

On the timing of megafaunal extinction and associated floristic consequences in Australia through the lens of functional palaeoecology

Matthew Adesanya Adeleye^{a,b,c,*}, Samuel Charles Andrew^d, Rachael Gallagher^e, Sander van der Kaars^{f,g}, Patrick De Deckker^h, Quan Huaⁱ, Simon Graeme Haberle^{b,c}

^a Department of Geography, University of Cambridge, 20 Downing Pl, CB2 3EL, Cambridgeshire, United Kingdom

^b School of Culture, History and Language, 9 Fellows Rd, HC Coombs, The Australian National University, Acton, ACT, 2600, Australia

^c Australian Research Council Centre of Excellence for Australian Biodiversity and Heritage, 9 Fellows Rd, HC Coombs, The Australian National University, Acton, ACT, 2600, Australia

^d The Commonwealth Scientific and Industrial Research Organisation (CSIRO), 101, Clunies Ross Street Black Mountain, ACT, 2601, Australia

^e Hawkesbury Institute for the Environment, Western Sydney University, L9, Science Rd, Richmond, NSW, 2753, Australia

^f School of Earth, Atmosphere and Environment, Monash University, 9 Rainforest Walk, Clayton, VIC, 3800, Australia

^g Department of Earth Sciences, Vrije Universiteit Amsterdam, Amsterdam, the Netherlands

^h Research School of Earth Sciences, The Australian National University, 142 Mills Rd, Acton, ACT, 2600, Australia

ⁱ Australian Nuclear Science and Technology Organisation, New Illawarra Rd, Lucas Heights, NSW, 2234, Australia

ARTICLE INFO

Handling Editor: Donatella Magri

Keywords:

Megafaunal extinction
Plant traits
Functional palaeoecology
Sporormiella
Charcoal
AMS ¹⁴C dating
Human activity

ABSTRACT

The timing and cause of megafaunal extinctions are an enduring focus of research interest and debate. Despite the developments in the analysis of coprophilous fungal spores (CFS), the proxy for reconstructing past megaherbivore changes, the environmental consequences of this fauna loss remain understudied. This is partly due to the general obscurity of such a signal in pollen records, as well as limitations in disentangling human and extinction ecological impact, and the lack of spatial information of megafauna changes in site-level sedimentary records. In Australia, the debate centres on the possibility that habitat loss through climate change, vegetation-fire change, human intervention, or a combination of these factors led to the extinction of some large animals during the Late Pleistocene. Pollen and plant isotope studies have also demonstrated that vegetation-fire responses following the Late Pleistocene megafaunal extinctions were characterized by increased vegetation density and fire activity due to reduced grazing/browsing pressure. Here, we use a well-dated marine sedimentary core record from the Murray Darling Basin in southern Australia and apply palynological and functional palaeoecological approaches to reconstruct the Late Pleistocene megafaunal abundance changes, the timing and potential cause of extinction across the basin and investigate if extinction was associated with any signal of trait-based vegetation changes. We infer megafaunal abundance changes from the abundance of CFS and compare this with climatic proxies from the same core. We then link modern observations of fruit, seed and fire response traits of plant genera within the basin to the fossil pollen record to reconstruct palaeo vegetation community traits and determine if extinction was associated with any changes in plant community trait composition. Closely-spaced ¹⁴C dates obtained from planktonic foraminifera and $\delta^{18}\text{O}$ tie points place a major decline in CFS, and thus the timing of extinction, within the basin at ~43.3 ka. While climate-driven environmental changes largely controlled megafaunal presence, human arrival and frequent landscape burning are considered the most likely primary cause of extinction or, at the very least, megafauna decline in the Murray Darling Basin. We also found that the proposed period of megafaunal decline was also accompanied and followed by a decline in the prevalence of plants with larger seeds and fruits that were likely to have been once dispersed by megaherbivores. Our study supports the idea of a human-driven megafaunal extinction in mainland Australia and that the extinction caused changes in vegetation due to reduced plant dispersal and herbivory. However, high fire activity primarily linked to these vegetation changes was not observed, as humans were already practicing landscape burning before the period of megafaunal extinction and likely continued to do so afterward.

* Corresponding author. Department of Geography, University of Cambridge, 20 Downing Pl, CB2 3EL, Cambridgeshire, United Kingdom.

E-mail addresses: ma2073@cam.ac.uk (M. Adesanya Adeleye), sam.andrew@csiro.au (S. Charles Andrew), rachael.gallagher@westernsydney.edu.au (R. Gallagher), sander.vanderkaars@monash.edu (S. van der Kaars), patrick.dedeckker@anu.edu.au (P. De Deckker), qhxa@ansto.gov.au (Q. Hua), simon.haberle@anu.edu.au (S.G. Haberle).

<https://doi.org/10.1016/j.quascirev.2023.108263>

Received 3 April 2023; Received in revised form 2 August 2023; Accepted 5 August 2023

Available online 11 August 2023

0277-3791/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).

1. Introduction

The timing, cause(s), and legacy effect of the extinction of megafauna (animals >40 kg) remain topics of global interest (Brook and Bowman, 2002; Wroe et al., 2013; Meltzer, 2020). While the timing of megafaunal extinction has been established in many parts of the world, the causes and impact on the environment remain contested (Brook and Bowman, 2002; Wroe et al., 2013; Barnosky et al., 2016; Villavicencio et al., 2016). Extinction is thought to have been primarily driven by climatic shifts (including a shift in Earth's geomagnetic field) (Brook and Bowman, 2002; Wroe et al., 2013; Cooper et al., 2021; Stewart et al., 2021) or human overhunting/habitat modification (Miller et al., 2005; Turney et al., 2008; Rule et al., 2012; van der Kaars et al., 2017) or a combination of both (Villavicencio et al., 2016; Bradshaw et al., 2021a, 2021b; David et al., 2021; Nürnberg et al., 2022). However, the environmental consequences which followed megafaunal extinction are still poorly understood in many parts of the world, including in Australia. This is partly due to the paucity of animal-plant interactions in conventional pollen records and human-land transformations around the time of extinction (Miller et al., 2005; Turney et al., 2008; Johnson, 2009; Lopes dos Santos et al., 2013a; De Deckker et al., 2021). These limitations have prompted the use of other plant proxies (e.g., stable carbon isotopes) to examine vegetation response to megafaunal extinctions (Miller et al., 2005; Lopes dos Santos et al., 2013a). The relatively few existing studies on this topic in Australia and beyond suggest that changes, including increases in vegetation density and increased fire activity, occurred across landscapes following the extinction of megafauna (Miller et al., 2005; Johnson, 2009; Rule et al., 2012; Lopes dos Santos et al., 2013a; Pym et al., 2023). However, this trend can also vary spatially as demonstrated by Perrotti et al. (2022) in their study, which shows woody taxa expansion following megafaunal extinction in northern and central United States, and wood taxa expansion preceding extinction in southern United States. Our goal here is to use a palynological and functional palaeoecological (Brussel and Brewer, 2021; Adeleye et al., 2023) approach to (i) identify the timing and potential cause of megafaunal extinction, and (ii) to chart associated changes in the functional characteristics of vegetation and fire activity in southern Australia.

We use a highly-resolved record of coprophilous fungal spores (CFS)

in the upper 15 m of a deep-sea marine sediment core (MD03-2607) taken from offshore Kangaroo Island in southern Australia to infer temporal changes in megafaunal abundance across the Murray Darling Basin ($\sim 1.10^6 \text{ km}^2$ in size) since the core is located opposite the mouth of the Murray River (De Deckker et al., 2021) (Fig. 1). The CFS record is then quantitatively compared to independent indicators of past climates and fire regimes to identify the possible drivers of megafaunal extinction in the area. The amount of compositional change in the already published fossil pollen record (De Deckker et al., 2021) through time is also estimated here to identify major vegetation shifts that may have followed megafaunal extinction. We then link contemporary observations (Falster et al., 2021) of fruit, seed and fire response traits of plant genera to the fossil pollen record. Based on the aforementioned studies (e.g., Miller et al., 2005; Johnson, 2009; Rule et al., 2012; Lopes dos Santos et al., 2013a; Pym et al., 2023) and existing knowledge of Murray Darling Basin's vegetation history (De Deckker et al., 2021), we hypothesize four scenarios of megafaunal-vegetation change trajectory during the Late Pleistocene which are highlighted below, and all scenarios assume an open pre-extinction vegetation with less fires (Fig. 2). Under all scenarios, we also expect that megafaunal extinction caused changes in fruit, seed and fire response traits in plant communities (Gröcke, 1997; Miller et al., 2005; Johnson, 2009; Lopes dos Santos et al., 2013a). These expected changes across the extinction boundary include progressive exclusion of plant species with larger seeds and fruits that require dispersal by large herbivores for successful establishment (Lord, 2004; Corlett, 2010), shifts in dispersal mode away from animal dispersal with a consequent and corresponding increase in the proportion of non-animal related dispersal modes in plant communities (Pym et al., 2023), and expansion of plants tolerant to high frequency fires.

For the first scenario (scenario 1), we expect human-pressure (including hunting and burning during a period of initial human occupation of the landscape) to drive megafaunal extinction, followed by an increase in vegetation density due to a decline in herbivory, resulting in high fire activity. Alternatively, under more intensive human-landscape management scenario (scenario 2), we expect no major changes in vegetation, which is maintained burning by humans following extinction. Given the progressive cooling and drying trends that generally characterize the Late Pleistocene (De Deckker et al., 2021), in the third scenario, we expect climate to drive an opening of vegetation and

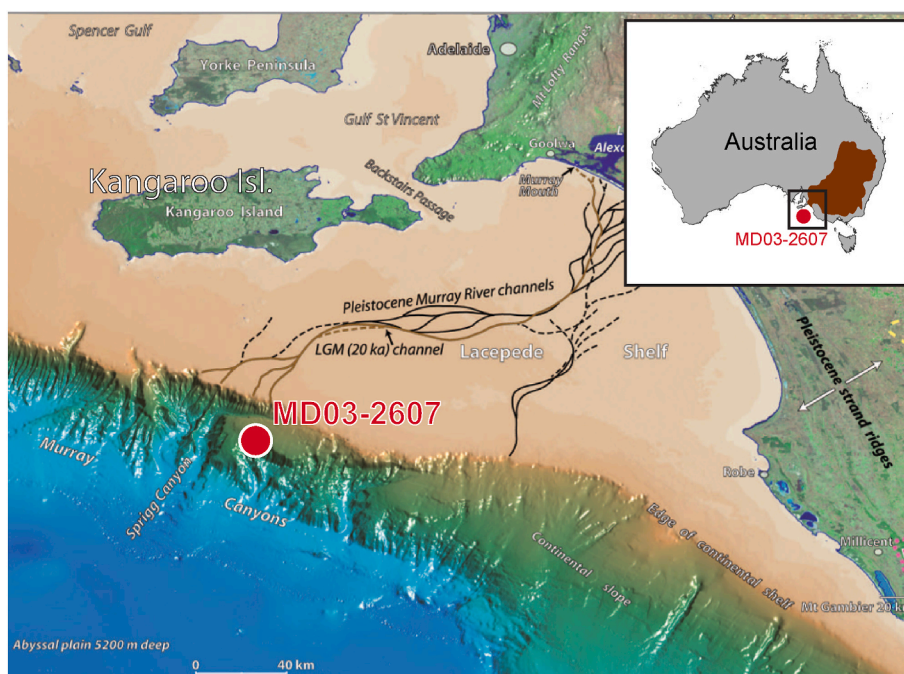


Fig. 1. Location of deep-sea sediment core MD03-2607 sediment core (solid red circle) taken offshore Kangaroo Island in southern Australia (De Deckker et al., 2021). The site is away from the canyons. Light-brown shaded area adjacent to the Australian coastline between Kangaroo Island and Millicent to the south relates to the shallow (<200 m) Lacepede Shelf and on this are the postulated positions of ancient channels of the Murray River during low sea levels (Hill et al., 2009). The dark, brown-shaded area in the inset map indicates the Murray Darling Basin, which is $\sim 1.10^6 \text{ km}^2$ in size.

megafaunal decline during periods of cooling, with no/minor increase in vegetation density and fire activity following extinction. In scenario 4 we expect a combination of human pressure and climate variability to drive vegetation change and megafaunal extinction, with open vegetation maintained by cool, dry climate and human burning after extinction.

2. Methods

2.1. Fungal spores, pollen analysis and charcoal analysis

Deep-sea sediment core MD03-2607 was obtained offshore Kangaroo Island (36° 57.64'S, 137° 24.39'E, 865 m water depth) opposite (~200 km today and ~15 km during the low sea-level stand at the Last Glacial Maximum) the mouth of the River Murray in South Australia (Fig. 1). The pollen record from the core was previously published, spanning the last 125,000 years (De Deckker et al., 2021). For the present study, we analyse the core for coprophilous fungal spore (CFS) assemblages and re-examine the pollen record using a functional palaeoecological method. Coprophilous fungi are saprobes in large herbivore dungs and their fossil spores are used to infer past changes in megafaunal biomass/density and extinction (Lee et al., 2022; van Asperen et al., 2020,

2021; Baker et al., 2013). We also use the abundance changes in CFS in core MD03-2607 to infer temporal changes in megafaunal abundance and the timing of extinction across the Murray Darling Basin. The CFS were counted on pollen slides and expressed as concentrations with log transformation (log_spore counts/mg of sediment) (Pym et al., 2023; van Asperen et al., 2020; Baker et al., 2016; Gill, 2014). CFS concentration was estimated by spiking samples with a known number (20,848 spores) of exotic *Lycopodium* spores (Batch no: 483216).

A Detrended Correspondence Analysis (DCA) was also conducted on the pollen record and first DCA axis scores were extracted to quantify compositional changes in vegetation through time. The DCA was performed in R using the 'vegan' package (Oksanen et al., 2022). Additionally, the microscopic charcoal record from core MD03-2607 is re-analysed for charcoal accumulation rates (CHAR) with peak identification using the 'tapas' package in R (Finsinger, 2022), which is the R version of the CharAnalysis program (Higuera et al., 2009). A globally-defined threshold at 0.95 with Gaussian mixed models is used for peak detection.

2.2. Plant functional trait analysis

Plant species currently distributed across the Murray Darling Basin

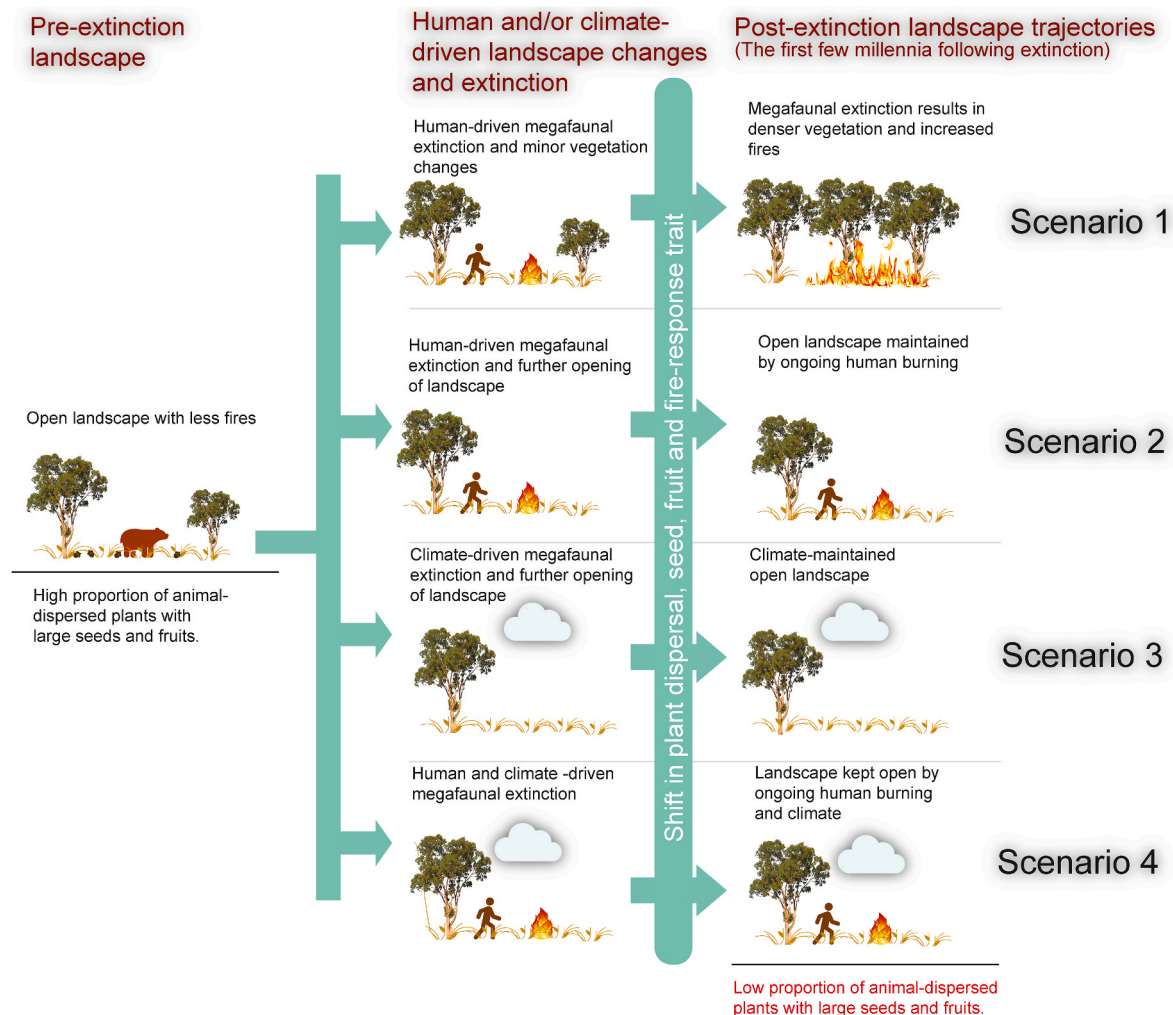


Fig. 2. Hypothesized scenarios (1–4) of megafaunal-environmental changes trajectory during the Late Pleistocene. All show an open, pre-extinction vegetation with less fires, human or/and climate driven landscape changes and megafauna extinction. Post-extinction trajectory included dense vegetation formation and biomass burning due to a decline in herbivory (scenario 1) or open vegetation maintained by human land use or/and climate (scenarios 2–4). Decline in the proportion of plants with large fruits and seed dispersed by large herbivores is expected following extinction. A shift in fire response trait across the extinction boundary is also expected, especially in scenario 1.

were identified using cleaned occurrence records associated with digitised herbarium specimens (Andrew et al., 2021). These occurrences include 236,620 observations for 4015 plant species. Values for five traits were obtained for these species from the AusTraits database (Falster et al., 2021) (<https://austraits.org/>) with 101,386 trait observations in total being available for the target species. The traits used include seed mass (mg), seed length (mm), fruit length (mm), dispersal modes, and fire response (Table 1, Fig. 3). To obtain representative trait values where more than one observation of a trait was available for a species, continuous traits were averaged and for categorical traits the most common phenotype was recorded, and the species level traits were subsequently aggregated for each of the 23 groups/families (Table 1). Mean log-transformed plant traits were then linked to corresponding square root-transformed fossil pollen (23 taxa/types) abundance to calculate community-weighted means (CWM) for each trait down core, performed in R using the 'FD' package (Laliberté et al., 2014). FD is a distance-based framework that measures trait diversity and at the same time calculates trait CWM in a multidimensional space (Laliberté et al., 2014).

2.3. Change point analysis and generalized additive modelling

A change point analysis is performed on all palaeoecological datasets (including plant trait reconstructions) and palaeoclimate records from core MD03-2607 to determine the timing of major shift in trends and the sequence of shifts particularly across the boundary of the megafaunal extinction. Change point analysis is performed using a Bayesian trans-dimensional Markov chain Monte Carlo test with 100,000 iterations (Gallagher et al., 2011) using PAST program version 4.11 (Hammer et al., 2001). A generalized additive model with non-linear smoothing and Gaussian distribution is used to assess the relationships between CFS, pollen DCA, CHAR, plant traits and climate records to identify major drivers of megafaunal extinction and vegetation change. In line with the goal of study, data points younger than 30 ka (i.e. 30 ka–present) are not included in the fitted models. Generalized additive modelling is performed in R using the 'mgcv' package (Wood, 2023). In order to remove the effect of temporal autocorrelation from fitted models, random resampling of each variable at a lower resolution is performed and each model fitted 100 times. The climate variables were previously published independent records of sea-surface temperatures (alkenone-based temperatures) and pollen-based annual rainfall

reconstructions for the MD03-2607 core (Lopes dos Santos et al., 2013b; De Deckker et al., 2021). All datasets are smoothed to the same temporal resolution (1000-yr interval on average) as the fungal spore record before fitting the models.

2.4. Core chronology

All reported dates are based on a chronology developed for core MD03-2607 using a combination of accelerator mass spectrometry (AMS) ^{14}C dates, optically stimulated luminescence (OSL) dates and foraminifera $\delta^{18}\text{O}$ isotopic dating tie points linked to the global marine isotope stratigraphy (see De Deckker et al., 2021; De Deckker et al., 2021 for details). ^{14}C dates are calibrated, after correction for local marine radiocarbon reservoir ages, using the latest Southern Hemisphere calibration curve—SHCal20 (Hogg et al., 2020). The age-depth model is built using a Bayesian OxCal P sequence with variable deposition rates and a general outlier analysis (see Supplementary Fig. 1 for age-depth model and De Deckker et al., 2021 for methodology details).

3. Results

Total coprophilous fungal spore (CFS) concentration, as well the results of the DCA, functional trait reconstruction and charcoal analysis for MD03-2607 core are presented in Fig. 4. The CFS recorded include *Sporormiella* (which makes up ~95%), *Sordaria* and *Podospora* (see Supplementary Fig. 2 individual CFS raw count diagram.). Change point analyses show a major shift (decline) in total CFS concentration at ~43.3 ka and a shift in pollen taxa composition (DCA1) occurred at ~73 ka. In the considered plant traits, seed mass, seed length, and fruit length show major changes across the boundary of major decline in CFS abundance; however, the percentage change point is highest for seed and fruit traits (Fig. 4). Charcoal analysis reveals the most peaks between 60 and 43 ka and with the greatest peak at ~47 ka. Among the previous palaeoecological and palaeoclimatic datasets from MD03-2607 core re-analysed for change point analysis, only the records of C4 plants (Lopes dos Santos et al., 2013a) and sea-surface temperatures (SST) (De Deckker et al., 2021) show major changes around the timing of CFS abundance decline (Fig. 5).

The generalized additive modelling result identifies SST and DCA1 as the significant ($p < 0.05$) predictors of the observed changes in CFS concentrations, with SST being the strongest predictor with an F-statistic

Table 1

Mean log-transformed and categorical plant trait data for pollen taxa recognised in core MD03-2607. DM = Dispersal modes (see text for further details), FR = Fire response (Os—obligate seeders, Res—resprouters), FL = Fruit length (mm), SM = Seed dry mass (mg), SL = Seed length (mm).

Taxa/pollen type	DM	DM%	FR	FR%	FL	SM	SL
<i>Acacia</i>	zoochory	77.5	Os	72.7	4.328	2.694	1.52
<i>Banksia</i>	anemochory	94.1	Os	52.2	2.327	2.949	2.194
<i>Callitris</i>	anemochory	100	Os	100	3.219	2.035	1.625
<i>Casuarina</i>	anemochory	100	Os	80	1.732	0.126	1.438
<i>Coprosma</i>	endozoochory	100	Os	50	NA	1.511	1.564
<i>Dodonaea</i>	anemochory	96.4	Os	75	2.744	1.324	0.915
<i>Elaeocarpus</i>	endozoochory	66.7	Res	75	2.292	5.665	1.799
<i>Epacris</i>	zoochory	83.3	Os	37.5	NA	−3.34	−0.443
<i>Eucalyptus</i>	barochory	72.1	Res	74.1	2.066	0.277	0.49
<i>Euphorbia</i>	zoochory	72.7	Os	100	1.589	0.79	0.793
<i>Gyrostemon</i>	myrmecochory	100	Os	100	NA	−0.177	0.693
<i>Melaleuca</i>	anemochory	100	Res	70	0.896	−2.38	−0.073
Amaranthaceae	epizoochory	36.7	Os	69	1.903	0.051	0.756
Asteraceae	anemochory	72.2	Os	65.2	0.556	−1.211	0.659
Centrolepidaceae	barochory	90	Os	100	NA	−3.113	−0.462
<i>Cyathaea</i>	anemochory	100	Res	66.7	NA	NA	NA
Cyperaceae	barochory	29.2	Res	66.2	0.486	−0.911	0.517
Haloragaceae	zoochory	42.6	Res	54	NA	−0.642	0.338
<i>Plantago</i>	barochory	48.7	Res	59	NA	−2.043	0.373
Poaceae	epizoochory	52.1	Res	48.2	0.724	−0.596	0.937
Rhamnaceae	zoochory	62.5	Os	90.4	2.081	−0.009	0.754
Scrophulariaceae	barochory	40	Res	56.7	1.775	0.403	0.947
<i>Typha</i>	anemochory	100	Res	100	NA	−1.915	0.46

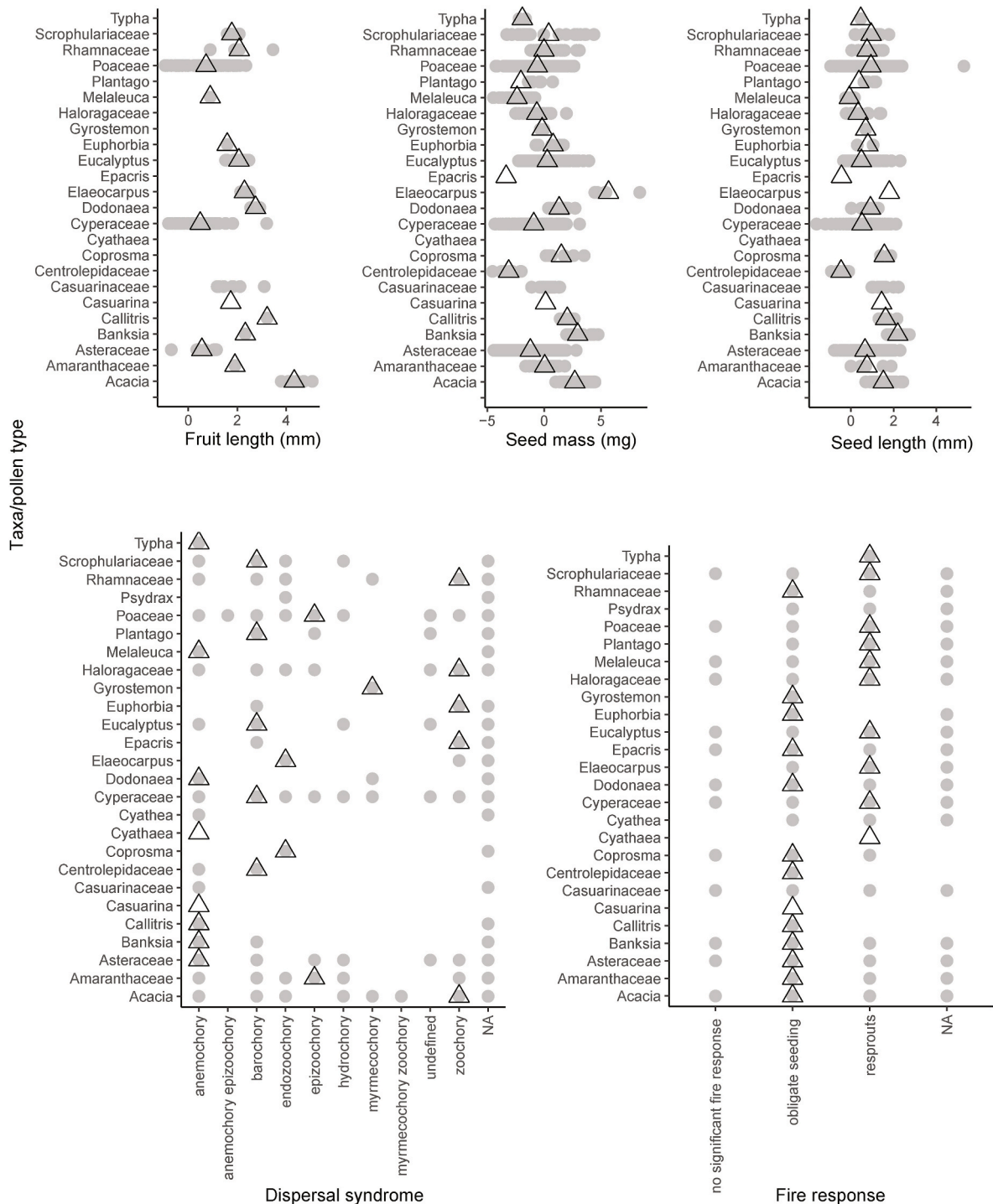


Fig. 3. The distribution (grey solid circles) and mean/dominant (black hollow triangles) trait observations in each pollen type/genus examined in the MD03-2607 core record.

value of 9.2 (Table 2). All predictors significantly ($p < 0.05$) explain DCA1; however, SST and annual rainfall have the highest F values. In addition to CFS, CHAR significantly ($p < 0.05$) explain changes in seed mass and SST significantly ($p < 0.05$) predict fruit length (Table 2).

4. Discussion

4.1. Methodological considerations

Coprophilous fungal spores (CFS) of herbivore dung are widely used

as a proxy to infer changes in herbivore density, including megafauna, in the past (Johnson, 2009; van der Kaars et al., 2017; Perrotti, 2018; van Asperen et al., 2020; Baker et al., 2013, 2016; Gill, 2014); however, this is not straight forward (Chepstow-Lusty et al., 2019; Davies et al., 2022). The accumulation of spores in sedimentary deposits can be influenced by various factors, such as dispersal medium (water and wind), biotic and abiotic factors affecting spore germination and growth, and catchment conditions (e.g., size and changes in water levels) (Kuthubutheen and Webster, 1986; Krug et al., 2004; Johnson, 2009; Raczka et al., 2016; Chepstow-Lusty et al., 2019). To reflect herbivore density and

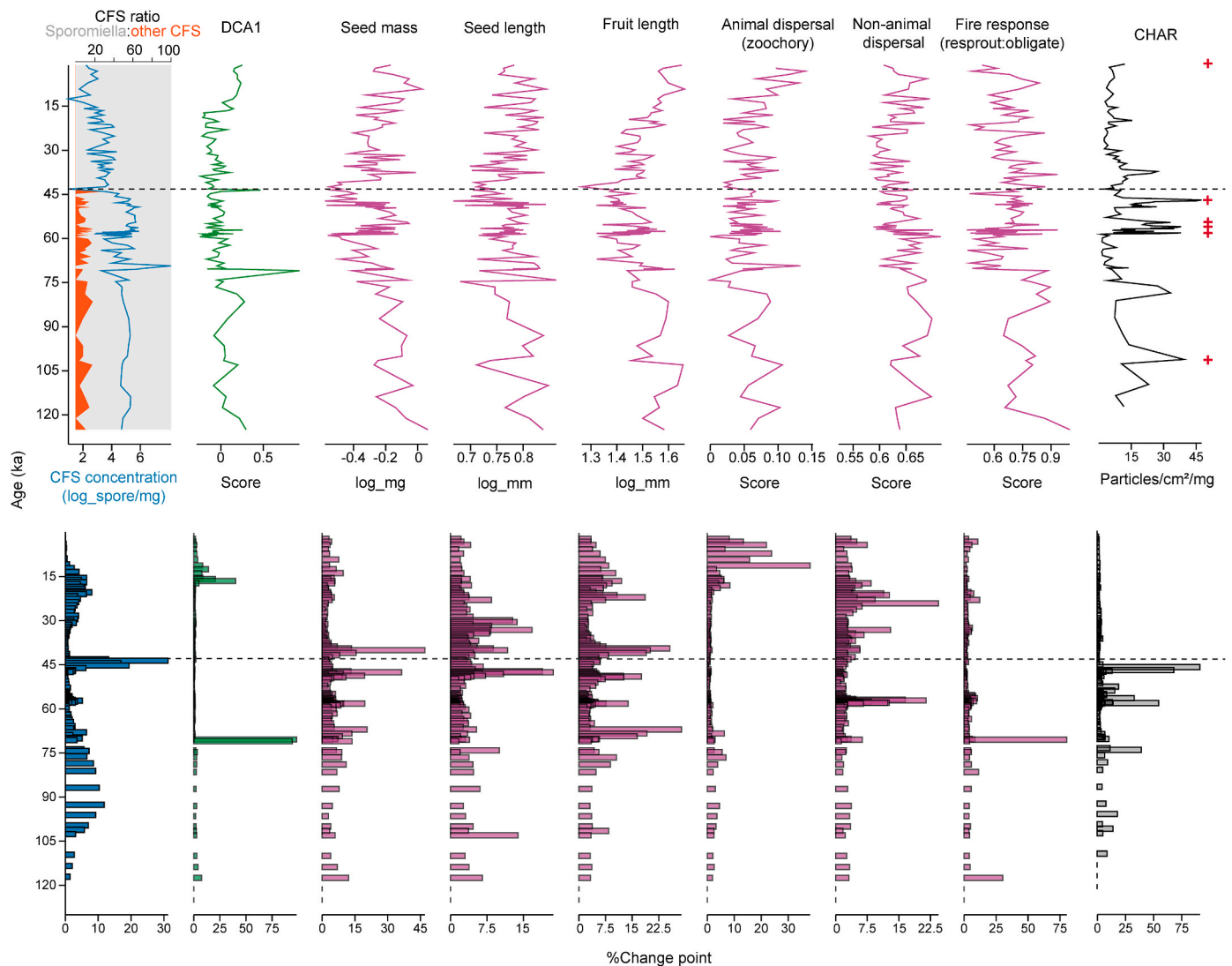


Fig. 4. The coprophilous fungal spore (CFS) record from deep-sea core MD03-2607 compared with vegetation changes (DCA1), plant traits (community-weighted means) and charcoal analysis result (CHAR-charcoal accumulation rates), as well as their corresponding change point analysis results. The black dashed horizontal lines indicate the timing of major decline in CFS at ~43.3 ka determined by changepoint analysis, which is taken as the timing of megafaunal extinction. Red crosses in CHAR curve are significant charcoal peaks.

temporal abundance shifts more accurately, it has been found that using spore concentration (Raczka et al., 2016; Johnson et al., 2015; Pym et al., 2023) and influx (Wood and Wilmshurst, 2013; van Asperen et al., 2020) provide better results compared to spore percentages. Additionally, considering multiple species of CFS during analysis yields a more robust estimate of herbivore density, thus minimizing the impact of interspecific responses to the aforementioned factors (Krug et al., 2004; Pym et al., 2023). In this study, we have also used CFS concentration to infer changes in megafauna density during the Late Pleistocene. Our concentration estimate includes multiple coprophilous fungal species, such as *Sporomiella*, *Podospira*, and *Sordaria*. Our concentration and influx estimates also exhibit a significant similarity ($R = 0.91$; Supplementary Figure 3).

While accumulated macroscopic charcoal particles in contiguously-sampled sedimentary records are known to provide a more accurate indication of past fire activity, microscopic charcoal particles in pollen slides are also used to infer fire history, despite the associated uncertainties (Whitlock and Larsen, 2001; Mooney and Tinner, 2011). We acknowledge the potential sources of error that may be associated with our microscopic charcoal record, particularly due to the non-contiguous nature of the samples and the processing methods used. The

millennial-scale sampling intervals may have resulted in missed fire events or episodes in the record, and the delicate nature of fossil charcoal raises the possibility of introducing artifacts through the rigorous chemical treatments and mixing involved in pollen processing (Clark, 1984; Mooney and Tinner, 2011). However, in order to enhance the representation of past fire activity in the Murray Darling Basin through our microscopic charcoal record, we are expressing our results as charcoal accumulation rates (Mooney and Tinner, 2011).

4.2. The timing and cause of Late Pleistocene megafaunal extinction in mainland Australia

The age of a single bone specimen (*Zygomaturus trilobus*) reported by Westaway et al. (2017) from the Willandra Lakes in western New South Wales implies a megafaunal presence in Australia at ~36–32 ka; however, the ages of several specimens reported by Roberts et al. (2001) across the continent suggest the disappearance of the large animals around 46 ka. The ~36–32 ka age is yet to be confirmed in other sites in Australia. While it is possible that a scanty number of the megafauna persisted for millennia in some parts of Australia after 46 ka (Westaway et al., 2017), it is likely that there was at least a major population or

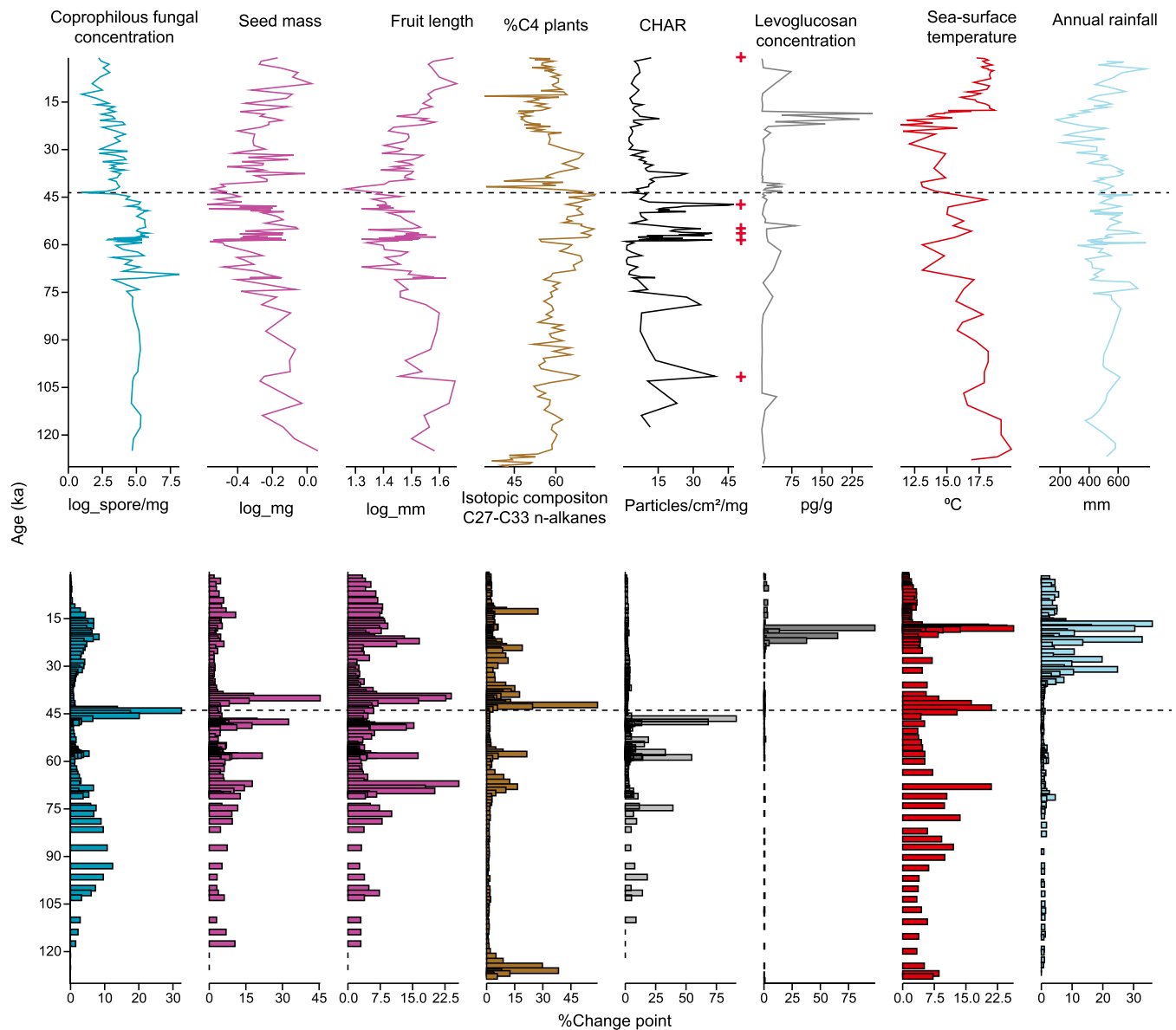


Fig. 5. Selected records from Fig. 4, as well as the changepoint analysis results for vegetation (%C4 plants), fire (levoglucosan concentration) and climate records (sea-surface temperatures and annual rainfall) previously published from deep-sea core MD03-2607 (Lopes dos Santos et al., 2013a; De Deckker et al., 2021). The black dashed horizontal lines indicate the timing of the major decline in coprophilous fungal spores at ~43.3 ka determined by changepoint analysis, which is taken as the timing of megafaunal extinction. Red crosses in CHAR curve are significant charcoal peaks.

diversity decline of the animals around 46 ka (Roberts et al., 2001).

Our CFS record presents one of the few pieces of evidence for the timing of Australia's megafaunal disappearance and indicates the presence of megaherbivores around the Murray-Darlin Basin in southern Australia until ~43.3 ka or at least a major decline in their presence in the area at this time (Fig. 6). The CFS trend indicates this marked decline was brief and decline in megafaunal presence in the basin was generally gradual from this time, as previously reported in some other parts of the world (e.g., interior Alaska) where megafauna extinction was also not an abrupt event (Conroy et al., 2020). While our recorded timing of ~43.3 ka is comparable to previous age estimates of megafaunal extinction ranging from ~50 to 40 ka on the Australian mainland (Roberts et al., 2001; Miller et al., 2005; Gillespie et al., 2006; van der Kaars et al., 2017; Hocknull et al., 2020; David et al., 2021), the robust chronological control and relatively higher sampling resolution of the core MD03-2607 (supplementary Fig. 4) provide a more precise age estimate of the timing of megafaunal decline in the Murray Darling Basin.

There is an ongoing debate on the cause of megafaunal extinction in Australia, and many arguments have been put forward to explain the cause(s). The low rank in the trophic network and fewer predators are thought to have rendered Australian megafauna vulnerable to external forcings and extinction (Llewellyn et al., 2022). These external forcings have been proposed to be caused by a climate-driven hydrological shift (Cohen et al., 2022), anthropogenic pressure (Rule et al., 2012; van der Kaars et al., 2017) and a combination of climatic and anthropogenic influences (David et al., 2021; Nürnberg et al., 2022). These patterns are reflected in our hypothesized scenarios for the trajectory of Late Pleistocene megafaunal extinction and landscape changes in Fig. 2.

4.2.1. Climate driven-changes in megafaunal presence

The overall importance ($p < 0.001$) of sea-surface temperature (SST) in our generalized additive models indicates the key role of climate in driving changes in megafaunal presence and vegetation in the Murray Darling Basin during the Late Pleistocene (Table 2). However, the fitted

Table 2

Results of generalized additive modelling with a non-linear smoothing, showing relationships between changes in coprophilous fungal spore (CFS) abundance, vegetation compositional change (DCA1), fire (CHAR), plant traits (seed mass and fruit length) and climate (annual rainfall—rain and sea-surface temperatures—SST). Traits selected are those with the highest percentage changepoint across the boundary of CFS abundance decline. Significance codes: ‘***’ < 0.001, ‘**’ < 0.01, ‘*’ < 0.05, ‘.’ < 0.1, ‘’ < 1.

CFS	edf	Ref.df	F	p-value	Significance
DCA1	6.081	6.883	2.939	0.0231	*
CHAR	1.39	1.662	1.307	0.3449	
SST	5.715	6.679	9.183	1.12E-05	***
Rain	1.191	1.351	2.27 E+00	0.1802	
DCA1					
CFS	8.46	8.857	2.527	0.02371	*
CHAR	1	1	7.268	0.01124	*
SST	1	1	11.394	0.002	**
Rain	1	1	11.757	0.00173	**
Seed mass					
CFS	1.388	1.676	4.56	0.02747	*
CHAR	2.584	3.173	4.687	0.00631	**
SST	2.315	2.856	2.024	0.15624	
Rain	1	1	1.167	0.28742	
Fruit length					
CFS	1.701	2.125	3.377	0.0453	*
CHAR	2.382	2.886	2.26	0.073	.
SST	7.962	8.615	2.161	0.0462	*
Rain	3.117	3.86	0.662	0.5707	

models for seed and fruit size suggests changes in megafaunal presence would have in turn had some influence on vegetation communities in the landscape in addition to the effect of background climate (e.g., increased dormancy and reduced germination success, Zhou et al., 2021), especially from 125 to 41 ka (Table 2). The previously published pollen record from core MD03-2607 (De Deckker et al., 2021) and our new CHAR analysis for the core show that megafauna would have roamed a landscape characterized by open woodland with infrequent fires in the basin from 125 to 70 ka, and the stability of CFS abundance suggests a consistent presence of the large animals in the area as well (Fig. 6). During the last 125 ka, the first major climatic shift occurred at ~70 ka (as detected by changepoint analysis), featuring a decline in SST, especially for the next ~10,000 years, and a major further opening of the landscape with herbaceous communities largely replacing woody ones (De Deckker et al., 2021). A grassland or savanna-like vegetation would have characterized the Murray Darlin Basin at this time. This climate-driven shift in vegetation composition (DCA1) may have featured a fluctuation in megafaunal presence in the area as indicated by the oscillating abundance of CFS during this period, which in turn perhaps contributed to the decline in the proportion of large-seeded and/or fruited plants due to reduced dispersal. A minor climate amelioration occurred after ~60 ka, with warming associated with a more stable megafaunal presence and an increase in the proportion of plants with large seeds and/or fruits (Fig. 6). However, the composition and perhaps structure of vegetation remained largely the same with the persistence of herb-dominated landscapes through and after the timing of major decline in megafaunal presence at ~43.3 ka. The large animals’ decline at/from this time may be related to climate cooling and was also accompanied by a decline in large-seeded and/or fruited plants until about 41 ka before recovery. The increase in the proportion of plants with large seeds and/or fruits after 41 ka may be due to the minor increase in temperature at this time or/and the recovery of some large herbivores in the Murray Darlin Basin (Fig. 6).

4.2.2. Human driven-changes in megafaunal presence

Ongoing changes in climate, especially the legacy effect of preceding cool and perhaps dry climatic episodes may have contributed to the decline in megafaunal presence at ~43.3 ka (Nürnberg et al., 2022). However, the degrees of temperature drop around 43.3 ka is similar to

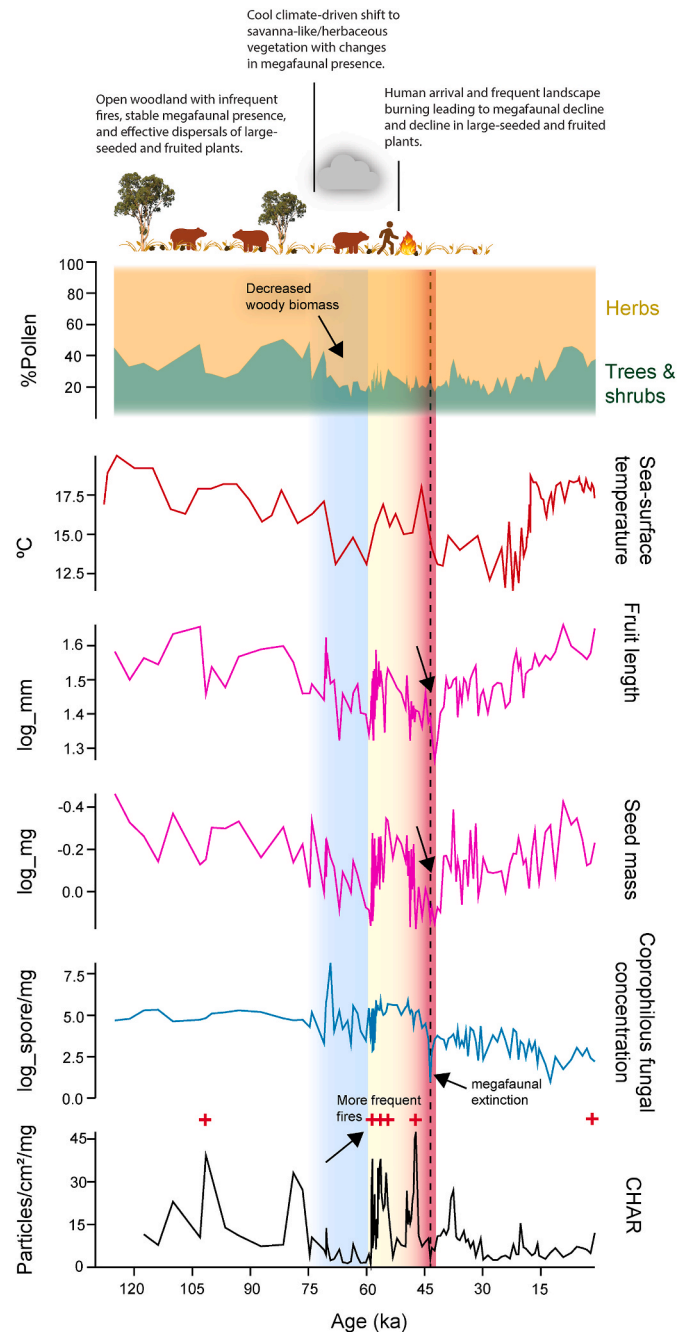


Fig. 6. Coprophilous fungal spore (CFS) abundance compared with charcoal accumulation rates (CHAR), seed and fruit trait reconstructions and sea-surface temperature reconstructions (Lopes dos Santos et al., 2013b; De Deckker et al., 2021) from MD03-2607 core. Also shown is the percentage total of tree and shrub and herb pollen from the core (De Deckker et al., 2021) from core MD03-2607. Blue-shaded zone indicate a period of marked climatic change (cooling) featuring a major shift from open woodland landscape to grassland or savanna like landscape, decline in the proportion of plants with large seeds, and low-fluctuating abundance of CFS. The yellow-red gradient zone indicates the period of human occupation in Australia with the onset of occupation (red zone) around the Murray Darling Basin within ~49–43 ka (O’Connell et al., 2018). The black dashed horizontal line indicates the timing of major decline in CFS at ~43.3 ka determined by changepoint analysis, which is taken as the timing of megafaunal extinction or at least major decline. (see Supplementary Fig. 4 for full records from core MD03-2607 and Supplementary Fig. 5 for percentage abundance of large-seeded/fruited pollen taxa across the extinction boundary).

the decline between 70 and 60 ka, but the latter featured a greater decline in megafaunal presence than the former. Also, cooling between 70 and 60 ka featured a major shift in vegetation which is not the case at ~43.3 ka (Fig. 6). Other factor(s) superimposed on background climate likely drove a major megafaunal decline at ~43.3 ka, which in this case is likely anthropogenic (Rule et al., 2012; van der Kaars et al., 2017; Llewellyn et al., 2022). Increased frequency of fire peaks from ~58 ka despite the prevalence of low-biomass herbaceous vegetation in the landscape suggests human presence (Fig. 6). Humans are thought to have arrived in northern Australia around 65 ka (Clarkson et al., 2017) and across the continent from about 50 ka (Tobler et al., 2017; O'Connell et al., 2018; Bradshaw et al., 2021b). Specifically, the most securely dated archaeological evidence from sites within the Murray Darling Basin (Lake Menindee) indicates human occupation from at least within ~48–43 ka with a median age of ~46 ka and nearby site west of the basin is Lake Warraty, with a human occupation start date range of ~49–47 ka and median age of ~48 ka (O'Connell et al., 2018). Although there is no direct evidence of overkilling yet in Australia (e.g., speared megafaunal bones), the possibility of multi-millennial human occupation and landscape burning (David et al., 2021) reducing megafaunal habitats/useable niches (Llewellyn et al., 2022) cannot be dismissed. People likely burned grasslands in the Murray Darling Basin during this time period or perhaps targeted existing small areas of woodland. Ongoing burning would have prevented any possible recovery of pre-existing woodland under the improved climatic condition at this time, leading to the gradual decline of megafaunal presence from ~46.5 ka, reaching a minimum at ~43.3 ka (Fig. 6). The peak in landscape burning at ~46.5 ka not only coincides with the timing of human spread across Australia (Williams, 2013), but also its local presence in the Murray Darling Basin (O'Connell et al., 2018); this can be linked to the major decline in megafaunal presence at ~43.3 ka. Shrinking habitats, such as the loss of suitable open woodland habitats, would have further rendered megafaunal populations more susceptible to a climate change impact and also successful hunting (Llewellyn et al., 2022). The delayed decline of megafaunal presence after human arrival on the continent suggests there was a stable coexistence that was likely disrupted by a rapid increase in human population or its rapid spread from ~46.5 ka (Williams, 2013), with increased widespread burning and perhaps hunting pressure on megafaunal species (Fig. 5). Increased human presence of this kind could be explained by innovations that helped human populations adapt to the Australian continent. Such innovations could be driven by a growing knowledge of the unique Australian flora for cultivation (fire-stick farming, e.g., Bliege Bird et al., 2018) and medicinal uses.

4.3. Megafaunal-extinction associated vegetation changes

The profile of plant community seed and fruit traits likely reflects shifts in vegetation community composition following the megafaunal decline in the Murray Darling Basin (Fig. 4). Particularly evident is the decline in size of seeds and/or fruits between 44 and 41 ka, which is also supported by the generalized additive model results (Table 2, Fig. 6). Plant community characteristics appear to have shifted, with large-seeded and/or fruited plant species fully or partially reliant on mega-herbivores for effective dispersal (e.g., *Acacia*, *Elaeocarpus*, *Banksia*), becoming less prevalent in the landscape within the first 2.5 millennia after the extinction.

Previous studies of the Late Pleistocene environmental changes from Australia and beyond (Johnson, 2009; Lopes dos Santos et al., 2013a; Pym et al., 2023) have also suggested that the megafaunal extinction was followed by vegetation thickening and higher fire activity, and decline in animal-dispersed plants, especially within the first few millennia after the extinction. However, this is not consistent with our results. Only seed and fruit traits showed a major shift (high percentage changepoint) after the decline in megafaunal presence in the Murray Darling Basin at ~43.3 ka (Fig. 6). Additionally, our plant fire response

trait reconstruction, CHAR and changepoint analysis all show no evidence of fire activity that may have been primarily driven by a megafaunal decline on the landscape (Figs. 4–6). A previous record of C4 plants and levoglucosan (marker for biomass burning) from core MD03-2607 shows an increase in C4 plants and levoglucosan concentration within the first three millennia following megafauna extinction, suggesting increased vegetation density and fires in Murray Darling Basin due to the decline in herbivory (Lopes dos Santos et al., 2013a). Though the abundance of C4 plants markedly declines between 44 and 42 ka, changepoint analysis for levoglucosan indicates no major change (Fig. 5). While changes such as vegetation thickening (Lopes dos Santos et al., 2013a) and reduced average seed size of plant communities may have followed megafaunal extinction, there is no clear evidence of increased fire activity that can be primarily linked to megafaunal extinction, given the existing roles of humans (Fig. 6). There is a possibility that the observed fire activity (CHAR and levoglucosan concentration) following ~43.3 ka is a reflection of ongoing human burning in the area, which later reduced upon the onset of the full glacial climate at ~30 ka (Figs. 5 and 6; Adeleye et al., 2021; Cadd et al., 2021).

5. Conclusion

In this study, our objective was to reconstruct Late Pleistocene megafaunal changes and identify the timing and potential causes of extinction across the Murray Darling Basin in southern Australia. We also aimed to investigate if the extinction was associated with any signal of trait-based vegetation change. Furthermore, we hypothesized four potential trajectories of Late Pleistocene megafaunal, vegetation, and fire-regime changes, as illustrated in Fig. 2.

By utilizing a detailed chronology based on high-resolution ^{14}C dates and tie points of the $\delta^{18}\text{O}$ record of marine planktic foraminifera, we provide, for the first time in Australia, a well-defined timing of megafaunal decline at approximately 43.3 ka. Our results also mostly support the first hypothesized scenario in Fig. 2 (scenario 1), in which we expect that frequent human burning and landscape transformation primarily drove the decline of megafauna and decrease in the proportion of large-seeded and/or fruited plants, and increased vegetation density following extinction. However, our findings do not indicate any increased fire activity that may be primarily associated with these post-extinction changes due to the already existing presence of humans and fire usage on the landscape before the extinction. Until we are able to distinguish between natural and anthropogenic fires during this period, it is best to associate fire activity in the first few millennia after extinction with human burning or, at least, a combination of human burning and vegetation thickening as a result of the decline in herbivory.

This study reveals the usefulness of functional palaeoecological method (Carvalho et al., 2019; Brussel and Brewer, 2021) on the fossil pollen records to detect plant–animal interactions in past vegetation communities. Applying a similar approach to other Late Pleistocene (MIS 4–3) records in Australia may provide a better understanding of the variability in spatial response of Australian ecosystems to megafaunal extinction. This may also assist in projecting the potential impacts of animal population/diversity changes in present-day ecosystems.

Author contribution

SGH and PDD co-developed the idea to examine the MD03-2607 core for evidence of coprophilous fungal decline and funded the analysis of the samples for pollen and coprophilous fungi. SGH and MAA co-developed the idea to analyse the data using a functional palaeoecological approach. SvdK counted pollen and coprophilous fungi in core MD03-2607 and co-interpreted the pollen and spore record with MAA, PDD and SGH. QH analysed MD03-2607 core samples by accelerator mass spectrometry radiocarbon dating, calibrated the dates, and built the sequence's age-depth model. SCA and RG extracted and checked plant trait data for study taxa, and RG initiated the AusTraits

project. PDD led and funded MD03-2607 marine coring expedition. MAA conducted the functional palaeoecological analysis and wrote the original manuscript draft. All authors contributed to manuscript revisions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Pollen and Sporormiella data are stored at <https://doi.pangaea.de/10.1594/PANGAEA.928645>. Plant trait data can be accessed through the AusTraits database (<https://zenodo.org/record/5112001>).

Acknowledgements

The authors acknowledge field and laboratory assistance from Yvon Balut (Manager of the RV *Marion Dufresne*) and Martine Hagen for processing the core samples for pollen and spore count. MAA and SGH acknowledge funding from the Australian Research Council (ARC) Centre of Excellence for Australian Biodiversity and Heritage (CE170100015) and PDD acknowledges funding from the French Polar Institute, the National Oceans Office as well as an ARC DP grant (DP0344932). We thank three anonymous reviewers for their valuable feedback that helped improved the manuscript quality.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2023.108263>.

References

- Adeleye, M.A., Haberle, S.G., Gallagher, R., Andrew, S.C., Herbert, A., 2023. Changing plant functional diversity over the last 12,000 years provides perspectives for tracking future changes in vegetation communities. *Nat Ecol Evol* 7, 224–235. <https://doi.org/10.1038/s41559-022-01943-4>.
- Adeleye, M.A., Haberle, S.G., McWethy, D., Connor, S.E., Stevenson, J., 2021. Environmental change during the last glacial on an ancient land bridge of southeast Australia. *J. Biogeogr.* 48, 2946–2960. <https://doi.org/10.1111/jbi.14255>.
- Andrew, S.C., Mokany, K., Falster, D.S., Wenk, E., Wright, I.J., Merow, C., Adams, V., Gallagher, R.V., 2021. Functional diversity of the Australian flora: strong links to species richness and climate. *J. Veg. Sci.* 32, e13018 <https://doi.org/10.1111/jvs.13018>.
- Baker, A.G., Bhagwat, S.A., Willis, K.J., 2013. Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quat. Sci. Rev.* 62, 21–31.
- Baker, A.G., Cornelissen, P., Bhagwat, S.A., Vera, F.W.M., Willis, K.J., 2016. Quantification of population sizes of large herbivores and their long-term functional role in ecosystems using dung fungal spores. *Methods Ecol. Evol.* 7, 1273–1281. <https://doi.org/10.1111/2041-210X.12580>.
- Barnosky, A.D., Lindsey, E.L., Villavicencio, N.A., Bostelmann, E., Hadly, E.A., Wanket, J., Marshall, C.R., 2016. Variable impact of late-Quaternary megafaunal extinction in causing ecological state shifts in North and South America. *Proc. Natl. Acad. Sci. USA* 113, 856–861. <https://doi.org/10.1073/pnas.1505295112>.
- Bliege Bird, R., Bird, D.W., Fernandez, L.E., Taylor, N., Taylor, W., Nimmo, D., 2018. Aboriginal burning promotes fine-scale pyrodiversity and native predators in Australia's Western Desert. *Biol. Conserv.* 219, 110–118. <https://doi.org/10.1016/j.biocon.2018.01.008>.
- Bradshaw, C.J.A., Johnson, C.N., Llewellyn, J., Weisbecker, V., Strona, G., Saltré, F., 2021a. Relative demographic susceptibility does not explain the extinction chronology of Sahul's megafauna. *Elife* 10, e63870. <https://doi.org/10.7554/eLife.63870>.
- Bradshaw, C.J.A., Norman, K., Ulm, S., Williams, A.N., Clarkson, C., Chadœuf, J., Lin, S. C., Jacobs, Z., Roberts, R.G., Bird, M.I., Weyrich, L.S., Haberle, S.G., O'Connor, S., Llamas, B., Cohen, T.J., Friedrich, T., Veth, P., Leavesley, M., Saltré, F., 2021b. Stochastic models support rapid peopling of Late Pleistocene Sahul. *Nat. Commun.* 12, 2440. <https://doi.org/10.1038/s41467-021-21551-3>.
- Brook, B.W., Bowman, D.M.J.S., 2002. Explaining the Pleistocene megafaunal extinctions: models, chronologies, and assumptions. *Proc. Natl. Acad. Sci. USA* 99, 14624–14627. <https://doi.org/10.1073/pnas.232126899>.
- Brussel, T., Brewer, S.C., 2021. Functional paleoecology and the pollen-plant functional trait linkage. *Front. Ecol. Evol.* 8.
- Cadd, H., Petherick, L., Tyler, J., Herbert, A., Cohen, T.J., Sniderman, K., Barrows, T.T., Fulop, R.H., Knight, J., Kershaw, A.P., Colhoun, E.A., Harris, M.R.P., 2021. A continental perspective on the timing of environmental change during the last glacial stage in Australia. *Quat. Res.* 102, 5–23. <https://doi.org/10.1017/qua.2021.16>.
- Carvalho, F., Brown, K.A., Waller, M.P., Bunting, M.J., Boom, A., Leng, M.J., 2019. A method for reconstructing temporal changes in vegetation functional trait composition using Holocene pollen assemblages. *PLoS One* 14, e0216698. <https://doi.org/10.1371/journal.pone.0216698>.
- Chepstow-Lusty, A.J., Frogley, M.R., Baker, A.G., 2019. Comparison of Sporormiella dung fungal spores and oribatid mites as indicators of large herbivore presence: evidence from the Cuzco region of Peru. *J. Archaeol. Sci.* 102, 61–70. <https://doi.org/10.1016/j.jas.2018.12.006>.
- Clark, R.L., 1984. Effects on charcoal of pollen preparation procedures. *Pollen Spores* 26, 559–576. <http://hdl.handle.net/102.100.100/280801?index=1>.
- Clarkson, C., Jacobs, Z., Marwick, B., Fullagar, R., Wallis, L., Smith, M., Roberts, R.G., Hayes, E., Lowe, K., Carah, X., Florin, S.A., McNeil, J., Cox, D., Arnold, L.J., Hua, Q., Huntley, J., Brand, H.E.A., Manne, T., Fairbairn, A., Shulmeister, J., Lyle, L., Salinas, M., Page, M., Connell, K., Park, G., Norman, K., Murphy, T., Pardoe, C., 2017. Human occupation of northern Australia by 65,000 years ago. *Nature* 547, 306–310. <https://doi.org/10.1038/nature22968>.
- Cohen, T.J., Arnold, C.S.M., Gázquez, F., May, J.-H., Marx, S.K., Jankowski, N.R., Chivas, A. R., García, A., Cadd, H., Parker, A.G., Jansen, J.D., Fu, X., Waldmann, N., Nanson, G. C., Jones, B.G., Gadd, P., 2022. Late quaternary climate change in Australia's arid interior: evidence from kati thanda – lake eyre. *Quat. Sci. Rev.* 292, 107635 <https://doi.org/10.1016/j.quascirev.2022.107635>.
- Conroy, K.J., Baker, A.G., Jones, V.J., Hardenbroek, M. van, Hopla, E.J., Collier, R., Lister, A.M., Edwards, M.E., 2020. Tracking late-Quaternary extinctions in interior Alaska using megaherbivore bone remains and dung fungal spores. *Quat. Res.* 97, 99–110. <https://doi.org/10.1017/qua.2020.19>.
- Cooper, A., Turney, C.S.M., Palmer, J., Hogg, A., McGlone, M., Wilmshurst, J., Lorrey, A. M., Heaton, T.J., Russell, J.M., McCracken, K., Anet, J.G., Rozanov, E., Friedel, M., Suter, I., Peter, T., Muscheler, R., Adolphi, F., Dosseto, A., Faith, J.T., Fenwick, P., Fogwill, C.J., Hugen, K., Lipson, K., Liu, J., Nowaczyn, N., Rainsley, E., Bronk Ramsey, C., Sebastianelli, P., Soulimi, Y., Stevenson, J., Thomas, Z., Tobler, R., Zech, R., 2021. A global environmental crisis 42,000 years ago. *Science* 371, 811–818. <https://doi.org/10.1126/science.abb8677>.
- Corlett, R.T., 2010. Megafaunal extinctions and their consequences in the tropical Indo-Pacific. In: Haberle, S.G., Stevenson, J., Prebble, M. (Eds.), *Altered Ecologies, Fire, Climate and Human Influence on Terrestrial Landscapes*. ANU Press, pp. 117–132.
- David, B., Arnold, L.J., Delannoy, J.-J., Freslöv, J., Urwin, C., Petchey, F., McDowell, M. C., Mullett, R., Mialanes, J., Wood, R., Crouch, J., Berthet, J., Wong, V.N.L., Green, H., Hellstrom, J., 2021. Late survival of megafauna refuted for Cloggs Cave, SE Australia: implications for the Australian Late Pleistocene megafauna extinction debate. *Quat. Sci. Rev.* 253, 106781 <https://doi.org/10.1016/j.quascirev.2020.106781>.
- Davies, A.L., Harrauld, L., Milek, K., McClymont, E.L., Dallimer, M., Hamilton, A., Warburton, J., 2022. A multiproxy approach to long-term herbivore grazing dynamics in peatlands based on pollen, coprophilous fungi and faecal biomarkers. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 598, 111032 <https://doi.org/10.1016/j.palaeo.2022.111032>.
- De Deckker, P., van der Kaars, S., Haberle, S., Hua, Q., Stuut, J.-B.W., 2021. The pollen record from marine core MD03-2607 from offshore Kangaroo Island spanning the last 125 ka; implications for vegetation changes across the Murray-Darling Basin. *Aust. J. Earth Sci.* 68, 928–951. <https://doi.org/10.1080/08120099.2021.1896578>.
- Falster, D., Gallagher, R., Wenk, E.H., Wright, I.J., Indriarto, D., Andrew, S.C., Baxter, C., Lawson, J., Allen, S., Fuchs, A., Monro, A., Kar, F., Adams, M.A., Ahrens, C.W., Alfonzetti, M., Angevin, T., Appagua, D.M.G., Arndt, S., Atkin, O.K., Atkinson, J., Auld, T., Baker, A., von Balthazar, M., Bean, A., Blackman, C.J., Bloomfield, K., Bowman, D.M.J.S., Bragg, J., Brodribb, T.J., Buckton, G., Burrows, G., Caldwell, E., Camac, J., Carpenter, R., Catford, J.A., Cawthray, G.R., Cernusak, L.A., Chandler, G., Chapman, A.R., Cheal, D., Cheesman, A.W., Chen, S.-C., Choat, B., Clinton, B., Clode, P.L., Coleman, H., Cornwell, W.K., Cosgrove, M., Crisp, M., Cross, E., Crous, K.Y., Cunningham, S., Curran, T., Curtis, E., Daws, M.I., DeGabriel, J.L., Denton, M.D., Dong, N., Du, P., Duan, H., Duncan, D.H., Duncan, R.P., Duretto, M., Dwyer, J.M., Edwards, C., Esperon-Rodriguez, M., Evans, J.R., Everingham, S.E., Farrell, C., Firn, J., Fonseca, C.R., French, B.J., Frood, D., Funk, J.L., Geange, S.R., Ghanoun, O., Gleason, S.M., Gosper, C.R., Gray, E., Groom, P.K., Grootemaat, S., Gross, C., Guerin, G., Guja, L., Hahs, A.K., Harrison, M.T., Hayes, P.E., Henery, M., Hochuli, D., Howell, J., Huang, G., Hughes, L., Huisman, J., Illic, J., Jagdish, A., Jin, D., Jordan, G., Jurado, E., Kanowski, J., Kasel, S., Kellermann, J., Kenny, B., Kohout, M., Kooyman, R.M., Kotowska, M.M., Lai, H.R., Laliberté, E., Lambers, H., Lamont, B.B., Lanfear, R., van Langevelde, F., Laughlin, D.C., Laugier-Kitchener, B.-A., Laurance, S., Lehmann, C.E.R., Leigh, A., Leishman, M.R., Lenz, T., Lepshi, B., Lewis, J.D., Lim, F., Liu, U., Lord, J., Lusk, C.H., Macinnis-Ng, C., McPherson, H., Magallón, S., Manea, A., López-Martínez, A., Mayfield, M., McCarthy, J.K., Meers, T., van der Merwe, M., Metcalfe, D.J., Milberg, P., Mokany, K., Moles, A.T., Moore, B.D., Moore, N., Morgan, J.W., Morris, W., Muir, A., Munroe, S., Nicholson, A., Nicolle, D., Nicotra, A.B., Niinemets, Ü., North, T., O'Reilly-Nugent, A., O'Sullivan, O.S., Oberle, B., Onoda, Y., Ooi, M.K.J., Osborne, C.P., Paczkowska, G., Pekin, B., Guilherme Pereira, C., Pickering, C., Pickup, M., Pollock, L.J., Poot, P., Powell, J.R., Power, S.A., Prentice, I.C., Prior, L., Prober, S.M., Read, J., Reynolds, V., Richards, A. E., Richardson, B., Roderick, M.L., Rosell, J.A., Rossetto, M., Rye, B., Rymer, P.D., Sams, M.A., Sanson, G., Sauquet, H., Schmidt, S., Schönenberger, J., Schulze, E.-D., Sendall, K., Sinclair, S., Smith, B., Smith, R., Soper, F., Sparrow, B., Standish, R.J., Staples, T.L., Stephens, R., Szota, C., Taseski, G., Tasker, E., Thomas, F., Tissue, D.T.,

- Tjoelker, M.G., Tng, D.Y.P., de Tombeur, F., Tomlinson, K., Turner, N.C., Veneklaas, E.J., Venn, S., Vesk, P., Vlasveld, C., Vorontsova, M.S., Warren, C.A., Warwick, N., Weerasinghe, L.K., Wells, J., Westoby, M., White, M., Williams, N.S.G., Wills, J., Wilson, P.G., Yates, C., Zanne, A.E., Zemunik, G., Ziemińska, K., 2021. AusTraits, a curated plant trait database for the Australian flora. *Sci. Data* 8, 254. <https://doi.org/10.1038/s41597-021-01006-6>.
- Gallagher, K., Bodin, T., Sambridge, M., Weiss, D., Kylander, M., Large, D., 2011. Inference of abrupt changes in noisy geochemical records using transdimensional changepoint models. *Earth Planet Sci. Lett.* 311, 182–194. <https://doi.org/10.1016/j.epsl.2011.09.015>.
- Gillespie, R., Brook, B.W., Baynes, A., 2006. Short overlap of humans and megafauna in Pleistocene Australia. *Alcheringa Australas. J. Palaeontol.* 30, 163–186. <https://doi.org/10.1080/03115510609506861>.
- Gill, J.L., 2014. Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytol.* 201, 1163–1169. <https://doi.org/10.1111/nph.12576>.
- Gröcke, D.R., 1997. Distribution of C3 and C4 plants in the late pleistocene of south Australia recorded by isotope biogeochemistry of collagen in megafauna. *Aust. J. Bot.* 45, 607–617. <https://doi.org/10.1071/bt96040>.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. *PAST: paleontological statistics software package for education and data analysis*. *Palaeontol. Electron.* 4, 9.
- Hill, P.J., De Deckker, P., von der Borch, C., Murray-Wallace, C.V., 2009. Ancestral Murray River on the Lacedpede Shelf, southern Australia: late Quaternary migrations of a major river outlet and strandline development. *Aust. J. Earth Sci.* 56, 135–157. <https://doi.org/10.1080/08120090802546993>.
- Hocknull, S.A., Lewis, R., Arnold, L.J., Pietsch, T., Joannes-Boyau, R., Price, G.J., Moss, P., Wood, R., Dosseto, A., Louys, J., Olley, J., Lawrence, R.A., 2020. Extinction of eastern Sahul megafauna coincides with sustained environmental deterioration. *Nat. Commun.* 11, 2250. <https://doi.org/10.1038/s41467-020-15785-w>.
- Hogg, A.G., Heaton, T.J., Hua, Q., Palmer, J.G., Turney, C.S., Southon, J., Bayliss, A., Blackwell, P.G., Boswijk, G., Ramsey, C.B., Pearson, C., Petchey, F., Reimer, P., Reimer, R., Wacker, L., 2020. SHCal20 southern hemisphere calibration, 0–55,000 Years cal BP. *Radiocarbon* 62, 759–778. <https://doi.org/10.1017/RDC.2020.59>.
- Johnson, C., Rule, S., Haberle, S., Turney, C., Kershaw, P., Brook, B., 2015. Using dung fungi to interpret decline and extinction of megaherbivores: problems and solutions. *Quat. Sci. Rev.* 110, 107–113. <https://doi.org/10.1016/j.quascirev.2014.12.011>.
- Johnson, C.N., 2009. Ecological consequences of Late Quaternary extinctions of megafauna. *Proc. R. Soc. B Biol. Sci.* 276, 2509–2519. <https://doi.org/10.1098/rspb.2008.1921>.
- Krug, J.C., Benny, G.L., Keller, H.W., 2004. 21 - coprophilous fungi. In: Mueller, G.M., Bills, G.F., Foster, M.S. (Eds.), *Biodiversity of Fungi*. Academic Press, Burlington, pp. 467–499. <https://doi.org/10.1016/B978-0-12509551-8/50024-6>.
- Kuthubutheen, A.J., Webster, J., 1986. Water availability and the coprophilous fungus succession. *Trans. Br. Mycol. Soc.* 86, 63–76. [https://doi.org/10.1016/S0007-1536\(86\)80118-8](https://doi.org/10.1016/S0007-1536(86)80118-8).
- Laliberté, E., Legendre, P., Shipley, B., 2014. *FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology*.
- Lee, C.M., van Geel, B., Gosling, W.D., 2022. On the use of spores of coprophilous fungi preserved in sediments to indicate past herbivore presence. *Quaternary* 5, 30. <https://doi.org/10.3390/quat5030030>.
- Llewellyn, J., Strona, G., McDowell, M.C., Johnson, C.N., Peters, K.J., Stouffer, D.B., de Visser, S.N., Saltré, F., Bradshaw, C.J.A., 2022. Sahul's megafauna were vulnerable to plant-community changes due to their position in the trophic network. *Ecography*. <https://doi.org/10.1111/ecog.06089>, 2022.
- Lopes dos Santos, R.A., De Deckker, P., Hopmans, E.C., Magee, J.W., Mets, A., Sinninghe Damsté, J.S., Schouten, S., 2013a. Abrupt vegetation change after the Late Quaternary megafaunal extinction in southeastern Australia. *Nat. Geosci.* 6, 627–631. <https://doi.org/10.1038/ng eo1856>.
- Lopes dos Santos, R.A., Spooner, M.I., Barrows, T.T., De Deckker, P., Sinninghe Damsté, J.S., Schouten, S., 2013b. Comparison of organic (UK'37, TEXH86, LDI) and faunal proxies (foraminiferal assemblages) for reconstruction of late Quaternary sea surface temperature variability from offshore southeastern Australia. *Paleoceanography* 28, 377–387. <https://doi.org/10.1002/palo.20035>.
- Lord, J.M., 2004. Frugivore gap size and the evolution of fruit size and shape in southern hemisphere floras. *Austral Ecol.* 29, 430–436. <https://doi.org/10.1111/j.1442-9993.2004.01382.x>.
- Meltzer, D.J., 2020. Overkill, glacial history, and the extinction of North America's Ice Age megafauna. *Proc. Natl. Acad. Sci. USA* 117, 28555–28563. <https://doi.org/10.1073/pnas.2015032117>.
- Miller, G.H., Fogel, M.L., Magee, J.W., Gagan, M.K., Clarke, S.J., Johnson, B.J., 2005. Ecosystem collapse in pleistocene Australia and a human role in megafaunal extinction. *Science* 309, 287–290. <https://doi.org/10.1126/science.1111288>.
- Mooney, S., Tinner, W., 2011. *The analysis of charcoal in peat and organic sediments*. Mires Peat 7.
- Nürnberg, D., Kayode, A., Meier, K.J.F., Karas, C., 2022. Leeuwin Current dynamics over the last 60 kyr – relation to Australian ecosystem and Southern Ocean change. *Clim. Past* 18, 2483–2507. <https://doi.org/10.5194/cp-18-2483-2022>.
- O'Connell, J.F., Allen, J., Williams, M.A.J., Williams, A.N., Turney, C.S.M., Spooner, N. A., Kamminga, J., Brown, G., Cooper, A., 2018. When did Homo sapiens first reach Southeast Asia and Sahul? *Proc. Natl. Acad. Sci. USA* 115, 8482–8490. <https://doi.org/10.1073/pnas.1808385115>.
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szöcs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlenn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T., Weedon, J., 2022. *Vegan: Community Ecology Package*.
- Perrotti, A.G., 2018. Pollen and Sporormiella evidence for terminal Pleistocene vegetation change and megafaunal extinction at Page-Ladson, Florida. In: *Quat. Int., from Taphonomy to Human Paleoeecology: A Commemorative Issue Celebrating the Career of Gary Haynes*, INQUA-HABCOM President from 2003–2011 466, pp. 256–268. <https://doi.org/10.1016/j.quaint.2017.10.015>.
- Perrotti, A.G., Kiahtipes, C.A., Russell, J.M., Jackson, S.T., Gill, J.L., Robinson, G.S., Krause, T., Williams, J.W., 2022. Diverse responses of vegetation and fire after pleistocene megaherbivore extinction across the eastern US. *Quat. Sci. Rev.* 294, 107696. <https://doi.org/10.1016/j.quascirev.2022.107696>.
- Pym, F.C., Franco-Gaviria, F., Espinoza, I.G., Urrego, D.H., 2023. The timing and ecological consequences of Pleistocene megafaunal decline in the eastern Andes of Colombia. *Quat. Res.* 1–17. <https://doi.org/10.1017/qua.2022.66>.
- Raczka, M.F., Bush, M.B., Folcik, A.M., McMichael, C.H., 2016. *Sporormiella* as a tool for detecting the presence of large herbivores in the Neotropics. *Biota Neotropica* 16, e20150090. <https://doi.org/10.1590/1676-0611-BN-2015-0090>.
- Roberts, R.G., Flannery, T.F., Ayliffe, L.K., Yoshida, H., Olley, J.M., Prideaux, G.J., Laslett, G.M., Baynes, A., Smith, M.A., Jones, R., Smith, B.L., 2001. New ages for the last Australian megafauna: continent-wide extinction about 46,000 Years ago. *Science* 292, 1888–1892. <https://doi.org/10.1126/science.1060264>.
- Rule, S., Brook, B.W., Haberle, S.G., Turney, C.S.M., Kershaw, A.P., Johnson, C.N., 2012. The aftermath of megafaunal extinction: ecosystem transformation in pleistocene Australia. *Science* 335, 1483–1486. <https://doi.org/10.1126/science.1214261>.
- Stewart, M., Carleton, W.C., Groucutt, H.S., 2021. Climate change, not human population growth, correlates with Late Quaternary megafauna declines in North America. *Nat. Commun.* 12, 965. <https://doi.org/10.1038/s41467-021-21201-8>.
- Tobler, R., Rohrlach, A., Soubrier, J., Bover, P., Llamas, B., Tuke, J., Bean, N., Abdullah-Highfold, A., Agius, S., O'Donoghue, A., O'Loughlin, I., Sutton, P., Zilio, F., Walshe, K., Williams, A.N., Turney, C.S.M., Williams, M., Richards, S.M., Mitchell, R. J., Kowal, E., Stephen, J.R., Williams, L., Haak, W., Cooper, A., 2017. Aboriginal mitogenomes reveal 50,000 years of regionalism in Australia. *Nature* 544, 180–184. <https://doi.org/10.1038/nature21416>.
- Turney, C.S.M., Flannery, T.F., Roberts, R.G., Reid, C., Fifield, L.K., Higham, T.F.G., Jacobs, Z., Kemp, N., Colhoun, E.A., Kalin, R.M., Ogle, N., 2008. Late-surviving megafauna in Tasmania, Australia, implicate human involvement in their extinction. *Proc. Natl. Acad. Sci. USA* 105, 12150–12153. <https://doi.org/10.1073/pnas.0801360105>.
- van Asperen, E.N., Perrotti, A., Baker, A., 2021. Coprophilous fungal spores: NPPs for the study of past megaherbivores. In: Marret, F., O'Keefe, J., Osterloff, P., Pound, M., Shumilovskikh, L. (Eds.), *Applications of Non-pollen Palynomorphs: from Palaeoenvironmental Reconstructions to Biostratigraphy*. Geological Society of London. <https://doi.org/10.1144/SP511>.
- van Asperen, E.N., Kirby, J.R., Shaw, H.E., 2020. Relating dung fungal spore influx rates to animal density in a temperate environment: implications for palaeoecological studies. *Holocene* 30, 218–232. <https://doi.org/10.1177/0959683619875804>.
- van der Kaars, S., Miller, G.H., Turney, C.S.M., Cook, E.J., Nürnberg, D., Schöndelf, J., Kershaw, A.P., Lehman, S.J., 2017. Humans rather than climate the primary cause of Pleistocene megafaunal extinction in Australia. *Nat. Commun.* 8, 14142. <https://doi.org/10.1038/ncomms14142>.
- Villavicencio, N.A., Lindsey, E.L., Martin, F.M., Borrero, L.A., Moreno, P.I., Marshall, C. R., Barnosky, A.D., 2016. Combination of humans, climate, and vegetation change triggered Late Quaternary megafauna extinction in the Última Esperanza region, southern Patagonia, Chile. *Ecography* 39, 125–140. <https://doi.org/10.1111/ecog.01606>.
- Westaway, M.C., Olley, J., Grün, R., 2017. At least 17,000 years of coexistence: modern humans and megafauna at the Willandra Lakes, South-Eastern Australia. *Quat. Sci. Rev.* 157, 206–211. <https://doi.org/10.1016/j.quascirev.2016.11.031>.
- Whitlock, C., Larsen, C., 2001. Charcoal as a fire proxy. In: Smol, J.P., Birks, H.J.B., Last, W.M., Bradley, R.S., Alverson, K. (Eds.), *Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, Developments in Paleoenvironmental Research*. Springer Netherlands, Dordrecht, pp. 75–97. https://doi.org/10.1007/0-306-47668-1_5.
- Williams, A.N., 2013. A new population curve for prehistoric Australia. *Proc. R. Soc. B Biol. Sci.* 280, 20130486. <https://doi.org/10.1098/rspb.2013.0486>.
- Wood, J.R., Wilmshurst, J.M., 2013. Accumulation rates or percentages? How to quantify Sporormiella and other coprophilous fungal spores to detect late Quaternary megafaunal extinction events. *Quat. Sci. Rev.* 77, 1–3. <https://doi.org/10.1016/j.quascirev.2013.06.025>.
- Wood, S., 2023. *Mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation*. CRAN package.
- Wroe, S., Field, J.H., Archer, M., Grayson, D.K., Price, G.J., Louys, J., Faith, J.T., Webb, G.E., Davidson, I., Mooney, S.D., 2013. Climate change frames debate over the extinction of megafauna in Sahul (Pleistocene Australia-New Guinea). *Proc. Natl. Acad. Sci. USA* 110, 8777–8781. <https://doi.org/10.1073/pnas.1302698110>.
- Zhou, L., Yu, H., Yang, K., Chen, L., Yin, W., Ding, J., 2021. Latitudinal and longitudinal trends of seed traits indicate adaptive strategies of an invasive plant. *Front. Plant Sci.* 12.