85
1284	Layer J	MC-10	Youngest flowstone	Min. age	6.8	447	74

Note: Ratios in parentheses are activity ratios calculated from the atomic ratios. The ages are calculated using Ken Ludwig's Isoplot/EX program. Corr. and uncorr. denote corrected and uncorrected. The corrected ^{230}Th ages and initial (^{234}U/^{238}U) ratios include a negligible to small correction for non-radiogenic Th using average crustal ^{232}Th/^{238}U atomic ratio of 3.8±1.9 (^{230}Th, ^{234}U and ^{238}U are assumed to be in secular equilibrium).

from less than 0.1 m^3 to more than 4 m^3. Hence, relative abundances were not analysed (Appendix A).

Pair-wise, Euclidean cluster analysis of mammalian presence/absence data was utilised to determine the similarity of fossil faunas to one another and to known modern and fossil faunas from a broad range of habitat types. Generic-level mammal lists were generated from the literature and included taxa from hydric, mesic and xeric habitats, such as; tropical rainforest, dry vine forests, open-forests, open woodlands, heathlands, shrublands, grasslands and chenopod shrublands. Vegetation classifications follow Webb and Tracey (1981) for closed-forest vegetation (e.g. tropical rainforest, dry vine forest) and Specht (1981) for all other open vegetation types. Cluster analyses were performed using PAST software (Hammer et al., 2001).

3. Results

3.1. Faunal ages

Sites within the study area that have produced dated faunas range in age from ~7 ka to greater than 500 ka, at the limit of the uranium-series technique employed. Table 1 summarises site ages with a full listing and imagery available as supplementary materials in Appendix A.

Queensland Museum Locality (QML)1284 and QML1284a, considered to be the two oldest faunas, are located on Limestone Ridge, east of Mt Etna. QML1284 has been dated based on several *in situ* flowstone layers associated within the fossil beds. Layer B is stratigraphically the oldest and Layer J the youngest, with calcite fillings from within bone derived from the fossil bed in between flowstone layers G and H. Such dates, especially those for purer flowstone samples with higher U contents and higher ^{230}Th/^{232}Th activity ratios, (e.g. MC-02mid and MC-09) and thus more precise results, approximate the application limit (~500 ka) of the TIMS U-series dating method. The analytical precisions for the calcite fillings are poor due to small sample sizes and extremely low U, and thus the age results are only indicative, but they are consistent with the ~500 ka assignment for the site. The capping flowstone MC-01, which covers patches of the underlying fossil deposit, yields an age of 284±9 ka, suggesting that the fossil-bearing horizons were exposed in cross-section prior to ~280 ka. Subsequently a capping flowstone formed over this wall, which has once again been eroded to expose the underlying bone-bearing sediments. Fauna was collected in blocks from the wall and floor having come from the area bracketed by Layers B and G. QML1284a is located on open karst above and to the northwest of QML1284. QML1284a is considered to be older than QML1284 as it occurs in weathered karst terrain outside the main entrance to QML1284 indicating an older collapsed chamber (Hocknull, 2005).

QML1311H yielded a minimum age of 454±48 ka based on calcite infilling of bone and is directly below QML1311J which yielded a minimum age of 337±15 ka. Unfortunately the speleothem associated with QML1311H was too contaminated by detritus or decalcified to retrieve a reliable basal age. However, it is suspected to be close to the limits of U-series technique (~500 ka) because the speleothem of QML1311H contacts QML1311F, which has a minimum age of 432±54 ka.

A minimum age of QML1383A was obtained from a flowstone that divides the lower unit A from B (ROK F) and yielded a basal age of 419±28 ka. The base of the flowstone is inter-laminated within the top sediments of QML1383A. Therefore, speleothem deposition occurred as sedimentation was slowing down, and thus QML1383A fauna is considered to be close to the age of the flowstone's base.

Two sites were deposited at least 330 000 years ago: QML1311J and QML1384LU. QML1311J and QML1384LU are separate deposits located on the western side of Mt Etna. Both sites have yielded minimum ages close to 330–340 ka based on calcite fillings in bone (e.g. ROK24, ROK27 cal).

One site located on the western side of Mt Etna was deposited after 330 ka (QML1311C/D). QML1311C/D contacts with QML1311F deposit via a large continuous basal flowstone layer. The maximum age of QML1311C/D is based on the minimum age (326±22 ka) of the basal flowstone (ROK04/04), which is also supported by stratigraphically consistent dates for ROK04/15 and ROK04/46 (Table 1).

A capping flowstone of QML1313 provides a minimum age of 283±7 ka based on the weighted mean of two dates (ROK02-4 and 5). The base of the flowstone is inter-laminated with the uppermost centimetres of the bone-bearing sediment. Therefore, the flowstone is considered to have begun deposition as sedimentation rates decreased and not a considerable time after that. Thus, the fauna of QML1313 is considered to date close to 280 000 years old.

QML1312 was dated using bone, teeth, shell and incorporated pieces of broken flowstone and straw. The oldest age derived from bone, teeth and shell provided a minimum age for the deposit, whereas the youngest dated broken flowstone pieces and straw provided a maximum age. Thus the deposit dates between 169±9 ka (snail shell, ROK-10) and 205±4 ka (calcite straw, QML1312-6).

Floor sediments (0–10 cm) from within Icicle and Honey Moon Suite Chambers (Olsen's Cave) yielded a diverse subfossil fauna. Calcite cement was used to date the Icicle Chamber deposit, returning an age of 7.6±0.2 ka (OC-07), whilst macropod enamel returned an age of 6.3±0.2 ka (ROK-07) for the Honey Moon Suite

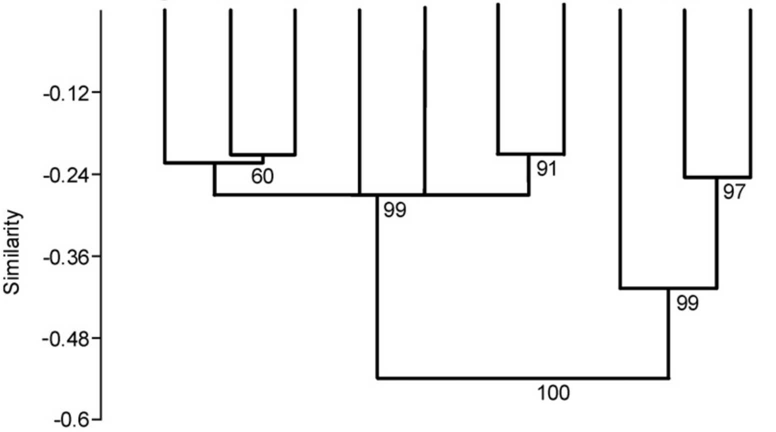

Fig. 2. Chronometrically constrained, bootstrapped, similarity cluster analysis of dated fossil and modern faunas of the present study.

Chamber deposit. Both deposits are considered to be Holocene in age.

3.2. Site faunal groupings

To test whether the chronology of deposits was consistent with the fossil faunas within them, a chronometrically constrained, bootstrapped, cluster analysis was performed using the dated faunas (Fig. 2). The analysis returned very strong support (99% bootstrap value) for two main clusters, those sites that are older than ~280 ka, and those sites that are younger than ~205 ka. Within the cluster of sites older than ~280 ka, there was very strong support (91%) for the position of deposits aged between ~280 ka and ~330 ka and good support (60%) for the position of deposits considered to be between ~450 ka and ~500 ka. The remaining sites, QML1384LU, QML1383A and QML1284a, were not faunally supported in their chronological position. This lack of support may reflect the presence of transitional faunas in the case of QML1383A where the age of this deposit is better defined, or incorrect chronological placement in the case of QML1384LU and QML1284a where we only have minimum ages. Within the sites younger than ~205 ka there was very strong support for the entire chronological sequence.

Similarities between fossil and modern faunas are summarised in a cluster analysis (Fig. 3). Three main faunal groupings are observed for modern habitats; 1) Faunas occurring in New Guinean and northern Australian hydric habitats (tropical rainforest), 2) Faunas occurring in Australian mesic habitats (dry vine forests to woodlands), and 3) Faunas occurring in Australian xeric habitats (open woodlands, arid grasslands and shrublands). Fossil faunas from the present study cluster amongst each of these three groupings.

All of the dated sites older than ~280 ka cluster together and with the New Guinean and northern Australian tropical rainforest faunas. Several fossil taxa of frogs, lizards and mammals are presently restricted to rainforest environments and are considered to be rainforest specialists (Table 2), which strongly supports the previous contention that these faunas represent a tropical rainforest habitat (Hocknull, 2005). The high diversity of mammalian arboreal folivores and hylid frog species reflects a palaeoecology with complex vegetative structure, whilst the presence of microhylid frogs and freshwater turtles indicates permanent water bodies (Hocknull, 2005).

A single fauna (QML1312), dated to between 205 and 170 ka, clusters with xeric habitats of central and southern Australia. These arid and semi-arid faunas occur in a great variety of habitats (e.g. Open woodlands, hummock grasslands, tussock grasslands and chenopod shrublands). Several of the taxa present in this deposit are considered to be arid-adapted taxa that specialise in arid habitats (Table 2). Contrary to the dominant arid/semi-arid signal, a

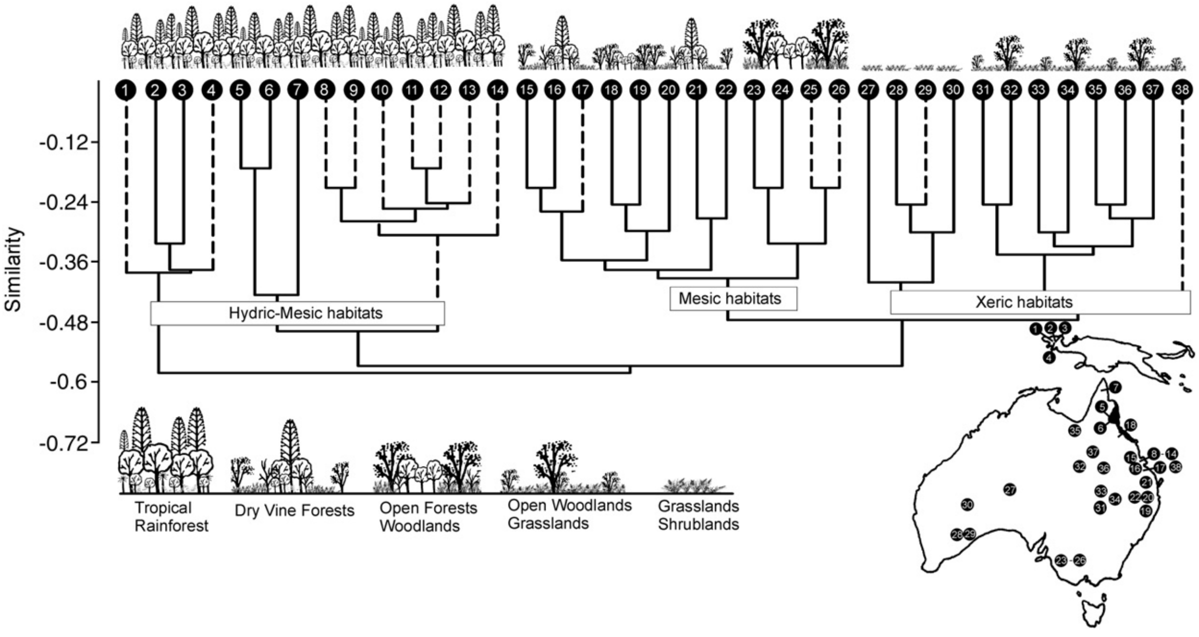

Fig. 3. Similarity cluster analysis of modern and fossil faunas associated with hydric (1–14), mesic (15–26) and xeric (27–38) habitats. Dashed lines indicate fossil faunas. Site locations and references are provided as a supplementary table in Appendix A.

Table 2
Middle Pleistocene fossil taxa considered to be rainforest or arid specialists with the annual precipitation range* of their closest living relatives

Rainforest taxa

Taxon	Closest living relative	Rainforest location	Annual precipitation (mm)*
Cercartetus sp.	*Cercartetus caudatus*	WT/New Guinea (NG)	1879–3060
Dactylopsila sp. 1	*Dactylopsila palpator*	NG	1091–5544
Dactylopsila sp. 2	*Dactylopsila kambuayai*	NG (Holocene)	Montane
Dendrolagus sp. 1	*Dendrolagus matschiei*	NG	1261–3644
Dendrolagus sp. 2	*Dendrolagus* spp.	NG	1261–3644
Dendrolagus sp. 3	*Dendrolagus* spp.	NG	1261–3644
Dendrolagus sp. 4	*Dendrolagus* spp.	NG	1261–3644
Hypsilurus sp.	*Hypsilurus* spp.	NG/WT/Southeast QLD (SEQ)	1074–5427
Kyarranus spp.	*Kyarranus* spp.	SEQ	1092–2110
Lechriodus spp.	*Lechriodus* spp.	SEQ/NG	1301–2074
Microhylids	Microhylids	WT/NG	1017–4005
Nyctimystes spp.	*Nyctimystes* spp.	WT/NG	1099–6795
Petauroides sp. 1	*Petauroides ayamaruensis*	NG (Holocene)	Montane
Petauroides sp. 2	*Petauroides ayamaruensis*	NG (Holocene)	Montane
Petauroides sp. 3	*Petauroides ayamaruensis*	NG (Holocene)	Montane
Phalanger sp. 1	*Phalanger gymnotis*	NG	2119–6580
Phalanger sp. 2	*Phalanger* spp.	NG	1706–6580
Pogonomys sp.	*Pogonomys* spp.	WT/NG	1675–5692
Pseudochirops sp 1.	*Pseudochirops* spp.	WT/NG	1261–5544
Pseudochirops sp. 2	*Pseudochirops* spp.	NG	1261–5544
Pseudochirops sp. 3	*Pseudochirops* spp.	NG	1261–5544
Pseudochirulus sp 1.	*Pseudochirulus canescens/mayeri*	NG	2722–5544
Pseudochirulus sp. 2	*Pseudochirulus forbesi*	NG	1296–5544
Pseudochirulus sp. 3	*Pseudochirulus* spp.	WT/NG	1296–5544
Thylogale sp. (small)	*Thylogale christenseni*	NG (Holocene)	Montane
Uromys sp.	*Uromys hadrourus*	WT	1211–3436

Arid taxa

Taxon	Closest living relative	Annual precipitation (mm)[a]
Chaeropus ecaudatus	*Chaeropus ecaudatus*	144–333
Macrotis lagotis	*Macrotis lagotis*	132–722
Notomys spp.	*Notomys* spp.	129–1273
Perameles bouganville	*Perameles bouganville*	208–391
Planigale sp. 2	*Planigale tenurostris*	140–743
Pogona sp.	*Pogona minor/michelli*	163–996
Sminthopsis macroura	*Sminthopsis macroura*	129–996
Tympanocryptis sp.	*Tympanocryptis cephalus*	181–539

[a] Annual precipitation range (mm) was determined for closest living relatives by using DIVA-GIS 5.2 bioclimatic software (Hijmans et al., 2005) and taxon distribution data taken from OZCAM BioMaps online databases (OZCAM community, 2006).

proportion of the fauna does not occur in these dry regions today and are indicative of more mesic environments. For example, a single calcaneum represents a species of *Dendrolagus*, an arboreal rainforest-dwelling macropod, and as it is unlikely to be reworked, the taxon was rare but present in the surrounding habitat. The presence of this, and other arboreal taxa, indicates that treed habitat occurred proximal to the cave entrance, possibly in the form of a refugium.

Two fossil faunas (Icicle Chamber and Honey Moon Suite Chamber) cluster with the modern mesic habitat in the study area, which includes grassy open-forests with refugial dry vine forests (semi-evergreen vine-thickets). This is not surprising as both deposits are considered to be Holocene in age.

3.3. Faunal succession

The middle Pleistocene is characterised by two distinct faunas; 1) a tropical rainforest fauna that existed at least between 500 ka and ~280 ka ago, spanning three glacial cycles from Marine Isotope Stage (MIS) 8 through MIS13, and 2) a xeric-adapted fauna with refugial elements, dated to 205–170 ka ago. Sites considered to represent the latest Pleistocene are yet to be adequately dated and will be the focus of future work. Holocene sites are characterised by a typically modern mesic-adapted fauna.

Approximately 50% reduction in species richness of small to medium-sized mammal species was observed between the older rainforest faunas (>280 ka; 28–35spp.) and those of the Holocene and present day (16–12spp. respectively) (Fig. 4a). This reduction in species richness is not considered to be an artefact of taphonomy or collection size because deposits with similar accumulation modes and collection sizes show markedly different species richness [e.g., QML1284 (30spp.) vs. Icicle Chamber (16spp.)].

Furthermore, the middle Pleistocene deposits that preserve large to megafaunal-sized mammalian taxa illustrate a similar massive reduction in species richness compared to the present day fauna at Mt Etna. The reduction includes the total extinction of megafaunal species (>100 kg) and a reduction of more than 50% species richness for both large-sized (3–15 kg) and very large-sized (15–100 kg) mammalian species.

Although the overall species richness of mammals decreased by more than 50% since the middle Pleistocene to present day levels, the loss and replacement of taxa was at times proportionally much greater. Loss of taxa in deposits dated between >500 ka and ~280 ka was low, varying between 0 and 13%, whilst replacement with new taxa was similarly low (0–14%), suggesting a relatively low rate of faunal turnover and a stable level of species richness for over 200 000 years (Fig. 4a). Between ~280 ka and ~205 ka major faunal reductions occurred with the loss of over 80% of small to medium-sized mammalian taxa (Fig. 4c). Losses also occurred in frog and lizard faunas with local extinction of the lizard *Hypsilurus* and the frogs, *Crinia*, *Etnabatrachus*, *Kyarranus*, *Lechriodus*, *Nyctimystes* and microhylids. Replacement of new mammalian taxa was proportionally lower than species losses, but it was still very high at over 75% (Fig. 4b), which accounts for the overall decrease in species richness from 33 to 21spp. Frog species richness decreased overall with replacement by some new forms, such as *Cyclorana* and *Neobatrachus*. Lizard species richness increased with appearance of new xeric-adapted taxa, including *Amphibolurus*, *Tympanocryptis* and *Pogona*.

The local extinction of more than 65% of small to medium-sized mammalian species occurred between the youngest middle Pleistocene fauna (205–170 ka) and the Holocene fauna (<10 ka). Replacement with new species was low, approximately 38%, which accounts for another drop in overall species richness from 21 to 13spp. (Fig. 4a). Frog and lizard species richness remained relatively stable over this period of time, but the three agamids present at 205–170 ka were replaced by three others, *Pogona barbata*, *Chlamydosaurus kingii* and *Diporiphora bilineata*.

3.4. Speleothem formation

U–Th isotopic data for all speleothems (e.g., *in situ* and broken flowstones and straws, and calcite fillings)

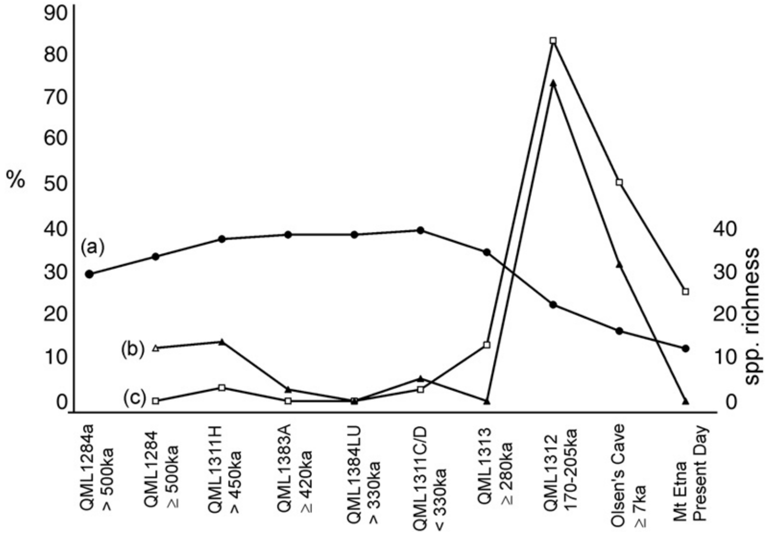

Fig. 4. Species richness and faunal turnover through time for medium and small-sized mammal species for the study area. (a) species richness (count of spp.), (b) percentage of new species, (c) percentage of species loss.

are listed in Appendix A, where a ^{230}Th/^{238}U vs. ^{234}U/^{238}U evolution diagram is illustrated. The data from the Mt Etna sites show that (1) the growth of all such speleothems occurred mainly during interglacials or interstadials, consistent with relatively wetter climatic conditions during those times; and (2) 23 (or more than 68%) of the 34 dated Pleistocene speleothem samples (randomly collected) are older than 300 ka, implying that climate conditions were wetter and more favourable for speleothem development prior to 300 ka. Indeed, most of the >300 ka speleothems are either *in situ* or broken flowstones that are volumetrically more significant than those younger than 300 ka, which are mainly calcite fillings or capping flowstones.

4. Discussion

4.1. Implications for biocorrelation

The present sites previously were interpreted as a suite of early Pliocene, Plio-Pleistocene and Holocene sites, and the rainforest assemblages were considered to be Pliocene in age on the basis of biocorrelation (Hocknull, 2005). Biocorrelation of these sites was based primarily on the very few chronometrically dated Pliocene sites in Australia. Since that time, several of the Pliocene-aged taxa that were once considered robust markers are now recorded in younger early Pleistocene sites (Piper, 2007).

Likewise, the new radiometric dates presented here extend the temporal ranges of several taxa into the middle Pleistocene. In particular, we present the youngest Australian records for the following taxa: *Pseudokoala* (Early Pliocene–early Pleistocene), '*Petauroides*' (Early Pliocene) *Kurrabi* (Pliocene), *Thylacoleo hilli* (Miocene–early Pleistocene), *Palorchestes* cf. *P. pickeringi* (Early Pliocene–early Pleistocene) and *Protemnodon* cf. *P. devisi* (Pliocene). In addition this study fills a significant gap in the Australian fossil record of extant vertebrate lineages with a fossil record previously restricted to the Oligo-Miocene and Pliocene; such as *Dactylopsila*, *Dendrolagus*, *Pseudochirops*, *Kyarranus* and *Lechriodus*. Moreover, we provide the first fossil record in Australia for several extant lineages; such as *Pseudochirulus*, *Pogonomys*, *Uromys*, *Mesembriomys*, *Hypsilurus* and *Nyctimystes.*

One important implication of these results is that other sites in Australia that have been dated only on the basis of biocorrelation may have incorrectly assigned ages. Importantly, it illustrates the need for, 1) a more robust biocorrelative synthesis of the temporal and geographic ranges of Australian Neogene vertebrate taxa and 2) more extensive chronometric dating of Neogene sites.

4.2. Responses of middle Pleistocene vertebrate faunas to climate change

Understanding the responses of middle Pleistocene vertebrate communities to Quaternary climate change is of crucial importance when attempting to infer the affects of late Pleistocene climate change on fauna without the superimposition of anthropogenic activities. Well-dated and faunally rich middle Pleistocene faunas from Australia are rare with three exceptions—two localities from southern Australia, Naracoorte (Moriarty et al., 2000; Prideaux et al., 2007b) and Nullarbor Caves (Prideaux et al., 2007a) and the present study area (Fig. 5).

The Cathedral Cave record from the Naracoorte Caves World Heritage Area, South Australia, is of particular importance because it spans a similar timeframe to the present study (Prideaux et al., 2007b). Demonstrated faunal stability at Naracoorte during the middle Pleistocene suggests that the influence of glacial cycles at that time were not severe enough to cause extinctions there. However, it was shown that relative abundance and community composition did fluctuate with climate (Prideaux et al., 2007b). Furthermore, a large proportion of the modern non-megafaunal taxa found in the area today are the same taxa found in the middle Pleistocene deposits, suggesting that faunal stability continued throughout the middle and late Pleistocene to the present day. These results inferred a faunal resilience to climate change in southern Australia. This trend is also suggested for the fossil record from the Nullarbor Caves (Prideaux et al., 2007a). We corroborate this faunal stability in the faunal cluster analysis where middle Pleistocene faunas from the Naracoorte and Nullarbor caves cluster most closely with their respective modern day faunas (Fig. 3).

The faunal succession documented in southern Australia contrasts with that documented here, where after an interval of faunal stability for over 200 000 years, a major faunal turnover occurred, which replaced the majority of taxa present in the area prior to 280 ka. Since before 500 ka until ~280 ka, the Mt Etna area possessed a diverse tropical rainforest habitat. However, between ~280 ka and ~205 ka large proportions of the vertebrate fauna were driven locally extinct, being replaced by a xeric-adapted fauna. The presence of xeric-adapted taxa indicates a marked drop in precipitation during the faunal turnover at Mt Etna, presumably a greater reduction in precipitation than what had occurred during previous glacials. Interestingly, this period of faunal turnover and reduced precipitation approximates a period of aridity observed at Naracoorte (270–220 ka) indicated by both speleothems and local faunal

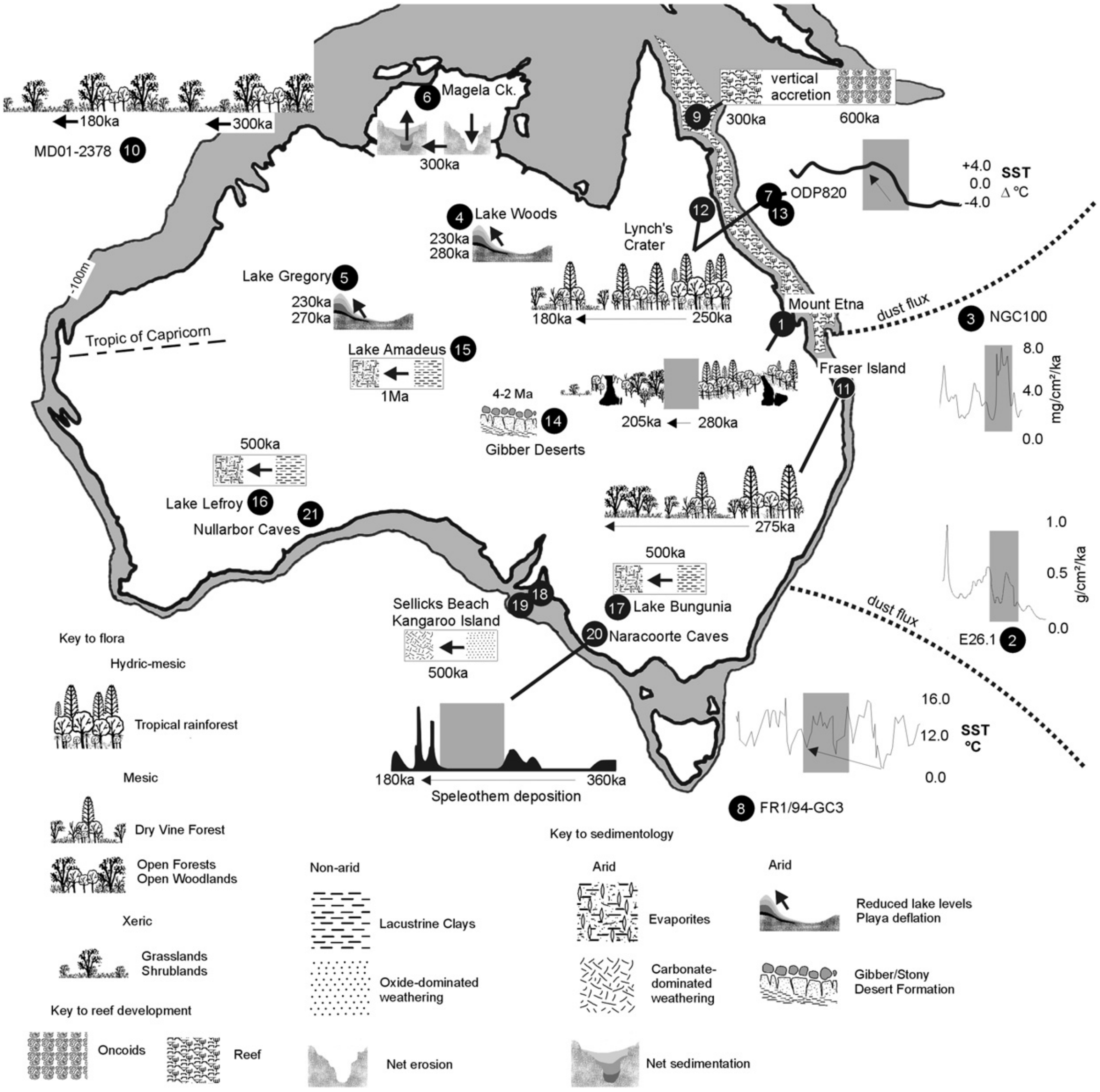

Fig. 5. Australia's middle Pleistocene palaeoclimatic record showing the differential timing of the shift to intensifying aridity and climatic variability in northern, central and southern Australia. The vertical grey bar represents the time of faunal turnover during the middle Pleistocene at Mt Etna (~280–205 ka). 1–13. Intensifying aridity in northern Australia since ~300 ka; 1. Mt Etna faunal turnover, 2–3. Aeolian dust records from the Tasman (Hesse, 1994) and Coral Seas (Kawahata, 2002), 4–5. Lake level reduction and playa deflation (Bowler et al., 2001), 6. Magela Ck. net sedimentation post 300 ka (Nanson et al., 1993), 7–9. Sea Surface Temperature (SST) increase along the East Australian Current with reef development (Peerdeman et al., 1993; Isern et al., 1996; Pelejero et al., 2006; International Consortium for Great Barrier Reef Drilling, 2001; Webster and Davies, 2003), 10–13. Palynological records from northwest Australia (Kawamura et al., 2006; Longmore and Heijnis, 1999; Moss and Kershaw, 2007). 14–15. Intensifying aridity in central Australia since 4 Ma; 14. Gibber–Stony desert formation (Fujioka et al., 2005), 15. Lake Amadeus arid shift (Chen and Barton, 1991). 16–20. Intensifying aridity in southern Australia since ~600 ka; 16–17. Southern lakes shift to aridity (Bowler, 1981; An et al., 1986; Stephenson, 1986; Zheng et al., 2002; English et al., 2001), 18–19. Southern weathering shift to aridity (Pillans and Bourman, 2001), 20. Dry phase between 270 and 220 ka at the Naracoorte Caves recorded from speleothems (Moriarty et al., 2000; Prideaux et al., 2007a).

composition (Prideaux et al., 2007b). The striking difference between the northern and southern records is that the northern non-megafaunal fauna was driven extinct during this arid event, whilst the southern non-megafaunal fauna was resilient through to the present day.

Sometime after ~205–170 ka the xeric-adapted taxa were lost, and by the Holocene (~7 ka) a more mesic fauna had established. The late Pleistocene record for Mt Etna is not securely dated and thus the record is missing the last two glacial maxima, a time of extreme climatic change (EPIC Community Members, 2004) the arrival of humans and extinction of megafauna (Wroe et al., 2004). Therefore, the Holocene mesic fauna most likely represents the local habitat returning to an interglacial state and may reflect one of many faunal changes since the middle Pleistocene. The return to mesic conditions did not result in the return of the wet-adapted fauna present prior to ~280 ka.

The interval for the major faunal turnover at Mt Etna (~280–205 ka) occurred during an hypothesised shift towards greater El Niño–Southern Oscillation (ENSO) variability (Kershaw et al., 2003a) and a weakening of the northern monsoon (Kawamura et al., 2006), culminating in intensifying aridity throughout northern Australia (Fig. 5). Our data support a large body of accumulating evidence for a long-term shift towards increasing aridity overlain on a more abrupt shift to greater amplitude of climatic change in individual glacial cycles initiated at the mid-Brunhes Climate Event (MBE) (~430–300 ka).

Dome C (Antarctica) ice core data show a strong contrast in climate before and after ~430 ka (MBE) (EPIC Community Members, 2004). The ice core δD‰ data show an overall warming trend after ~430 ka and much higher amplitude swings in glacial–interglacial temperatures, suggesting a less equable climate after ~430 ka. Dust records also show increasing dust volume at glacial maxima after ~430 ka (EPIC Community Members, 2004).

Sediment core data from MD97-2140 (de Garidel-Thoron et al., 2005), Western Pacific, show greater amplitude and closer swings in Sea Surface Temperatures (SST) between glacial and interglacials after ~450 ka. Sediment core data from Ocean Drilling Program (ODP) hole 806B (Medina-Elizalde and Lea, 2005), Western Pacific, also show greater amplitude swings in glacial–interglacial SST after around 450 ka.

Records of terrigenous dust transported by aeolian processes into the Indian Ocean (SO-14-08-05) (Hesse and McTainsh, 2003), Tasman Sea (E26.1 core) (Hesse, 1994) and Coral Sea (GR100 core) (Kawahata, 2002) all suggest increased aridity in Australia after 350 ka, with particular peaks after 300 ka, 200 ka and 50 ka.

The Lake Woods and Gregory basins illustrate increased aridity through the progressive reduction of lake sizes and development of playas and lunettes since 300 ka (Bowler et al., 2001). Magela Ck., Northern Territory records a shift to aridity after 300 ka by a net increase in sedimentation throughout the tributary after a long period of incision and sediment evacuation (Nanson et al., 1993). Such a shift is consistent with a decrease in long-term discharge.

SSTs over the last 800 000 years or so have been reconstructed for the western Coral (Peerdeman et al., 1993; Davies and Peerdeman, 1998; Lawrence and Herbert, 2005; Isern et al., 1996) and Tasman Seas (Pelejero et al., 2006), illustrating an increase in SST leading up to, and during, the period of faunal turnover. This suggests that the SST along the entire East Australian Current was rising at the time, and rising SST has been invoked as evidence for the onset of ENSO activity (Kershaw et al., 2003a, 2005). Although increased SST does not indicate mainland aridity directly, increased ENSO activity would produce a climatic variability not conducive for rainforest habitat, which requires a relatively aseasonal climate (Nix, 1982). Timing of initiation of the growth of the Great Barrier Reef supports the increases in Coral Sea SSTs that are inferred from δ^{18}O records and may be associated with the initiation of the western Pacific warm pool (Kershaw et al., 2003b; International Consortium for Great Barrier Reef Drilling, 2001). Intermittent carbonate deposition dominated by coralline algal facies began in outer shelf regions around 600±280 ka, but true vertically accreting reef facies only began to accumulate between 452 and 365 ka (International Consortium for Great Barrier Reef Drilling, 2001; Webster and Davies, 2003). Thus, initiation of true reef growth may coincide with an increase in Coral Sea SST.

Palynological records from northern Australia indicate a progressive increase in open-arid vegetation, beginning ~300 ka and intensifying further since ~180 ka (Kawamura et al., 2006). Pollen records to the south (Longmore and Heijnis, 1999) and north (Moss and Kershaw, 2007) of the study site record shifts from rainforest taxa to drier-land taxa reflecting increased aridity from ~275 ka and ~250 ka ago respectively.

We hypothesise that the trend toward drier and more variable climate ~300–200 ka ago in northern Australia made rainforest habitats unsustainable in central-eastern Queensland, particularly during the increasingly dry glacial maxima, and that pattern contrasts strongly with earlier long periods of more equable climates and relative faunal stability.

In contrast, southern and central Australia experienced increased aridity earlier than northern Australia with records showing aridification starting from 600–500 ka in southern regions and as early as 4–2 million years ago (Ma) in central regions.

In central Australia, Gibber and Stony Deserts were formed 4–2 Ma (Fujioka et al., 2005), whilst Lake

Amadeus underwent an arid shift from uniform lacustrine clays to evaporites and dunes after ~1.2–1.0 Ma (Jansen et al., 1986; Chen and Barton, 1991; Bowler, 1981).

In the south, Lake Bungunnia underwent an arid shift from lacustrine clays to saline clays and dunes after ~600 ka (Jansen et al., 1986; An et al., 1986; Stephenson, 1986). Lake Lefroy preserves evidence of an arid shift from freshwater clays to evaporitic gypsum-dominated sediments around 500 ka (Jansen et al., 1986; Zheng et al., 2002). Lake Lewis underwent a shift from uniform lacustrine clays to more heterogenous deposits representing greater aridity and fluctuating salinity (between 600 and 500 ka) (Jansen et al., 1986; English et al., 2001). Sellicks Beach and Kangaroo Island preserve weathered dune systems that show a change to aridity 600–500 ka ago characterised by oxide-weathering zones changing to carbonate-weathering zones (Pillans and Bourman, 2001).

The faunal stability demonstrated at Naracoorte throughout the middle Pleistocene to present day for non-megafaunal taxa may reflect a prolonged adaptation to this earlier onset of climatic variability and aridity, where entire faunal assemblages became resilient to increased climatic variability. Conversely, northern faunas responding to a later onset of aridity would not have had as much time to adapt to a new climatic regime, and as such, may remain relatively unstable to change, climate or otherwise.

4.3. Implications for megafaunal extinction hypotheses

We provide the first direct evidence of Quaternary rainforest megafauna in Australia. Therefore, any hypotheses of megafaunal extinction must take into account their extinction from rainforest habitats. Evidence will need to determine whether the reduction of rainforest habitat to its present state was primarily due to pre-human climate change and that this was sufficient to drive the megafauna extinct from rainforest habitat, or whether the addition of human hunting and habitat modification was necessary to tip the balance.

Faunal stability throughout the middle-late Pleistocene, during periods of climate change and prior to human arrival, has been used to argue against climate change as a mitigating factor in the extinction of the late Pleistocene megafauna (Prideaux et al., 2007a,b). It is argued that the southern faunas, including megafauna, were resilient to climate change and thus the extinction of megafauna must have included other factors, of which anthropogenic impacts are favoured (Prideaux et al., 2007a,b).

Our results cannot preclude climate change, in particular increased climatic variability and aridity, as a mitigating factor in the extinction of Pleistocene fauna in northern Australia. Although we are yet to determine the direct affects of climate change on megafaunal species, we argue that the climate changes during the middle, and presumably late Pleistocene, in northern Australia dramatically influenced the composition and stability of both the flora and fauna before first human occupation ~50 ka. Hence, the response of fauna and flora to climate change and the impacts of human occupation may have been very different in different regions of Australia owing to differential timing of major climate-induced habitat modifications.

4.4. Palaeobiogeographic implications

The middle Pleistocene rainforest faunas of Mt Etna provide new data on the paleobiogeography of taxa endemic to the tropical rainforests of New Guinea and the Wet Tropics bioregion of Australia. Of particular interest are the small, herbivorous, arboreal and terrestrial mammals that are common in Holocene deposits and in extant montane rainforests throughout New Guinea (e.g. †*Thylogale christenseni*, *Thylogale calabyi*, †*Dactylopsila kambuyai*, †‘*Petauroides*’ *ayamauruensis* and *Pseudochirulus mayeri* (Flannery, 1995; Hope et al., 1993; Aplin et al., 1999)). These small-bodied taxa are absent from the existing Wet Tropics rainforests of northern Australia, however, closely related taxa are found approximately 800 kms to the south of the Wet Tropics in the middle Pleistocene deposits at Mt Etna (Hocknull, 2005). This indicates that they were present in Australia during the Pleistocene, however, were driven extinct on mainland Australia sometime after ~280 ka.

Similarly, middle Pleistocene species of possum (*Pseudochirulus* and *Phalanger*) and tree-kangaroo (*Dendrolagus* “short-foot” clade) from Mt Etna share closer phylogenetic relationships with New Guinean taxa than they do with extant Wet Tropics taxa, suggesting that they too were driven extinct on mainland Australia after ~280 ka. Therefore, the continental extinction of several taxa, including entire guilds, and not just those that were megafauna, occurred within Australian rainforests during the Pleistocene.

Palaeoclimatic models have been used to hypothesise relatively recent (i.e. 7500–6000 years ago) arrivals of New Guinean taxa into the Wet Tropics region (e.g. *Cercartetus caudatus*, *Dactylopsila trivirigata*, *Uromys caudimaculatus*, and *Pogonomys mollipilosus*) (Winter, 1997). However, species from each of these genera occur in the middle Pleistocene of Mt Etna, and, with the exception of *Uromys* sp., none of them are considered to be conspecific with modern forms. This suggests a complex interchange of faunas between New Guinea and Australia during the Quaternary, with the current "New Guinea species" in the Wet Tropics representing one of at least two possible invasions, the first arriving before the middle Pleistocene and reaching as far south as Rockhampton. Alternatively, "New Guinea species" that presently occur in the Wet Tropics may share a refugial status with the Wet Tropics endemics, representing species and/or lineages present on mainland Australia for much longer than previously was thought.

The Wet Tropics bioregion possesses a group of mammals that are not present in either New Guinea or the middle Pleistocene sites of Mt Etna (e.g. *Hypsiprymnodon*, *Bettongia* and *Hemibelideus*). The absence of these mammals from the Mt Etna deposits is an enigma and cannot be explained taphonomically because collecting has been thorough and similarly-sized taxa are found in abundance in most of the deposits. Each of these three genera represent deeply divergent clades (Archer et al., 1999), two of which are rainforest specialists (*Hypsiprymnodon* and *Hemibelideus* (Winter, 1997)), and two possess a long fossil record associated with interpreted rainforest palaeoecologies (i.e. *Hypsiprymnodon* and *Bettongia* (Oligo-Pliocene) (Archer et al., 1999)). Likewise, *Dorcopsis*, now endemic to New Guinea has an early Pliocene record in Australia, however, it is absent from the middle Pleistocene deposits at Mt Etna (Turnbull and Lundelius, 1970)). Thus, the middle Pleistocene rainforest faunas at Mt Etna represent a mixture of taxa that are now differentially isolated in New Guinea and the Wet Tropics. This mixture has included or excluded taxa with long histories associated with rainforests, illustrating the complex taxonomic filters operating in Australopapuan rainforests throughout the Neogene. The extinct rainforest assemblage presented here illustrates a diversity of taxa and guilds unlike that found in present day Australian tropical rainforests. These results emphasise the dominance of extinction, via climate change, as the major driving force in shaping Australia's present day tropical rainforest faunas.

5. Conclusions

Fossiliferous cave deposits from Mt Etna, central-eastern Queensland represent the only Quaternary rainforest vertebrate fossil record known in Australia. The deposits were previously thought to be Pliocene in age based on biocorrelation, but direct chronometic dating has revealed that most of these sites are in fact middle Pleistocene in age, dating from before 500 ka to approximately 280 ka. This result extends the temporal range of several Pliocene and early Pleistocene taxa into the middle Pleistocene.

After a long period of relative faunal stability at Mt Etna, a major faunal turnover occurred between ~280 ka and ~205 ka, wherein a diverse rainforest fauna was replaced by a xeric-adapted fauna, lending the first vertebrate fossil evidence to the large-scale climatic shifts to aridity in northern Australia, documented by numerous other palaeoclimatic methods. At least one more faunal change occurred since that time to produce the Holocene and modern mesic-adapted fauna, which we suggest is a continued response of northern Australian habitats to the sustained shift to increased climatic variability. However, additional anthropogenic influences are not ruled out in the most recent faunal changes.

These results contrast with Quaternary records from southern Australia which show remarkable faunal stability over the last 500 ka for non-megafaunal taxa. That stability may reflect long-term adaptation to increasing aridity, which began earlier in southern Australia.

Our results illustrate the presence of a suite of rainforest taxa without any present day Australian representative and indicate a longer connectivity between the faunas of northern Australia and New Guinea than previously was thought. Understanding the causes for the extinction of these taxa on mainland Australia is fundamental when considering the vulnerabilities of present day rainforest taxa in far north Queensland, a bioregion under several climatic and human induced threats.

We demonstrate here that Quaternary climate change influenced regions of the Australian continent in different ways over a similar period of time and to a degree previously not recorded. Although this is in itself an intuitive statement, it does illustrate the inherent complexity in determining what the responses of fauna and flora to climate change may be in the future.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.epsl.2007.10.004.

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