Rapid expansion of meso-megathermal rainforests into the southern high latitudes at the onset of the Paleocene-Eocene Thermal Maximum

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ABSTRACT

Current knowledge of terrestrial ecosystem response to the Paleocene-Eocene Thermal Maximum (PETM; ~56 Ma) is largely based on the mid-latitudes of the Northern Hemisphere. To more fully reconstruct global terrestrial ecosystem response to the PETM, we generated vegetation and biomarker proxy records from an outcrop section on the southern coast of Australia (~60° S paleolatitude). We document a rapid, massive, and sustained vegetation turnover as a response to regional PETM warming of approximately 1–4 °C, abruptly transitioning from a warm temperate to a meso-megathermal rainforest similar to that of present-day northeastern Queensland, Australia. The onset of this vegetation change precedes the characteristic PETM carbon-isotope excursion (CIE) by several thousand years. The reconstructed ecosystem change is much stronger than in other Southern

Hemisphere records, highlighting the need for consideration of regional paleoceanographic, paleogeographic, and biogeographic characteristics to fully understand the global terrestrial ecosystem response to PETM climate forcing.

INTRODUCTION

The PETM (~56 Ma) was a ~200 thousand year (kyr)-long hyperthermal event triggered by a massive injection of ^{13}C-depleted carbon into the atmosphere within 1–5 kyrs (Kirtland-Turner et al., 2017). Due to the rapidity of the carbon injection, the onset of the PETM represents a paleo-analog to current climate change, albeit occurring over a few thousand rather than a few hundred years (Foster et al., 2018). Thus, temporally well resolved paleovegetation data from the PETM can help understand terrestrial ecosystem dynamics in response to atmospheric CO_2 increase and associated climate change. Previous work has shown that the PETM regionally triggered plant migrations and, to various extents, extirpations and originations (e.g., Wing et al., 2005; Jaramillo et al., 2010). However, current knowledge of PETM-induced vegetation change is strongly skewed towards the Northern Hemisphere, where the megafloral record from the Bighorn Basin (Wyoming, USA) in particular has yielded detailed insight into the vegetation response to increased CO_2 and rapid warming (Wing et al., 2005; Wing and Currano, 2013). In contrast, the terrestrial ecosystem response to PETM warming in the Southern Hemisphere is largely unknown, as available floral records are of low temporal resolution (Ocean Drilling Program [ODP] Site 1172, East Tasman Plateau; Contreras et al., 2014) or from geographically isolated islands (New Zealand; e.g., Crouch and Brinkhuis, 2005; Handley et al., 2011).

Here we present a detailed vegetation record for the latest Paleocene to earliest Eocene (~56.1–55.9 Ma) based on sporomorphs from a high-deposition-rate, nearshore marine setting in southern Australia. With a paleo-latitude of ~60° S (van

Hinsbergen et al., 2015), our record resolves vegetation change during the initiation and peak of the PETM for the first time at a high southern-latitude site. Our pollen- and biomarker-based temperature estimates provide further insight into the temporal relationships between terrestrial ecosystem change and PETM-related environmental forcing.

MATERIAL AND METHODS

Site description

Situated on the southern coast of Australia near Princetown, Victoria (38°43’28.8” S, 143°10’35.0” E; Fig. 1), the Point Margaret outcrop exposes upper Paleocene–lower Eocene pro-delta deposits of the Pember Mudstone of the Dilwyn Formation (Holdgate and Gallagher, 2003). We studied an interval of the Pember Mudstone spanning the PETM onset and extending into the body of the PETM CIE (47.0–52.3 m section height; Frieling et al., 2018). High carbon/nitrogen ratios throughout the study section indicate a dominance of terrestrial organic matter (OM) and minimal influence of OM sourcing on the bulk organic $\delta^{13}C$ signal (Frieling et al. 2018). Sporomorphs and biomarkers at Point Margaret likely derive from proximal lowland, near-coastal settings based on the lack of marked paleorelief in the hinterland (Joyce, 1992), the depositional setting off a river mouth (Holdgate and Gallagher, 2003), and the fact that river transport is responsible for most sporomorphs deposited in nearshore marine settings (Farley, 1987).

Palynology

Sporomorphs were studied in 26 samples (sampling resolution: 0.50–0.05 m) from Point Margaret. Palynological processing involved the treatment with hydrochloric and hydrofluoric acids and sieving through a 10 µm mesh (Pross et al., 2012). At least 300 sporomorphs were counted per sample and identified to the species level.

Mean annual air temperatures (MAATs) were estimated from the sporomorph data using the Nearest Living Relative (NLR) approach (Reichgelt et al., 2015; Greenwood et al., 2017). Generalists and relictual taxa were omitted, and the presence of particular taxa was considered insignificant when the abundance was <10th percentile. Probability-density distributions were calculated from the individual climatic ranges of the NLRs of the fossil taxa (Table DR2; Hijmans et al., 2005), and a maximum likelihood analysis was performed using the fossil dataset (Greenwood et al., 2017).

Organic Geochemistry

Branched glycerol dialkyl glycerol tetraethers (brGDGTs) were analyzed in 54 samples. The polar fractions separated from total lipid extracts were analyzed for brGDGTs by high-performance liquid chromatography/mass spectrometry after Hopmans et al. (2016). Source-assessment parameters indicate strong dominance of soil and peat-derived brGDGTs in the samples (see Text DR1, Fig. DR1), allowing calculation of MAATs following the $\mathrm{MBT'}_{5me}$ index and soil-based transfer function of Naafs et al. (2017). The root mean square error of this function (±4.0 °C) is most relevant when comparing absolute temperatures between sites; the intra-site (i.e., sample-to-sample) error is much smaller (Peterse et al., 2012), giving confidence to more subtle trends in our record.

Relative timing of proxy-signal shifts

Cross-correlation functions (CCFs) were used to quantify the stratigraphic offset between the various proxy signals across the CIE onset. These analyses are employed in a similar manner as in Frieling et al. (2019) (see also Text DR2). The results of these analyses are used to interpret phase relationships between the $\delta^{13}C$ signal, brGDGT-derived temperature change, and vegetation turnover.

RESULTS AND DISCUSSION

Latest Paleocene to earliest Eocene vegetation at Point Margaret

Sporomorph assemblages are well preserved and highly diverse in all studied samples from the Point Margaret section (Fig. 2), and visual inspection and ordination techniques reveal three distinct assemblages (Fig. 3). Analysis of similarities (ANOSIM) yields a strong dissimilarity between the late Paleocene and the PETM assemblages ($R = 0.99$; $p < 0.001$; $n = 9999$). The samples from the uppermost Paleocene to the onset of the PETM CIE (47.3–50.8 m) contain elements that are characteristic of today's mesothermal rainforests in New Caledonia, New Guinea, and New Zealand (Macphail et al., 1994). Based on the ecology of their NLRs (Table DR2), *Podocarpus*, *Dacrydium* (both Podocarpaceae), and Araucariaceae formed the forest canopy, while Proteaceae, *Trimenia,* and ferns (Cyatheaceae, Gleicheniaceae, and parent plants of *Laevigatosporites* spp.) made up the understory. Sclerophyll Proteaceae and Ericaceae pollen indicates the presence of open areas with heath-like vegetation. Importantly, insect-pollinated taxa such as Arecaceae (palms), *Strasburgeria,* and *Xylomelum* also occur; their pollen dispersal in extant rainforests is typically <100 m (Bush and Rivera, 1998), confirming that the sporomorphs were deposited close to their source area. Mesothermal conditions in the uppermost Paleocene (47.3–50.5 m) are supported by our pollen-based climate estimates, with NLR-based MAATs of 18.0 °C on average (standard error [SE]: 0.2 °C). Independently, the brGDGT proxy yields an average MAAT of 21.7 °C (SE: 0.1 °C; Fig. 2).

The onset of the PETM CIE at 50.8 m is associated with extensive vegetation turnover from a mesothermal to a meso-megathermal rainforest (Fig. 2). Within a transitional interval between 50.9 and 51.3 m, meso- to megathermal trees and shrubs (e.g., *Austrobuxus*, *Gymnostoma*), ferns (e.g., *Todisporites, Pteris, Lygodium*), and the megathermal mangrove palm *Nypa* increase to up to 75% of the assemblage at the expense of *Podocarpus*/*Dacrydium* and Araucariaceae (Fig. 2). A fern-spore peak at 51.00–51.05 m suggests a brief stage of disturbed vegetation cover (Vajda et al., 2001) within this vegetation-turnover interval. During peak CIE (above 51.2 m), NLR and brGDGT-based estimates yield average MAATs of 21.7 ºC (SE: 0.2 ºC) and 22.9 ºC (SE: 0.1 ºC), respectively – a warming of 3.7 ºC (NLR) and 1.2 ºC (brGDGT) compared to the uppermost Paleocene baseline.

Terrestrial ecosystem response to PETM-related environmental forcing

The high temporal resolution of our records, which is on the order of 1–3 kyr for the PETM interval based on the available age control (Frieling et al., 2018), allows insight into the phase relationships between vegetation change and PETM-related environmental forcing. Megathermal taxa (e.g., *Nypa*) appear at 50.57 m, approximately 25 cm below the onset of the CIE (Fig. 2; see also Fig. DR2). At the same stratigraphic level, the NLR-derived MAAT increases by ~3 °C. CCF analysis of the NLR-based MAAT and $\delta^{13}C$ records suggests that the NLR-based warming leads the $\delta^{13}C$ shift in the depth domain by 5–10 cm (Fig. 4). Based on a mean sedimentation rate of ~7 cm/kyr for the Point Margaret section (Frieling et al., 2018), the onset of vegetation-derived warming as documented by the advent of megathermal taxa therefore precedes the CIE by several (~1–4) kyr.

Our data are the first to document a vegetation response to pre-CIE warming in the Southern Hemisphere, and the magnitude of the pollen-based, pre-CIE warming (NLR MAAT) is similar to that previously reported from marine (Thomas et al., 2002; Sluijs et al., 2007; Frieling et al., 2019) and terrestrial records (Secord et al., 2010). Further analysis shows that brGDGT-derived MAAT increased after the CIE onset (at 51.1 m; Fig. 2) and lags the $\delta^{13}C$ shift by 15–20 cm (Fig. 4). Quantitatively, the fraction of soil-derived OM, which carries the brGDGT MAAT signal, is likely low in Point Margaret sediments compared to the plant-derived OM fraction, which dominates the bulk $\delta^{13}C$ signal. Additionally, elevated fern-spore abundance indicates disturbed vegetation cover within the PETM transition interval. The apparent lag in soil warming relative to the CIE onset may therefore result from delivery of a mixture of contemporaneous and older eroded soil material, as similarly interpreted in other shallow-marine PETM sequences (Schneider-Mor and Bowen, 2013; see also Text DR2).

Supraregional vegetation and temperature change across the PETM

The meso-megathermal rainforest biome that established at Point Margaret during the PETM contains numerous meso- to megathermal taxa typical of modern subtropical–tropical environments in Australia, New Caledonia, and New Guinea. In Australia, the closest extant analog to this biome are the coastal tropical rainforests of northeastern Queensland at a latitude of ~15° S (AVH, 2018). Hence, climate conditions during the PETM facilitated the growth of similar vegetation ~45° latitude further south than today.

Although the coastal lowlands of southern Australia likely provided migration corridors for the expansion of thermophilous plant taxa to the Point Margaret region, lowland migration cannot explain the conspicuously early arrival of the mangrove palm *Nypa* at Point Margaret, which predates the colonization by all other megathermal taxa (Fig. 2). In contrast to other megathermal elements, *Nypa* seeds are water dispersed (Tomlinson, 1986). During the Paleogene, the southwestern and southern coast of Australia was bathed by the Proto-Leeuwin Current that originated in the lower latitudes (Huber et al., 2004; Fig. 1). The early *Nypa* appearance may thus have resulted from a favorable surface-current configuration allowing direct transport of seeds from lower-latitude settings. *Nypa* is known from Paleocene strata of northwest Australia (Macphail and Hill, 2018), where it co-occurs with several other meso-megathermal elements (*Anacolosa*, Arecaceae, *Austrobuxus*, *Gymnostoma*, and Strasburgeriaceae) that also appear at Point Margaret during the PETM, further supporting such a scenario.

The PETM-induced increase in meso-megathermal elements at Point Margaret is much stronger than at ODP Site 1172 in the Southwest Pacific (Contreras et al., 2014; Fig. 1). This may be due to the (i) paleogeographic position of the Point Margaret section, which allowed rapid immigration of meso-megathermal plant taxa from more northerly, pre-PETM habitats via lowland migration corridors, and/or (ii) favorable paleoceanographic conditions in the Australo-Antarctic Gulf. In contrast, Site 1172 was located within the northward-flowing Tasman Current, which bathed southeastern Antarctica before reaching eastern Tasmania (Huber et al., 2004; Fig. 1). Thus, the sporomorphs at Site 1172 are likely sourced from catchment areas on Tasmania and the Antarctic margin, thereby representing an integrated vegetation signal that comprises a wide spectrum of different, mostly cooler climate conditions between ~62–72° S (van Hinsbergen et al., 2015; Fig. 1). Despite the appearance of *Nypa*, vegetation change in New Zealand was relatively minor during the PETM (e.g., Crouch and Visscher, 2003, Handley et al. 2011). This may be attributable to a diminished regional temperature response (Frieling et al., 2017) and the geographical isolation of New Zealand, which hampered rapid colonization by immigrant taxa (Wing and Currano, 2013).

Our MAAT estimates for the southern Australian coast also pose a challenge for supraregional terrestrial–marine integration of PETM temperature histories and circulation reconstructions. This problem is exemplified by inferred sea-surface temperatures at Site 1172 and Deep Sea Drilling Project (DSDP) Site 277 (Fig. 1) that are ~10 °C warmer (~32–33°C; Sluijs et al., 2011; Hollis et al., 2015) than MAATs at Point Margaret during the PETM (~21–23°C; Fig. 2). These differences are likely due to as-yet-unexplained biases in the biotic and geochemical temperature proxies (Contreras et al., 2014) and require attention in future studies.

CONCLUSIONS

Our new data from Point Margaret in southern Australia (~60° S paleolatitude) reveal extensive vegetation turnover from a warm temperate to a meso-megathermal rainforest in conjunction with the PETM, accompanied by ~1–4 °C warming. This terrestrial ecosystem re-organization was much stronger than previously recognized in the Southern Hemisphere. Southern Australia may have been particularly prone to short-term climate-induced vegetation turnover due to the presence of coastal lowland migration corridors and coast-parallel surface currents originating in the lower latitudes. This underscores that a spatially differentiated perspective, including associated boundary conditions, is required in order to fully understand terrestrial ecosystem change in response to past and future rapid climate forcing.

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FIGURE CAPTIONS

Figure 1. A). Location of the Point Margaret outcrop within present-day Australia. Land mass in green, submerged continental crust <3000 m water depth in blue. **B).** Early Eocene paleogeography and paleoceanography of the Southwest Pacific region with surface-water currents (warm and cool currents in red and blue, respectively) and locations mentioned in the text. AAG = Australo-Antarctic Gulf, PLC = Proto-Leeuwin Current, 1172 = ODP Site 1172, 277 = DSDP Site 277, KC = Kumara-2 (Handley et al., 2011), MH = Moeraki-Hampden (Crouch and Brinkhuis, 2005), TW = Tawanui (Crouch and Visscher, 2003). After Huber et al. (2004). Color coding as in Figure 1A.

Figure 2. Selected sporomorph taxa from the uppermost Paleocene–lowermost Eocene at Point Margaret, grouped into mesothermal (14–20 °C), meso-megathermal (20–24 °C), and megathermal (>24 °C) elements, along with mean annual air temperature derived from organic geochemistry and palynology. Lithology

and $\delta^{13}C_{org}$ data from Frieling et al. (2018). The onset and body of the CIE are marked by shaded bars.

Figure 3. Non-Metric Multidimensional Scaling of the Point Margaret sporomorph assemblages, showing the first two axes of a 3D-ordination using the Bray-Curtis dissimilarity index. Data were transformed by calculating the square root and applying a Wisconsin Double transformation. Three distinctly different assemblages can be recognized (see text for details).

Figure 4. A) Topmost ~3 m interval of the Point Margaret section showing the $\delta^{13}C_{org}$ excursion, mean annual air temperature based on palynology and organic geochemistry, and percentage of meso-megathermal elements. Orange shading marks the CIE. **B)** Correlation coefficients between $\delta^{13}C_{org}$ and $MAAT_{NLR}$, $MAAT_{brGDGT}$, and meso-megathermal elements, showing leads and lags in the depth domain. Arrows mark the positions of the highest cross-correlation coefficents for each proxy.

[1] GSA Data Repository item 201Xxxx, Table DR1 (nearest living relatives of the encountered sporomorphs), Table DR2 (climatic parameters and modern distribution of the nearest living relatives), Text DR1 including Figure DR1 (source of the encountered biomarkers), Text DR2 (timing of individual proxy signals), Figure DR2 and DR3 (plates with photographs of encountered sporomorphs), is available online at www.geosociety.org/pubs/ft20XX.htm, or on request from editing@geosociety.org. Data used in this paper are also available in the Pangaea database (www.pangaea.de).