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Paleo-leaf economics reveal a dramatic shift in ecosystem function associated with the end-Triassic mass extinction event

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Climate change has likely altered the ecological functioning of past ecosystems, and likely will alter functioning in the future; however, the magnitude and direction of such changes are difficult to predict. Here we use a deep-time case study to evaluate the impact of a well constrained CO_2-induced global warming event on the ecological functioning of dominant plant communities. We use leaf mass per area (LMA), a widely used trait in modern plant ecology, to infer the paleoecological strategy of fossil plant taxa. We show that paleo-LMA can be inferred from fossil leaf cuticles based on a tight relationship between LMA and cuticle thickness (CT) observed among extant gymnosperms. Application of this new paleo-LMA proxy to fossil gymnosperms from East Greenland reveals significant shifts in the dominant ecological strategies of vegetation found across the Triassic-Jurassic (Tr–J) transition. Late Triassic forests, dominated by low LMA taxa with inferred high transpiration rates and short leaf life spans, were replaced in the Early Jurassic by forests dominated by high LMA taxa that likely had slower metabolic rates. We suggest that extreme CO_2-induced global warming selected for taxa with high LMA associated with a stress-tolerant strategy

and that adaptive plasticity in leaf functional traits such as LMA contributed to post-warming ecological success.

Introduction

The functioning of modern terrestrial ecosystems is determined largely by the ecological strategies of dominant plant taxa as these influence the rate at which elements and energy are moved through the whole system[1]. Theoretical, experimental and modelling studies have all forecasted that rising CO_2 will alter the ecological composition of future plant communities[2,3] but the direction and functional implications of these changes in the long-term remain unclear. One promising way forward is to study how ecosystem properties changed in response to analogous climate change – global warming events in the deep past. Here we investigate whether increased atmospheric CO_2[4-6] and global warming[7] resulted in a shift in ecosystem-scale ecological strategy and function across the Tr–J boundary (201.36 ± 0.17 Ma[8]). To do this we estimated the LMA of 109 fossil taxa from Astartekløft in East Greenland (Bennettitales and Ginkgoales) across Tr–J transition[9-11], and analysed these data together with information on changes in the relative abundance of these taxa [12], and other paleoecological and climatological data[4,11,13,14]. The Astartekløft locality provides evidence for an extreme CO_2-induced global warming event, an abrupt decline in plant diversity, regional turnover of dominant taxa and ultimately to alteration in species composition and vegetation structure[5,12,15]. Palynological evidence has shown that the floral turnover at Astartekløft coincides with the end-Triassic marine mass extinction event (ETE) in St. Audrie's Bay, UK[10] and was broadly contemporaneous with a major decline in conifers and woody taxa in other global localities[9,16]. A rapid doubling of atmospheric carbon dioxide to c. 2000-2500 ppm[4] (Fig. S1) was accompanied by emissions of SO_2 and other volcanic gases[17,18], and mean global temperature increased by up to 4° C[7]. Our study taxa, Ginkgoales and Bennettitales (an extinct group of “seed ferns”), showed contrasting ecological fates: the former predominated in the post-Tr–J warming interval following near extirpation in East Greenland, and the latter were common in the Late Triassic but underwent sharp ecological decline across the Tr–J transition, and eventually becoming locally extinct in the post-warming interval[12].

Leaf mass per area, LMA, is a key trait in the measurement and categorization of plant ecological strategies[19,20]. It represents the dry mass and nutrient construction costs per unit leaf area, and is tightly correlated with many important functional attributes of a leaf including its life span, nitrogen concentration, maximum potential photosynthetic rate and defence chemistry[21,22].

Results

Paleo-LMA proxy development. To investigate ecological change across the Astartekløft Tr–J transition, we developed a paleo-LMA proxy by quantifying a tight linear scaling relationship between cuticle thickness and LMA among 20 species of extant flat-leaved gymnosperms (Fig. 1a). The positive relationship between LMA and leaf life span underpins a leaf economic spectrum that runs from slow-return species with high LMA, long leaf life spans, low nutrient concentrations and slow physiological rates, to low-LMA fast-return species with short leaf life spans and high nutrient concentrations and physiological rates[21-23]. Similarly, leaf cuticle has many intrinsically linked functions of ecological significance such as defence, protection against harsh environments, water repellence and mechanical support [24]. Ultimately, the cuticle protects the costly biological mass within leaves. For these reasons, and also because cuticle material is relatively dense and constitutes a substantial proportion of leaf mass (average of 15.35% , 13 species)[25], LMA and cuticle thickness are expected to be tightly correlated among flat-leaved taxa independent of their phylogenetic history as demonstrated in Fig. S2 (see Supplementary Information Section 1).

The presence of well-preserved cuticle in all fossil leaf material investigated was confirmed firstly by auto-fluorescence of the cuticular membranes under epifluorescence microscopy (appearing red using green excitation fluorescence filter, 510–560 nm) and secondly by the presence of the outermost plant cuticle layer, that is, the lamellate cuticle proper followed by cuticle layer in Transmission Electron Microscopy (TEM) sections (Fig. 1b–f) (see Supplementary Information Section 1 and Dataset 1). Subsequently, we inferred paleo-LMA for each of the 109 Tr–J fossil leaves for which we measured cuticle thickness, based on the extant gymnosperm cuticle thickness-LMA relationship (Fig. 1a). To support the results of the cuticle-based LMA proxy (hereafter "cuticle-LMA"), we compared the paleo-LMA of Ginkgoales with two independent paleo-LMA proxy methods. The first is based on relationships between petiole width and leaf blade area (hereafter "petiole-LMA") shown for woody dicots[26], gymnosperms[27] and Ginkgo biloba[28] . The second is based on a relationship between LMA and the density of adaxial epidermal cells (hereafter "epidermal-LMA"), which has been demonstrated on extant Ginkgo biloba[28] only (see section 'Paleo-LMA trend across geologic time').

Bennettitales and Ginkgoales functional groups. Paleo-LMA estimates of all 109 fossil cuticles (Dataset 2) were used to deduce their likely functional grouping by comparison with LMA values of extant plant functional groups. The mean LMA of Tr–J Ginkgoales (95.3 gm^{-2}, 95% prediction interval, $PI_{95\%}$: 86.0, 105.2) is considerably higher than Bennettitales, 65.4 ($PI_{95\%}$: 56.8, 75.0) gm^{-2} (Fig. 2a, Table S1) (probability, $P(LMA_{Ginkgoales} > LMA_{Bennettitales}) \approx 1$, see Methods for details). The median LMA of Tr–J Ginkgoales (94 gm^{-2}) lies between those of extant deciduous trees (75 gm^{-2}) and evergreen angiosperm trees (106 gm^{-2}), while the median LMA of Bennettitales (60 gm^{-2}) is lower than values of all extant woody groups (Fig. 2b). Our paleo-LMA data therefore support the proposition that Bennettitales and Ginkgoales were likely distinctly different functional groups within the Astartekløft ecosystem. The lower LMA of Bennettitales suggests that their ecological strategies were further towards the fast-return end of the leaf economic spectrum than those of Ginkgoales, and that their leaves typically had higher leaf N concentrations, higher maximum photosynthetic rates and faster leaf turnover (shorter leaf life spans)[20,21,23]. This is independently corroborated by the observation (based on stomatal morphology[11]) that maximum estimated stomatal and canopy transpiration rates of Bennettitales at Astartekløft were on average 40% higher than Ginkgoales in all Tr–J beds, as would be expected for a lower LMA taxon. The corollary is that Bennettitales would likely have required greater N and H_2O inputs than coeval Ginkgoales to maintain their higher photosynthetic rates. Perhaps these Bennettitales were understory and/or open floodplains taxa while Ginkgoales studied here were overstory trees[12], since understory vegetation is generally more nitrogen-demanding than overstory[29]. In this context, accumulations of bennettite leaves into fossil leaf mats, which are common in the Tr beds at Astartekløft, likely represent rapid burial of low LMA deciduous leaf litter rather than longer term accumulation of high LMA evergreen litter with slow decomposition rates. These new ecological inferences (Fig. 2a-b) provide a new insight on the functional groupings of the dominant plants in the Astartekloft assemblages[12].

Paleo-LMA trends across geologic time. Temporal trends in the LMA of Bennettitales and Ginkgoales were estimated across the Tr–J transition in order to examine long-term (geologic scale) trends in leaf economic traits (Fig. 2c–d, Fig 3a–b, Table S2–S4). For these analyses data were pooled into pre-warming (Beds 1–4), peak warming (Beds 5–6) and post-warming periods (Beds 7–8) (Fig. 2c–d); this arrangement best corresponds to the prevailing paleoatmospheric carbon dioxide concentrations (Fig. 3a). Although initial warming at Astartekloft started at Bed 4, Mander et al.[10] suggested a possibility of a hiatus between Bed 4 and 5, which is an additional reason for our chosen grouping. For Bennettitales, average LMA increased 55% from the pre-warming (59.4 gm^{-2}, $PI_{95\%}$: 51.0, 69.3) to the peak warming period (92.2 gm^{-2}, $PI_{95\%}$: 77.0, 109.9) ($P(LMA_{peak\text{-}warming} > LMA_{pre\text{-}warming}) \approx 1$) (Fig. 2c): this is interesting because considering that the average Bennettitales LMA is lower than Ginkgoales, the high mean LMA seen during the peak-warming period was within the range more typical of Ginkgoales (Fig. 2c-d, Table S3-4). Only one specimen was measured during the post-warming, from Bed 7 with LMA value of 66.5 gm^{-2} ($PI_{95\%}$: 40.4, 103.4), which more or less corresponds to the average values obtained during the pre-warming–warming period ($P(LMA_{post\text{-}warming} > LMA_{pre\text{-}warming}) = 0.64$). Therefore, we cannot confidently describe this as a meaningful shift to either the pre- or peak-warming periods ($P(LMA_{post\text{-}warming} > LMA_{peak\ warming}) = 0.08$). In Ginkgoales, LMA increases from the pre-warming (88.0 gm^{-2}, $PI_{95\%}$: 77.4, 99.9) to the post-warming period (101.8 gm^{-2}, $PI_{95\%}$: 90.9, 114.2) ($P(LMA_{post\text{-}warming} > LMA_{pre\text{-}warming}) = 0.98$). The prediction intervals surrounding the estimate of peak-warming LMA (81.6 gm^{-2}, $PI_{95\%}$: 55.9, 115.8) were sufficiently wide due to small sample size, that we could not distinguish any meaningful trend in relation to either the pre- or post-warming periods (Fig. 2d, Table S4).

Paleo-LMA values derived from the petiole-LMA and epidermal-LMA proxies, strongly corroborate the LMA trends for Ginkgoales and Bennettitales (Fig. S3) inferred using cuticle thickness, despite yielding somewhat different absolute LMA values (Fig. 2e, Table S5) when applied to the same fossil leaf specimens, or different specimens from the same plant beds. LMAs inferred from the petiole-LMA (woody dicot) and epidermal-LMA proxies are systematically c. 40% and c. 10% higher, respectively than cuticle-LMA derived values (Fig.

2e). However, using the gymnosperm and Ginkgo biloba calibrations of the petiole-based LMA proxy resulted in substantially higher LMA estimates (by c. 70% and c. 105%, respectively) compared to the cuticle-LMA proxy (Fig 2e) (See discussion in Supplementary Information Section 1). Importantly, differences in absolute LMA values derived using alternative LMA proxies (Fig 2e) do not compromise the interpretability of our results because we find that LMA trends over time are robust to the choice of proxy (Fig S3).

Selection for stress-tolerance. Considering all taxa together and on a bed-by-bed basis, average LMA increased across the Tr–J transition (Fig. 2f, Table S6). We suggest that this trend can be attributed to both direct and indirect effects of elevated atmospheric CO_2. Atmospheric CO_2 directly increases LMA in the short term via acclimation, by increasing the total non-structural carbohydrate content of leaves (i.e., starch accumulation)[30, 20]. Indirect and long-term effects on LMA include CO_2-induced environmental stress at Astartekløft, such as increasing atmospheric temperature [31] and through reduced soil nutrient status caused by increasing terrestrial runoff and erosion [11]. Other possible abiotic factors such as salinity, water availability and light intensity that could potentially affect LMA in general, but are not applicable at Astartekløft, are discussed in Supplementary Information Section 2. The abovementioned short-term CO_2 effect on LMA is further supported by simulated paleoatmosphere experiments[32] that showed extant plants from ancient lineages (cycad, tree fern, ginkgo) exhibiting 40% higher mean LMA when grown at 1500 vs. 380 ppm CO_2 (p-value < 0.05; Fig. S4). This demonstrates that extant tree ferns, ginkgos and cycads have the capacity to acclimate their leaf economics in elevated CO_2. Notably, the addition of high CO_2 to a low O_2 treatment always significantly increased LMA compared to an exclusively low O_2 treatment[32]. Although low atmospheric O_2 (< 21%) is likely to have been a feature of much of the Mesozoic[33,34], paleoatmosphere experiments convincingly rule out < 21% atmospheric O_2

as a primary driver of increased LMA without a stronger over-riding influence of elevated CO_2[35]. In addition to CO_2, Central Atlantic magmatic province (CAMP) volcanic SO_2 emissions are also likely to have caused biotic stress during the ETE[17,36].

At Astartekløft, Bacon et al.[37] identified a significant change in fossil leaf shape (increased roundness) associated with likely elevated SO_2 in beds 2 to 6 and particularly beds 4 and 5. The same study identified a similar increase in leaf roundness in controlled environment experiments when nearest living equivalent taxa were exposed to SO_2, supporting the detection of elevated SO_2 likely related to CAMP-volcanic activity at Astartekloft. Furthermore, the same experiments[38] demonstrated a trend of decreasing LMA for Agathis australis (D.Don) Lindl., Lepidozamia hopei (W.Hill) Regel, Lepidozamia peroffskyana Regel, Nageia nagi (Thunb.) Kuntze and Ginkgo biloba in response to SO_2 fumigation (2000 ppb) relative to control treatment (380 ppm CO_2, no SO_2) (Figure S5). Other independent studies on the responses of LMA to SO_2 reveal species-specific trends; Garsed et al.[39] reported no change in LMA of three flowering tree species and an increase in one; Temple et al.[40] reported decreased LMA in Phaseolus vulgaris L.; Whitmore and Mansfield[41]; Jones and Mansfield[42] and Bell et al.[43] all reported decreased LMA in several grass species. However, when different species are exposed to a combined elevated SO_2 (2000 ppb) and elevated CO_2 treatment (2000 ppm), mimicking those of the ETE, a consistent increase in LMA is observed in all taxa but no significant change in G. biloba[35] (Figure S5). Based on these experimental results we conclude that although SO_2 likely played an important role in the biotic extinction across the ETE[17,36], elevated atmospheric SO_2 cannot account for rising LMA observed in the plant taxa which survived the ETE at Astartekløft. We propose therefore that high CO_2 was among the primary drivers of increasing LMA across the Tr–J in the short-term via direct effects of acclimation, and in the long-term by honing selection for higher-LMA, stress-tolerant taxa[19] to emerge.

Theory suggests that stress-tolerant strategies with slow leaf turnover (longer leaf life spans) and higher LMA enable species to persist under the continuously low-productivity conditions that arise from environmental stress and resource depletion[19]. In the case of Bennettitales, the observed shift in ecological strategy from low to high LMA was not apparently sufficient to confer ecological resilience compared with competing plant taxa because the group underwent near local extinction in Beds 5 and 6 when CO_2 concentration and associated environmental change reached peak levels (Fig. 3c). The higher LMA reconstructions for Ginkgoales than Bennettitales, suggests that Ginkgoales had lower N-requirements and generally lower ecophysiological rates, aiding them in surviving peak environmental upheaval and allowing them to flourish in the post-warming interval represented by Beds 7 and 8 (Fig. 3c).

Phenotypic plasticity in paleo-LMA. Considering the entire LMA dataset, Gingkoales show higher LMA variation than Bennettitales with pooled coefficient of variation (CV) in Beds 1–4 of 0.31 ($PI_{95\%}$: 0.22, 0.41) versus Bennettitales pooled CV of 0.26 ($PI_{95\%}$: 0.19, 0.35) ($P(CV_{Ginkgoales} > CV_{Bennettitales}) = 0.78$). Pooled Ginkgoales CV in Triassic Beds 1–4 (CV = 0.31 ($PI_{95\%}$: 0.22, 0.41) was higher than that of Jurassic Beds 7–8 (CV = 0.28, $PI_{95\%}$: 0.21, 0.31) with the probability, $P(CV_{Beds\ 1–4} > CV_{Beds\ 7–8}) = 0.64$. The wider variation in Ginkgoales LMA, both within the same sampling bed and across evolutionary time, suggests that there was higher functional diversity in leaf economic traits within this group than in the Bennettitales, and perhaps also greater adaptive phenotypic plasticity (i.e. plasticity that enhances fitness of the genotype). Adaptive phenotypic plasticity, when occurring in functional traits, is expected to facilitate rapid adaptation to new environments[44] and to improve persistence thus enabling subsequent adaptive evolution [45]. This plasticity could have positively contributed to the recovery of Ginkgoales in the post-warming interval as the potential for the diversification of taxa with more stress-tolerant ecological strategies (indicated by relatively higher LMAs), was already present. Supporting evidence for high ecological adaptability in Ginkgoales can be found in the recent and Cretaceous–Miocene epoch where Ginkgo was able to adapt to highly disturbed habitats by adopting a competitive-ruderal strategy despite having life-history traits that are not classically associated with such habitats[46,47].

Dramatic shift in community-mean paleo-LMA. Overall, our findings show that the most dominant plant group of the Late Triassic plant community, changed in response to CO_2-induced global warming. Pre-warming, the ecological strategies of the most dominant plant group were ‘fast-return’, characterised by low LMA taxa such as Bennettitales (> 38% relative abundance, Beds 1–5[12]). During peak and post-warming periods, there was a shift to dominance by ‘slow-return’ strategies characterised by high LMA taxa such as Ginkgoales (> 37% relative abundance, Beds 6–8[12]). Average community-mean LMA (average LMA values weighted by taxon abundance) increased by 36% from the pre- to the peak-warming period (61.6 gm^{-2}, $PI_{95\%}$: 53.2, 71.0; vs. 83.9 gm^{-2}, $PI_{95\%}$: 69.7, 100.3 respectively), and from there a further 21% to the post-warming period (101.7 gm^{-2} , $PI_{95\%}$: 90.5, 114.2) (Fig. 3d, Table S7, See supplementary Fig. S6 and Table S8 for bed-by-bed community-mean LMA). To the best of our knowledge, this study represents the first time that shifts in community-LMA have been estimated across the Tr–J transition, but not the first quantification of LMA-shifts across geological warming/cooling events. Using the petiole-based proxy described above, Currano et al.[48] estimated angiosperm LMAs across the Paleocene–Eocene Thermal Maximum global warming event (PETM; ca. 55 Ma), finding no general trend. That study has special relevance because, like the Tr–J event, the PETM included rapid increases in both atmospheric temperature and CO_2. Using the same petiole-based proxy, Blonder et al.[49] found a decrease in mean LMA and its variance among taxa during and after the dramatic global cooling associated with the Cretaceous–Paleogene boundary (KPB; ca. 66 Ma): post-KPB is similar in trend to post-Tr–J event in showing a decline in LMA CV (0.29 at pre-KPB to 0.2 at post-KPB). Put together with our results there are still too few examples to make any claims for or against generality of LMA-shifts in response to major perturbances in global temperature and atmospheric composition. Certainly, we encourage future studies to take into account information on taxon relative abundance, rather than treating all fossil taxon occurrences with equal weight. Here, for example, this led to a clearer picture of landscape-level trends in LMA (e.g. in our own study, see the contrasting LMA trends between Fig 3b and 3d).

Future outlook for a high CO_2 world

A substantial increase in community-mean LMA across the Tr–J transition is likely to have had significant feedback effects on ecosystem functioning such as potential decreases in insect herbivory[20,26,48] and reduction in litter decomposition rate[50], with follow-on effects to the rate at which nutrients were re-cycled through ecosystems. Although no evidence of insect herbivory on the fossil samples in Astartekløft has been found in this study (see Dataset 2), we can deduce from the LMA trend that high paleoatmospheric CO_2 incurred an irreversible ecological change to the dominant plant communities with probable indirect consequences on the local ecosystems across the Tr–J transition.

Our study highlights that the Tr–J global warming event created a very strong ecological filter whereby only plants with more conservative, stress-tolerant strategies were able to persist and this included many of the Ginkgoales and only the highest-LMA Bennettitales.

However, our results also suggest that recovery success following this extreme global warming event of the Tr–J favoured plant orders with high adaptive plasticity in functional traits such as LMA. Selection for high LMA taxa associated with a stress-tolerant strategy could in part explain the worldwide proliferation of Cheirolepidiaceae, a high LMA conifer, in many global localities during the Hettangian following the end-Triassic extinction event [36,51] but this supposition requires further study. Ecophysiological investigations of extant taxa predict future elevated atmospheric CO_2 will favour plants with high mesophyll resistance, hence robust and high LMA plants such as gymnosperm and evergreen angiosperms[2,52]. This concurs with the geographical expansion of evergreen angiosperms during the Eocene[53] – a time of high CO_2 induced global warmth, and with this study across the Tr–J transition . Our findings allow us to examine how past global warming episodes influenced plant taxa with contrasting functional strategies and functional trait dynamics. If the same trend can be observed to hold true for other past global warming events then we can conclude that a similar ecological dynamic may apply under a future global warming scenario where plants with a more conservative resource use strategy with high LMA will be favoured. Such ecological shifts would have significant consequences for the rate at which important societal resources such as water, carbon and nitrogen will flow through terrestrial ecosystems.

Materials and Methods

Modern gymnosperm samples, sites and LMA. LMA and leaf cuticle thickness were quantified for 57 leaf samples from 20 species (15 genera and 8 families) of flat-leaved gymnosperms growing at Macquarie University, Sydney Royal Botanic Gardens, University College Dublin and the National Botanic Gardens, Ireland (see Dataset 1). Healthy and fully-expanded leaves were sampled from outer-canopy shoots because they are taphonomically more likely to be fossilized than shade leaves [54]. A small section of each leaf lamina was excised and fixed with 4% paraformaldehyde for measurements of cuticle properties. Leaves were digitally scanned and area was calculated using ImageJ software [55]. Leaves were then dried at 70°C to constant weight, for determination of leaf dry mass and LMA (dry mass divided by surface area in g m^{-2}).

Fossil cuticle samples and site. Astartekløft, East Greenland, harbours nine fossil plant beds within the Kap Stewart Group spanning the Late Triassic (Mid to Late Rhaetian age: Beds 1, 1.5, 2, 3 and 4), latest Late Rhaetian (Bed 5) and Early Jurassic (Hettangian age: Bed 6, 7 and 8) [10]. The first six beds are crevasse splay deposits, Bed 6 is a poorly developed coal swamp and Bed 7 and 8 are abandoned channels [12]. Fossil materials from 51 Bennettitales (Anomozamites and Pterophyllum) and 58 Ginkgoales (Baiera, Ginkgoites and Sphenobaiera) (Dataset 2) used here were collected and identified to order-level or generic-level in a previous study by McElwain, et al. [12] (detailed collections and method therein). Ginkgoales fossil samples were low or absent in some plant beds but this was not caused by inadequate sampling protocol (See Supplementary Information Section 3 for detail). Fossil cuticles were handpicked coalified compression fragments or macerated bulk rock mesofossils. The leaf cuticles in Bed 5 are fragmentary and therefore cuticle traits alone were used to identify specimens to order level: identification to morphogeneric level within Bennettitales requires intact leaflets (whole macrofossils) where Anomozamites is differentiated from Pterophyllum based on width-length ratio [13].

Microscopy. Leaf samples were dehydrated using a graded series of ethanol and then gradually infiltrated with LR White Resin before being embedded into a block. The procedure for generating thin cross-sections of extant gymnosperm lamina and fossil cuticle are the same except for the duration of infiltration with LR White Resin: fossil cuticles were left for two weeks at the last stage of 100% resin concentration while modern gymnosperm lamina only required an overnight infiltration. Following embedding, thin sections (0.7 – 0.9 µm) were cut with a Leica EM UC7 ultramicrotome, mounted and stained with Methylene Blue. Images of the sections were taken with a Scion CFW-1310C camera at 60x –100x magnification. Samples were also examined using an epifluorescence microscope to detect cuticle autofluorescence. One sample (Pterophyllum, sample ID 47154) was prepared for TEM following Dykstra (1993) [56].

Cuticle thickness measurements. For modern samples, cuticle thickness was measured ten times for each abaxial and adaxial side using ImageJ and the total 20 measurements were then averaged. For fossil samples, cuticle thickness was measured ten times on each side in the parts of the cuticle cross section that showed no obvious folds, compression or damage, and the total averaged (see Supplementary Information Section 1).

Comparison of Ginkgoales cuticle-LMA with other independent paleo-LMA proxies. Petiole-LMA [26] and epidermal cell-LMA[28] proxies were applied to Ginkgoales fossil leaves from the same plant beds, using a combination of different or the exact same fossil samples (Datasets 3 and 4). Due to having a limited number of Astartekløft macrofossil samples with sufficiently well preserved and intact petioles and unfragmented leaf blades (Bennettitales and Ginkgoales), we only applied the petiole-LMA proxy to 32 Ginkgoales fossil samples from Baiera (Bed 1 and 3) and Ginkgoites (Bed 1, 2 and 7), excluding Sphenobaiera. Bennettitales were excluded in this comparative study because firstly, there were limited macrofossils available with sufficiently well-preserved petioles and secondly ,the Ginkgo biloba cell-LMA proxy cannot be used to infer Bennettitales LMA. Paleo-LMA proxy comparison was made at plant beds where the respective morphogenera were found and when two or three proxies could be used. The macrofossils were photographed and the resulting digital images were analysed using ImageJ for blade area (A) and petiole thickness (PW) [37]. For the epidermal cell-LMA proxy, adaxial surfaces of 47 fossil cuticle samples of Baiera (Bed 1 and 3), Ginkgoites (Bed 1, 2 and 7) and Sphenobaiera (Bed 3, 7 and 8) of mostly the same samples that were used in cuticle-LMA proxy were imaged using epifluorescence microscopy (Leica DM5500B). Adaxial epidermal cell density (CD) from each fossil sample was obtained from an average of three to four 0.09 mm^2 grid counts, made using ImageJ (see Supplementary Dataset). The training datasets used here were from petiole-LMA (gymnosperm[27], $\log_{10}LMA = 0.3076\log_{10}(PW^2/A) + 3.015$, $n = 93$, $R^2 = 0.44$; Ginkgo biloba [28], $\log_{10}LMA = 0.2851\log_{10}(PW^2/A) + 2.8832$, $n = 36$, $R^2 = 0.21$), and epidermal-LMA[28] (Ginkgo biloba, $\log_{10}LMA = 1.4064\log_{10}CD - 1.8986$, $n = 36$, $R^2 = 0.66$) proxies. These training datasets together with fossil blade-petiole and fossil adaxial epidermal cell density were used in Bayesian linear regressions to obtain grouped mean and 95% prediction interval (PI) values (see ‘Analyses’ section). Fossil LMAs inferred from woody dicot petiole-LMA relationship were calculated from equations in Royer et al.[26] ($\log_{10}LMA = 0.3820\log_{10}(PW^2/A) + 3.070$, $n = 667$, $R^2 = 0.55$). All LMA estimates were made using $\log_{10}$-transformed data, then back-transformed so as to be reported in the original units.

Analyses. Generally, there was a large overlap among the LMA of morphogenera within the same order-level compared to between different orders (Fig. S7). These observations justify the pooling of LMA values to the taxonomic rank of order in subsequent analyses. All statistical analyses were undertaken using JAGS 4.1.0. [57] and R statistical software [58] on Supplementary Information Dataset. Linear least square regression on the training dataset ($\log_{10}LMA$ as dependent variable and $\log_{10}$leaf cuticle thickness and/or $\log_{10}$tissue thickness as independent variables) was performed using the lm function in R. Additonally, Bayesian linear regression using JAGS, through the R package rjags[59] interface, on the same variables yield similar results: inference of each parameter was made from Markov Chain Monte Carlo (MCMC) sampling from 6,000 samples of the posterior distribution from three chains, each with 10,000 iterations with a burn-in of 2,000 and thin rate of 4 [60]. Normal distribution priors with mean zero and variance 100 were used for intercept and slope parameters while a uniform (0, 10) prior was used for the standard deviation on the variance terms. Convergence was checked by visual assessment of MCMC chains and using the Gelman-Rubin statistic[60]. 95% credible intervals of parameter estimates were calculated as the 2.5% and 97.5% quantile of the posterior distributions. Predicted fossil LMAs and their 95% PI were obtained from sample predictive distributions by inputting the fossil cuticle thickness values into the model, running MCMC and antilog of the sampled posterior distribution values. Grouped mean, CV and average community-mean LMA together with their 95%PI were all calculated from posterior distribution values of fossil samples: statistical comparisons between groups were made by calculating the probability of grouped differences bigger than or smaller than zero[61]. E.g., ‘$P(x > y) = z$’ denote the probability of variable ‘x’ bigger than variable ‘y’, given the data, is ‘z’. Community-mean LMA was estimated for each plant bed based on mean LMA data for each morphogenus and available relative abundance data [12] (See details in Supplementary Information Section 4). Phylogenetic independence contrast analysis was conducted using R package ape and phylogenetic tree was constructed using Phylomatic website[62] and Phylocom[63] software (see Supplementary Information Section 1) . Extant Ginkgo biloba data in Fig. 2a and 2e were taken from Christianson and Niklas [64], and Haworth et al.[28].

Data availability. Data supporting the findings of this study are available within the article and its Supplementary Information files.

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Supplementary Information is available in the online version of the paper.

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Author contributions

W.K.S., I.J.W. and J.M.C. designed the study, interpreted the data and wrote the paper with feedback from all authors; W.K.S. and A.C.P. performed the statistical analyses; W.K.S. and T.I.L. conducted the microscopy work; W.K.S. contributed to the cell-LMA proxy data; K.L.B contributed to the paleoatmosphere experiment and petiole-LMA proxy results; M.S. contributed to the macrofossil morphotype and herbivory data.

Figure legends

Fig. 1. Paleo-LMA proxy development. **a**. Relationship between LMA and cuticle thickness (CT) among extant gymnosperms: $\log_{10}$LMA = 0.601$\log_{10}$CT + 1.744; R^2 = 0.78, n =57, shaded area is 95% confidence interval band. **b.** TEM cross section of Pterophyllum (ID 47154), showing a lamellate cuticle proper (I and inset, bar = 100 nm), cuticle layer (II) and coalified 'mesophyll' layer (III); bar = 500 nm. **c.** Ginkgoites (ID 47103a), cuticle cross section autofluorescing in bright red; bar = 10 µm. **d**. Baiera (ID 47200a), cuticle cross section, 'cell-like' structure represents chattering effect, white line across cuticle is measured thickness; bar = 10 µm. **e**. Ginkgoites, sample ID 47103a, cuticle cross section, white line across cuticle is measured thickness, bar = 10 µm. **f**. extant Ginkgo biloba (ID 11-84), showing uncompressed leaf cross section with mesophyll tissue; bar = 10 µm.

Fig. 2. Leaf mass per area (LMA) of fossil plant species from Astartekløft in East Greenland, pooled by plant groups and plant beds: dotplots represent mean value, whiskers indicate 95% prediction intervals except for Ginkgo biloba, of which whiskers show the 95% confident interval. Number of samples are given in brackets. Prediction interval indicates the level of uncertainty in the inferred LMA values which in turn depends on the sample size and proxy calibration. **a**, Comparison of LMA estimates for Tr–J Bennettitales, Tr–J Ginkgoales and extant Ginkgo biloba. **b**, Boxplots showing a comparison of Bennettitales (green) and Tr–J Ginkgoales (red) LMAs with LMAs of modern plant functional groups from Poorter et al.[30] in ascending order of median values. Numbers above boxplots are median LMAs. Boxes represent the interquartile range (IQR), horizontal lines within the boxes represent medians, and whiskers are the 10th and the 90th percentile. **c**, Comparison of LMA estimates for Bennettitales pooled across Beds 1–4, Beds 5–6 and Bed 7. **d**, Comparison of LMA estimates

for Ginkgoales pooled across Beds 1–4, Beds 5–6 and Beds 7–8, for sample size less than 5, individual sample values are indicated by black dots. **e**, Comparison of LMA estimates for Triassic-Jurassic (Tr–J) Ginkgoales made with three independent proxies: cuticle thickness (cuticle-LMA), petiole width-blade area (petiole-LMA[26,27]), and adaxial epidermal cell density (epidermal cell-LMA[28]). Three version of the petiole-LMA approach were used (calibrations made for woody dicots, gymnosperms, and Ginkgo biloba). Mean LMA and 95% prediction interval ($PI_{95\%}$) of Tr–J Ginkgoales inferred using the cuticle-LMA proxy (95.3 gm^{-2}, $PI_{95\%}$: 86.0, 105.2) and the epidermal cell-LMA proxy (104.5 gm^{-2}, $PI_{95\%}$: 96.0, 113.8) overlap with the LMA of extant Ginkgo biloba (98.1 gm^{-2}, 95% confidence interval: 95.5, 100.6). **f**, LMA trend across fossil beds. Plot illustrating the relationship between mean LMA inferred from cuticle-LMA proxy and bed height (LMA = 0.50Bed depth + 54.93; R^2 = 0.55) indicated by red regression line, shaded area is 95% confidence interval band, plant bed numbers are indicated below plots.

Fig. 3. Ecological traits of Bennettitales and Ginkgoales plotted against Triassic-Jurassic (Tr–J) geologic time scale, indicated by plant sporomorph zonation [10] and global warming period. **a**, Simplified schematic log of the Astartekløft section showing the position of plant beds and the depositional setting of each bed [65], and estimated atmospheric CO_2 concentration [4]. **b**, Temporal trends in mean leaf mass per area (LMA) for Bennettitales and Ginkgoales, with 95% prediction interval whiskers. **c**, Relative abundance of Bennettitales and Ginkgoales [12]. **d**, Temporal trends in community-mean LMA of Beds 1–4, Beds 5–6 and Bed 7–8 for combined Ginkgoales and Bennettitales, with 95% prediction interval whiskers, and sample numbers in brackets.