

When flowering plants ruled Antarctica: evidence from Cretaceous pollen grains

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Summary

- The replacement of seed-free plants and gymnosperms by flowering plants during the Cretaceous is one of the most important biotic events in the evolution of life. However, the magnitude of this global turnover remains largely unknown.
- Here we present sampling-standardized diversity estimates from a high resolution palynological record of the Late Cretaceous (85–66 Ma) from Antarctica, in the context of the past climatic events.
- Our fossil evidence reveals the occurrence of a rich Campanian flora peaking at *c.* 80 Ma, with angiosperms as the most diverse group of plants for the first time in Antarctica. This peak of diversity was followed by a period of a stepwise deterioration; 60% of ferns and 40% of gymnosperms became locally extinct from the early/mid-Campanian to the late Maastrichtian. Although angiosperms also faced several extinctions – 25% became extinct – they were far less affected than nonangiosperms.
- The onset of deterioration of the greenhouse conditions at the end of the Cretaceous – low CO₂ and global cooling trends – would have led to our observed pattern of change. Overall, our study reveals the beginning of a profound floristic turnover in the highest southern latitudes that pre-dates the major extinction event of the end of the Cretaceous by 15 Myr.

Introduction

The Cretaceous period witnessed a major reorganization of vascular plant diversity and composition all over the world. During the Early Cretaceous, seed-free plants (i.e. bryophytes, lycophytes and ferns) and gymnosperms exceeded angiosperms in diversity and dominance (Lidgard & Crane, 1990; Lupia *et al.*, 1999). During the Late Cretaceous, however, angiosperms rose to ecological prominence, from their earlier dominance in the tropics by the Cenomanian (*c.* 96 Ma) to a later near-cosmopolitan presence everywhere else by the end of the Cretaceous (Crane & Lidgard, 1989; Lupia *et al.*, 1999). During the angiosperm rise, seed-free plants and nonconifer gymnosperms declined (Crane & Lidgard, 1989; Wing & Sues, 1992; Wing *et al.*, 1993; Lupia *et al.*, 1999; Nagalingum *et al.*, 2002; Friis *et al.*, 2011). Although widely accepted, the timing and magnitude of this 'Cretaceous terrestrial revolution' (Meredith *et al.*, 2011) remain poorly quantified, especially in the Southern Hemisphere.

Fluctuations of atmospheric CO₂ – one of the most important greenhouse gases – in deep time have traditionally been linked to vascular plant diversifications (Willis & McElwain, 2014). Atmospheric CO₂ concentrations are predicted to have been relatively high in the Early Cretaceous, declining by the end of this period to values comparable to those of the present day (McElwain *et al.*, 2005; Fletcher *et al.*, 2008; Bond & Scott, 2010; Li &

Elderfield, 2013). The analysis of fossil data – largely spores and pollen grains from North America (Lupia *et al.*, 1999) and Australia (Nagalingum *et al.*, 2002) – demonstrates that angiosperms increased in richness and abundance in local floras with declining CO₂ concentrations, whereas gymnosperms and seed-free plants decreased (McElwain *et al.*, 2005). Compelling evidence indicates that hydraulic innovations of angiosperms (i.e. high-order reticulate venation, vessels and more efficient stomatal control mechanisms) changed dramatically during their radiation probably in response to the physiological drought imposed by a CO₂-starved atmosphere of the Late Cretaceous (Brodribb *et al.*, 2010; Feild *et al.*, 2011). Palaeotemperatures also declined, especially in the high southern latitudes, from the extreme warmth conditions of the Cretaceous Thermal Maximum (Turonian–Santonian), to a long-term cooling since the Campanian, which culminated in Cretaceous temperature minima during the Maastrichtian (Huber *et al.*, 2018).

Here, we explore the patterns of floristic turnover in the high southern latitudes for the Late Cretaceous – a period of a global climate reorganization – based on the palynological analyses of fossil-bearing sediments from Antarctica (Santa Marta, Snow Hill Island and López de Bertodano Formations; Fig. 1; Supporting Information Fig. S1). Although the plant fossil record from the Cretaceous of Antarctica has been widely explored and substantial changes among lineages through time have been recognized

(Dettmann & Thomson, 1987; Askin, 1990; Baldoni, 1992; Cantrill & Poole, 2002, 2005, 2012; Cantrill, 2018; see Notes S1 for further contributions), the magnitude of the floristic replacements remains largely unknown because of the lack of accurate estimations. We use both a raw empirical approach and a more rigorous sampled-based estimation to reconstruct palaeodiversity on the basis of the spore and pollen record. Our study demonstrates that angiosperms exceeded gymnosperms and seed-free plants in diversity for the first time in Antarctica at *c.* 80 Ma, *c.* 20 Myr later than at low palaeolatitudes (Lupia *et al.*, 1999; Friis *et al.*, 2011), in a context of relatively warm conditions (Poole *et al.*, 2005; Francis *et al.*, 2008). We also detect a dramatic drop in diversity of all groups of plants, in particular, lycophytes, ferns and gymnosperms during the cooler Maastrichtian (Poole *et al.*, 2005; Bowman *et al.*, 2013, 2014; Huber *et al.*, 2018).

Materials and Methods

Palynology

Rock samples were recovered by EO from the Santonian/Maastrichtian Santa Marta, Snow Hill and López de Bertodano Formations on the James Ross and Vega islands, in Antarctica (Figs 1, S1). Thirty-seven samples were chemically treated following standard palynological techniques; 30 of them yielded abundant and well-preserved fossil spores, pollen grains and dinocysts. The slides are housed in the palynological collection of the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina): BAPal, ex CIRGEO Palin 603–615, 693–707, 962–965. Fossil spores and pollen grains were identified to species level whenever possible (Table S1). We explored the modern

botanical affinity of fossil morphotypes and grouped them in taxonomic categories (i.e. class, orders or families). A minimum of 200 continental specimens were counted in each sample, except in samples 3, 14, 21 and 24, for a total of 9609 counted specimens.

Diversity estimates

Three major types of methods were used to evaluate species diversity. First, we estimated raw species richness (or ‘within-flora diversity’ *sensu* Lupia *et al.*, 1999) for comparison with previous published data from North America (Lupia *et al.*, 1999) and Australia (Nagalingum *et al.*, 2002), calculating the percentage of species belonging to each major plant group relative to the diversity of the entire sample. Shannon–Wiener Index and Simpson’s Index also were estimated. Secondly, we also estimated Standing Diversity using the range-through method which assumes that a taxon is present in a sample if it is found both above and below it (Boltovskoy, 1988), and hence it tends to minimize facies effect. Thirdly, we used rarefaction curves from relative abundance data of fossil spore–pollen assemblages, to estimate species diversity relative to sample size. We used this method because the count sizes for the samples slightly differed. Rarefaction allowed us to down-sample those larger samples until they are the same size as the smallest sample, making fair comparisons between incomplete samples. Rarefaction has been widely used to reconstruct past diversity trends based on plant fossil data (Wilf *et al.*, 2003; Jaramillo *et al.*, 2006). These methods were applied to the entire fossil assemblage (i.e. vascular plants). We applied the function breakpoints from R/STRUCCHANGE for simultaneous estimation of multiple breakpoints to the diversity estimates adjusted for sample-size; Bayesian Information Criterion (BIC) values were used as model selection. This method has been used to quantify temporal changes in biodiversity (Dornelas *et al.*, 2013). We define temporal bins according to the identified breakpoints. These bins were used to contrast patterns of diversity through time. Each bin includes from 6 to 9 samples (Table 1). We also used R/GGPlot2 to conduct smooth analysis on selected curves.

We compared our rarefied diversity estimates with the reconstructed net-CO₂ drawdown for the last 100 Myr (Li & Elderfield, 2013) interpreted to be consistent with proxy-based reconstructions of the atmospheric CO₂ partial pressure (Li & Elderfield, 2013; Torres *et al.*, 2014). We also compared our rarefied diversity estimates with the main climatic states of temperature defined by Huber *et al.* (2018) for the Late Cretaceous.

Quantitative analyses

We conducted a cluster analysis to explore sample associations (Q-mode). We used the ‘chclust’ function of R/RIOJA (Juggins, 2012) that performs a constrained cluster analysis of a distance matrix, with clusters constrained by sample order. The distance matrix used was the Bray–Curtis metric (Bray & Curtis, 1957) and the agglomeration method was the coniss (Juggins, 2012). As opposed to unconstrained cluster analysis, only stratigraphically adjacent

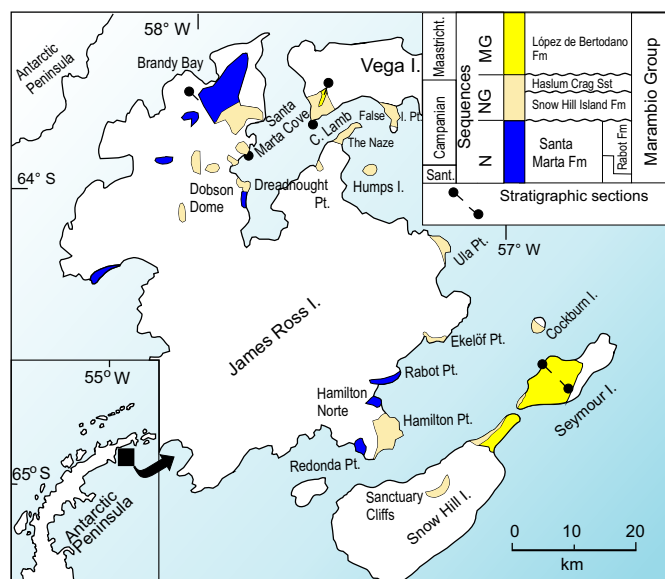


Fig. 1 Location map and geological sketch showing the distribution of Late Cretaceous rocks of Santa Marta, Snow Hill Island and López de Bertodano Formations. The studied sections in Brandy Bay–Santa Marta Cove, James Ross Island; Cape Lamb, Vega Island and Seymour Island also are indicated. Adapted from Olivero (2012).

clusters are considered for merging. The main resulting groups of samples were used to contrast patterns of abundance of selected lineages through time: Bryophytes, Lycophytes, Pteridophytes (Osmundaceae, Schizaeaceae, Dicksoniaceae, Gleicheniaceae, Matoniaceae, Polypodiaceae), Gymnosperms (Araucariaceae, Podocarpaceae, *Lagarostrobos* type), Angiosperms (Non-Eudicots, Proteaceae, Nothofagaceae). All analyses were run on square-root transformation, which partially reduces the problems associated with closed sum percentage data, improves normality, and it is highly recommended when using count variables (Sokal & Rohlf, 1995).

Results

We identified 253 spore and pollen species (Table S1) representing 6 bryophytes, 17 lycophytes, 68 pteridophytes, 24 gymnosperms and 138 angiosperms from biostratigraphically constrained sediments from Antarctica assigned to the Santonian–Maastrichtian (*c.* 85–66 Ma) (Olivero, 2012). A detailed description of the sampling localities and sections (thickness and

Table 1 Rarefaction results and standard error of the total flora for all the analysed samples

Epoch	Samples	Rarefaction		Diversity phases
		Tf	SE	
Late Santonian	1	37.57	2.99	First
	2	38.83	2.26	
	3	33.91	1.68	
Early Campanian	4	38.89	3.04	
	5	40.59	3.41	
	6	46.23	2.93	
	7	39.68	2.92	
	8	44.63	2.86	
	9	33.56	2.55	
	10	47.15	3.04	
Mid-Campanian	11	47.14	3.33	Second
	12	46.70	3.44	
	13	44.41	3.18	
	14	41.67	2.19	
	15	41.93	3.02	
Late Campanian	16	49.67	3.13	Third
	17	41.23	2.48	
	18	32.03	2.64	
	19	36.15	2.29	
	20	37.86	2.39	
	21	38.34	1.93	
Early Maastrichtian	22	37.59	2.52	Fourth
	23	36.28	2.99	
Late Maastrichtian	24	31.00	0.00	
	25	29.14	2.45	
	26	33.51	2.70	
	27	30.65	2.98	
	28	31.24	2.76	
	29	32.78	2.70	
	30	31.40	2.68	

The age of the samples and the four phases determined by our breakpoint analysis are shown on the first and fourth columns, respectively. Diversity estimates were used in Figs 2 and 4 (cutoff = 127).

lithology) along with the temporal constraint of these fossil-bearing sediments is given in the Supporting Information (Methods S1; Fig. S1).

We explored two different approaches to assess major changes in the spore-pollen assemblages through time: (1) a breakpoint analysis based on diversity estimates adjusted for sample size (rarefied diversity) (Table 1); and (2) a constrained cluster analysis based on abundance data. Both analyses generated compatible results, as we will describe in the following paragraphs.

(1) Our breakpoint analysis identified four major phases through the Santonian to the Maastrichtian (Figs 2a, 3, Tables 1, S2). The first phase (late Santonian/early Campanian; *c.* 85.5–82 Ma) represents a moderately diverse interval. Seed-free plants showed the highest estimates of diversity (within-flora diversity or richness and adjusted for sample size estimations or rarefaction), with a spectacular variety of ferns (Fig. 2c; Tables S2, S3). On the one hand, apart from ferns and allies, gymnosperms were fairly rich. Angiosperms, on the other hand, underwent a two-fold increase in richness during this first identified phase (Fig. 2d; Table S3). The second phase (early Campanian/mid-Campanian; *c.* 82–79 Ma) marks the climax of the Antarctic palaeoflora, with the highest values of rarefied diversity and within-flora diversity (richness), among other estimates (Fig. 2a; Tables S2, S3). Seed-free plants showed a decreasing trend in overall richness through this phase (Fig. 2c; Tables S2, S3). Gymnosperms remained virtually unchanged relative to the first phase. Angiosperms, by contrast, became a highly rich plant group with high representation of Non-Eudicots. The third phase (middle Campanian/earliest Maastrichtian; *c.* 79–71.4 Ma) shows a decreasing trend in rarefied diversity of all plant groups (Fig. 2a; Table 1). Seed-free plants experienced the most remarkable drop according to all our estimates (Fig. 2c; Tables S2, S3). Although angiosperms appear to have diversified according to our richness results, adjusted for sample size, estimations (rarefaction) indicate that they also declined in diversity relative to the former phases (Table S2). The fourth and last phase (early Maastrichtian/late Maastrichtian; *c.* 71.4–66 Ma) represents the least diverse interval of the Antarctic palaeoflora (Fig. 2a, Table 1). Seed-free plants experienced a greater than two-fold decrease in diversity relative to the previous phases (Tables S2, S3). Gymnosperms became reduced whereas angiosperms increased in rarefied diversity and richness.

(2) Our Q-mode cluster analysis recognized four major groups of samples with similar spore and pollen composition (Fig. 4). The most important break among the samples split the late Santonian–early Campanian samples (Groups A1 and A2) from the middle Campanian–late Maastrichtian samples (Groups A1 and A2). The Santonian–early Campanian samples (Groups A1 and A2; Fig. 4) included seed-free plants as a dominant component (*c.* 50%) with lycopods and at least five leptosporangiate fern groups (e.g. Gleicheniales, Cyatheales, Polypodiales, Osmundales and Schizaeales), some of them highly abundant (Figs 4, S2). Gymnosperms (*c.* 40%) also are well represented, including Podocarpaceae (*Podocarpus*, *Microcachrys* types), Araucariaceae (e.g. *Araucaria* and *Agathis/Wollemia* types) and Cycadophyta; these two last families showed a slight decrease towards Group A2. Angiosperms underwent a progressive increase in abundance

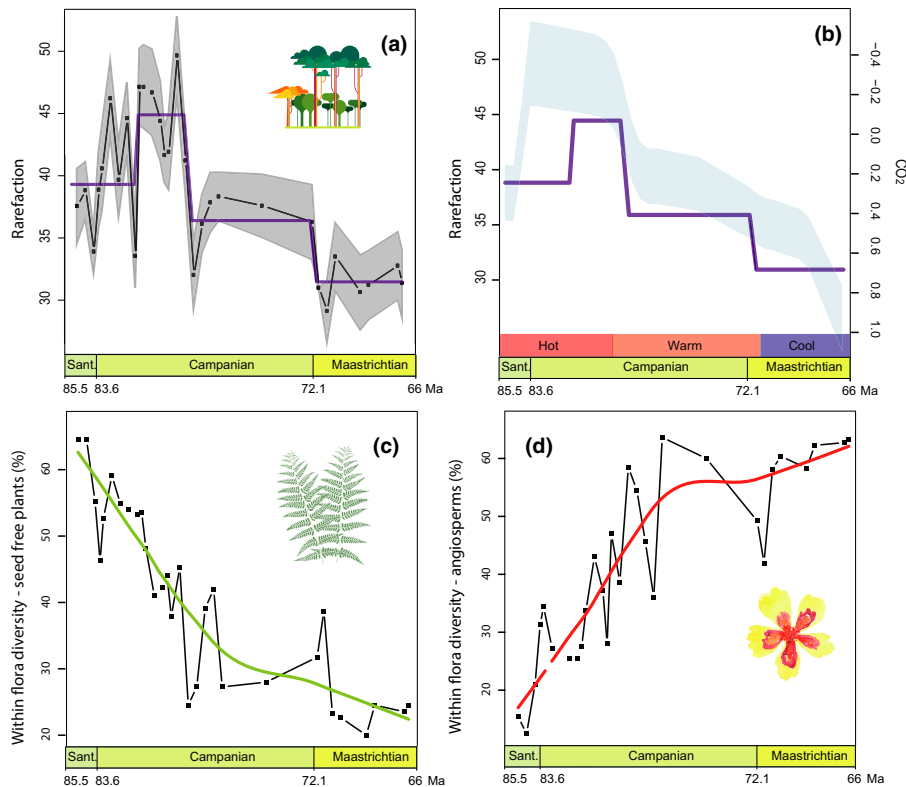


Fig. 2 Fluctuations of the palaeoflora diversity through time in the context of the palaeoclimate. (a) Diversity estimates adjusted for sample size (rarefied diversity) through the Santonian (Sant.) to the Maastrichtian (cutoff = 127) with standard error (grey shadow) and the four major phases according to our breakpoint analysis of the rarefied estimates (solid violet line). (b) Comparison between our four major phases of rarefied estimates, and both the climatic states of temperature defined by Huber *et al.* (2018) (background colours representing: hot (red), warm (orange) and cool (blue) intervals), and the atmospheric CO₂ partial pressure based on the reconstructed net-CO₂ drawdown for the last 100 Myr (Li & Elderfield, 2013) (smooth curve of light blue shadow). Note the close correspondence between our phases of rarefied estimates and the climatic variables (temperature and atmospheric CO₂ partial pressure). (c, d) Trends of within-flora diversity through time: (c) seed-free plants, (d) angiosperms. Solid lines represent a smooth curve. Note the marked contrast trend in richness between the fall of seed-free plants (c) and the rise of angiosperms (d).

with about a two-fold increase (*c.* 8% in Group A1 to *c.* 17% in Group A2); overall there was a high representation of non-Eudicots (i.e. Piperales (Chloranthaceae), Arecales, Laurales, and Alismatales) across Group A. The earliest records of the Protea (*Beauprea*, cf. *Carnarvonina* and Grevilleoideae types) and southern beech (ancestral *Nothofagus*) families also occurred throughout this Group A (Fig. 5; Table S1). The mid-Campanian–late Maastrichtian samples (Groups B1 and B2; Fig. 4) included angiosperms as the most abundant plant group (*c.* 40%), dominating at mid-Campanian times (*c.* 78 Ma) for the first time in Antarctica. Gondwanan lineages, largely Nothofagaceae (mean 17%, *Nothofagus* ancestral groups, and *Nothofagus* and *Lophozonia* types) and Proteaceae (mean 16%, including *Beauprea*, *Embothrium*, cf. *Carnarvonina*, and Persoonioideae, Proteoideae and Grevilleoideae types) markedly increased in abundance (Fig. S2). Also we found Myrtales, Aquifoliales, Ericales, Malvales, Gunnerales, Asterales, Poales, Piperales (Lactoridaceae) and Santalales (Loranthaceae) (Fig. 5), particularly in Group B2 (Table S1). By contrast, noneudicot angiosperms (Chloranthaceae, some Arecaceae, Lauraceae) progressively decreased in abundance. Gymnosperms remained abundant (37%), represented mainly by podocarps (e.g. *Podocarpus*, *Microcachrys*, *Dacrycarpus*, *Lagarostrobos*); among them, *Lagarostrobos* type peaked in Group B2 (23%). Nonconifer gymnosperms and Araucariaceae became clearly reduced through these groups (Figs 4, S2). Seed-free plants (*c.* 23%) decreased in

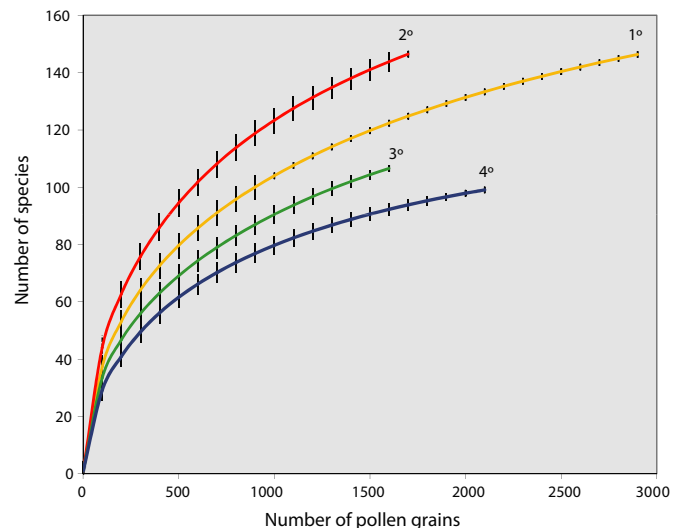


Fig. 3 Rarefaction curves and standard error of the total flora. These curves represent the four phases determined by our breakpoint analysis (Table 1, Fig. 2a). (1) First phase, late Santonian/early Campanian (orange line, high diversity estimates, samples 1–9); (2) Second phase, early/mid-Campanian (red line, highest diversity estimates, samples 10–17); (3) Third phase, mid-Campanian/earliest Maastrichtian (green line, moderate diversity estimates, samples 18–23); (4) Fourth phase, Maastrichtian (blue line, low diversity estimates, samples 24–30). Note that rarefaction curves provide information on both richness and evenness; hence the decline in richness is genuine and not just an effect of changing relative abundance distributions.

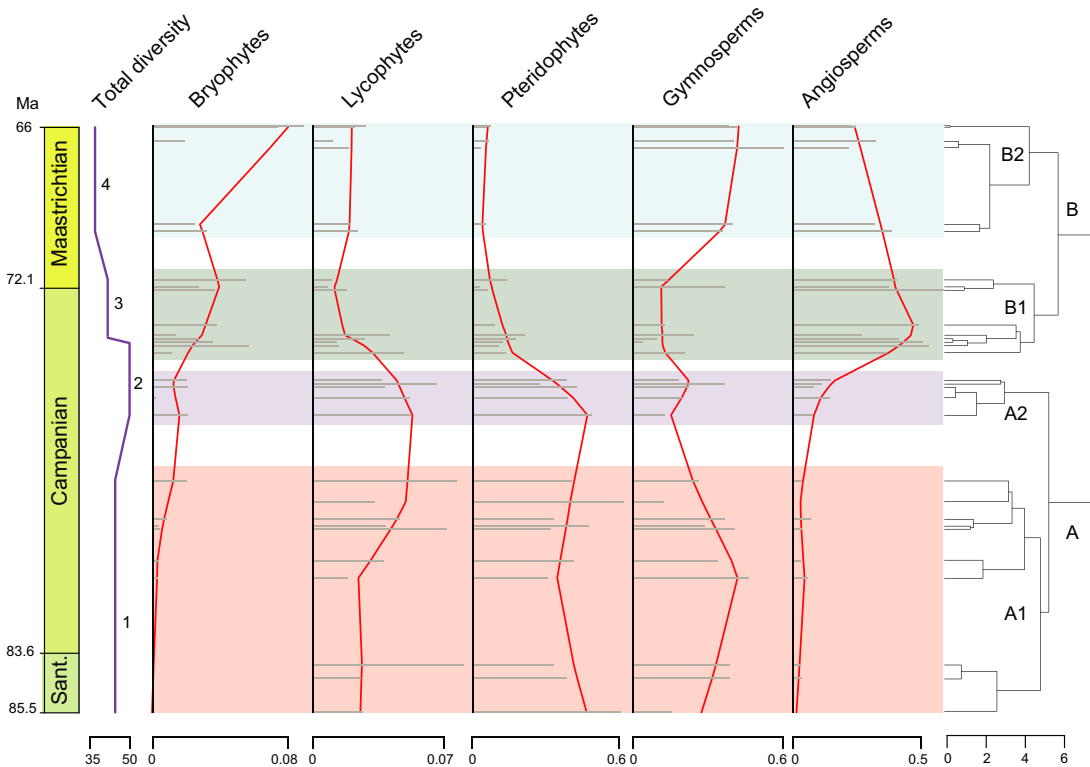


Fig. 4 Trends in abundance and diversity of major plant groups through time. Cluster analysis (Q-mode) revealed four major groups of samples, the most important break splits the late Santonian–early Campanian samples (groups A1 and A2) from the middle Campanian–late Maastrichtian samples (groups B1 and B2). Spore and pollen abundance diagrams are shown as percentage abundances in a sample. Red line represents a smooth curve ('sm.fun' function of R/R_{IOJA}). Note the important change in abundance from ones dominated by seed-free plants (groups A1 and A2) to others dominated by angiosperms (Groups B1 and B2). Groups A1 and A2 include fern spores (mean 45%) and gymnosperms (mean 39%), subordinate angiosperms (mean 10.5%) and lycophytes (mean 5%), and uncommon bryophytes (mean 0.5%). Groups B1 and B2 include angiosperms (mean 40.5%), followed by gymnosperms (mean 37%), and subordinate ferns (mean 17%) and lycophytes (mean 2.5%). Bryophytes reach their highest values of abundance (mean 3%, reaching 7% in the youngest sample 29). Violet line represents the four phases (1–4) recognized by the breakpoint analysis based on rarefied diversity values of the total flora (see Table 1, Fig. 2a).

abundance relative to our Groups A1 and A2. Most fern families (Schizaeaceae, Osmundaceae, Gleicheniaceae, Dicksoniaceae and Matoniaceae) showed a marked decreasing trend from Group A to Group B (Figs 4, S2). Group B largely includes polypods (Polypodiaceae, Pteridaceae and smooth monolete spores of *Laevigatosporites*). Bryophytes reached their highest values of abundance (mean 3%), reaching 7% in Group B2 (Fig. S2).

Taking both analyses together – breakpoint analysis based on total rarefied diversity and cluster analysis based on abundance – we identified four major phases in the evolution of the Late Cretaceous flora from Antarctica (Fig. 4). These are: (1) the late Santonian/early Campanian (moderately diverse samples, with dominance of nonangiosperm groups, in particular pteridophytes); (2) the early/mid-Campanian (most diverse samples, with peak abundances of pteridophytes and lycophytes; angiosperms began to increase in abundance for the first time); (3) the middle Campanian/earliest Maastrichtian (poorly diverse samples, with peak abundances of angiosperms, but decreases in pteridophytes and gymnosperms); and (4) the early Maastrichtian/late Maastrichtian (the least diverse samples, with angiosperms and gymnosperms as the most abundant components. Seed-free plants became the least represented group of plants).

Discussion

Our new empirical analysis of the fossil record from Antarctica reveals a splendid diversity peak of the floras during the Late Cretaceous, *c.* 80 Ma, coinciding with the radiation of other terrestrial groups including some Mesozoic mammals (Wilson *et al.*, 2012). This bloom phase was followed by a period of floristic impoverishment, across the Maastrichtian, when several gymnosperms and seed-free plant species became locally extinct. Although we did detect a reduction in angiosperm rarefied diversity, it was less pronounced than in other vascular plant groups. Overall, the drop in plant diversity that we detected towards the end of the Cretaceous (late Maastrichtian) in Antarctica based on our diversity estimates adjusted for sample size seems not to be an artifact of sampling; very close rarefied estimates were recorded elsewhere on the basis of the palynological record, either at low (De la Parra, 2009) or high (Barreda *et al.*, 2012; Vajda & Bercovici, 2014) palaeolatitudes (Table S4). A similar floristic replacement to the one recognized here – in particular related to the rise of angiosperms and the decline of seed-free plants – was detected previously in Antarctica based on fossil spore–pollen, leaves and wood records. However, the lack of rigorous sample-based estimations in previous studies complicates the analysis of

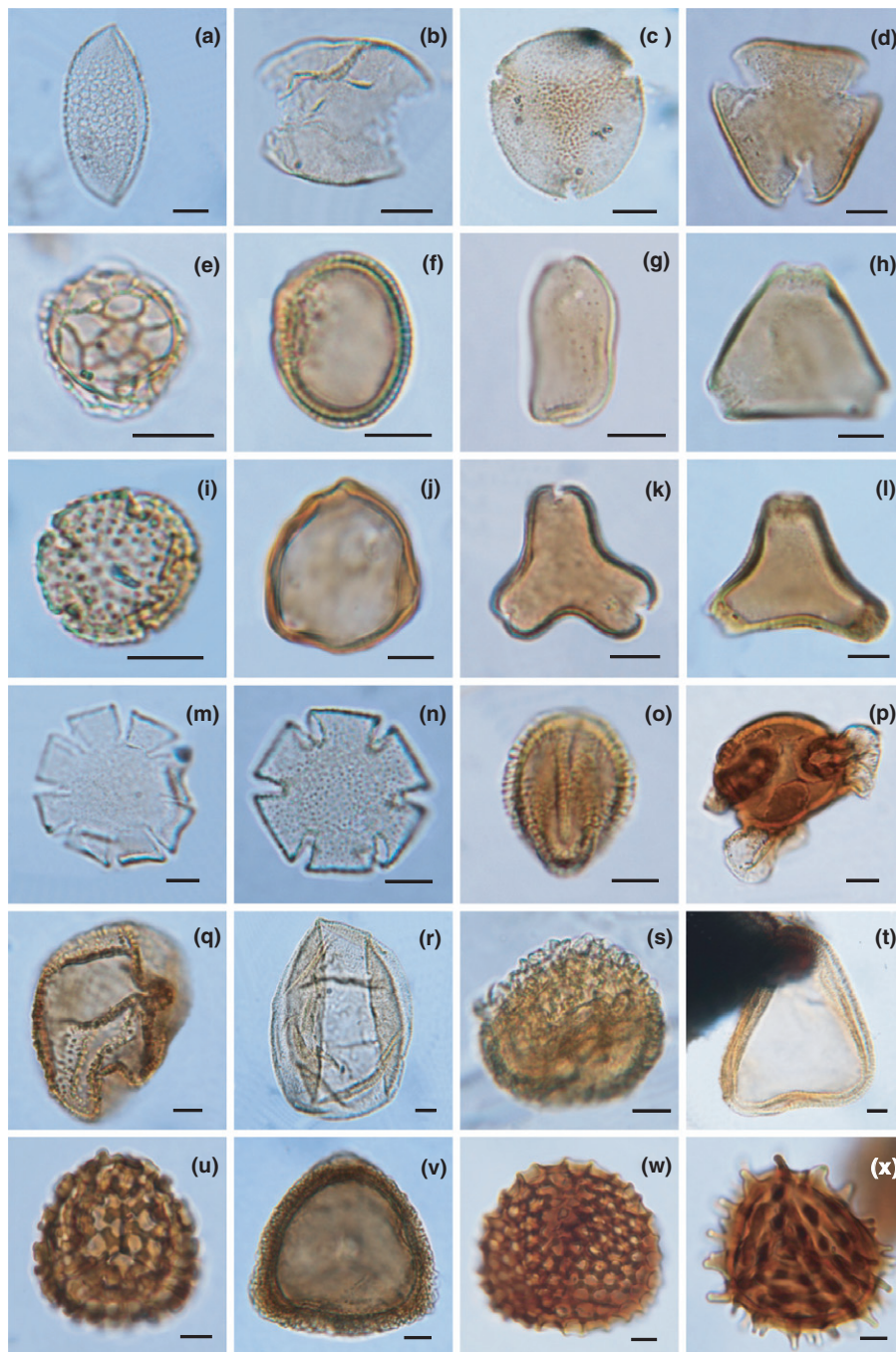


Fig. 5 Selected fossil spores and pollen grains from the Santonian/Maastrichtian of Antarctica. Bar, 5 μ m. Authorities are given in Supporting Information Table S1. (England Finder coordinates) (a) *Liliacidites* sp. 4 (similar to pollen of extant *Puya*, Bromeliaceae, BAPal. ex CIRGEO Palin 695b₁, E51. (b) *Dicolpopollis* sp. BAPal. ex CIRGEO Palin 697b, S30-4. (c) *Stellidiopollis annulatus* BAPal. ex CIRGEO Palin 606b, E32-3. (d) *Peninsulapollis gillii* (*Beauprea*, Proteaceae), BAPal. ex CIRGEO Palin 611b, U40-1. (e) *Pennipollis peroreticulatus* (Alismatales), BAPal. ex CIRGEO Palin 697b, E28-2. (f) *Clavatipollenites* sp. (*Ascarina*, Chloranthaceae), BAPal. ex CIRGEO Palin 698b, U30-1. (g) *Granodiporites nebulosus* (*Embothrium*, Proteaceae), BAPal. ex CIRGEO Palin 695b₂, F53-3. (h) *Lewalanipollis senectus* (Proteaceae), BAPal. ex CIRGEO Palin 606b, H29. (i) *Nothofagidites senectus* (*Nothofagus*, Nothofagaceae), BAPal. ex CIRGEO Palin 707b, R32-4. (j) *Haloragacidites harrisii*, BAPal. ex CIRGEO Palin 610b, G55-2. (k) *Gambierina rudata*, BAPal. ex CIRGEO Palin 704b, U35. (l) *Propylipollis reticulosabratus* (Proteaceae), BAPal. ex CIRGEO Palin 606b, U43. (m) *Nothofagidites* cf. *suggatei* (*Nothofagus* subgenus *Lophozonia*, Nothofagaceae), BAPal. ex CIRGEO Palin 695b₁, V42. (n) *Nothofagidites dorotensis* (*Nothofagus*, Nothofagaceae), BAPal. ex CIRGEO Palin 611b, W42. (o) *Ilexpollenites clifdenensis* (*Ilex*, Aquifoliaceae), BAPal. ex CIRGEO Palin 694b₁, P49-1. (p) *Phyllocladidites* sp. (rare specimen with 3 sacci, *Lagarostrobos*, Podocarpaceae), BAPal. ex CIRGEO Palin 694a, W49. (q) *Dilwynites granulatus* (*Agathis/Wollemia*, Araucariaceae), BAPal. ex CIRGEO Palin 703a, E43. (r) *Araucariacites australis* (*Araucaria*, Araucariaceae), BAPal. ex CIRGEO Palin 611a, X38-1. (s) *Lygistepollenites florinii* (*Dacrydium*, Podocarpaceae), BAPal. ex CIRGEO Palin 703a, X34-2. (t) *Inaperturopollenites* sp. (*Saxegothea?*, Podocarpaceae), BAPal. ex CIRGEO Palin 611a, V31-2. (u) *Rugulatisporites mallatus* (Dicksoniaceae), BAPal. ex CIRGEO Palin 698a, M52-2. (v) *Densoisporites velatus* (Selaginellaceae), BAPal. ex CIRGEO Palin 702a, J33-4. (w) *Retitriletes circolumenus* (*Lycopodium*, Lycopodiaceae), BAPal. ex CIRGEO Palin 698a, G42-2. (x) *Nodosisporites macrobaculatus* (*Anemia*, Schizaeaceae), BAPal. ex CIRGEO Palin 698a, O47-2.

the magnitude of the Late Cretaceous floristic turnovers. In this context, Dettmann & Thomson (1987), Askin (1990) and Baldoni (1992) recognized a substantial vegetation change through the Late Cretaceous, with a marked increase in angiosperm abundance and species richness (particularly Nothofagaceae and Proteaceae) from the Campanian to the Maastrichtian and a parallel decrease in ferns. Cantrill & Poole (2002, 2012) obtained comparable results by analysing trends in 'within flora' diversity of major plant groups; they also found an increase in angiosperm diversity at the expense of ferns and gymnosperms and a close correspondence with the palaeoclimate. Cantrill & Poole (2005) and Cantrill (2018) marked the Campanian as a period of change in the Antarctic vegetation with the appearance, diversification and rise to dominance of Nothofagaceae based on both pollen and wood records (see Notes S1 for further discussion).

Our analysis indicates that plants appear to have experienced a gradual rather than an abrupt change across the late Campanian and more importantly during the Maastrichtian. This gradual decrease in diversity of virtually all plant groups across this interval leads us to suspect that the main cause of this ecological disturbance might be climatically driven. The end of the greenhouse conditions of the latest Cretaceous, particularly the drop of atmospheric CO₂ concentrations (Li & Elderfield, 2013), and the increasing cooler conditions (Poole *et al.*, 2005; Bowman *et al.*, 2013, 2014; Huber *et al.*, 2018), may have played a critical role in changes of the flora diversity. The very similar trends observed in the rarefied diversity of the palaeoflora vs the fluctuations of atmospheric CO₂ concentrations lead us to infer that this greenhouse gas, joined with palaeotemperatures, were the major drivers of floristic turnover (Fig. 2b). Although the low CO₂ concentration of the Late Cretaceous was perceived as a major trigger of angiosperm diversification (McElwain *et al.*, 2005), this group also decreased in diversity during the starved-CO₂ world according to our adjusted for sample size estimates (except those biased by the closed-sum effect, i.e. within-flora diversity, standing diversity). The magnitude of the diversity loss was far more important for nonangiosperm (up to c. 60%) groups (i.e. ferns, lycophytes, nonconifer gymnosperms) than for angiosperms (up to c. 30%) (Table S2). The lower impact on angiosperms is likely to be related to the evolution of novel physiological and morphological traits in response to the new environmental conditions.

The onset of angiosperm radiation occurred earlier in the low palaeolatitudes, than in the high latitudes, as has been reported widely (Lupia *et al.*, 1999; Friis *et al.*, 2011); Antarctica is not the exception. However, by the end of the Cretaceous, within-flora diversity estimates of angiosperms from Antarctica closely resemble those reported from low latitudes for the Maastrichtian (Table S5). We assume that the evolution of the southern Gondwanan lineages (e.g. Proteaceae, Nothofagaceae) may have played a leading role in the rapid angiosperm radiation of the latest Cretaceous of Antarctica.

Overall, the onset of a profound ecological disturbance in the highest southern latitudes pre-dates the major extinction event of the end of the Cretaceous by 15 Myr. The progressive latest

Cretaceous reduction of plant diversity would have had a significant impact on the fauna as vascular plants constitute the base of the terrestrial food chain.

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Author contribution

VDB analysed fossil pollen samples; VDB and LP designed the research, analysed data and wrote the paper; and EBO conducted the fieldwork and devised the stratigraphic scheme.

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References

- Askin RA. 1990. Campanian to Paleocene spore and pollen assemblages of Seymour Island, Antarctica. *Review of Palaeobotany and Palynology* 65: 105–113.
- Baldoni A. 1992. Palinología de la formación Santa Marta, Cretácico superior de la isla James Ross, Antártida. In: Rinaldi CA, ed. *Geología de la isla James Ross*. Instituto Antártico Argentino, Buenos Aires, Argentina, 359–374.
- Barreda VD, Cúneo NR, Wilf P, Currano ED, Scasso RA, Brinkhuis H. 2012. Cretaceous/Paleogene floral turnover in Patagonia: drop in diversity, low extinction, and a *Classopollis* spike. *PLoS ONE* 7: e52455.
- Boltovskoy D. 1988. The range-through method and first-last appearance data in paleontological surveys. *Journal of Paleontology* 62: 157–159.
- Bond WJ, Scott AC. 2010. Fire and the spread of flowering plants in the Cretaceous. *New Phytologist* 188: 1137–1150.
- Bowman VC, Francis JE, Askin RA, Riding JB, Swindles GT. 2014. Latest Cretaceous–earliest Paleogene vegetation and climate change at the high southern latitudes: palynological evidence from Seymour Island, Antarctic Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology* 408: 26–47.
- Bowman VC, Francis JE, Riding JB. 2013. Late Cretaceous winter sea ice in Antarctica? *Geology* 41: 1227–1230.
- Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349.
- Brodribb TJ, Feild TS, Sack L. 2010. Viewing leaf structure and evolution from a hydraulic perspective. *Functional Plant Biology* 37: 488–498.
- Cantrill DJ. 2018. Cretaceous to Paleogene vegetation transition in Antarctica. In: Krings M, Harper CJ, Cúneo NR, Gar W, Rothwell GW, eds. *Transformative paleobotany*. Cambridge, MA, USA: Academic Press, 645–659.
- Cantrill DJ, Poole I. 2002. Cretaceous patterns of floristic change in the Antarctic Peninsula. In: Crame JA, Owen AW, eds. *Palaeobiogeography and biodiversity change: the ordovician and mesozoic-cenozoic radiations*. Geological Society, London, UK, Special Publication 194, 141–152.

- Cantrill DJ, Poole I. 2005. Taxonomic turnover and abundance in Cretaceous to Tertiary wood floras of Antarctica: implications for changes in forest ecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 215: 205–219.
- Cantrill DJ, Poole I. 2012. The origin of southern temperate ecosystems. In: Cantrill DJ, Poole I, eds. *The vegetation of Antarctica through geological time*. Cambridge, UK: Cambridge University Press, 249–307.
- Crane PR, Lidgard S. 1989. Angiosperm diversification and paleo-latitude gradients in Cretaceous floristic diversity. *Science* 246: 675–678.
- De la Parra F. 2009. *Palynological changes across the Cretaceous-Tertiary boundary in Colombia, South America*. MSc thesis, University of Florida, Gainesville, FL, USA.
- Dettmann ME, Thomson MRA. 1987. Cretaceous palynomorphs from the James Ross Island area, Antarctica — a pilot study. *British Antarctic Survey Bulletin* 77: 13–59.
- Dornelas M, Magurran AE, Buckland ST, Chao A, Cazdon RL, Colwell RK, Curtis T, Gaston KJ, Gotelli NJ, Kosnik MA *et al.* 2013. Quantifying temporal change in biodiversity: challenges and opportunities. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 280: 20121931.
- Feild TS, Brodribb TJ, Iglesias A, Chatelet DS, Baresch A, Upchurch GR Jr, Gomez B, Mohr BAR, Coiffard C, Kvacek J *et al.* 2011. Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. *Proceedings of the National Academy of Sciences, USA* 108: 8363–8366.
- Fletcher BJ, Brentnall SJ, Anderson CW, Berner RA, Beerling DJ. 2008. Atmospheric carbon dioxide linked with Mesozoic and early Cenozoic climate change. *Nature Geoscience* 1: 43–48.
- Francis JE, Cantrill DJ, Crame JA, Howe J, Stephens R, Tosolini AM, Thorn V. 2008. 100 million years of Antarctic climate evolution: evidence from fossil plants. In: Couper AK, Barrett PJ, Stagg H, Storey B, Stump E, Wise W, the 10th ISAES editorial team, eds. *Antarctica: a keystone in a changing world, Proceedings of the 10th International Symposium on Antarctic Earth Science, Washington, DC*. The National Academies Press, Washington, DC, USA.
- Friis EM, Crane PR, Pedersen KR. 2011. *Early flowers and angiosperm evolution*. Cambridge, UK: Cambridge University Press.
- Huber BT, MacLeod KG, Watkins DK, Coffin MF. 2018. The rise and fall of the Cretaceous Hot Greenhouse climate. *Global and Planetary Change* 167: 1–23.
- Jaramillo C, Rueda MJ, Mora G. 2006. Cenozoic plant diversity in the Neotropics. *Science* 311: 1893–1896.
- Juggins S. 2012. *Rioja: analysis of quaternary science data*. R package v.0.7-3. [WWW document] URL <http://cran.r-project.org/package=rioja>. [accessed 26 April 2018].
- Li G, Elderfield H. 2013. Evolution of carbon cycle over the past 100 million years. *Geochimica et Cosmochimica Acta* 103: 11–25.
- Lidgard S, Crane PR. 1990. Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Paleobiology* 16: 77–93.
- Lupia R, Lidgard S, Crane PR. 1999. Comparing palynological abundance and diversity: implications for biotic replacement during the Cretaceous angiosperm radiation. *Paleobiology* 25: 305–340.
- McElwain JC, Willis KJ, Lupia R. 2005. Cretaceous CO₂ decline and the radiation and diversification of angiosperms. In: Ehleringer JR, Cerling TE, Dearing MD, eds. *History of atmospheric CO₂ and its effects on plants, animals and ecosystems*. New York, NY, USA: Springer, 133–165.
- Meredith RW, Janecka JE, Gatesy J, Ryder OA, Fisher CA, Teeling EC, Goodbla A, Eizirik E, Simao TLL, Stadler T *et al.* 2011. Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on mammal diversification. *Science* 334: 521–524.
- Nagalingum NS, Drinnan AN, Lupia R, McLoughlin S. 2002. Fern spore diversity and abundance in Australia during the Cretaceous. *Review of Palaeobotany and Palynology* 119: 69–92.
- Olivero EB. 2012. Sedimentary cycles, ammonite diversity and palaeoenvironmental changes in the Upper Cretaceous Marambio Group, Antarctica. *Cretaceous Research* 34: 348–366.
- Poole I, Cantrill D, Utescher T. 2005. A multi-proxy approach to determine Antarctic terrestrial palaeoclimate during the Late Cretaceous and Early Tertiary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 222: 95–121.
- Sokal RR, Rohlf FJ. 1995. *Biometry, 3rd edn*. New York, NY, USA: Freeman WH & Co.
- Torres MA, West AJ, Li G. 2014. Sulphide oxidation and carbonate dissolution as a source of CO₂ over geological timescales. *Nature* 507: 346–349.
- Vajda V, Bercovici A. 2014. The global vegetation pattern across the Cretaceous–Paleogene mass extinction interval: a template for other extinction events. *Global and Planetary Change* 122: 29–49.
- Wilf P, Cúneo NR, Johnson KR, Hicks JF, Wing SL, Obradovich JD. 2003. High plant diversity in Eocene South America: evidence from Patagonia. *Science* 300: 122–125.
- Willis K, McElwain J. 2014. *The evolution of plants*. Oxford, UK: Oxford University Press.
- Wilson GP, Evan AR, Corfe IJ, Smits PD, Fortelius M, Jernvall J. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. *Nature* 483: 457–483.
- Wing SL, Hickey LJ, Swisher CC. 1993. Implications of an exceptional fossil flora for Late Cretaceous vegetation. *Nature* 363: 342–344.
- Wing SL, Sues HD. 1992. Mesozoic and early Cenozoic terrestrial ecosystems. In: Behrensmeier AK, Damuth JD, DiMichele WA, Potts R, Sues HD, Wing SL, eds. *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. Chicago, IL, USA: University of Chicago Press, 327–416.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Analysed stratigraphic sections.

Fig. S2 Spore–pollen abundance diagrams of selected plant groups.

Methods S1 Supporting materials and methods.

Notes S1 Previous palaeobotanical works.

Table S1 Species list recovered from selected fossiliferous localities.

Table S2 Diversity estimates of major plant groups for the four major phases determined by our breakpoint analysis

Table S3 Within-flora diversity estimates (richness) for all samples.

Table S4 Previous late Maastrichtian rarefaction estimates from elsewhere.

Table S5 Previous within-flora diversity estimates from elsewhere.

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