



Quantitative reconstruction of Early Pleistocene climate in southeastern Australia and implications for atmospheric circulation

J.M.K. Sniderman^{a,*}, N. Porch^b, A.P. Kershaw^a

^aSchool of Geography and Environmental Science, Monash University, Wellington Road, Monash, Victoria 3800, Australia

^bDepartment of Archaeology and Natural History, Research School of Pacific and Asian Studies, Australian National University, Canberra, ACT 0200, Australia

ARTICLE INFO

Article history:

Received 8 April 2009

Received in revised form

4 August 2009

Accepted 5 August 2009

ABSTRACT

Today, southeastern Australia experiences a winter-dominated rainfall regime, governed by the seasonal migration of the highly zonal Southern Hemisphere subtropical anticyclone. The late Cenozoic history of this rainfall regime is poorly understood, but it has been widely accepted that its onset was a product of the intensification and northward migration of the subtropical anticyclone, driven by steepening of hemispheric temperature gradients associated with the initiation of extensive Northern Hemisphere glaciation, ~2.6 million years ago (Ma). Here, we use fossil beetle remains from Stony Creek Basin, a small palaeolake record in upland southeastern Australia deposited over ~280,000 years between ~1.84 and 1.56 Ma, to quantitatively reconstruct regional climate during the Early Pleistocene. Climate reconstructions based on coexistence of extant beetle taxa indicate that temperatures were consistently 1–3 °C warmer than present, and rainfall as high as or substantially higher than today, throughout the record. In particular, beetle data indicate that rainfall was similar to today during winter, but 2–2.4 times higher than today during summer. This is consistent with the presence of diverse rainforest pollen also present in the record, and indicates that the modern, winter-dominated rainfall regime was not yet in place by ~1.5 Ma, at least one million years later than previously thought. We suggest that the Southern Hemisphere anticyclonic circulation must have been much less intense during the Early Pleistocene than today, rather than shifted meridionally as previously argued.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Southern Australian climate is dominated at present by the seasonal migration of the anticyclonic subtropical high, the synoptic scale manifestation of the descending limb of the Hadley circulation (Hobbs, 1999). During austral winter, the subtropical high occupies its most northerly position over the Australian continent (Fig. 1). This directs dry easterly trade winds over the north of the continent, while frontal lows embedded within the mid-latitude westerlies are directed over southern Australia, which experiences its wet season. During austral summer, in response to a decreased hemispheric temperature gradient, the subtropical high migrates poleward, occupying a position near Australia's southern margin. This migration permits the southerly penetration of the intertropical convergence zone, bringing monsoon rains to Australia's north. At the same time, subsiding air beneath the anticyclone brings primarily dry summer weather to southern

Australia, as the westerlies are pushed south of the continent (Gentili, 1972).

The late Cenozoic history of this synoptic regime is poorly known. Fossil evidence for formerly extensive rainforest floras and faunas suggests that climates with substantially higher annual and summer rainfall were widespread in Australia throughout much of the Cenozoic (Greenwood, 1994; Kershaw, 1997; Macphail, 1997). Bowler (1982) attempted to explain the transition in southern Australia from mid Cenozoic ever-wet climates to Quaternary winter-wet climates in synoptic terms. He suggested that shallow hemispheric thermal gradients associated with early to mid Cenozoic greenhouse climates were characterised by a weaker, and more poleward-centred subtropical anticyclone, while the Australian continent was surrounded by warm oceans that encouraged convective rainfall. Bowler (1982) suggested that progressive Antarctic cooling since the Middle Miocene drove the intensification and northward movement of the anticyclonic subtropical high. In his view, this occurred in two distinct stages, corresponding to two distinct synoptic regimes in southern Australia. The first stage occurred in response to the development of a relatively small Antarctic ice sheet during the Late Miocene to Pliocene. At this stage, during austral winter, the high tracked south of the Australian

* Corresponding author. Tel.: +61 3 9905 4622; fax: +61 3 9905 2948.

E-mail address: kale.sniderman@arts.monash.edu.au (J.M.K. Sniderman).

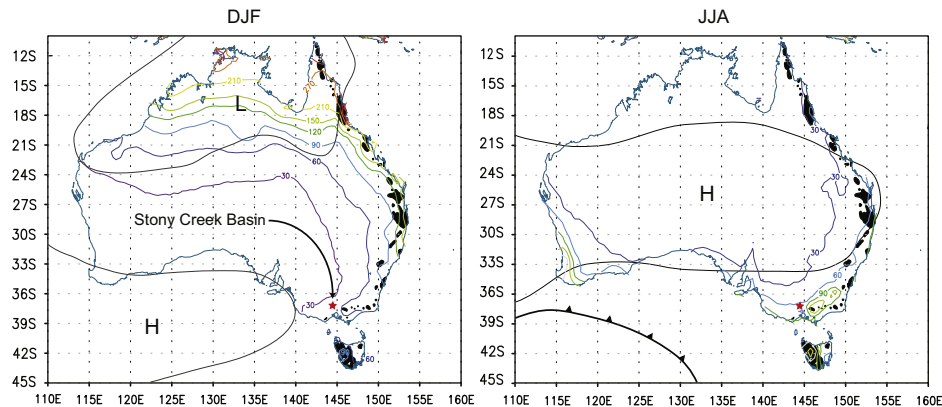


Fig. 1. Summer (DJF) and winter (JJA) seasonal mean of monthly precipitation (mm/month), derived from CRU TS 1920–1995 climatology, plotted with Climate Explorer (<http://climexp.knmi.nl>) (van Oldenborgh et al., 2009). Schematic winter and summer mean sea level pressure and frontal position derived from Tapper and Hurrell (1993). Modern distribution of Australian rainforest shown in black, based on Webb and Tracey (1981).

continent, which was then several degrees further south than today due to ongoing northward drift of the Australian tectonic plate. During austral summer, shallowing of the hemispheric temperature gradient shifted the subtropical high well poleward of the continent. By explicit analogy with the modern synoptic climatology of northern Australia, Bowler (1982) invoked, for this Late Miocene–Early Pliocene stage, an intensely dry winter season in southern Australia dominated by the trade easterlies, alternating with a summer, monsoonal wet season.

In the second stage, during the Late Pliocene or Early Pleistocene, Bowler (1982) proposed that Southern Hemisphere temperature gradients steepened further in response to continued cooling of the Antarctic margin. The corresponding compression of zonal circulation intensified the subtropical anticyclone and pushed it further equatorward into the latitudes it now occupies, overtaking the slow northward drift of the continent. This new position of the subtropical high initiated, for the first time, the familiar pattern of summer-dry, winter-wet climate that characterises southern Australia today.

However, fossil pollen evidence for the persistence of moisture-sensitive rainforest taxa during the Early–Middle Pliocene, including *Nothofagus* subgenus *Brassospora* in southeastern Australia (Kershaw et al., 1991; Macphail, 1997) and Podocarpaceae and *Agathis* (Araucariaceae) in southwestern Australia (Dodson and Macphail, 2004), is difficult to reconcile with the intense winter drought during the Pliocene suggested by Bowler (1982). Instead, it suggests that relatively high annual and summer rainfall persisted in southern Australia throughout the Early and Middle Pliocene. However, the subsequent transition from relatively aseasonal (or at least summer moist) ‘Tertiary’ climates to drier ‘Quaternary’ climates, with predominantly winter rainfall in the south, has eluded documentation. Given the profound changes in global climate that coincided with the onset of extensive Northern Hemisphere glaciation at ~2.7 Ma (Raymo and Nisancioglu, 2003; Haug et al., 2005), it has been assumed that this critical transition in southern Australian climate occurred near the Pliocene–Pleistocene boundary (Kershaw et al., 1994; Macphail, 1997). Yet the causes, nature and timing of the transition remain uncertain. In this paper, we use fossil beetle remains to generate new quantitative reconstructions of Early Pleistocene climate in southeastern Australia, which indicate that a high annual- and summer-rainfall climate persisted in southern Australia until ~1.5 Ma.

2. The Stony Creek Basin record

Stony Creek Basin (SCB, 144.13°E, 37.35°S, 550 m above sea level) (Fig. 1) is a small (c. 10 ha), infilled palaeolake of probable volcanic

origin in upland southeastern Australia. A drill core taken in 2000 recovered 40 m of partly annually laminated silty-clay lacustrine sediments that were subjected to sediment and pollen analysis, palaeomagnetism and fission track dating. A chronology was established from the insertion of a floating varve record into the geological timescale using an observed palaeomagnetic polarity change and fission track ages from pyroclastic zircons, then astronomically tuned by pattern matching the amplitude-modulated, climatically sensitive rainforest angiosperm pollen record to similarly amplitude-modulated, precession-dominated summer insolation. It was determined that the sediment sequence was deposited over ~280 kyr between ~1835 and 1555 ka (Sniderman et al., 2007). Pollen and macrofossil analyses demonstrated that Early Pleistocene vegetation in upland southeastern Australia alternated between diverse rainforest composed of both gymnosperms and angiosperms, and sclerophyllous, open forest dominated by *Eucalyptus*, Casuarinaceae and Cupressaceae (Fig. 2) with a diverse, micro-sclerophyllous understorey (Jordan et al., 2007). Rhythmic alternation between these two forest types was paced by the ~23 kyr period of orbital precession, presumably through the effect of changing summer insolation on temperature, effective precipitation, or both.

Today, SCB is located well beyond the continental distribution of moisture-demanding, fire-sensitive rainforest (Fig. 1). The diverse rainforest in the pollen record (Fig. 2) has floristic affinities to warm-temperate rainforests of eastern Australia and lowland New Zealand. Qualitatively, this suggests that southeastern Australian climate at the time of deposition of the SCB record was wetter than present, since modern rainfall during the summer quarter-year at SCB (150 mm) is too low to support rainforest today. In relation to temperature, previous studies using nearest living relative (NLR) approaches (Macphail et al., 1994; Macphail, 1996, 1997; Hill and Scriven, 1997; Kershaw, 1997) have suggested that late Cenozoic extinctions have eliminated the high latitude ranges of a number of rainforest genera and families (Jordan, 1997a,b; Sniderman et al., 2007), so NLR palaeoclimate reconstructions for southern Australia are likely to be biased towards warm climates if they are based on extant Australian plant taxa.

In order to avoid this bias, in this paper we do not rely on NLRs of SCB pollen types to estimate palaeoclimate parameters. Instead, we have estimated climate parameters solely from fossil beetle remains, which are abundant within SCB sediments. For several reasons, palaeoclimate estimates from beetles should be more accurate than those from plant fossils, especially fossil pollen. Their great vagility and short generation times make beetles more likely than plants to have geographic ranges in equilibrium with climate,

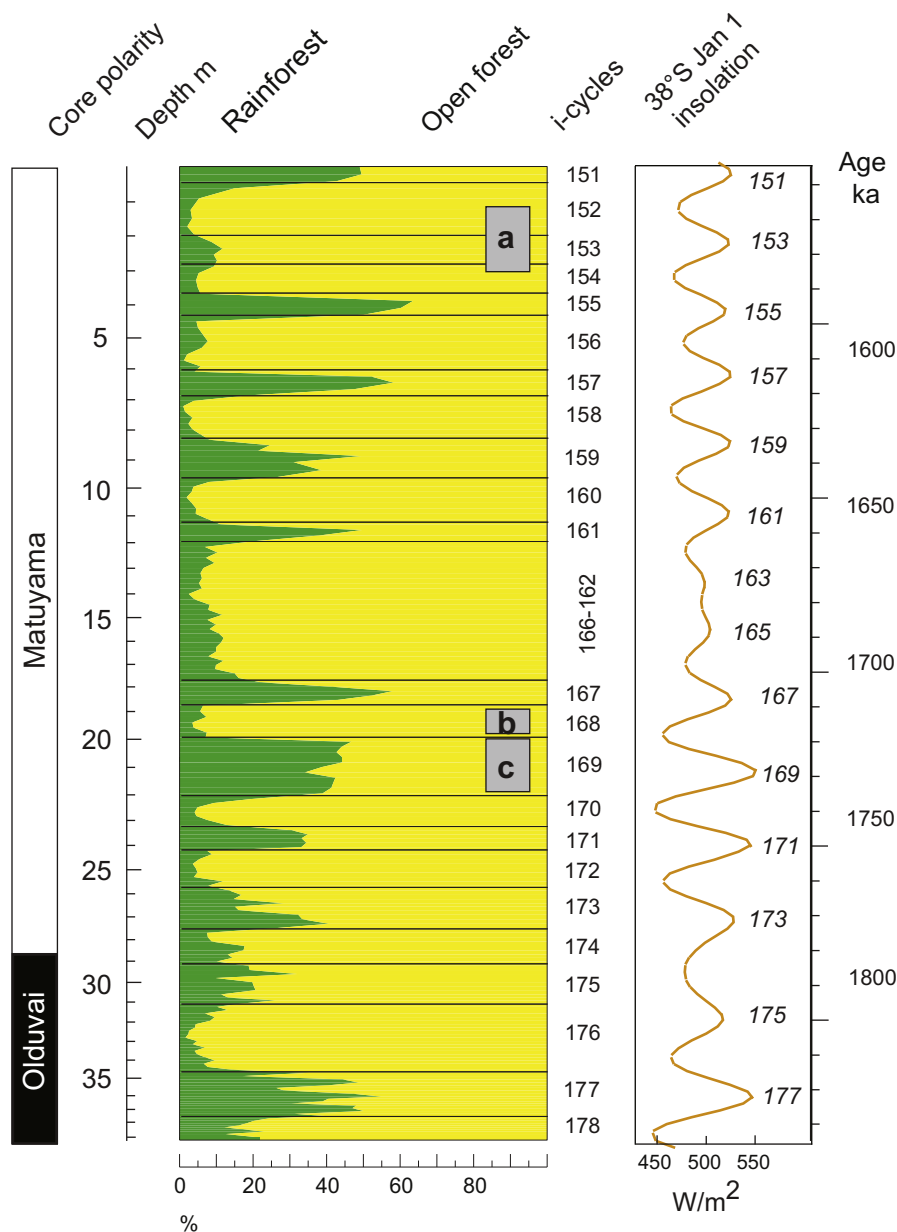


Fig. 2. Summary pollen diagram from the Stony Creek Basin core, core magnetic polarity and correlation with Southern Hemisphere summer insolation (see Sniderman et al., 2007); numbered insolation cycles follow Lourens et al. (1996). Grey boxes indicate stratigraphic positions of sediment samples from which beetle samples A–C were recovered.

and more able to change their ranges in response to dramatic climatic fluctuations (Porch and Elias, 2000; Porch, 2007). Additionally, fossil beetles can routinely be identified to the level of genus or species, whereas pollen types typically cannot be resolved below the level of family or genus. Hence bioclimatic envelopes associated with beetle remains are likely to be both more accurate and more precise than those associated with pollen.

3. Methods

Fossil beetles were extracted and analysed from only a small portion of the SCB sediment record due to time constraints and limited sediment availability. However, because the pollen record alternates bimodally between rainforest-rich and sclerophyll-rich intervals, we hypothesized that most of the range of climate experienced at SCB during its 280 kyr infill history could be

captured by characterising the climates of these rainforest-rich and sclerophyll-rich modes. To this end, assemblages of well preserved, fossil beetle sclerites were recovered for palaeoclimatic analysis by wet sieving selected, 1–2 m long sections of 7 cm diameter SCB drill core, in contiguous, 10 cm thick subsamples. These sections corresponded to pollen-defined zones previously correlated to the astronomic timescale by Sniderman et al. (2007) and labelled following the *i*-cycle codification of Lourens et al. (1996) (Fig. 2). Beetle sample A, from 2.5 to 4 m down core, is correlated with *i*-cycles 152–153, at 1590–1570 ka (thousands of years ago). It was selected as representative of the climate during intervals when sclerophyllous taxa were dominant. Because the sediment volumes available from drill core for beetle recovery were still very limited (core material for sample A constituted ~2.5 kg of sediment), an open excavation of the lacustrine sediments was undertaken by backhoe in 2002 to a depth of 5 m, in the hope of increasing the

number of taxa contributing to sample A. The excavation, located c. 5–10 m west of the drill core locality, was easily correlated, both palynologically and in terms of its beetle fauna, with the upper 5 m of the SCB drill core. This correlation allowed beetle remains recovered from the excavation (based on c. 15 kg of sediment) to be confidently aggregated with the core-derived beetle sample A assemblage. Beetle sample B (based on c. 1.4 kg of sediment), from 19 to 20 m down core, is correlated with *i*-cycle 168 (1725–1715 ka). It was analysed to test whether the beetle assemblage of sample A was in fact representative of assemblages deposited during other sclerophyll-forest dominated intervals. Beetle sample C (based on 6.7 kg of sediment), from 20 to 22 m down core, is correlated with *i*-cycle 169 (1735–1725 ka). It was selected as representative of the climate during intervals when rainforest taxa were most abundant.

We generated quantitative climate estimates for the selected intervals based on the modern climatic range of identified fossil beetle genera and species. Modern bioclimatic envelopes were produced for a wide range of species and genera using BIOCLIM (Houlder et al., 2000) analysis of geocoded distribution data derived from literature records, museum collections and focussed field collecting (Porch, 2007). BIOCLIM allows the determination of 35 temperature, precipitation, radiation and moisture parameters from three-dimensionally geocoded distribution data. The bioclimatic data for each taxon, referred to as the bioclimatic profile, formed the basic data for estimation of palaeoclimates. This was accomplished using a coexistence approach, widely used for palaeoclimatic reconstruction using taxon-based assemblage data, including beetles (Kershaw and Nix, 1988; Mosbrugger and Utescher, 1997; Marra et al., 2006; Elias, 2007; Porch, 2007). For the purposes of this study, we reconstructed three temperature and three precipitation parameters describing annual and seasonal variability in thermal and moisture regimes.

These parameters are mean annual temperature (MAT) and mean annual precipitation (MAP), temperature and precipitation of the warmest quarter (TwarmQ and PwarmQ), and temperature and precipitation of the coldest quarter (TcoldQ and PcoldQ). MAT is calculated as the mean of all weekly mean temperatures, based on BIOCLIM's 1920–1995 climatology; MAP is the sum of all monthly precipitation estimates in this climatology; and the other four parameters approximate summer and winter climates as the warmest and coldest quarter year, determined to the nearest week (Houlder et al., 2000). We report MAT ranges in terms of thermal response groups (de Candolle, 1874; Wolfe, 1975) as refined for the Australian continent by Nix (1991): microthermal = MAT < 12 °C; microtherm/mesotherm interzone = MAT 12–14 °C; mesotherm = MAT 14–24 °C. We note that seasonal temperatures are strongly correlated with annual temperatures in Australia, so that reconstruction of both is somewhat redundant. However, we report seasonal temperature estimates in order to better characterise summer and winter environments, because across Australia seasonal precipitation is not correlated with annual precipitation.

For some Australian beetle taxa, collection records are relatively few, and may not capture the full climatic range of a taxon. Faced with a similar problem in New Zealand, Marra et al. (2006) used maximum likelihood methods to estimate actual climatic ranges. Here, we use approaches developed by Porch (2007) which examine the impact that addition of new records to an existing bioclimatic profile has on the range of individual parameters. For temperatures, an empirically derived estimate of the actual temperature range for each taxon was developed, on the basis of relationships between old profiles and new, data-enhanced profiles, that takes into account the observed parameter range (maximum value – minimum value) for each taxon, and the number of geocoded records available for it:

$$\text{Estimated temperature error} = 4 \times (\text{maximum value} - \text{minimum value}) / \text{number of geocoded records}$$

This value was added to the maximum and minimum values to produce a best estimate of the actual taxon temperature range.

For precipitation parameters, the approach was similar but, because of the positive skew of most precipitation parameters, required different approaches to estimation of minimum and maximum values. For estimates of minimum values, the parameter range was derived from the 0 to 75 percentile range, to exclude the influence of the outlier and extreme values at the high end of the range. For estimates of maximum values, the entire observed range was used, because of the necessity of including extreme, high values. For precipitation errors, the best estimates were found to require five times the parameter range/number of records value. However, for taxa with strongly restricted precipitation values, whose distributions include spatially restricted, very high rainfall regions (e.g. isolated mountain tops which tend not to be sampled unless a taxon is extremely well collected), precipitation estimates may more realistically be considered as minimum values.

The value of these climatic range estimates ('error' values) was tested in modern Australian climate space using 54 assemblages from localities across Australia. For each locality, BIOCLIM estimates of the modern temperature and precipitation values for the site ('observed') were compared with beetle assemblage-based estimates ('predicted'). These assemblage-based estimates were jack-knifed, i.e. the parameter data for each taxon from a test site was not used in the determination of the value for that site. For all temperature and precipitation parameters tested, comparison of the observed vs predicted relationships showed that the observed value was included within the beetle-predicted range for 51 of the 54 assemblages, or 94.4% of cases. Several reasons explain the failure to overlap in three cases: errors associated with BIOCLIM estimation of parameter values; presence of assemblages at the edge of climate space; and, occurrence of taxa significantly outside their usual climatic range.

4. Results

4.1. Fossil beetle assemblages

Because of the relatively large sediment volumes contributing to beetle sample A, this was a large and diverse assemblage that contained a mixture of eastern Australian mesotherm taxa and southeastern Australian microthermal taxa including many that do not occur in the SCB region today (Table 1). Sediment subsamples from the excavation, representing c. 10 cm of stratigraphy, all contained the southeastern Australian microtherms *Cyphotrechodes gibbipennis* Blackburn (Carabidae) undescribed southern species of *Austrorhysus* Steel (Staphylinidae), the genus *Catoposchema* Jeannel (Leiodidae) and the eastern Australian mesotherms *Ataenius strigifrons* Schmidt (Scarabaeidae) and *Lepanus Balthasar* (Scarabaeidae) (several species belonging to eastern Australian species groups, including *Lepanus australis* Matthews). A number of less frequent taxa support the general climatic signature of these common taxa. The assemblage from sample B (from 19 to 20 m down core), although based on limited sediment volumes from drill core and therefore with fewer taxa (Table 1), is very similar in composition to the assemblage from sample A, suggesting that they were deposited at times of very similar climate. This is not surprising since their associated palynofloras (both dominated by the sclerophyll taxa *Eucalyptus* and/or Casuarinaceae, with traces of rainforest taxa) are similar. Hence, we consider that climate reconstructions based on the

Table 1
Coleoptera taxa contributing to climate reconstructions. (Abbreviations refer to Figs. 3–6).

Taxon	Samples			Abbreviation
	A	B	C	
Cupedidae				
<i>Adinolepis</i> sp.			2	Adinolepis
Carabidae				
<i>Bembidion blackburni</i>	2	1		Bembblac
<i>Pericompsus semistriatus</i>	5	2		Perisemi
<i>Cyphotrechodes gibbipennis</i>	23	6	1	Cyphgibb
<i>Trechobembix b. baldiensis</i>	30	4	3	Trecbald
<i>Mecyclothorax 'punctatus' grp. n.sp</i>	1			Mecypunc
<i>Mecyclothorax</i> sp. 3 (<i>cordicollis</i> grp.)	1		2	Mecycord
Hydrophilidae				
<i>Limnoxenus 'zelandicus'</i>	2	3		Limnoxen
Leiodidae				
<i>Catoposchema cf. tasmaniae</i>	7	2		Catoposc
<i>Eublackburniella</i> sp.				Eublack
<i>Myrmicholeva</i> spp.	6	1		Myrmchol
Staphylinidae: Proteininae				
<i>Austrorhysus</i> spp.	16	3		Austrorh
<i>Austrorhysus</i> sp. B			1	AustroB
<i>Anepis koebelei</i>	1	1		Anepkoeb
Staphylinidae: Piestinae				
<i>Prognathoides mjoergei</i>	1		2	Progmjob
Staphylinidae: Osoriinae				
<i>Thoracophorus</i> spp.	7	4	3	Thoracoph
Staphylinidae: Steninae				
<i>Stenus (Hemistenus)</i> n.sp.	1			Hemisten
<i>Stenus (Hypostenus)</i> sp.	3	2		Hyposten
Scarabaeidae				
<i>Lepanus</i> (eastern Australian spp.)	25	5		LepanusE
<i>Demarziella</i> n.sp.	2			Demarz
<i>Ataenius strigifrons</i>	8	1		Ataestri
<i>Saprosites clydensis</i>	1			
<i>Saprosites nitidicollis</i>	3	1		Saprniti
Buprestidae				
<i>Germarica cf. lilliputana</i>	9	1	2	Germarica
Derodontidae				
<i>Nothoderodontus darlingtoni</i>	1			Nothoder
Myrabolidae				
<i>Myrabolia</i> spp.	11	2		Myrabolia
Latridiidae				
Genus indet.			4	Latridiinae
Rhynchophoridae				
<i>Dryophthorus</i> sp.	1			Dryophth

larger assemblage of sample A also apply, in broad terms, to the interval (*i*-168) during which the smaller assemblage of sample B was deposited.

The assemblage of sample C (Table 1), from the rainforest-rich pollen zone correlated with *i*-169, is smaller than that recovered from sample A, because of limited sediment volumes available from drill core. However, there are compositional differences between the beetle assemblages from rainforest and sclerophyll intervals that are not related to sample size effects. Microthermal taxa present in sclerophyll samples A and B are either rare (*C. gibbipennis*) or completely absent in rainforest sample C. Significantly, the species of *Austrorhysus* present in the rainforest assemblage is different to those from sclerophyll assemblages A and B, and matches an undescribed taxon from eastern Australia. Fig-wasps (*Pleistodontes* Saunders), which have an obligate association with *Ficus* section *Malvanthera* (Lopez-Vaamonde et al., 2002) are present in all 10 cm subsamples throughout the 2 m thick rainforest sample C, but are

completely absent from the sclerophyll samples A and B. Additionally, a large number of unidentified taxa differentiate the rainforest and sclerophyll assemblages.

4.2. Climate reconstructions

4.2.1. Beetle assemblages (samples A and B) associated with sclerophyllous vegetation

MAT during deposition of samples A and B was 13.2 ± 0.9 °C, or 1.3–3.1 °C higher than modern MAT of 11 °C (Fig. 3b, Table 2). TWarmQ was 18.0 ± 0.9 °C, or 0.6–2.4 °C higher than modern TWarmQ of 16.5 °C (Fig. 3a). TColdQ was 8.0 ± 1.7 °C, or 0.5–3.9 °C higher than modern TColdQ of 5.8 °C (Fig. 3c). Hence, during these two intervals dominated by sclerophyllous vegetation, temperatures were warmer than modern values, whether these are reconstructed for winter, summer, or annually. Best estimates of the temperature differences between sclerophyll-dominated intervals (samples A and B) and modern climate at SCB (SCB_{SCl} – modern) are 2.2 °C (MAT), 1.5 °C (TWarmQ), and 2.2 °C (TColdQ) (Table 2). Relatively narrow envelopes result primarily from the limited thermal overlap between microthermal taxa, now confined largely to southeastern Australian upland and montane habitats, and mesothermal taxa, confined to lowland southeastern Australian and upland eastern Australian habitats.

The reconstruction of MAP is 1390 ± 481 mm, 3–113% higher than the modern MAP of 879 mm (Fig. 4b, Table 2). PWarmQ was 325 ± 30 mm, 96–136% higher than modern PWarmQ of 150 mm (Fig. 4a). PColdQ was 281 ± 95 mm, 38% less than, to 25% higher than, modern PColdQ of 293 mm (Fig. 4c). Hence, precipitation may have been similar to today during winter, and was somewhat higher (up to 2× modern values) than today annually, but was clearly dramatically higher (2–2.4× modern values) during summer (Table 2). Although the precise nature of beetles' physiological responses to rainfall gradients are poorly understood (Tauber et al., 1998), it seems likely that the upper limits of our precipitation estimates are primarily artefacts of limited collections and of the restricted geographic extent of perhumid habitats in Australia.

4.2.2. Beetle assemblage (sample C) associated with rainforest vegetation

MAT during the rainforest-dominated interval corresponding to assemblage C was 13.3 ± 1.9 °C, or 0.4–4.2 °C higher than modern MAT of 11 °C (Fig. 5b, Table 2). TWarmQ was 17.8 ± 1.8 °C, or between 0.5° lower and 3.1 °C higher than modern TWarmQ of 16.5 °C (Fig. 5a). TColdQ was 8.5 ± 3.3 °C, or between 0.6° lower and 6.0 °C higher than modern TColdQ of 5.8 °C (Fig. 5c). Hence, as for samples A and B deposited during a time of sclerophyll-dominated vegetation, temperatures during deposition of sample C, when local vegetation was rainforest-rich, were as warm or warmer than modern values, both seasonally and annually. Best estimates of the temperature differences between the rainforest interval (sample C) and modern climate at SCB (SCB_{Rf} – modern) are 2.3 °C (MAT), 1.3 °C (TWarmQ), and 2.7 °C (TColdQ) (Table 2). Errors are larger for this interval than for the sclerophyll-dominated interval simply because of smaller beetle sample size, but collectively samples A, B and C indicate that temperatures were warmer than present during both sclerophyll- and rainforest-dominated intervals. The reconstruction of MAP is 1133 ± 232 mm, 2.5–55% higher than modern MAP (Fig. 6b, Table 2). PwarmQ was 306 ± 58 mm, 66–143% higher than modern PwarmQ (Fig. 6a). PcoldQ was 299 ± 127 mm, 43% less than, to 42% higher than modern PcoldQ (Fig. 6c). These values are similar to those reconstructed for the sclerophyll-dominated intervals of samples A and B.

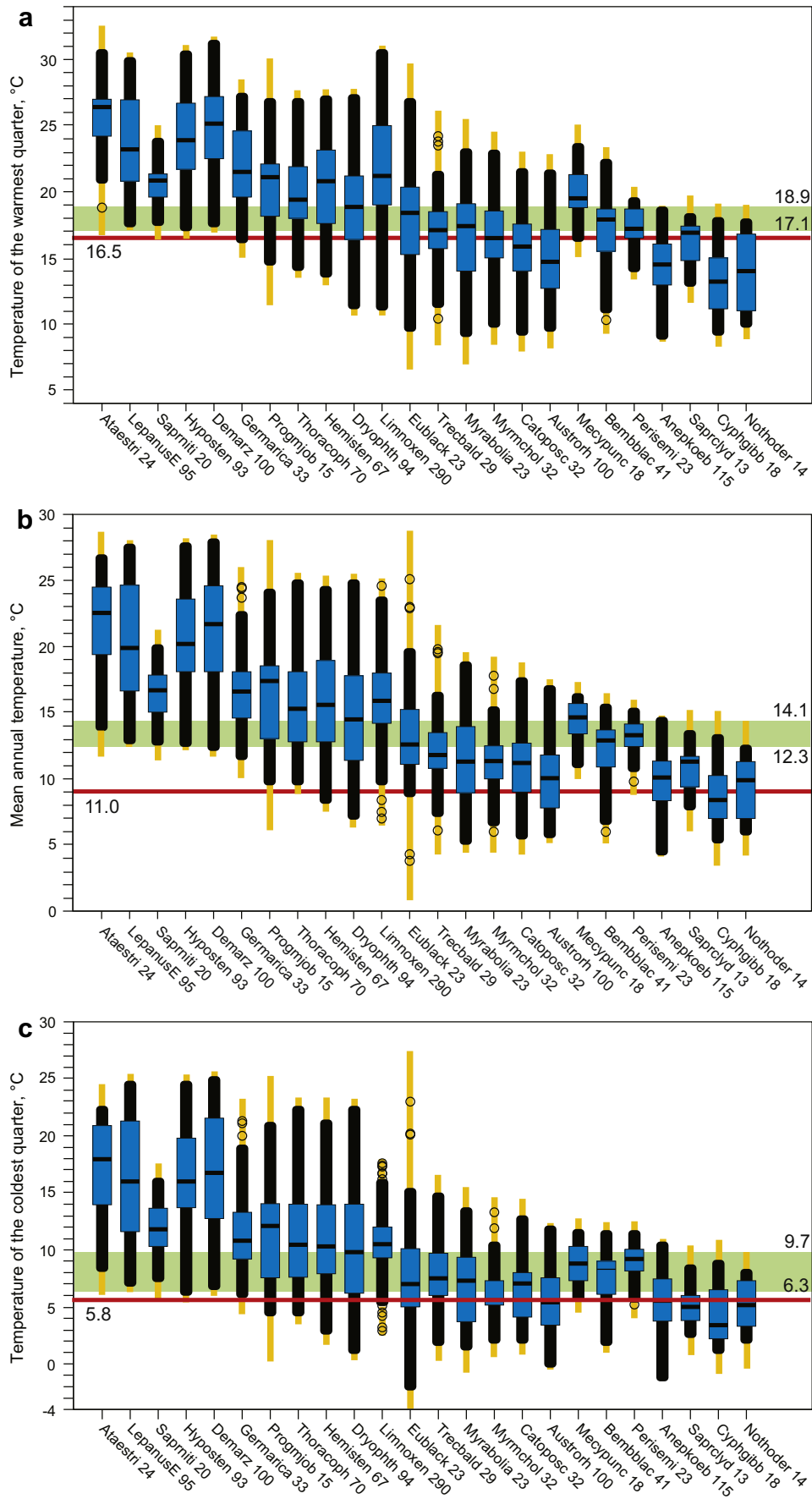


Table 2

Modern climate at Stony Creek Basin, and palaeoclimate estimates for sclerophyll- and rainforest-dominated vegetation intervals, using selected climate parameters.

	Modern	Assemblages A and B (sclerophyll-dominated intervals)	Assemblage C (rainforest- dominated)
MAT	11.0°	13.2° ± 0.9°	13.3° ± 1.9°
TWarmQ	16.5°	18.0° ± 0.9°	17.8° ± 1.8°
TColdQ	5.8°	8.0° ± 1.7°	8.5° ± 3.3°
MAP	879 mm	1390 ± 481 mm	1133 ± 232 mm
PWarmQ	150 mm	325 ± 30 mm	306 ± 58 mm
PColdQ	299 mm	281 ± 95 mm	299 ± 127 mm
Δ SCB – modern			
		SCB_{Sci} – modern	SCB_{Rf} – modern
ΔMAT, °C		+2.2 ± 0.9°	+2.3 ± 1.9°
ΔTWarmQ, °C		+1.5 ± 0.9°	+1.3 ± 1.8°
ΔTColdQ, °C		+2.2 ± 1.7°	+2.7 ± 3.3°
ΔMAP, %		+3% to +113%	+2.5% to +55%
ΔPWarmQ, %		+96% to +136%	+66% to +143%
ΔPColdQ, %		–38% to +26%	–42.5% to +42%

5. Discussion

5.1. Climate reconstructions

Our climate reconstructions are based on beetle assemblages from only three intervals of the SCB record – one rainforest-rich interval (sample C) and two sclerophyll-rich intervals (samples A and B), suggesting that we may not have captured the full range of climate experienced during deposition of the SCB record. However, the strongly bimodal nature of the vegetation record, and the similarity of the beetle assemblages from samples A and B (Table 1), despite the c. 150 kyr age difference between them, suggests that any individual rainforest- or sclerophyll-dominated interval in the record is at least generally representative of the climate of the other rainforest- and sclerophyll-dominated intervals, respectively. Therefore, we infer that, to first approximation, our reconstructions embrace the range of variability experienced at the site for ~280 kyr of the Early Pleistocene, between ~1835 and 1555 ka. One caveat is that slightly higher percentage values for the conifer family Araucariaceae during rainforest intervals in the lowermost 6 m of the SCB record (Sniderman et al., 2007) may imply that slightly different climates occurred during the early part of the record.

Our climate reconstructions indicate that, during deposition of the SCB record, temperatures, both seasonally and annually, were consistently 1–3 °C warmer than modern in upland southeastern Australia. By contrast, precipitation estimates differ between winter and summer. Winter precipitation estimates for both rainforest and sclerophyll intervals symmetrically straddle the modern value for SCB (299 mm), so we consider that winter precipitation was most likely similar to today. On the other hand, annual precipitation was at least slightly higher, and as much as 2× higher than today, while summer precipitation was 2–2.4× the

modern value at SCB of 150 mm. Interestingly, these estimates differ little between intervals of sclerophyll-dominated vegetation (samples A and B), and the interval of diverse rainforest-dominated vegetation (sample C). This is surprising, since we expected that the repetitive alternation between these floristically distinct vegetation types would have been driven by rhythmically alternating, clearly distinguishable climate states. In particular, we assumed that the local to regional expansion and contraction of rainforest would have been driven by alternating intervals of higher and lower rainfall, particularly during summer. The vegetation changes at SCB were paced by the 23 kyr period of orbital precession through its influence on summer insolation (Sniderman et al., 2007). We expected this to have led to enhanced rainfall during summer insolation maxima, caused either by higher regional sea surface temperatures, increased land–sea contrast, or both. Instead, we can detect no difference between the relatively warm and wet climates experienced during both sclerophyll- and rainforest-dominated vegetation intervals, because for all climate parameters the mean values for rainforest and sclerophyll intervals are similar, with overlapping errors.

We are uncertain of the cause(s) of our inability to differentiate the climates of rainforest- and sclerophyll-dominated intervals. However, the beetle assemblages, from rainforest and sclerophyll intervals, are both dominated by southern and eastern Australian wet forest taxa. This implies, in the first place, that any temperature difference between these vegetation states was modest in amplitude. On the other hand, with the exception of rare *C. gibbipennis*, microthermal beetle taxa are absent from the beetle assemblage of rainforest-rich sample C. Hence it is possible that actual temperatures during the rainforest interval were close to the upper end of the predicted climatic envelopes. If so, the rainforest interval may, within error, have been as much as 1–2 °C warmer than the sclerophyll-dominated intervals. However, for precipitation, the presence of the obligate wet forest species *Prognathoides mjobergi* Bernhauer in both sclerophyll- and rainforest-dominated faunas indicates that summer precipitation was at least twice the modern value, during both the sclerophyll and rainforest intervals. The vegetation is consistent with this, given that several poorly dispersed rainforest pollen types persist at trace levels throughout sclerophyll-dominated intervals. This implies that local or regional climate during these intervals remained at least marginally adequate for these drought- and fire-sensitive plant taxa. Therefore, our data indicate that higher than modern temperatures, along with substantially higher annual and summer precipitation, were perennial features of southeastern Australian uplands during the Early Pleistocene, through multiple, precessional scale climate cycles. One explanation for the dramatic vegetation cyclicity in the SCB record may be that the basin was located within a sensitive ecotone between vegetation types. Alternatively, since microcharcoal counts are generally lower during rainforest-rich intervals (Sniderman, unpublished data), relatively modest precessional scale changes in rainfall seasonality may have been responsible for large changes in fire regime that alternately encouraged and discouraged rainforest expansion.

Fig. 3. Estimates of (a) Temperature of the warmest quarter, (b) Mean annual temperature, and (c) Temperature of the coldest quarter, for the aggregated samples A and B, associated with sclerophyll-rich vegetation. The modern bioclimatic profiles for individual beetle taxa are represented as box plots. The lower and upper boundaries of blue boxes represent the first ($x_{.25}$) and third ($x_{.75}$) quartiles, respectively, with the median shown as a horizontal black band. Vertical black bars represent minimum and maximum non-outlier values, while outliers, defined as values less than $1.5 \times \text{IQR} - x_{.25}$, or greater than $1.5 \times \text{IQR} + x_{.75}$ (interquartile range (IQR) = $x_{.75} - x_{.25}$), are shown as open circles. Vertical yellow bars represent best estimates of the actual lower and upper limits of each bioclimatic profile, taking into account possible sampling error at the margins of each taxon's range (see Methods). Climate estimates (green horizontal bar, with upper and lower boundaries labelled) are based on the zone of climatic overlap of all taxa, defined by the lowest maximum (best estimate) value (in this case, *Nothoderodontus darlingtoni*), and the highest minimum (best estimate) value (in this case, eastern Australian *Lepanus* spp.). Modern value at SCB shown (labelled, red horizontal line) for comparison. Abbreviated taxon names (see Table 1), and the number of occurrence records on which their bioclimatic profile is based, appear along the bottom.

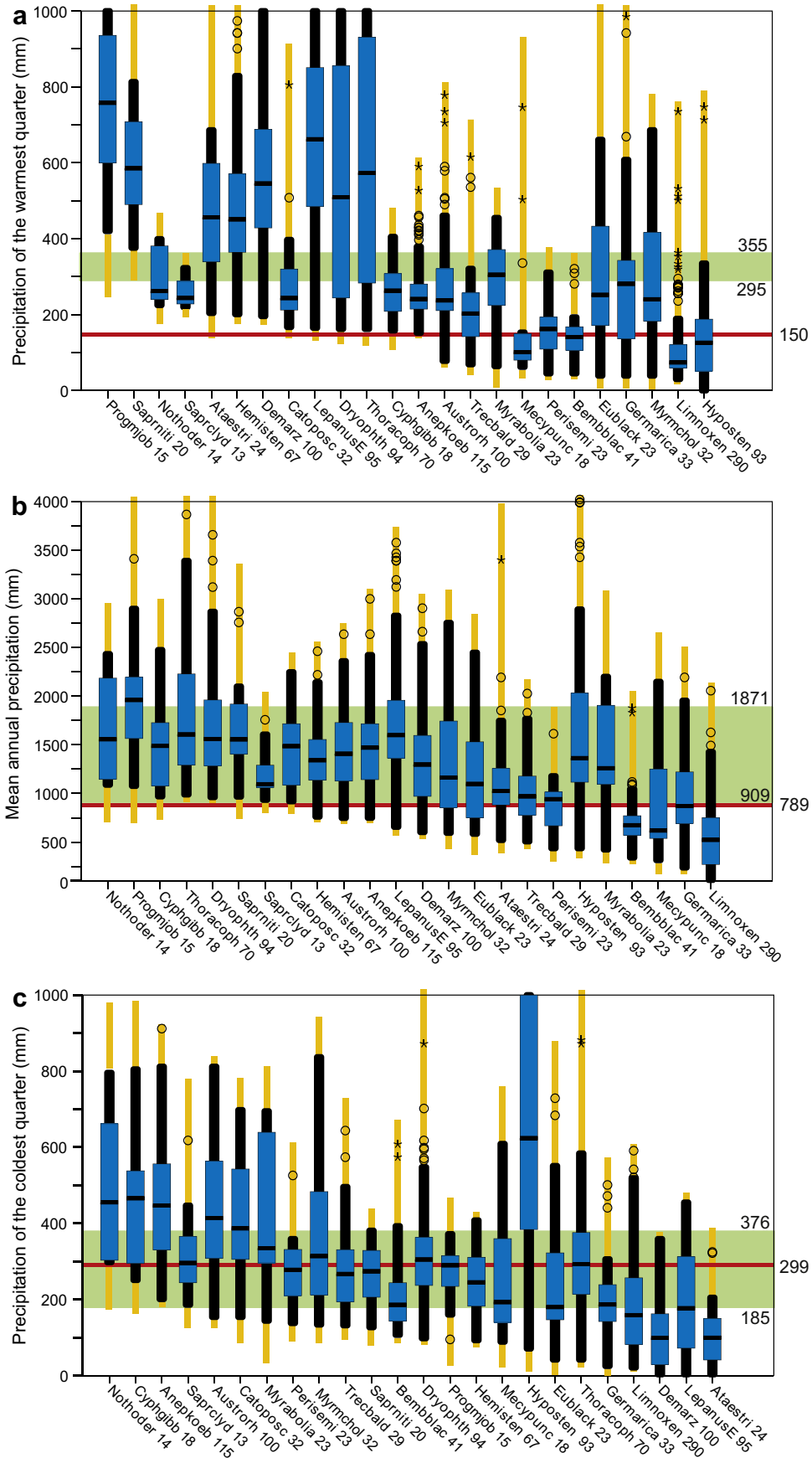


Fig. 4. Estimates of (a) Precipitation of the warmest quarter, (b) Mean annual precipitation, and (c) precipitation of the coldest quarter, for the aggregated samples A and B, associated with sclerophyll-rich vegetation. For explanation, see caption of Fig. 3. Extreme high precipitation outliers, values greater than $3 \times \text{IQR} + \chi_{.75}$, are shown as stars.

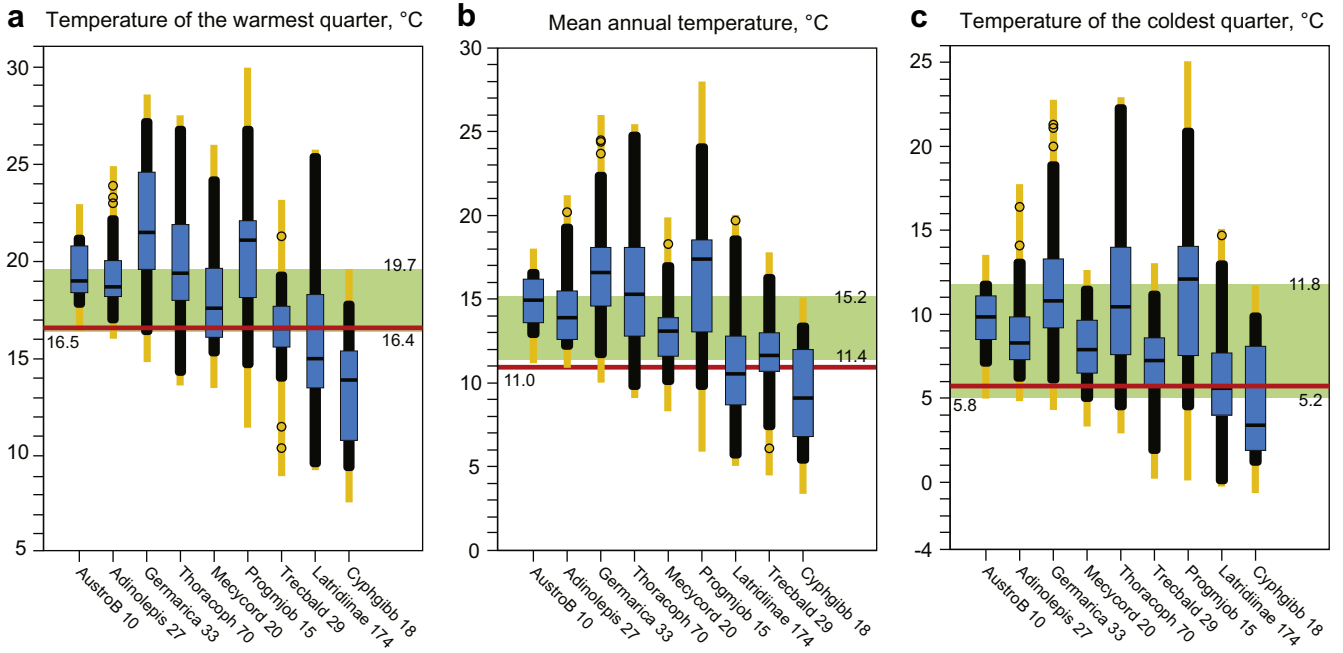


Fig. 5. Estimates of (a) Temperature of the warmest quarter, (b) Mean annual temperature, and (c) Temperature of the coldest quarter, for sample C, associated with rainforest-rich vegetation. For explanation, see caption of Fig. 3.

5.2. Implications for Early Pleistocene Australian synoptic climatology

Bowler’s (1982) hypothesis for the genesis of the modern southern Australian climate argued that the transition from a summer-wet Pliocene to a winter-wet Quaternary was a function primarily of a northward shift in the mean tracking position of the anticyclonic circulation. Below, we examine the plausibility of this and other synoptic scenarios as explanations for our climate reconstructions at SCB.

On a range of palaeoclimate timescales, substantial latitudinal shifts of the subtropical high and associated westerly storm tracks have provided appealing synoptic mechanisms to explain both Greenhouse (Bowler, 1982; Farrell, 1990; Pole, 2003) and Icehouse (Chylek et al., 2001; Toggweiler et al., 2006) climates of the past. However, Bowler’s (1982) explanation of high Pliocene summer rainfall in terms of a poleward-shifted subtropical high effectively requires that the summer intertropical convergence zone expanded to southern Australian latitudes, implying a shift of zonal circulation belts by probably more than ten degrees of latitude (cf. the

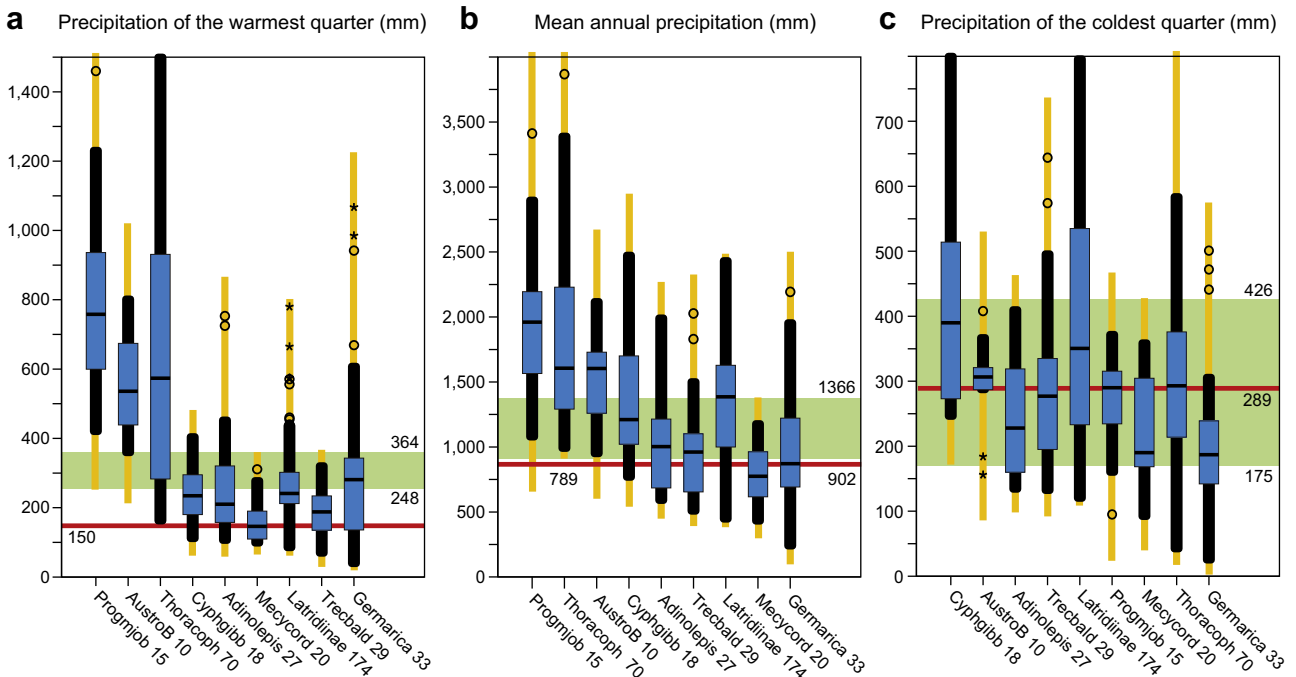


Fig. 6. Estimates of (a) Precipitation of the warmest quarter, (b) Mean annual precipitation, and (c) precipitation of the coldest quarter, for sample C, associated with rainforest-rich vegetation. For explanation, see caption of Fig. 3. Extreme high precipitation outliers, values greater than $3 \times IQR + x_{.75}$, are shown as stars.

modern summer tracking latitude over Australia, c. 36–38°S). For the Pliocene and Pleistocene, when global temperatures probably have not been more than ~3 °C warmer than modern (Haywood et al., 2000), this may be dynamically implausible, since models suggest that Hadley cell expansion in response to global warming is only c. 0.2–0.3° latitude per 1 °C (Frierson et al., 2007), consistent with the most extreme IPCC model projections (the A2 scenario of Meehl et al. (2007)) in which anthropogenic Hadley cell expansion is only of the order of 2° of latitude. In addition, a poleward-shifted subtropical high would have brought dry winters to southern Australia, yet our reconstructions indicate that winter precipitation was high during the Early Pleistocene at SCB.

The opposite possibility is that the Early Pleistocene subtropical high was shifted equatorward, allowing southern Australia to experience a year-round 'roaring 30s' (in analogy with the 'roaring 40s' climate experienced today in western Tasmania) climate more or less perennially exposed to the mid-latitude frontal lows. This seems implausible since equatorward contraction of zonal circulation is more likely to be consistent with periods of global cooling (Toggweiler et al., 2006), yet SCB temperatures, and by implication, regional/mid-latitude SH temperatures, were warmer than modern. If SCB moisture was explained by a roaring 30s scenario, we would expect to find SCB taxa and their relatives primarily in modern, western Tasmanian rainforests. Instead, the modern geographic range of most identified SCB beetle taxa extends in a montane arc from mainland southeastern Australia northward along the eastern Australian escarpment.

More fundamentally, the high precipitation at SCB during both winter and summer seems difficult to explain in terms of any combination of summer and winter positions of the subtropical high, unless those positions were separated by considerably more than their current 6–10° of latitude. That is, tropical lows might have brought high summer precipitation when the subtropical anticyclone was centred well south of the Australian margin during summer, and mid-latitude frontal lows might have brought high winter precipitation when the subtropical anticyclone was centred near its modern winter latitude of 28–30°S (Hobbs, 1999). However, in such a scenario wet summer and winter seasons would be separated by very dry spring and autumn seasons when the anticyclone migrated north or south over southern Australia. This seems implausible, because it is difficult to identify a mechanism for such high amplitude of seasonal migration of the anticyclone, and because the scenario is inconsistent with the presence of diverse rainforest plant and beetle taxa poorly adapted to aridity in any season. Based on the above, we conclude that simple latitudinal shifts of the subtropical anticyclone cannot explain the SCB palaeoclimate reconstructions of relatively high, year-round precipitation.

An apparently simpler possibility is that there was no synoptic scale circulation change at all, but that higher Southern and Indian Ocean sea surface temperatures increased regional rainfall simply by feeding greater moisture into mid-latitude frontal lows. However, this is contradicted by modelling studies of past (Haywood and Valdes, 2004) and future (Yin, 2005; Bengtsson et al., 2006; Lu et al., 2007, 2009) greenhouse conditions, and by recent observations of poleward expansion of zonal circulation (Seidel et al., 2007), which indicate that the zones of subtropical descent, and of mid-latitude storm tracks, expand poleward in response to warming at high latitudes. A year-round, poleward shift in storm tracks would divert the zone of reliable cool season frontal rain south of southern Australia, even in winter when these tracks are at their northernmost extent. Such an effect, which has already been observed in recent decades in southern Australia (Hope et al., 2006), seems unlikely to explain higher annual and summer precipitation at SCB.

Since these considerations of the position of the subtropical anticyclone cannot readily explain high year-round precipitation at

SCB, we seek an alternative explanation that draws on observations that the Hadley circulation, at least in the NH where meridional thermal gradients are shallower than in the SH, is predominantly a feature driven by winter radiative cooling (Lindzen and Hou, 1988) and that during summer there is little zonal mean subtropical descent (Rodwell and Hoskins, 1996; Cook, 2003; Trenberth and Stepaniak, 2003).

Southern Hemisphere (SH) mid-latitude atmospheric circulation is highly zonal (Simmonds and Keay, 2000; Trenberth and Stepaniak, 2003), because of the lack of landmasses between c. 35 and 65°S, and because of steep meridional gradients associated with very low temperatures at the Antarctic margin. This provides some basis for extrapolation to zonal changes in circulation from a single SH terrestrial palaeoclimate record, in contrast with the Northern Hemisphere (NH) where there is considerable longitudinal variability in the synoptic settings of subtropical latitudes (Rind and Perlwitz, 2004). Such extrapolation is currently difficult to test because of a lack of SH data with which to compare our precipitation and temperature estimates for the 1.8–1.5 Ma interval. However, the hypothesis of Raymo et al. (2006) that the East Antarctic ice sheet maintained a land-based melting margin throughout the Early Pleistocene is consistent with our evidence for SCB temperatures 1–3 °C higher than modern, and, if correct, implies that the warm Early Pleistocene climates reconstructed for SCB were hemispheric in extent.

We suggest that the strong subtropical anticyclones which dominate modern southern Australian climate during both winter and summer may have responded in different ways to higher middle-high latitude SH temperatures during the Early Pleistocene. Since hemispheric temperature gradients are steeper during winter, relatively high SCB winter precipitation may have been generated in much the same way as today, by the passage of mid-latitude frontal lows embedded within eastward flowing anticyclones. However, during summer, a reduced hemispheric temperature and pressure gradient may have been unable to spawn intense anticyclones. This would reduce the atmospheric subsidence that now routinely suppresses convection over southern Australia during summer, and may have permitted the regular development, or more regular migration from lower latitudes, of a heat low over the entire Australian continent. Such a scenario implies that with decreased meridional temperature gradients during the Early Pleistocene, SH atmospheric circulation was less strongly zonal than today, and the SH Hadley cell functioned in summer more like its counterpart in the NH, with longitudinal variability driven in part by convection over landmasses (Cook, 2003).

The high annual and summer rainfall at SCB may have been linked to the precessional dominance of SCB vegetation change. Some time after 1.55 Ma when deposition ceased at SCB, the orbital signal dominating southeastern Australian climate changed from precessional (presumably within-hemisphere) summer insolation (Sniderman et al., 2007) to globally synchronised, NH-driven ice-volume fluctuations (Kershaw et al., 2003). Both this transition, and the transition from a summer-wet to a summer-dry climate, may have been expressions of a major regional climate reorganisation (Ravelo et al., 2004) driven by, or coinciding with, expansion of the Antarctic cryosphere near the end of the Early Pleistocene (Raymo et al., 2006; Scherer et al., 2008; Villa et al., 2008). If steepened hemispheric temperature gradients associated with this cryosphere expansion intensified the subtropical anticyclonic circulation, this may have spawned stronger high pressure cells capable of suppressing summer convection over the Australian continent. This would have eliminated a major source of warm season rainfall for southern Australia, and ushered in the modern, winter-dominated rainfall regime. At the same time, insofar as the strength of this convection was sensitive at orbital scale to fluctuating summer

insolation, its suppression would have strongly reduced the importance of the precession signal in southern Australian climate variability.

6. Conclusions

Our data indicate that temperatures at Stony Creek Basin in the southeastern Australian uplands were consistently 1–3 °C warmer than present, for several 100 kyr of the Early Pleistocene. Annual average precipitation was slightly to substantially higher than today, and summer precipitation was 2–2.4 times higher than present. These values indicate that southern Australia's modern, winter-dominated rainfall regime was not yet in place by 1.5 Ma. We suggest that no combination of mean annual and seasonal shifts in the latitude of the subtropical anticyclone can explain high winter and summer precipitation at SCB. Instead, we interpret our data to imply that the strength of the subtropical anticyclone was weaker than today during Early Pleistocene summers, although it may have been similar to today during Early Pleistocene winters. There may be a causal link between higher annual and summer rainfall and the precession-pacing of the SCB vegetation record if both were the products of shallower hemispheric temperature gradients, or warmer hemisphere-wide temperatures, during the Early Pleistocene. This interpretation could be tested with a climate modelling study designed to ask what changes in SH circulation would be consistent with a combination of warmer temperatures and substantially higher summer rainfall in southern Australia.

Acknowledgments

This research was supported by the Australian Research Council through grants to Kershaw, and by Australian Postgraduate Awards to Sniderman and Porch. We thank J. Bowler, J.R. Brown and N. Nicholls for valuable comments on the manuscript or on ideas presented therein.

References

- Bengtsson, L., Hodges, K.I., Roeckner, E., 2006. Storm tracks and climate change. *Journal of Climate* 19, 3518–3543.
- Bowler, J.M., 1982. Aridity in the Late Tertiary and Quaternary of Australia. In: Barker, W.R., Greenslade, P.J.M. (Eds.), *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publications, Frewille, pp. 35–45.
- Chylek, P., Lesins, G., Lohmann, U., 2001. Enhancement of dust source area during past glacial periods due to changes of the Hadley circulation. *Journal of Geophysical Research* 106, 18477–18485.
- Cook, K.H., 2003. Role of continents in driving the Hadley cells. *Journal of the Atmospheric Sciences* 60 (7), 957–976.
- de Candolle, A., 1874. Constitution dans le regne vegetal des groupes physiologiques applicables a la geographie ancienne et moderne. *Archives des Sciences Physiques et Naturelles* 50 (N.S.), 5–42.
- Dodson, J.R., Macphail, M.K., 2004. Palynological evidence for aridity events and vegetation change during the Middle Pliocene, a warm period in Southwestern Australia. *Global and Planetary Change* 41, 285–307.
- Elias, S.A., 2007. Beetle records: overview. In: Elias, S.A. (Ed.), *Encyclopedia of Quaternary Science*. Elsevier, Amsterdam, pp. 151–163.
- Farrell, B.F., 1990. Equable climate dynamics. *Journal of the Atmospheric Sciences* 47, 2986–2995.
- Frierson, D.M.W., Lu, J.A., Chen, G., 2007. Width of the Hadley cell in simple and comprehensive general circulation models. *Geophysical Research Letters* 34, L18804.
- Gentili, J., 1972. *Australian Climate Patterns*. Thomas Nelson, Melbourne.
- Greenwood, D.R., 1994. Palaeobotanical evidence for Tertiary climates. In: Hill, R.S. (Ed.), *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 44–59.
- Haug, G.H., Ganopolski, A., Sigman, D.M., Rosell-Mele, A., Swann, G.E.A., Tiedemann, R., Jaccard, S.L., Bollmann, J., Maslin, M.A., Leng, M.J., Eglinton, G., 2005. North Pacific seasonality and the glaciation of North America 2.7 million years ago. *Nature* 422, 821–825.
- Haywood, A.M., Valdes, P.J., Sellwood, B.W., 2000. Global scale paleoclimate reconstruction of the Middle Pliocene climate using the UKMO GCM: initial results. *Global and Planetary Change* 25, 239–256.
- Haywood, A.M., Valdes, P.J., 2004. Modelling Pliocene warmth: contribution of atmosphere, oceans and cryosphere. *Earth and Planetary Science Letters* 218 (3–4), 363–377.
- Hill, R.S., Scriven, L.J., 1997. Palaeoclimate across an altitudinal gradient in the Oligocene–Miocene of northern Tasmania: an investigation of nearest living relative analysis. *Australian Journal of Botany* 45, 493–505.
- Hobbs, J.E., 1999. Present climates of Australia and New Zealand. In: Hobbs, J.E., Lindsay, J.A., Bridgman, H.A. (Eds.), *Climate of the Southern Continents: Present, Past and Future*. Wiley and Sons, Chichester, pp. 63–105.
- Hope, P.K., Drosowsky, W., Nicholls, N., 2006. Shifts in the synoptic systems influencing southwest Western Australia. *Climate Dynamics* 26, 751–764.
- Houlder, D.J., Hutchinson, M.F., Nix, H.A., McMahon, J.P., 2000. ANUCLIM User Guide, Version 5.1. Centre for Resource and Environmental Studies, Australian National University, Canberra.
- Jordan, G.J., 1997a. Contrasts between the climatic ranges of fossil and extant taxa: causes and consequences for palaeoclimatic estimates. *Australian Journal of Botany* 45, 465–474.
- Jordan, G.J., 1997b. Evidence of Pleistocene plant extinction and diversity from Regatta Point, western Tasmania, Australia. *Botanical Journal of the Linnean Society* 123, 45–71.
- Jordan, G.J., Bromfield, K.E., Sniderman, J.M.K., Crayn, D., 2007. Diverse fossil epacrids (Styphelioideae: Ericaceae) from Early Pleistocene sediments at Stony Creek Basin, Victoria, Australia. *International Journal of Plant Sciences* 168, 1359–1376.
- Kershaw, A.P., 1997. A bioclimatic analysis of Early to Middle Miocene brown coal floras, Latrobe Valley, South-eastern Australia. *Journal of Biogeography* 45, 373–387.
- Kershaw, A.P., Nix, H.A., 1988. Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant taxa. *Journal of Biogeography* 15, 589–602.
- Kershaw, A.P., D'Costa, D.M., McEwan Mason, J.R.C., Wagstaff, B.E., 1991. Palynological evidence for Quaternary vegetation and environments of mainland southeastern Australia. *Quaternary Science Reviews* 10, 391–404.
- Kershaw, A.P., Martin, H.A., McEwan Mason, J.R.C., 1994. The Neogene: a period of transition. In: Hill, R.S. (Ed.), *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 299–327.
- Kershaw, A.P., Moss, P., van der Kaars, S., 2003. Causes and consequences of long-term climatic variability on the Australian continent. *Freshwater Biology* 48, 1274–1283.
- Lindzen, R.S., Hou, A.Y., 1988. Hadley circulations for zonally averaged heating centered off the equator. *Journal of the Atmospheric Sciences* 45, 2416–2427.
- Lopez-Vaamonde, C., Dixon, D.J., Cook, J.M., Rasplus, J.-Y., 2002. Revision of the Australian species of *Pleistodontes* (Hymenoptera: Agaonidae) fig-pollinating wasps and their host-plant associations. *Zoological Journal of the Linnean Society* 136, 637–683.
- Lourens, L.J., Antonarakou, A., Hilgen, F.J., Van Hoof, A.A.M., Vergnaud Grazzini, C., Zachariasse, W.J., 1996. Evaluation of the Plio-Pleistocene astronomical time-scale. *Paleoceanography* 11, 391–413.
- Lu, J., Vecchi, G.A., Reichler, T., 2007. Expansion of the Hadley cell under global warming. *Geophysical Research Letters* 34, L06805.
- Lu, J., Deser, C., Reichler, T., 2009. Cause of the widening of the tropical belt since 1958. *Geophysical Research Letters* 36.
- Macphail, M.K., 1996. Neogene environments in Australia, 1: re-evaluation of microfloras associated with important Early Pliocene marsupial remains at Grange Burn, southwest Victoria. *Review of Palaeobotany and Palynology* 92, 307–328.
- Macphail, M.K., 1997. Late Neogene climates in Australia: fossil pollen- and spore-based estimates in retrospect and prospect. *Australian Journal of Botany* 45, 425–464.
- Macphail, M.K., Alley, N.F., Truswell, E.M., Sluiter, I.R.K., 1994. Early Tertiary vegetation: evidence from spores and pollen. In: Hill, R.S. (Ed.), *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 189–261.
- Marra, M.J., Shulmeister, J., Smith, E.G.C., 2006. Reconstructing temperature during the Last Glacial Maximum from Lyndon Stream, South Island, New Zealand using beetle fossils and maximum likelihood envelopes. *Quaternary Science Reviews* 25, 1841–1849.
- Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., Zhao, Z.-C., 2007. Global climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and NY, USA.
- Mosbrugger, V., Utescher, T., 1997. The coexistence approach – a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 134, 61–86.
- Nix, H.A., 1991. An environmental analysis of Australian rainforests. In: Werren, G., Kershaw, P. (Eds.), *The Rainforest Legacy: Australian National Rainforests Study. Flora and Fauna of the Rainforests, vol. 2*. Australian Government Publishing Service, Canberra, pp. 1–11.
- Pole, M., 2003. New Zealand climate in the Neogene and implications for global atmospheric circulation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 193, 269–284.
- Porch, N., 2007. Beetle records. In: Elias, S.A. (Ed.), *Encyclopedia of Quaternary Science*. Elsevier, Amsterdam, pp. 179–190.

- Porch, N., Elias, S., 2000. Quaternary beetles: a review and issues for Australian studies. *Australian Journal of Entomology* 39, 1–9.
- Ravelo, A.C., Andreasen, D.H., Lyle, M., Lyle, A.O., Wara, M.W., 2004. Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature* 429, 263–267.
- Raymo, M.E., Nisancioglu, K., 2003. The 41 kyr world: Milankovitch's other unsolved mystery. *Paleoceanography* 18, 1–6.
- Raymo, M.E., Lisiecki, L.E., Nisancioglu, K.H., 2006. Plio-Pleistocene ice volume, Antarctic climate, and the global $\delta^{18}\text{O}$ record. *Science* 313 (5786), 492–495.
- Rind, D., Perlwitz, J., 2004. The response of the Hadley circulation to climate changes, past and future. In: Diaz, H.F., Bradley, R.S. (Eds.), *The Hadley Circulation: Present, Past and Future*. Kluwer Academic, Dordrecht, pp. 399–435.
- Rodwell, M.J., Hoskins, B.J., 1996. Monsoons and the dynamics of deserts. *Quarterly Journal of the Royal Meteorological Society* 122, 1385–1404.
- Scherer, R.P., Bohaty, S.M., Dunbar, R.B., Esper, O., Flores, J.A., Gersonde, R., Harwood, D.M., Roberts, A.P., Tiviani, M., 2008. Antarctic records of precession-paced insolation-driven warming during early Pleistocene Marine Isotope Stage 31. *Geophysical Research Letters* 35.
- Seidel, D.J., Fu, Q., Randel, W.J., Reichler, T.J., 2007. Widening of the tropical belt in a changing climate. *Nature Geoscience* 1, 21–24.
- Simmonds, I., Keay, K., 2000. Mean Southern Hemisphere extratropical cyclone behavior in the 40-year NCEP-NCAR reanalysis. *Journal of Climate* 13, 873–885.
- Sniderman, J.M.K., Pillans, B., O'Sullivan, P.B., Kershaw, A.P., 2007. Climate and vegetation in southeastern Australia respond to southern hemisphere insolation forcing in the Late Pliocene–Early Pleistocene. *Geology* 35, 41–44.
- Tauber, M.J., Tauber, C.A., Nyrop, J.P., Villani, M.G., 1998. Moisture, a vital but neglected factor in the seasonal ecology of insects: hypotheses and tests of mechanisms. *Environmental Entomology* 27, 523–530.
- Tapper, N.J., Hurry, L., 1993. *Australia's Weather Patterns: an Introductory Guide*. Mount Waverley, Victoria, Dellsta, 130 pp.
- Toggweiler, J.R., Russell, J.L., Carson, S.R., 2006. Midlatitude westerlies, atmospheric CO_2 , and climate change during the ice ages. *Paleoceanography* 21, PA2005.
- Trenberth, K.E., Stepaniak, D.P., 2003. Seamless poleward atmospheric energy transports and implications for the Hadley circulation. *Journal of Climate* 16, 3706–3722.
- van Oldenborgh, G.J., Drijfhout, S.S., van Ulden, A., Haarsma, R., Sterl, A., Severijns, C., Hazeleger, W., Dijkstra, H., 2009. Western Europe is warming much faster than expected. *Climate of the Past* 5, 1–12.
- Villa, G., Lupi, C., Cobianchi, M., Florindo, F., Pekar, S.F., 2008. A Pleistocene warming event at 1 Ma in Prydz Bay, East Antarctica: evidence from ODP Site 1165. *Palaeogeography, Palaeoclimatology, Palaeoecology* 260, 230–244.
- Webb, L.J., Tracey, J.G., 1981. The rainforests of northern Australia. In: Groves, R.H. (Ed.), *Australian Vegetation*. Cambridge University Press, Cambridge, pp. 67–101.
- Wolfe, J.A., 1975. Some aspects of plant geography of the northern hemisphere during the Late Cretaceous and Tertiary. *Annals of the Missouri Botanical Garden* 62, 264–279.
- Yin, J.H., 2005. A consistent poleward shift of the storm tracks in simulations of 21st century climate. *Geophysical Research Letters* 32, L18701.