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Evaluation of a modern-analogue methodology for reconstructing Australian palaeoclimate from pollen

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ABSTRACT

Quantitative palaeoclimate reconstructions are widely used to evaluate climate model performance. Here, as part of an effort to provide such a data set for Australia, we examine the impact of analytical decisions and sampling assumptions on modern-analogue reconstructions using a continent-wide pollen data set. There is a high degree of correlation between temperature variables in the modern climate of Australia, but there is sufficient orthogonality in the variations of precipitation, summer and winter temperature and plant–available moisture to allow independent reconstructions of these four variables to be made. The method of analogue selection does not affect the reconstructions, although bootstrap resampling provides a more reliable technique for obtaining robust measures of uncertainty. The number of analogues used affects the quality of the reconstructions: the most robust reconstructions are obtained using 5 analogues. The quality of reconstructions based on post-1850 CE pollen samples differ little from those using samples from between 1450 and 1849 CE, showing that European post-settlement modification of vegetation has no impact on the fidelity of the reconstructions although it substantially increases the availability of potential analogues. Reconstructions based on core top samples are more realistic than those using surface samples, but only using core top samples would substantially reduce the number of available analogues and therefore increases the uncertainty of the reconstructions. Spatial and/or temporal averaging of pollen assemblages prior to analysis negatively affects the subsequent reconstructions for some variables and increases the associated uncertainties. In addition, the quality of the reconstructions is affected by the degree of spatial smoothing of the original climate data, with the best reconstructions obtained using climate data from a 0.5° resolution grid, which corresponds to the typical size of the pollen catchment. This study provides a methodology that can be used to provide reliable palaeoclimate reconstructions for Australia, which will fill in a major gap in the data sets used to evaluate climate models.

1. Introduction

Quantitative palaeoclimate reconstructions are widely used to evaluate climate model performance because meteorological records only extend back for about 250 years and encompass a relatively modest range of climate variability (Braconnot et al., 2012; Harrison et al., 2013; Schmidt et al., 2014). The palaeo-record provides opportunities to examine model performance in intervals when the forcing and the climate response were large and comparable to the changes expected during the 21st century (Braconnot et al., 2012).

Pollen records are the most spatially extensive and widely accessible sources of data for quantitative reconstructions of past climates (Whitmore et al., 2005; Bartlein et al., 2011). Their usefulness reflects the fact that climate exerts a strong control on vegetation distribution (Harrison et al., 2010) and because the records can be dated using radiocarbon techniques (Prentice, 1988; Whitmore et al., 2005). There is a long history of reconstructing palaeoclimate from pollen using techniques such as inverse regression (Webb, 1980; Bartlein et al., 1984; Huntley and Prentice, 1988), transfer functions (Webb and Bryson, 1972), modern analogues (Howe and Webb, 1983; Overpeck et al., 1985; Jackson and Williams, 2004) and response surfaces (Bartlein et al., 1986; Gonzales et al., 2009). Large-scale reconstructions have been made for many regions, including North America (Gajewski et al., 2000; Williams et al., 2000; Viau and Gajewski, 2009), Europe (Cheddadi et al., 1997; Davis et al., 2003; Jost et al., 2005), Georgia (Connor and Kvavadze, 2008), Eurasia (Tarasov et al., 1999; Wu et al., 2007), Africa (Peyron et al., 2000; Peyron et al., 2006; Wu et al., 2007), China (Guiot et al., 2008) and New Zealand (Wilmshurst et al., 2007).

Many pollen-based reconstructions are based on some form of modern-analogue technique, in which modern relationships between pollen assemblages and climate variables are applied to palaeo-assemblages to infer past climate states. Similarity between assemblages is measured using the squared chord distance (SCD) (Overpeck

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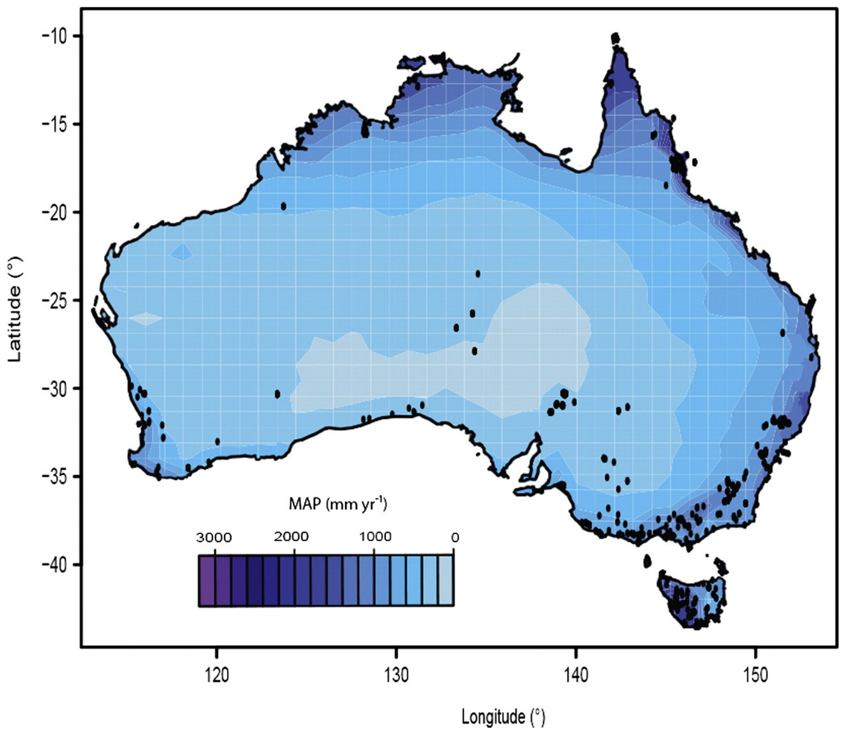

Fig. 1. Distribution of sites with pollen samples with ages <500 yr. BP (1450 to 2014 CE), used in the analyses. The sites are plotted on a map showing mean annual precipitation (MAP), to emphasise the relative paucity of sites from the arid interior of the continent.

et al., 1985), with modern analogues that pass a defined threshold being used to infer the climate of the palaeo-assemblage. However, there are a number of other analytical decisions that also need to be made to make modern-analogue reconstructions (for a review, see e.g. Simpson, 2012). The first is the choice of technique for selecting the appropriate analogues through cross-validation: jackknife leave-one-out (Efron and Efron, 1982) or bootstrapping (Freedman, 1981). The jackknife leave-one-out technique takes one assemblage at a time and compares it to all the others to see which matches most closely. Bootstrapping compares an assemblage to a subset of randomly selected assemblages and repeats the comparisons a predetermined number of times. The second decision is the optimal number of analogues to minimise the

Table 1
Performance statistics for reconstructions performed using two different analogue selection techniques, jackknife leave-one-out (leave-one-out) and bootstrapping (bootstrap), where the number of analogues was selected automatically to produce the lowest possible root mean square error of prediction (RMSEP). The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual temperature (MAT, °C), growing degree days above a baseline of 5 °C (GDD5), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant–available moisture index (α). The reconstructions made using the two different selection techniques are not significantly different from one another (95% confidence limit) nor are they significantly different (95% confidence limit) from the appropriate observed values.

Variable	Mean			RMSEP		r^2		Analogues	
	Observed	Leave-one-out	Bootstrap	Leave-one-out	Bootstrap	Leave-one-out	Bootstrap	Leave-one-out	Bootstrap
MTCO	10.2	10.1	10.1	1.7	2.0	0.93	0.94	2	1
MTWA	21.3	21.3	21.3	1.4	1.7	0.94	0.94	2	1
MAT	15.9	15.8	15.8	1.5	1.8	0.94	0.94	2	1
GDD5	4002	3987	3980	532	642	0.94	0.94	2	1
MAP	1122	1120	1120	209	240	0.92	0.93	2	2
α	0.71	0.72	0.72	0.07	0.08	0.94	0.95	2	2

Table 2
Performance statistics for reconstructions performed using a different pre-selected number of analogues, using the bootstrapping technique of analogue selection. The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual temperature (MAT, °C), growing degree days above a baseline of 5 °C (GDD5), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant–available moisture index (α). Results where the reconstructions made using the different numbers of analogues are significantly different from one another (95% confidence limit) are shown in italics; results where the reconstructions differ significantly (95% confidence limit) from the appropriate observed values are shown in bold; results where the reconstructions made using either 5 or 10 analogues different from the results obtained by automatic selection of the number of analogues, as shown in Table 1, are marked with an asterisk (*).

Variable	Mean			RMSEP		r^2	
	Observed	10 analogues	5 analogues	10 analogues	5 analogues	10 analogues	5 analogues
MTCO	10.2	**9.9***	**10.1**	2.5	2.3	0.88	0.91
MTWA	21.3	21.1	21.3	2.1	1.9	0.88	0.91
MAT	15.9	**15.6***	15.8	2.3	2.0	0.88	0.91
GDD5	4002	**3916***	3978	791	706	0.88	0.92
MAP	1122	**1120**	1122	269	248	0.88	0.91
α	0.71	***0.72***	*0.72*	0.10	0.09	0.90	0.93

Table 3
Correlations between climate variables. The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual temperature (MAT, °C), growing degree days above a baseline of 5 °C (GDD5), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant–available moisture index (α).

	MTCO	MTWA	MAT	GDD5	MAP	α
MTCO		0.69	0.93	0.93	0.31	−0.10
MTWA	0.69		0.91	0.90	−0.30	−0.64
MAT	0.93	0.91		1.00	0.11	−0.37
GDD5	0.93	0.90	1.00		0.03	−0.37
MAP	0.31	−0.30	0.11	0.03		0.84
α	−0.10	−0.64	−0.37	−0.37	0.84	

chances of either falsely determining two samples to be analogues (type 1 errors) or considering two analogous samples not to be analogues (type 2 errors). The normal practise is to use between 5 and 10 analogues (Luo et al., 2010), with the exact number determined using the lowest root-mean-square error of prediction (RMSEP).

The nature of the pollen samples themselves can also affect the reconstructions. Samples from cores taken in moderately sized lakes or peatbogs should provide a good record of the regional pollen rain (Prentice, 1985, 1988) and thus of regional vegetation and climate. However, practical considerations mean that it is not always possible to sample such sites, and thus surface samples from other sites within a basin or from other environments are frequently used either as a check on the representativeness of core samples or to extend the range of climate space sampled. However, both the representation and the preservation of pollen vary with the type of surface sample. Samples from wet sediments are less subject to preservation issues, for example, than surface soils (Wilmshurst and McGlone, 2005). Samples from closed-canopy vegetation are more likely to reflect the very local vegetation than samples from open vegetation (Tauber, 1967). Although several studies have highlighted the sampling differences between common surface sample types (e.g. Cundill, 1991; Vermoere et al., 2000), there has been limited research on the implications of sample selection on quantitative climatic reconstructions. One noticeable exception is the study by Goring et al. (2010) which examines the impact of using samples from different depositional environments in western North America on climate reconstructions obtained using several statistical techniques. They showed that the impact of sample type varied depending on the statistical technique used but could have a non-negligible influence on the reconstructions. Goring et al. (2010) point out that the impact may vary between different regions and floras; no such study has been conducted in Australia. Thus, our underlying question is how different can two pollen assemblages be before it makes a difference to the reconstruction of Australian climate?

This question also underlies decisions about temporal averaging. It is common practise in presenting palaeoclimate reconstructions to average or pool results within a selected time window, usually a 1000-year window for the Holocene and sometimes up to 2000 years during glacial periods (e.g. Gajewski et al., 2000; Bartlein et al., 2011). These fairly large time windows are designed to minimise dating and calibration uncertainties. They also ensure that, despite the tendency for the number of samples to decrease with time because of sediment compression, there are sufficient samples available across sites to reconstruct geographic patterns. Temporal averaging can either be performed on individual sample reconstructions or on a single composite sample created by averaging or pooling the counts of the individual pollen samples, but there has been no systematic evaluation of which technique is more appropriate.

A final consideration is the impact of the spatial resolution of the modern climate used. Analogue climate can be obtained by interpolation between meteorological stations or from a gridded climatology. The most widely available data sets are gridded at a resolution of 0.5° resolution (e.g. CRUTS3.1: Harris et al., 2014; HadCRUT4: Morice et al., 2012; GHCN: Peterson and Vose, 1997), but finer resolution data sets are now available for some regions (e.g. CRU CL2: New et al., 2002). Although the failure of interpolated or gridded climates to capture analogues for a specific site or sample has been raised in the literature (see e.g. discussion in Bartlein et al., 2011), the impact of changing the size of the climatic grid of the baseline climate data on analogue reconstructions has not been systematically evaluated.

There have been relatively few attempts to make quantitative climate reconstructions for Australia. The only continent-wide reconstruction to date is part of the PAGES 2k synthesis (Neukom et al., 2013; Neukom et al., 2014) and the Australian component of this synthesis is based on coral, tree ring and documentary records rather than pollen, and only spans the last millennium. However, there have been pollen compilations at a sub-continental (D'Costa and Kershaw, 1997; Cook and van der Kaars, 2006) and continental scale (Pickett et al., 2004). D'Costa and Kershaw (1997) document the climate ranges of key taxa using the South-East Australian Pollen Database (SEAPD) but do not make quantitative reconstructions. The goal of Pickett et al. (2004) was to reconstruct palaeovegetation patterns, although they do make qualitative inferences about past climates based on these patterns. Cook and van der Kaars (2006) used the SEAPD and a compilation of northern Australian pollen samples to test whether a transfer-function approach could be used to make quantitative climate reconstructions. Van der Kaars et al. (2006) subsequently applied this methodology to a single marine core from northwestern Australia and made reconstructions of several climate variables going back 100,000 years.

One of the difficulties in reconstructing palaeoclimate from pollen in Australia is the arid nature of much of the continent, which leads to serious preservation issues. Palaeo-sites are confined to limited areas and thus sample a limited range of climate space. This has led to extensive sampling of less typical environments, such as estuaries (Moss et al., 2005), river sediments (Van der Kaars et al., 2006) and artesian spring outflows (Boyd, 1990), to extend the sampled climate space. Another concern is the degree to which the introduction of exotic taxa, such as *Pinus* and *Plantago lanceolata*, during European settlement of Australia in the mid-19th century affects the reliability of modern samples as analogues. Several studies have found European settlement had significant impacts on the Australian environment, through introduction of new

Table 4
Performance statistics for reconstructions performed using samples dated to between 1450 and 1849 CE (i.e. 500 to 101 yr. B.P; pre-1850) and samples between 1850 and 2014 CE (i.e. 100 yr. BP to present; post-1850). The climate space sampled by the pre-1850 and post-1850 samples is slightly different, and so the observed mean values for each period are given for comparison. The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant–available moisture index (α). Results where the reconstructions made using the two different data sets are significantly different from one another (95% confidence limit) are shown in italics; none of the results are significantly different from observed values.

Variable	Mean				RMSEP		r^2	
	Pre-1850		Post-1850		Pre-1850	Post-1850	Pre-1850	Post-1850
	Observed	Reconstructed	Observed	Reconstructed				
MTCO	9.2	*8.7*	10.1	*10.3*	2.5	2.6	0.91	0.91
MTWA	20.9	*20.8*	21.6	*22.0*	1.9	1.9	0.90	0.91
MAP	1091	1092	1076	1061	191	185	0.95	0.94
α	0.76	*0.77*	0.72	*0.71*	0.09	0.08	0.93	0.95

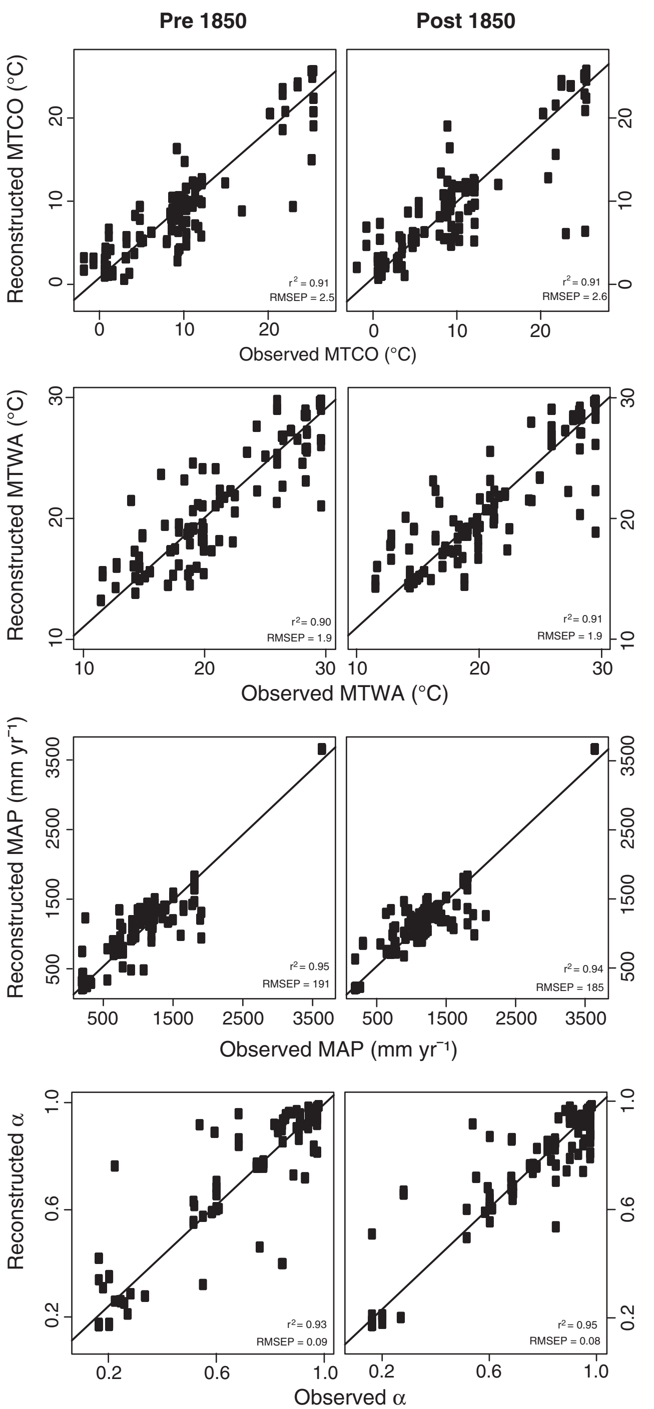

Fig. 2. Reconstructed versus observed values for mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant-available moisture index (α) for samples with ages dated to between 1450 and 1849 CE (i.e. 500 to 101 yr. B.P; pre-1850) and samples between 1850 and 2014 CE (i.e. 100 yr. BP to present; post-1850). The line represents the r^2 value shown. The associated RMSEP values are also shown.

species (exotic pollen), fire (charcoal) and erosion (magnetic susceptibility) (e.g. Gell et al., 1993; Mooney and Dodson, 2001; Dodson and Mooney, 2002; Fletcher and Thomas, 2010). Kershaw et al. (1994)

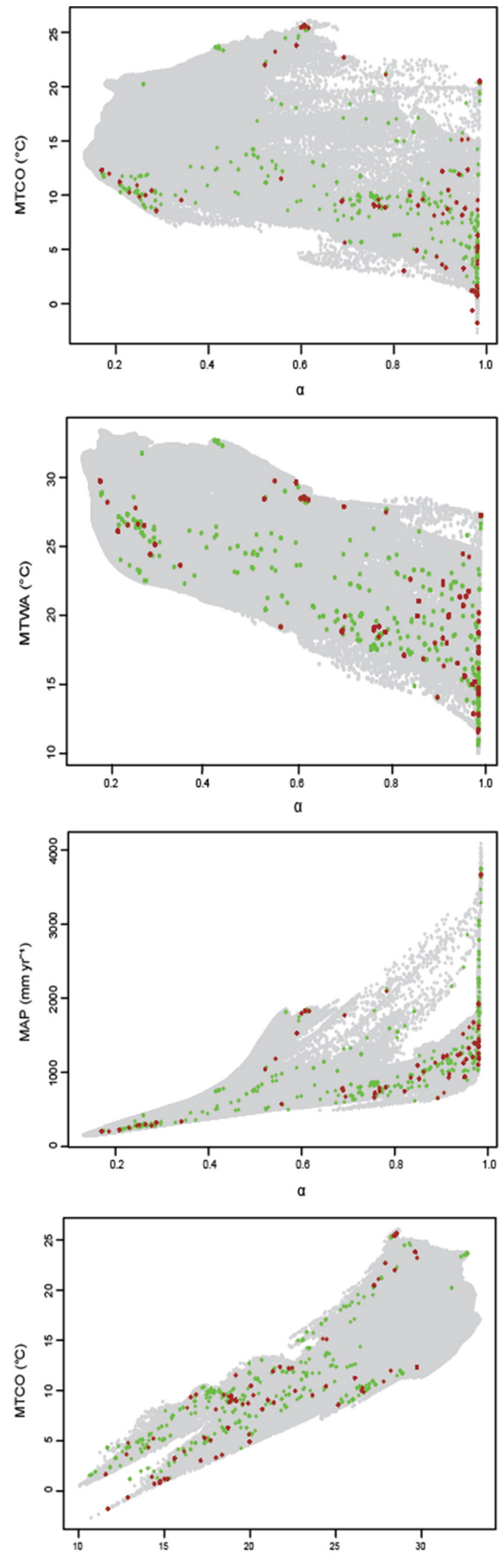

Fig. 3. The location of core top (brown points) and surface (green points) samples in climatic space, overlain on the total Australian climate space (grey dots), represented by (a) mean temperature of the coldest month (MTCO, °C) versus the Cramer–Prentice plant-available moisture index (α), (b) mean temperature of the warmest month (MTWA, °C) versus α, (c) MTCO versus MTWA and (d) mean annual precipitation (MAP) versus α.

Table 5
Performance statistics for reconstructions performed using samples only from cores (core top) and only from surface samples (surface) dated to post-1850 CE. The climate space sampled by core top and surface samples is slightly different and so the observed mean values for each period are given for comparison. The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant–available moisture index (α). Results where the reconstructions made using the two different data sets are significantly different from one another (95% confidence limit) are shown in italics; results where the reconstructions are significantly different (95% confidence limit) from the appropriate observations in bold.

Variable	Mean				RMSEP		r^2	
	Core top		Surface		Core top	Surface	Core top	Surface
	Observed	Reconstructed	Observed	Reconstructed				
MTCO	9.6	*9.6*	10.8	***10.6***	1.8	2.7	0.95	0.87
MTWA	21.3	*21.3*	21.2	*21.1*	1.5	2.1	0.95	0.89
MAP	1084	*1087*	1182	***1164***	133	316	0.97	0.86
α	0.74	*0.74*	0.71	*0.71*	0.06	0.10	0.97	0.90

thought the impact of European settlement on pollen assemblages sufficient to warrant only using averaged pre-European samples from the SEAPD as the modern samples for reconstructions, although they never tested the impact of using post-European samples. However, modern samples are used routinely and successfully for quantitative palaeoclimate reconstructions in other parts of the world, despite the presence of introduced species. So the question remains as to whether European settlement had sufficient impact to affect the ability of modern Australian pollen samples to provide reliable reconstructions of present-day climate and hence to provide suitable analogues for palaeo-reconstructions.

The purpose of this study is to test the impact of methodological decisions on the reliability of climate reconstructions for Australia using modern pollen samples in order to design an approach that can be applied to reconstruct past climates from pollen. Specifically, the study tests the methodological decisions, the basic assumptions and the impact of temporal and spatial averaging.

2. Methods

We used the pollen data set developed by Pickett et al. (2004), which was subsequently updated by the QUAVIDA working group (quest.bris.ac.uk/research/wkg-gps/QUAVIDA.html). Additional pollen samples, obtained directly from palynologists working in Australia, have been added to extend the range of sampled climate. The final data set (Fig. 1) comprises 1444 samples in the 0–500 yr. BP time window from 325 sites (for the full list of sites with coordinates and data sources, see supplementary information).

Climate data were obtained from the ANUCLIM software package (Xu and Hutchinson, 2011), which uses the ANUSPLIN thin-plate spline fitting package (Hutchinson, 2004) to interpolate meteorological data from the period 1970–1999 to a 0.05° grid cell resolution climatology. This is the climatology used by van der Kaars et al. (2006). These data were used to calculate a number of climatic and bioclimatic variables, including mean temperature of the coldest and warmest months (MTCO and MTWA, respectively), mean annual temperature (MAT), mean annual precipitation (MAP), growing degree days above 5 °C (GDD5) and the Cramer–Prentice plant–available moisture index (α, Cramer and Prentice, 1988). The bioclimatic variables, GDD5 and α, are considered to be more closely related to the controls on vegetation growth than standard meteorological variables (Harrison et al., 2010). GDD5 is calculated by linearly interpolating the monthly mean temperature to daily temperature then summing this for days where the mean temperature exceeds 5 °C. α is the ratio of actual to equilibrium evapotranspiration (Cramer and Prentice, 1988) and was calculated from monthly temperature, precipitation and percentage of sunshine hours using a simple soil water-balance model (Wang et al., 2013) with soil field water-holding capacity based on a single soil type for the continent. We choose these six variables because they are the variables included in the Bartlein et al. (2011) global benchmarking data set. However, as shown in Bartlein et al. (2011), it is not possible to reconstruct every variable at every site because of differential vegetation sensitivity to climate, e.g. tropical vegetation is unlikely to be sensitive to seasonal temperature and arid vegetation is more likely to be sensitive to drought. Thus, part of the purpose of this study is to test which variables can be reconstructed robustly from the Australian flora.

Taxa likely to represent local conditions (i.e. aquatic taxa, mangroves, parasitic plants, mosses, agricultural crops, obligate halophytes and ferns) were removed from the pollen data set, prior to analysis. Some taxa could be classified as belonging to one of these groups but also occur in other plant functional types (e.g. Chenopodiaceae can be halophytes but are also represented as succulents, forbs and shrubs), and these taxa have been retained in the data set because they represent non-excluded types. The sample counts were standardised to percentages, based on the sum of all remaining taxa. Reconstructions were performed using the Rioja package in R (Juggins, 2012), only using analogues with SCD-values lower than 0.9, the 2.5th percentile of the distribution of SCD values for this data set. In addition, no analogues were selected with SCD-values lower than 0.001, to reduce the risk of analogues being selected from the same site or the same core.

We ran number of separate tests to answer the following questions:

1. Does the choice of analogue selection method affect the reconstruction? Separate reconstructions were performed using jackknife

Table 6
Performance statistics for reconstructions performed using individual surface samples (individual) and after averaging or pooling all the surface samples (average and pooled) from a site dated to post-1850 CE. The mean climate of the two data sets is slightly different because of differences in the size of the populations, and so the observed mean values for each period are given for comparison. The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant–available moisture index (α). Results where the reconstructions made with the averaged samples differ from the individual samples, or where the pooled samples differ from the individual samples are shown in italics; results where the reconstructions are significantly different (95% confidence limit) from the appropriate observations in bold.

Variable	Mean						RMSEP			r^2		
	Individual		Averaged		Pooled		Individual	Averaged	Pooled	Individual	Averaged	Pooled
	Observed	Reconstructed	Observed	Reconstructed	Observed	Reconstructed						
MTCO	11.2	10.9	11.3	***10.5***	11.3	**10.6**	2.5	4.6	4.6	0.90	0.70	0.70
MTWA	21.5	21.3	21.7	21.4	21.7	21.4	1.8	3.7	3.7	0.93	0.70	0.71
MAP	1181	1195	1210	**1229**	1210	**1233**	243	486	483	0.93	0.67	0.68
α	0.69	0.70	0.70	0.68	0.70	0.68	0.08	0.18	0.18	0.94	0.67	0.67

leave-one-out and bootstrapping selection approaches. The number of selected analogues was chosen automatically to yield the lowest RMSEP.

2. Does the number of analogues selected affect the reconstruction? Separate reconstructions were made using 10 and 5 analogues. These reconstructions are also compared to the automatically selected number of analogues.
3. Are all climate variables equally well reconstructed using the Australian data set? In addition to evaluating the quality of the reconstructions performed in Step 1 and 2, we examined the cross-correlation between climate variables.
4. Do modern samples adequately reconstruct modern climate even though they may include exotic pollen? Separate reconstructions were performed based on samples dated to between 1450 and 1849 CE (500 to 101 yr. BP) and samples between 1850 and 2014 CE (i.e. 100 yr. BP to present). The date of 1850 CE is used by Mooney and Dodson (2001) as broadly corresponding to the time of European settlement and introduction of exotic pine in southeastern Australia.
5. Do surface samples adequately represent regional climate? Separate reconstructions were performed based on core top samples and surface samples. In addition, the proportion of climate space only represented by one of these groups was calculated by dividing the individual observations into sections of climate space and counting each section which is only represented by one of the two groups. In a separate test, we also examined whether averaging or pooling surface samples by site provided more robust reconstructions than the individual surface samples. Sites with only one surface sample were not used in this second test.
6. Does averaging or pooling samples within a specific time window produce similar reconstructions to those produced using individual samples? We separately averaged and pooled the pollen counts for all samples dated to post-1850 CE from each core and used these new assemblages for making the reconstructions. In addition to comparing the reconstructed climate values obtained by averaging versus pooling, we also compared these results to the reconstructions based on individual samples from each core.
7. Does the resolution of the gridded modern climate data affect the climate reconstructions? The original 0.05° gridded climate data was averaged to produce a climate data set at 0.5° resolution, which was then used to make reconstructions. We compared the results obtained using the two climatologies.

The performance of each reconstruction was measured by the RMSEP. The r^2 is used as a measure of the goodness-of-fit of the reconstructed and observed values. The best-fit regression line is not necessarily the same as the 1:1 regression line indicative of perfect prediction. We tested the distribution of the reconstructions for each variable separately using a Kolmogorov–Smirnov test, using the 95% confidence interval to determine significance. The selection of subsamples of the data (e.g. core tops versus surface samples) and averaging or pooling of samples (e.g. within time windows) means that the mean and range of observed climate used for evaluation can differ. Variations in the size of the populations were taken into account when determining the statistical significance of the tests. Different populations could sample different areas of climate space and this affects the mean and range of the target climates. Reconstructions are compared with the appropriate climate for each population, rather than attempting to sample a common area of climate space. As a final assessment, we compare the site-based reconstructions, where each site may be represented by multiple samples (in which case the median discrepancy is used), with the observed climate by overlaying the samples on our 0.5° gridded data set, using fixed intervals of each variable, based on their respective RMSEP, to indicate degree of discrepancy. No attempt has been made to standardise the discrepancies relative to the observations; thus, this comparison is particularly stringent for regions of high observed values of a given climate variable.

3. Results

3.1. Individual tests

3.1.1. Analogue selection approach

The climate reconstructions obtained using the jackknife leave-one-out and bootstrap approaches are statistically indistinguishable (Table 1). The RMSEP values are marginally better for the leave-one-out approach and the r^2 values are marginally better for the bootstrapping

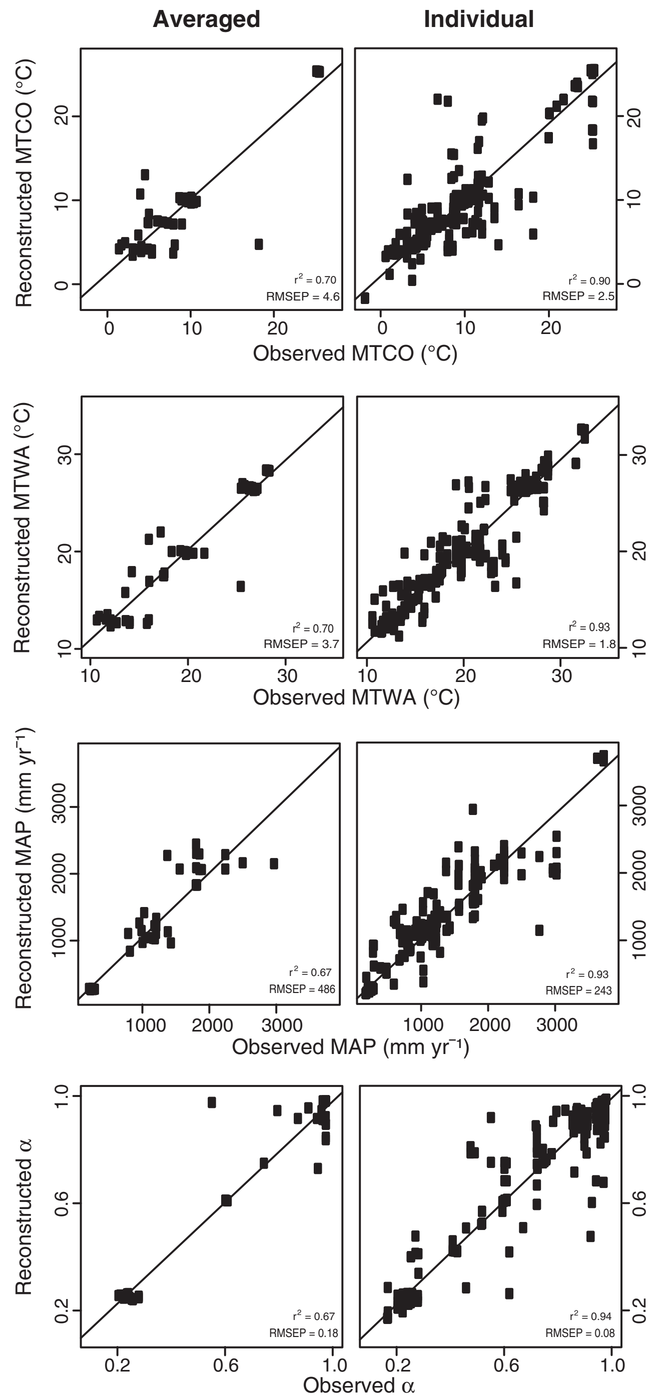

Fig. 4. Reconstructed versus observed values for mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant-available moisture index (α) for averaged and individual surface samples at a site. The line represents the r^2 value shown. The associated RMSEP values are also shown.

approach. Bootstrapping provides a more robust estimation of the variance of the distribution than the jackknife leave-one-out approach (Shao and Tu, 1995, pp. 86–90) and could also be used to estimate e.g. median values, and so it is used for all subsequent analyses.

3.1.2. Using varying numbers of analogues

The difference between reconstructions made using 5 or 10 analogues is not statistically significant, although the RMSEP values are slightly lower and the r^2 values slightly higher when only 5 analogues are used (Table 2). The reconstructions obtained using 5 analogues do not differ significantly from the automatically selected number of analogues (1 or 2) that gives the lowest RMSEP (Table 1), although the reconstructions of MTCO, MAT, α and GDD5 based on 10 analogues are significantly different from those obtained by automatic selection. Furthermore, the reconstructions based on 10 analogues are significantly different from the observed values whereas those based on 5 analogues (and the automatic selection) are not significantly different from observed. Increasing the number of analogues does not improve the reconstructions and we therefore use 5 analogues for all further analyses.

3.1.3. Choice of climate variables

The results of the first two tests suggest that all six of the climate variables can be reconstructed equally well: the bootstrap r^2 values are similar and the RMSEP values are of a similar magnitude. Nevertheless, some of these variables are highly correlated in the modern climate of Australia (Table 3). There is a particularly high degree of correlation amongst the temperature variables, for example, both MTCO and MTWA are strongly correlated with MAT ($r^2 \approx 0.90$) although less strongly correlated to one another ($r^2 = 0.69$). GDD5 is also strongly correlated with MAT ($r^2 = 1.00$). The degree of correlation is such as to rule out being able to distinguish the independent effects of these temperature variables on vegetation distribution. The performance statistics for MTWA are generally better than for the other temperature variables (Tables 1 and 2). Given that the correlation between MTCO and MTWA is the least strong, and that it is highly desirable to be able to reconstruct changes in temperature seasonality because this is a major feature of both Holocene and glacial climates (Izumi et al., 2013; Izumi et al., 2014), we have preserved these two variables but make no further attempt to reconstruct MAT or GDD5. The moisture variables are not well correlated with temperature: the correlation between MAP and MTWA is -0.3, and between MAP and MTCO is 0.3. There is also a negative correlation between α and seasonal temperature, which is moderately strong for MTWA (-0.6) but weak for MTCO (-0.1). Thus, there is probably sufficient independent information to be able to reconstruct moisture as well as seasonal temperature variables. MAP and α reflect different aspects of the moisture balance, i.e. input versus plant–water availability. The amount of plant–available water (α) is influenced by factors affecting evapotranspiration, including temperature and wind speed. MAP and α are quite highly correlated (0.84), but it should still be possible to reconstruct them independently. As a further test, we carried out a redundancy analysis (RDA; see Juggins and Birks, 2012) using all six variables to determine whether they have independent power to explain the variation in the pollen assemblages. MAP, α, MTWA and MTCO are all significant (99% level), confirming that there is sufficient information in the assemblages to reconstruct them independently, whereas MAT and GDD5 are not significant and therefore lack explanatory power.

3.1.4. Impact of European settlement

The reconstructions using pre-1850 CE and post-1850 CE samples are statistically different from one another (Table 4) for all variables except MAP. However, neither are significantly different from the appropriate observed climate, and the pre-1850 CE and post-1850 samples have comparable RMSEP and r^2 values (Fig. 2). Only 22% of the sites have pre-1850 CE samples compared to the 95% of the sites that have post-1850 CE samples. This suggests that reliable reconstructions can be obtained by using only the recent samples for analogues. In subsequent tests we only use the post-1850 CE samples.

3.1.5. Use of core tops or surface samples

The reconstructions of all the climate variables made using only core samples and only surface samples are significantly different from one another. This reflects the fact that the core tops sample a more limited amount of climate space (Fig. 3). In fact, about half of the bioclimatic space is only covered by surface samples (42–65%, depending on variable), with 0–6% being unique to core top samples. The core top reconstructions have lower RMSEP values and higher r^2 values (Table 5), reflecting the fact that several of the surface samples have very large errors and overall the reconstruction based on surface samples alone is much noisier. However, only MTCO and MAP from the surface sample reconstructions differ significantly from the observed climate (Table 5). Despite this, and given that the surface samples extend the range of sampled climate, it appears that combining surface sample and core top samples is appropriate in order to provide robust reconstructions.

3.1.6. Spatial averaging and pooling of surface samples

Surface samples are usually chosen to sample the variety of different vegetation types within a catchment. Combining multiple surface samples could potentially provide a more complete sampling of the vegetation and thus provide a better approximation of the regional pollen rain, and hence a better match to the regional climate signal.

Reconstructions made after amalgamating the surface samples from a site, whether by averaging the individual samples or by pooling them, are only significantly different from those based on the individual surface samples for MTCO (Table 6). However, the averaged and pooled samples have much higher RMSEP values and much lower r^2 values. The greater variance in the averaged or pooled samples (Fig. 4) probably reflects the reduction in the number of potential analogues. Thus, this test shows that it is better to use the individual surface samples as analogues and this is the procedure used in the final tests.

Table 7
Performance statistics for reconstructions performed using all core and surface samples from a site (individual) and after averaging or pooling all samples (average and pooled) dated to post-1850 CE. The mean climate of the two data sets is slightly different because of differences in the size of the populations and so the observed mean values for each period are given for comparison. The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm $yr.^{-1}$) and the Cramer–Prentice plant–available moisture index (α). Results where the reconstructions made with the averaged samples differ from the individual samples, or where the pooled samples differ from the individual samples are shown in italics; results where the reconstructions are significantly different (95% confidence limit) from the appropriate observations in bold.

Variable	Mean						RMSEP			r^2		
	Individual		Averaged		Pooled		Individual	Averaged	Pooled	Individual	Averaged	Pooled
	Observed	Reconstructed	Observed	Reconstructed	Observed	Reconstructed						
MTCO	10.7	*10.7*	10.3	***9.5***	10.3	***9.2***	2.2	5.0	5.0	0.93	0.57	0.58
MTWA	21.7	21.7	21.3	21.7	21.3	21.5	1.7	3.8	3.8	0.94	0.65	0.66
MAP	1112	1125	1149	1001	1149	1003	209	463	464	0.94	0.69	0.69
α	0.69	0.69	0.71	0.65	0.71	0.65	0.08	0.19	0.18	0.95	0.65	0.66

3.1.7. Temporal averaging and pooling of core samples

There are multiple samples within the post-1850 time window from some of the cores in the data set. This raises the issue of whether all of these samples should be treated as potential modern analogues, or whether it is better to average or pool the samples to derive a single analogue assemblage. Although the mean values of the reconstructions are not statistically different (apart from MTCO again; Table 7), the RMSEP values are very much higher and the r^2 values lower for the reconstructions based on averaged samples (Fig. 5). The same is true for the pooled samples (Table 7). As in the case of spatial averaging, this most likely reflects the reduction in the number of potential analogues. This test shows that it is better to use the individual core samples as analogues and this is the procedure used in the final tests.

3.1.8. Impact of the resolution of the climate data set

There is a significant difference between the reconstructions of all climatic variables based on analogue climates drawn from a 0.05° or a 0.5° grid (Table 8, Fig. 6). The MTCO reconstructions are significantly different from observed climate values at both resolutions, while α is also significantly different from observed for reconstructions using the 0.5° resolution grid. However, the RMSEP values for all climate variables are lower for the coarser grid. This presumably reflects the fact that the 0.5° resolution grid is closer to the size of the pollen source area (see e.g. Prentice, 1985) for most sites in the data set and suggests that it is better to use the coarser grid to derive analogues for the reconstructions. To test this, separate reconstructions were made for sites with small (<10 km^2), medium (10.1–500 km^2) and large (>500 km^2) catchments. There is a significant difference between these reconstructions for all climate variables, but none of them are significantly different from the appropriate observations (Table 9). The reconstructions based on medium-sized catchments have the lowest RMSEP values (and highest r^2) for all variables except α. Most of the medium-sized catchments occur at the saturated end of the α range and this probably contributes to the poorer performance for this variable. Reconstructions based on sites with large catchments are significantly worse than the other two sets of reconstructions, possibly because only 2% of the sampled sites are in this size range and the range of climate sampled is limited. Many of the larger basins occur in the central part of the continent, where there would otherwise be very limited sampling. Excluding reconstructions from such sites because of the large associated uncertainties would lead to a loss of information for a critical region.

3.2. Reliability of the reconstructions

There are 11 sites in our data set for which there are no analogues (i.e. no samples with an SCD value <0.9) elsewhere in the data set. For the remaining sites, there is moderately good agreement between the reconstructed and observed MTCO for individual samples from different sites (Fig. 7a). Most of the sites (61%) show agreement within 1 °C of the observed MTCO, with 78% agreeing within 2 °C. Discrepancies >2 °C occur in Queensland, and there is a single site in the far north (Groote Eylandt, 2 samples) and one in the northwest of the country (Dragon Tree Soak, 5 samples) that also show discrepancies >2 °C. There are also several sites in coastal situations in Western Australia, South Australia and the southeastern part of the country with samples that show large discrepancies. These coastal sites, and about half of the northern sites, also show large discrepancies (i.e. >2 °C) in MTWA (Fig. 7b). There are extremely steep temperature gradients inland from the coast around much of southern Australia (Sturman and Tapper, 2005, pp. 541; Jones et al., 2009), and the temperature discrepancies at coastal sites probably reflect the fact that the gridded climate data set does not capture such gradients. The discrepancies in northern Australia are more likely to reflect the comparative lack of surface samples from the tropical regions in our data set.

The worst agreement between the reconstructed and observed figures is for MAP (Fig. 7c). Only just over half of the sites (52%) show agreement to within 100 mm of the observed MAP, with 24% of sites showing disagreement >250 mm, though most of these are in areas of fairly high rainfall, such as Queensland or the southeast. Thus, these discrepancies are small compared to the actual amount of rainfall received at these sites. The reconstructions of α are moderately good, with most samples (81%) showing agreement of <0.1 (Fig. 7d). Very few sites (3%) show discrepancies of >0.3, and these are mostly sites in southwestern Australia where the temperature variables also show moderately large discrepancies. The only exceptions to this pattern are two sites in inland

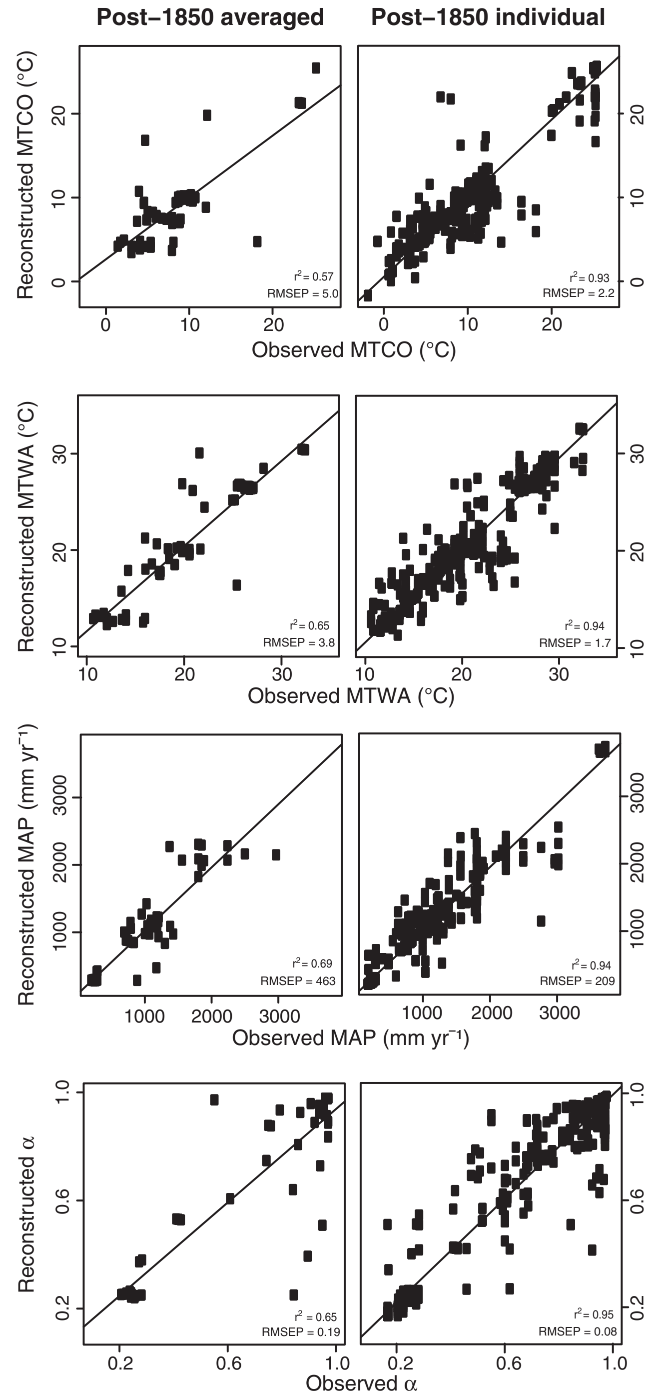

Fig. 5. Reconstructed versus observed values for mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant-available moisture index (α) performed using all samples dated to post-1850 CE from a single core and after averaging these samples. The line represents the r^2 value shown. The associated r^2 values are also shown.

Table 8
Performance statistics for reconstructions performed using modern climate values obtained from gridded climatologies of different resolution. The original climatology was on a grid of 0.05° resolution (0.05°) and second climatology was aggregated to 0.5° resolution (0.5°). The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant-available moisture index (α). Results where the reconstructions made using the two different data sets are significantly different from one another (95% confidence limit) are shown in italics; results which are significantly different (95% confidence limit) from the appropriate observed values are shown in bold.

Variable	Mean				RMSEP		r^2	
	0.05°		0.5°		0.05°	0.5°	0.05°	0.5°
	Observed	Reconstructed	Observed	Reconstructed				
MTCO	10.6	***10.4***	10.9	***10.7***	2.6	2.3	0.88	0.89
MTWA	21.4	*21.4*	21.9	*21.9*	2.1	1.8	0.89	0.90
MAP	1130	*1118*	1043	*1032*	280	233	0.89	0.90
α	0.70	*0.70*	0.69	***0.68***	0.10	0.09	0.91	0.91

NSW which show discrepancies of >0.2 in an area where the observed α is already low (<0.4) and also along the arid coastal area of southern Australia area where α is <0.3 (Fig. 7d). The discrepancies in these two regions are not driven by discrepancies in temperature, but likely reflect the fact that there are very few available analogues for such dry sites.

It is possible that part of the reason for poor performance reflects issues of the taxonomic resolution of some samples, particularly those from arid regions. Indeed, the use of samples dominated (>75%) by a single taxon has a significant and negative impact on the quality of the reconstructions, displaying some of the worst test statistics from any of our tests (Supplementary Table 1). However, the reconstructions still do not diverge significantly from the observed values, which highlights how robust our overall reconstructions are.

Much of Australia is characterised by large interannual variability in climate, chiefly associated with the El Niño-Southern Oscillation (ENSO) (Diaz and Markgraf, 1992). Rainfall variability leads to changes in the relative abundance of annual species between years. Given that most of the pollen samples used in this analysis integrate the pollen rain over years-to-decades, it is possible that the pollen assemblages reflect climate extremes rather than the long-term mean climate and that this might contribute to the rather large reconstruction biases particularly in MAP. However, there does not appear to be any geographic patterning in the reconstruction biases (Fig. 7) that could be linked to differences in climate variability. In general, the largest biases are for sites in regions with relatively few modern analogues. Thus, it seems likely that the uneven distribution of modern analogues is the primary explanation for the occurrence of larger reconstruction uncertainties.

4. Discussion and conclusions

Our analyses provide a methodology for the application of MAT to make palaeoclimate reconstructions for Australia. We have shown that the method of analogue selection does not significantly affect the reconstructions but the number of selected analogues does. Previous studies (e.g. Birks et al., 1990; Telford et al., 2004) have also suggested that such methodological decisions could be important.

We examined the same set of variables used in the global benchmark data set by Bartlein et al. (2011). All six of these variables (MAT, MTCO, MTWA, GDD5, MAP and α) could be reconstructed using our data set, with reasonable reliability. However, the four temperature variables (MAT, MTCO, MTWA and GDD5) are very highly correlated in the modern climate, and thus unlikely to provide independent palaeoclimate reconstructions. MTWA and MTCO were the least well correlated and produced reconstructions with good performance statistics, and thus we suggest it should be possible to provide a measure of seasonal temperature change. This is highly desirable given that changes in seasonality are a major signal in both interglacial and glacial climates (Izumi et al., 2013; Izumi et al., 2014). The moisture variables, MAP and α, show only moderate correlation with MTWA and MTCO, and thus it should also be possible to make palaeoclimate reconstructions of these aspects of the moisture balance. Again, this is highly desirable in the context of Australia because many of the largest changes in past climate have been attributed to changes in the hydrological cycle (Harrison, 1993; Harrison and Dodson, 1993, pp. 265–293; Shulmeister and Lees, 1995; Wyrwoll and Miller, 2001; Kershaw et al., 2003; Hesse et al., 2004; Pickett et al., 2004; Martin, 2006; Nanson et al., 2008; Kershaw and van der Kaars, 2012). RDA confirms that MAT and GDD5 have little explanatory power, whereas there is sufficient information in the pollen assemblages to make independent reconstructions of MAP, α, MTWA and MTCO. However, our choice of variables differs somewhat from that identified as optimal by Bartlein et al. (2011): they recommended the use of GDD5 and MTCO (rather than MTWA and MTCO) for temperature and suggested that MAP was likely to provide more robust reconstructions than α. This may reflect the preponderance of northern hemisphere extratropical sites in the data they analysed, where length of the growing season (as measured by GDD5) is likely to be more important as a control on vegetation distribution than heat stress (as measured by MTWA). In tropical and subtropical climates, heat stress may be more important (see e.g. Harrison et al., 2010). The robustness and coherency of the α reconstructions for Australia suggests that this is as valuable as MAP as a measure of the hydrological regime, and again the fact that Bartlein et al. (2011) found it to be less reliable may reflect the preponderance of samples from humid climates in their data set.

There has been considerable concern about the impact of European colonisation on Australian vegetation and whether it is possible to use modern pollen samples as analogues for palaeo-reconstructions (see e.g. D'Costa and Kershaw, 1997). While European settlement considerably altered Australian vegetation patterns (Carnahan, 1997), and indeed the presence of exotic pollen is widely used in Australia as a temporal marker in pollen diagrams (e.g. Williams et al., 2006; Black, 2006), we have shown that post-European pollen samples provide good reconstructions of the modern climate. As is true in other regions, the presence of some exotic pollen has little effect on the ability to reconstruct regional climate—in part because exotic species are also limited by climate factors and in part because they comprise a relatively small component of the regional pollen rain. Our results suggest that, other than in exceptional circumstances, human impact on the landscape of Australia has not substantially altered the regional vegetation patterns. Indeed, this is consistent with the results of Pickett et al. (2004) who were able to reconstruct local vegetation from pollen at >60% of the sites from mainland Australia. The ability to use modern (i.e. post-1850 CE) samples as palaeoclimate analogues is important because it increases the number of potential analogues in our data set by about 50%.

The interpretation of palynological data is often limited by taxonomic resolution. Although this problem is not unique to Australia, the Australian flora is characterised by a large number of genera of high diversity and broad climatic ranges. The classic case is *Eucalyptus*, with more than 700 species occupying almost all extant climatic niches across the continent. Although attempts have been made to distinguish broad ecological groups of *Eucalyptus* from their pollen morphology

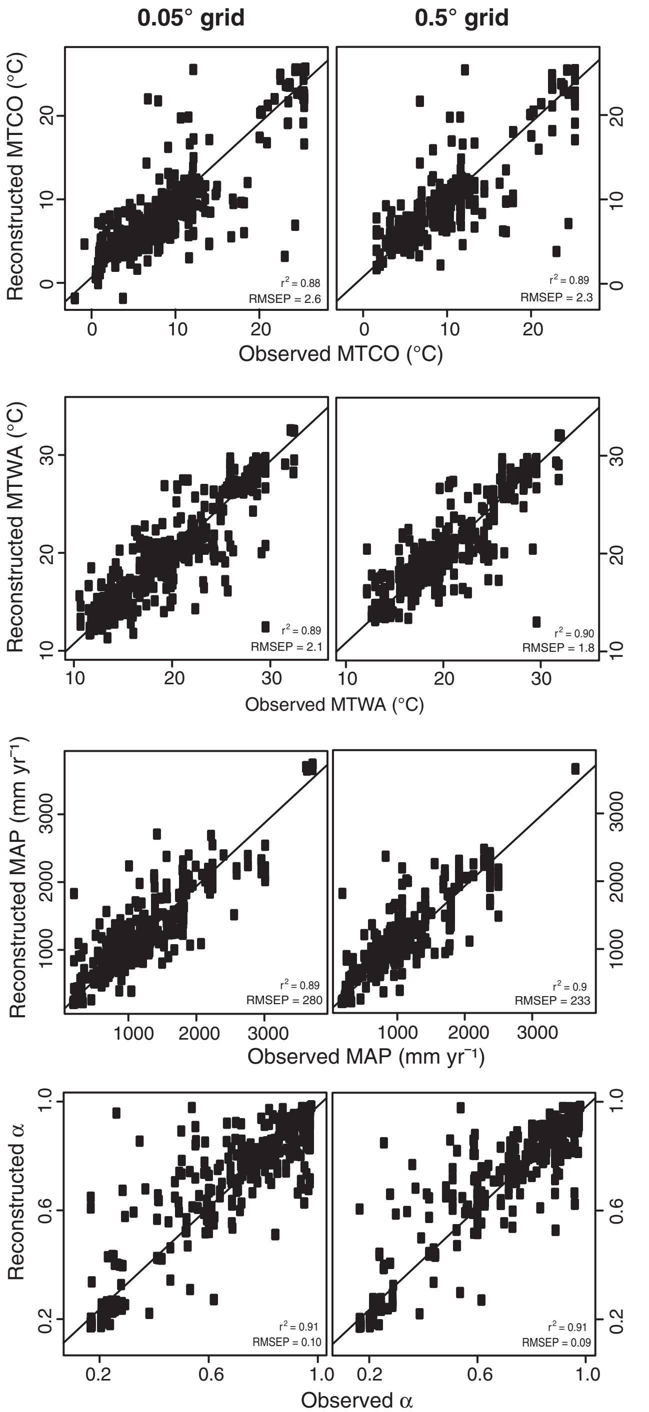

Fig. 6. Reconstructed versus observed values for mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant–available moisture index (α) based on climate data derived from a 0.05° gridded climatology and a 0.5° gridded climatology. The line represents the r^2 value shown. The associated r^2 values are also shown.

(see e.g. Pickett and Newsome, 1997), the lack of morphological variation generally precludes distinguishing individual species from one another. Other widespread genera which are generally not distinguished to species level in Australian pollen records include e.g. *Acacia* and *Casuarina* (Pickett et al., 2004). Our data set is not adequate to explicitly test the impact of taxonomic resolution on the climate reconstructions, but the quality of climate reconstructions is substantially downgraded in samples dominated (>75%) by a single taxon or characterised by only a very limited number of taxa. This suggests that, as Pickett et al. (2004) found in making vegetation reconstructions, the impact of poor taxonomic resolution may be overcome when the pollen assemblage includes a reasonably large number of individual taxa.

Averaging, both geographically and in time, does not significantly change the mean value of the reconstructions, but it does affect the variance. This suggests that it is better to make reconstructions using individual samples and then to average the results in order to obtain representative values for either specific time windows or regions. This is the approach generally used in providing regional reconstructions for model evaluation, which are usually averaged to the same spatial resolution as climate models (ca 2 × 2° latitude, longitude) and across time windows of ca 1000 years (see e.g. Bartlein et al., 2011). This approach has a second advantage of providing an additional measure of reconstruction uncertainty in terms of temporal or within-grid cell variability.

Although there has been discussion in the literature of the impact the choice of climate data set used to obtain analogues has on reconstructions (e.g. Schäfer-Neth and Paul, 2003, pp. 531–548; Bartlein et al., 2011), there has been little consideration of the impact the resolution of these data sets has on the final reconstructions. However, it is frequently noted that modern reconstructions using gridded climate data sets in areas of high topographic diversity often show large errors (Viau et al., 2006; Thompson et al., 2008; Bartlein et al., 2011), presumably because the gridded averages of climate variables are not representative of the climate at individual pollen sites. Our analyses show that the reconstructed ranges of the climate variables are often more limited than the observed ranges, with most noticeable underestimates for the cold end of the temperature range. This is consistent with the idea that it is difficult to obtain estimates of extreme climate values using analogues selected from gridded data sets, although relatively few sites in the Australian data set occur in complex topography or are particularly high-elevation sites. Nevertheless, we have shown that better reconstructions are obtained using climate variables from a 0.5° resolution grid than from a finer resolution grid. One explanation for this could be related to the pollen-source area sampled by analogue sites. Some of our sampling sites are large and many of the sites occur in relatively open vegetation. Both characteristics mean that the pollen-source area is relatively large (Prentice, 1985; Sugita, 1994; Bunting et al., 2004; Sugita, 2007a, 2007b) and this would be consistent with our finding that the coarser resolution grid produces better reconstructions. This conclusion is also supported by the finding that sites from medium-sized catchments generally provide better reconstructions than sites from large- or small-sized catchments. Some recent studies have attempted to take account of pollen-source area in reconstructing palaeoclimate (e.g. Wang et al., 2014), and our study suggests that this issue needs to be explored further in the context of determining the appropriate resolution of the climate data used as a basis for reconstruction.

The study by Cook and van der Kaars (2006) provides the only other attempt to reconstruct modern Australian climates quantitatively from pollen data and uses transfer functions developed for three regions (northern Australia, Tasmania and mainland Southeast Australia) separately to reconstruct a suite of 11 seasonal and annual measures of moisture and temperature. Cook and van der Kaars (2006) show that it is neither possible to reconstruct all of these measures in each region nor to derive a unique set of variables that apply to all three regions. Our analyses show that this is not surprising given the high degree of correlation between different temperature variables, and the fact that the relationship between MAP and α is not completely independent implies that similarly high degrees of correlation will be found between seasonal moisture variables. Indeed, Cook and van der Kaars (2006) obtain very low significance values for the seasonal moisture reconstructions. Despite the fact that different plant species will show differential sensitivity to specific aspects of climate (Jackson and Williams, 2004; Harrison et al., 2010; Bartlein et al., 2011), there is a limit to the amount of real climate information that can be derived

Table 9
Performance statistics for reconstructions performed using samples from sites with different catchment sizes. The different sizes are small (<10 km^2), medium (10.1–500 km^2) and large (>500 km^2). The climate variables are mean temperature of the coldest month (MTCO, °C), mean temperature of the warmest month (MTWA, °C), mean annual precipitation (MAP, mm yr.$^{-1}$) and the Cramer–Prentice plant-available moisture index (α). Results where the reconstructions made using the two different data sets are significantly different from both of the others (95% confidence limit) are shown in italics; results which are significantly different (95% confidence limit) from the appropriate observed values are shown in bold.

Variable	Mean						RMSEP			r^2		
	Large catchment		Medium catchment		Small catchment		Large	Medium	Small	Large	Medium	Small
	Observed	Reconstructed	Observed	Reconstructed	Observed	Reconstructed						
MTCO	21.1	*21.8*	10.4	*10.2*	9.4	*9.2*	2.6	2.3	2.3	0.63	0.93	0.90
MTWA	29.5	*29.6*	20.6	*20.5*	20.1	*20.0*	1.5	1.5	1.7	0.78	0.93	0.91
MAP	1678	*1809*	1207	*1198*	1204	*1206*	474	154	227	0.89	0.95	0.93
α	0.63	*0.66*	0.82	*0.82*	0.76	*0.76*	0.13	0.07	0.07	0.78	0.85	0.94

from pollen assemblages, and thus it is important to test explicitly whether the reconstructed variables are reasonably independent and to select variables that are most likely to influence plant physiology, growth and distributions.

A strict comparison of our results with those obtained by Cook and van der Kaars (2006) is not possible because the climate variables selected in each study are different. Nevertheless, examination of comparable variables suggests that a better fit is obtained using regional specific calibrations than the continental calibration used in our study. For example, we obtained an RMSEP of 0.09 for α, which can be compared with values of 0.05 and 0.09 in the Cook and van der Kaars (2006) study. Similarly, we obtained an RMSEP of 1.8 for MTWA,

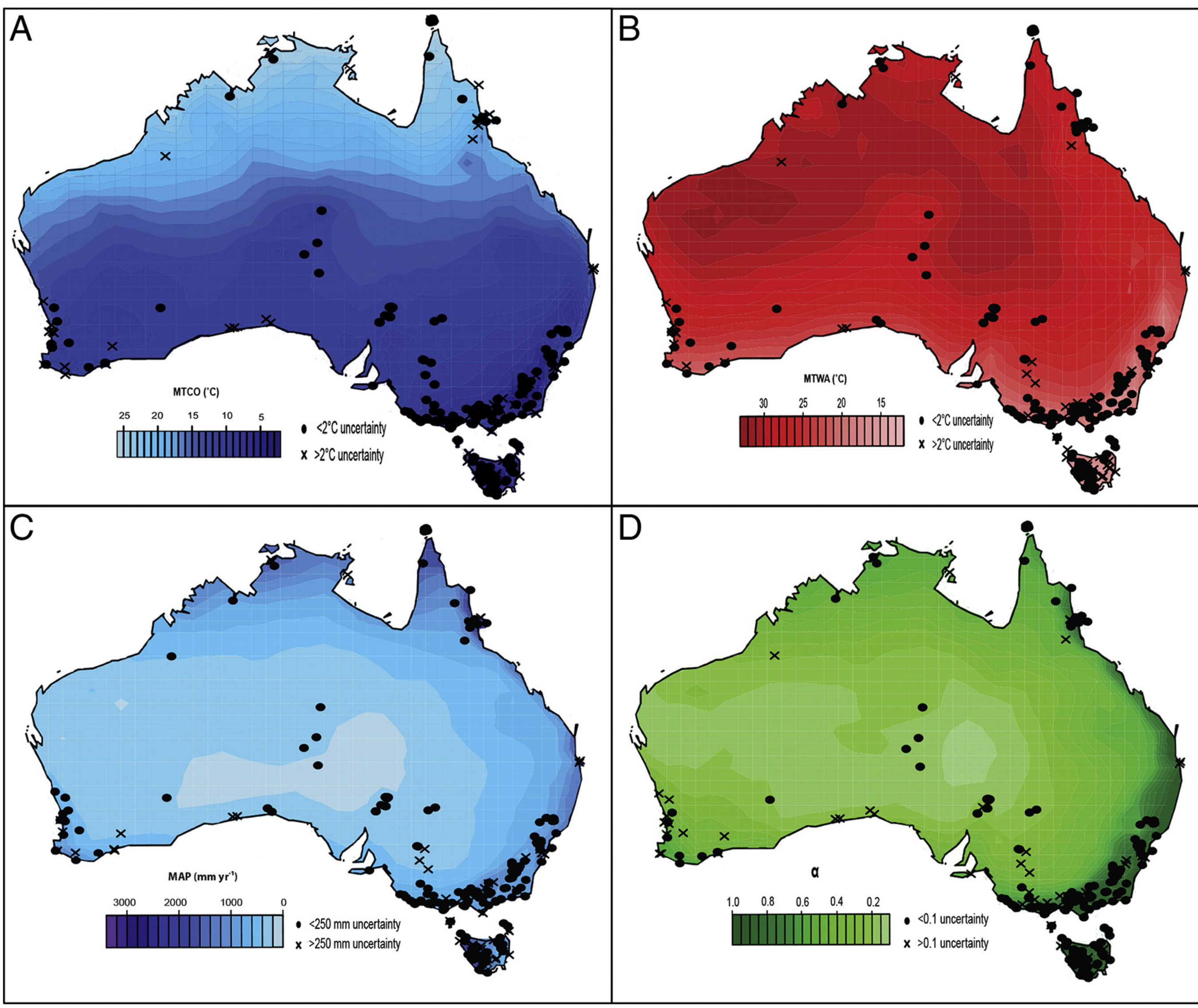

Fig. 7. Comparison of reconstructed and observed (a) mean temperature of the coldest month (MTCO, °C), (b) mean temperature of the warmest month (MTWA, °C), (c) mean annual precipitation (MAP, mm yr.$^{-1}$) and (d) the Cramer–Prentice plant-available moisture index (α). The underlying map shows the observed patterns based on the 0.5° gridded climatology. The symbols show how closely the reconstructed values capture the observed values, where the different symbols show if the discrepancies are greater or smaller than the associated RMSEP. No attempt has been made to standardise the discrepancies relative to the observations, thus this comparison is particularly stringent for regions of high observed values of a given climate variable.

which can be compared to values of 0.8 to 1.8 for mean summer temperature; an RMSEP of 2.3 for MTCO, which can be compared to values of 1.6 to 1.9 for mean winter temperature; and an RMSEP of 233 for MAP, compared to values of 159 to 474 for annual precipitation. However, as these comparisons show, even the improvement obtained by using a regionally specific calibration only pertains in some regions. Furthermore, limiting the area from which analogues can be selected will tightly constrain the palaeo-reconstructions and thus will make it more difficult to reconstruct climate radically different from present.

The ability to reconstruct modern climate from modern pollen samples does not guarantee that this approach will provide good reconstructions of palaeoclimates. Past climate changes may have led to situations that are not represented in the modern climate space (the non-analogue problem: Overpeck et al., 1985; Whitmore et al., 2005). Furthermore, under-sampling of the modern climate can lead to poor palaeo-reconstructions even though these past climates are represented in modern climate space. Despite the size of our data set, for example, cold temperatures are under-sampled, which could be problematic for reconstructions of glacial climates. Similarly, the fact that there are larger uncertainties associated with reconstructions of tropical climates suggests that we are also under-sampling this region of climate space. Nevertheless, our explorations suggest that it is worthwhile to apply the modern analogue reconstruction technique to the palaeorecord of Australia and have provided a methodology for doing so. Australia is a major gap in global target data sets (e.g. Bartlein et al., 2011). Our data compilation makes it possible to fill this gap, and our analyses provide a methodology for how to perform these reconstructions. This is important because Australia is a maritime continent, strongly influenced by the El Niño Southern Oscillation (McBride and Nicholls, 1983; Diaz and Markgraf, 1992; Fierro and Leslie, 2014). The ability to reconstruct large-scale patterns of climate change in the northern hemisphere (see e.g. Harrison et al., 2013; Izumi et al., 2013; Li et al., 2013) is no guarantee that state-of-the-art models can reliably reconstruct similar patterns in the southern hemisphere.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.revpalbo.2015.12.006.

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